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FIFTH NOTE ON THE DINOSAURS
OF BERNISSART

BY

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Engineer, Naturalist-aide at the Musée.

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Plates VI and VII.

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Since the publication of my *Quatrième Note sur les Dinosauriens de Bernissart* [1], I have had the occasion to make some observations on the *Iguanodon*s, which seemed to me to deserve particular attention. On the other hand, perusal of the fine works of Mssrs. Cope and Marsh suggested to me various reflections on several points regarding the general organization of dinosaurs. These are the observations and reflections which I wish to present today.

Towards this end, I will discuss the following subjects successively:

I. The proatlas;

II. The mandibular elevator muscles and their influence on the shape of the skull.

I.

THE PROATLAS.

In the sixth part of *Principal Characters of American Jurassic Dinosaurs* [2] by Mr. Marsh, the following passage may be read:

"In two genera of the *Sauropoda* (*Morosaurus* and *Brontosaurus*), and probably in all members of this order, there is a pair of small bones connected with the skull which have not hitherto been observed in any vertebrates. These bones, which may be called the *post-occipital* bones, were found in position in one specimen, and with the skull in several others. When in place, they are attached to the occiput just above the foramen magnum, and extend backward and outward, overlapping the lateral pieces of the atlas, thus protecting the spinal cord at this point, which would otherwise be much exposed.

These bones are short, flattened, and slightly curved, resembling somewhat a riblet. The anterior end is thickened and rugose for attachment to a roughened surface on the exoccipital just above and outside the foramen magnum. The shaft is flattened from above downward, and gradually converges to a thin posterior end. In *Morosaurus grandis*, these bones are about 65 mm. in length, and thirty along the surface which joins the occiput. The correspond in position to the muscle in mammals known as the *rectus capitis posticus minor*.

In the existing Cormorants (*Graculus*) a single slender bone is articulated to the occiput on the median line. This, however, does not correspond to the bones here described. To distinguish it from the post-occipitals, it may be called the *nuchal* bone."

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[1] L. DOLLO, *Quatrième Note sur les Dinosauriens de Bernissart* (BULL. MUS. ROY. HIST. NAT. BELG., 1883, vol. II, p. 223).

[2] O. C. MARSH, *Principal Characters of American Jurassic Dinosaurs.* Part VI. *Restoration of Brontosaurus.* [AMERICAN JOURNAL OF SCIENCE (SILLIMAN), 1883, vol. XXVI, p. 82].

While the eminent paleontologist from Yale College is content to note the existence of the bones which he names *post-occipitals*, he does not ascertain their morphological value. At most he establishes a positional connection between them and the *rectus capitis posticus minor* from human anatomy. This absence of information, which concerns an important point, led me to investigate the homologies of these elements. I have therefore, from some time previous, some ideas with regard to them. However, as it was impossible for me to examine Mr. Marsh's originals, I had abstained from publishing anything. Now that I have had the good fortune to find the post-occipitals of *Iguanodon*, I can speak with knowledge on this topic. I will add, besides, that to my great satisfaction this discovery only confirmed the interpretation which was first presented to my understanding.

Before placing the discussion on the grounds of comparative anatomy, I will briefly describe the vertebral column of *Iguanodon mantelli*, Ow. (individual T of the series from the Musée). This column is composed of:

> cervical vertebrae 10
> dorsolumbar vertebrae 18
> sacral vertebrae 5
> caudal vertebrae . . . . 32 (the rest of the tail is missing.)
> ‾‾‾‾‾‾‾
> TOTAL. 65

Just as in *I. bernissartensis*, Blgr., the cervical vertebral centra are opisthocoelous; those of the dorsal vertebrae, biplanar; and those of the caudal vertebrae, slightly amphicoelous.

Six pairs of ribs were counted in the dorsolumbar region. There were, as follows:

> dorsals 16
> lumbars 2
> ‾‾‾‾‾‾‾
> TOTAL. . . . . . 16 dorsolumbars.

Thus there is one dorsal fewer and one lumbar more than in *I. bernissartensis*.

All the cervical vertebrae (in the usual sense of the word) bear ribs, with the exception of the atlas.

Generally, the atlas presents the shape usually encountered in reptiles. The neurapophyses are synchondrosed together. Mutilation of the specimen does not permit observing if they are synostosed with the pseudocentrum or not. They show caudally well-developed postzygapophyses articulating with the axis. Cranially and dorsally, the neurapophyses support two small bones, one right and one left, which correspond in all points to the post-occipitals of Mr. Marsh. In profile, each of them delimits, with the neurapophysis of the same side, a fossa for the passage of the first cervical nerve (*N. suboccipitalis*, Winslow).

This stated, what is the morphological value of the post-occipitals, at present?

Four *a priori* hypotheses are admissible [1]:

> 1st - They are homologous to the nuchal plate of the sturgeon;
> 2nd - They are homologous to the nuchal bones of the cormorant;

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[1] It is evident, from their shape and position, that the post-occipitals have nothing in common with the "occipital ribs" of *Micropterus salmoides* [R. W. SHUFELDT, *Osetology of* Micropterus salmoides (SCIENCE, 1884, vol. III, no. 72, p. 749, *ocx*)].

3rd - They are homologous to the proatlas of crocodilians and rhynchocephalians;

4th - They constitute a *sui generis* element unknown in other vertebrates until now.

1st - In the second edition of his *Grundriss der vergleichenden Anatomie* [2], Mr. Gegenbaur figures the head of a sturgeon with the dermal bones represented and labeled. Among the latter, note an unpaired plate connected to the supraoccipital and which the illustrious anatomist from Heidelberg calls "*Nuchale*". It seems impossible to consider this plate as the homologue of the post-occipitals of Mr. Marsh. Indeed:

a) It is unpaired, while the post-occipitals number two, one on each side of the medial line;

b) It occupies an entirely superficial position, while the post-occipitals lie directly on the atlantal neurapophyses, with which they clearly articulated;

c) Considering its relationships with the subjacent organs, the nuchal plate is above the first six or seven cervical vertebrae which are fused together and with the skull [1], while the post-occipitals rest only on the atlas or second cervical vertebra (P. Albrecht).

2nd - The cormorant shows [2] a small bony stylet attached to the supraoccipital and in the medial plane of the body which, according to Mr. Shufeldt, is merely an ossification of the fascia situated between the neck extensors. According to the same author, there is reason to compare this stylet with the cranial portion of the cervical ligament (*lig. nuchae*) of mammals. Finally, we know from Yarrell that it serves to increase the surface of origin of the temporal muscles, the neck extensors returning to the occipital by passing below the supplementary fibers of the first.

It seems, as Mr. Marsh further admitted, that there can be no question of identifying the stylet of the cormorant with the post-occipitals. Because:

a) These are in pairs and the stylet is not;

b) The latter, receiving part of the nuchal ligament, is entirely independent of the atlas, since this is the only cervical vertebra on which the aforementioned ligament does not attach [3].

On the contrary, the post-occipitals are in immediate contact with the atlas, as has already been repeated several times.

So that the terms *nuchal plate* (of the sturgeon) and *nuchal bone* (of the cormorant) are not confused, which is clearly odd, I propose conserving the first name which was given by Mr. Gegenbaur, and attributing the qualification *intranuchal bone* to the second to express that this is an ossification within the nuchal ligament.

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[2] C. GEGENBAUR, *Grundriss der vergleichenden Anatomie*, p. 449, 2nd edition, Leipzig, 1878.

[1] T. H. HUXLEY, *Lectures on the elements of comparative Anatomy*, p. 204, fig. 82a, London, 1804.

[2] W. YARRELL, *On the Xiphoid Bone, etc... of the Cormorant* (ZOOLOGICAL JOURNAL, 1828, pp. 234-237, pl. VII, fig. 5 and 6); R. OWEN, *Anatomy of Vertebrates*, vol. II, pp. 64 and 93, London, 1866; E. SELENKA, *Vögel* in BRONN, *Klassen u. Ordnungen d. Thierreichs*, pl. VIII, fig. 5 and 6; A. H. GARROD, *Notes on the Anatomy of Plotus* Anhinga (PROC. ZOOL. SOC. LONDON, 1876, p. 336, pl. XXVIII, fig. 1*a*); R. W. SHUFELDT, *Remarks upon the Osteology of* Phalacrocorax bicristatus (SCIENCE, 1883, Vol. II, no. 41, p. 640, fig. 1); *Osteology of the Cormorant* (IBID, 1884, vol. III, no. 53, p. 143); *Osteology of the Cormorant* (IBID, 1884, vol. III, no. 63, p. 474); J. A. JEFFRIES, *Osteology of the Cormorant* (IBID, 1883, vol. II, no. 44, p. 739); Th. GILL, *Osteology of the Cormorant* (IBID, 1884, vol. III, no. 61, p. 404).

[3] R. OWEN, *Anatomy of Vertebrates*, vol. III, p. 48.

3rd - In crocodilians, the atlantal neurapophyses support an unpaired bony element which also contacts the supraoccipital and exoccipitals. This element, which is developed primitively from two lateral moieties, received the name "*dorsales Schlussstück des Atlas*" from Rathke [1]. Mr. P. Albrecht, who was since engaged by the importance which he admitted understanding, arrived at the conclusion [2] that they represent the last remnants of a vertebra lost by amniotes, a vertebra formerly situated between the skull and atlas. Pursuing these researches, this brilliant anatomist found his *proatlas* in *Hatteria* [3], but here with two rudiments of the right and left neurapophyses, still separate. Thus, it is enough to compare these two rudiments to the post-occipitals (as seen in *Iguanodon,* for example) to be convinced that there is complete agreement between them. Indeed:

a) They are both paired;

b) Also both articulate with the atlantal neurapophyses;

c) Finally, both rest cranially against the supraoccipital and exoccipitals.

In summary:

1st - The post-occipitals of Mr. Marsh are homologous neither with the *nuchal plate* of the sturgeon nor with the *intranuchal bone* of the cormorant;

2nd - They coincide so exactly with Mr. Albrecht's *proatlas* that it cannot be doubted to be the same structure in view of this;

3rd - Therefore they do not constitute a new element in the vertebrate skeleton, as suggested by the illustrious American paleontologist.

Note here a table of sauropsids in which the proatlas has currently been found:

PROATLAS OF SAUROPSIDS							
	CROCODILIANS			DINOSAURS			
RHYNCHO-CEPHALIANS	*Parasuchia*	*Mesosuchia*	*Eusuchia*	*Sauropoda*	*Stegosauria*	*Ornithopoda*	*Theropoda*
+	?	+	+	+	?	+	?
P. Albrecht (4).		E. E. Deslongchamps (2) E. Koken (3). L. Dollo (4).	Rathke (5). P. Albrecht (6).	O. C. Marsh (7).		L. Dollo (8).	

(1) P. ALBRECHT, *Note sur la présence*, etc. (v. *supra*).
(2) E. E. DESLONGCHAMPS, *Mémoires sur les Téléosauriens de lépoque jurassique du Départment du Calvados* (MÉMOIRES DE LA SOCIÉTÉ LINNÉENNE DE NORMANDIE, années 1860-61).

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[1] RATHKE, *Untersuchungen über die Entwickelung und den Körperban der Krokodile*, p. 49. Herausg. von v. Wittich. Braunschweig, 1866.
[2] P. ALBRECHT, *Ueber den Proatlas, einen zwischen dem Occipitale und dem Atlas der amnioten Wirbelthiere gelegenen Wirbel und den Nervus spinalis I. s. proatlanticus* (ZOOLOGISCHER ANZEIGER, 1880, p. 450).
[3] P. ALBRECHT, *Note sur la presernce d'un rudiment de Proatlas sur un exemplaire de* Hatteria punctata, *Gray.* (BULL. MUS. ROY. HIST. NAT. BELG., 1883, vol. II, p. 185).

(3) E. KOKEN, *Die Reptilien der norddeutschen unteren Kreide* (ZEITSCHR. D. DEUTSCH. GEOL. GESELLSCH., 1883, pp. 735 and 792).

(4) L. DOLLO, *Première Note sur les Crocodiliens de Bernissart* (BULL. MUS. ROY. HIST. NAT. BELG., 1883, vol. II, p. 319).

(5) RATHKE, *Untersuchungen*, etc. (v. *supra*).

(6) P. ALBRECHT, *Ueber den Proatlas*, etc. (v. *supra*).

(7) O. C. MARSH, *Principal Characters*, etc. Part VI, p. 82.

(8) L. DOLLO, *Cinquième Note sur les Dinosauriens de Bernissart* (v. *supra*).

II.

THE MANDIBULAR ELEVATOR MUSCLES AND THEIR INFLUENCE ON THE SHAPE OF THE SKULL.

When examining the skulls of *Iguanodon* [1] and *Diclonius* [2], serious divergences are doubtlessly observed. They can easily be compared, however, and it is permissible to say that the second is but an exaggeration of the first. Proceeding next to the skulls of *Diplodocus* [3] and *Ceratosaurus* [4], note that these are very removed from one another, as could be expected with regard to the entirely different diets of these two dinosaurs. However, in spite of the considerable differences noted between these skulls, common characters are still found in them and, curiously, characters that are possessed neither by *Iguanodon* nor *Diclonius*, both herbivores like *Diplodocus*. Surprised by these peculiarities, to which I will return in a more detailed manner in the course of this notice, I ask myself if it is not necessary to look for their cause in the more or less large development of certain head muscles, guided in this by the admirable researches of W. Kowalevsky [5] on ungulates and those of Mr. R. H. Traquair [6] on ganoids. Note, in the following pages, that their study provides precisely the key to the enigma.

Human anatomy demonstrates that there are mandibular elevator muscles, four on the right and four left; namely:

      1st - The temporalis muscles;
      2nd - The masseters;
      3rd - The internal pterygoids;
      4th - The external pterygoids.

I will consider them first in mammals, then in sauropsids.

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[1] L. DOLLO, *Quatrième Note sur les Dinosauriens de Bernissart* (BULL. MUS. ROY. HIST. NAT. BELG., 1883, vol. II).

[2] E. D. COPE, On the Characters of the Skull in the Hadrosauridae (PROC. ACAD. NAT. SCI. PHILADELPHIA, 1883).

[3] O. C. MARSH, *Principal Characters of American Jurassic Dinosaurs.* Part VII. *Diplodocidae, a new family of the Sauropoda.* [AMER. JOURN. SC. (SILLIMAN), 1884].

[4] O. C. MARSH, *Principal Characters*, etc.. Part VIII. *The order Theropoda.* [IBID., 1884].

[5] W. KOWALEVSKY, *Monographie der Gattung* Anthracotherium*, Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere* (PALAEONTOGRAPHICA, 1876, p. 277, pl. IX); *Osteologie des Genus* Entelodon, Aym. (IBID., 1876, p. 483).

[6] R. H. TRAQUAIR, *The Ganoid Fishes of the British Carboniferous Formations* (PALAEONTOGRAPHICAL SOCIETY OF LONDON, 1877 (*Palaeoniscus* and *Polyodon*, pp. 17 and 40, pl. I, fig 3*pa* and pl. VII, fig 2*LM*).

1st - *Mammals*. - The four pairs of muscles previously mentioned nearly always coexist in mammals, although the temporalis and masseters often enough show mingle together into one [1].

Be that as it may, these diverse muscles rarely show an equal development. Besides, it is easy to determine by the following formula the number of combinations of *n* objects taken from *r* to *r*:

$$C_n^r = \frac{n\,(n-1)\,...\,(n-r+1)}{1 \cdot 2 \cdot 3\,...\,r}\ .$$

expresses what everyone understands - the variations that the system of elevators can show; because:

If they are of the same force we have:

$$n = 4 \qquad r = 4 \qquad C_4^4 = \frac{4 \cdot 3 \cdot 2 \cdot 1}{1 \cdot 2 \cdot 3 \cdot 4} = 1.$$

If three are more developed than the fourth:

$$n = 4 \qquad r = 3 \qquad C_4^3 = \frac{4 \cdot 3 \cdot 2}{1 \cdot 2 \cdot 3} = 4.$$

If two are predominant:

$$n = 4 \qquad r = 2 \qquad C_4^2 = \frac{4 \cdot 3}{1 \cdot 2} = 6.$$

Finally, if one dominates:

$$n = 4 \qquad r = 1 \qquad C_4^1 = \frac{4}{1} = 4.$$

Thus, in total:

$$V = C_4^1 + C_4^2 + C_4^3 + C_4^4 = 4 + 6 + 4 + 1 = 15.$$

The system of mandibular elevators can thus have five different arrangements, by only being occupied by more powerful muscles and by supposing that they are equivalent among themselves. Therefore it is understandably impossible for me to describe these five systems without also setting aside my purpose. Still less am I trying to understand whether they are realized in mammals. For the understanding of what follows, I restrict myself to considering two from group C_4^2.

C_4^2. *The temporalis and masseter are the strongest; the pterygoids are weak and hardly distinct from each other* [1].

The corresponding modifications of the skull are:

    a) Strong sagittal crest;
    b) Long, massive mandibular coronoid process;
    c) Enormous temporal fossa;
    d) Tall, plainly recurved zygomatic arch;
    e) Deep masseteric fossa;
    f) Pterygoids acquire the shape of very slender stylets.

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[1] ALLEN, HARRISON, *On the Temporal and Masseter Muscles of Mammals* (PROC. ACAD. NAT. SCI. PHILADELPHIA, 1880, p. 385); ELLIOT COUES, *On the Osteology and Myology of* Didelphys virginiana (MEM. BOSTON SOC. NAT. HIST., 1872, p. 92).
[1] R. OWEN, *Anatomy of Vertebrates*, vol. III, p. 49.

C_4^2 . *Weak temporalis. More voluminous masseters, but incomparably smaller than those of the preceding case. Well-developed pterygoids* [2].

The corresponding modifications of the skull are:

    a) No sagittal crest;
    b) Very slender mandibular coronoid process;
    c) Small temporal fossa;
    d) Very narrow, nearly straight zygomatic arch;
    e) Some rugosities, but no masseteric fossa;
    f) Pterygoids acquire the shape of tall bony laminae.

The first of these two types are found in the order *Carnivora*; the second exists in recent *ungulates* in general, mostly in the *ruminants*. The former belong thus to *carnivores*; the latter to *herbivores*, or better *gramnivores* following the term proposed by W. Kowalevsky [3]:

2nd - *Sauropsids*. - Continuing on to sauropsids, note at first that fusion of the temporalis and masseter is the rule [1]. The entirety of variations of the system of elevators, under the same conditions as above, as a consequence will be:

$$n = 3 \qquad r = 3C_3^3 \quad = \frac{3 \cdot 2 \cdot 1}{1 \cdot 2 \cdot 3} \qquad\qquad = 1$$

$$n = 3 \qquad r = 2 \;\; C_3^2 \quad = \frac{3 \cdot 2}{1 \cdot 2} \qquad\qquad = 3$$

$$n = 3 \qquad r = 1 \;\; C_3^1 \quad = \frac{3}{1} \qquad\qquad = 3$$

$$\text{IN TOTAL: } 7$$

We will choose two from group C_3^1 .

C_3^1 . *Temporalis predominant* [2].

The corresponding modifications of the skull are:

    a) Strong sagittal crest;
    b) Well-developed mandibular coronoid process;
    c) Supratemporal fossae largely open;
    d) Weak pterygoids appear with the shape of narrow laminae and are nearly *parallel* to the median plane of the skull. Their quadrate shaft [3] remains membranous.
    e) No mandibular fontanelle.

C_3^1 . *Internal pterygoid predominant.*

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[2] R. OWEN, *Anatomy of Vertebrates*, vol. III, p. 48.
[3] W. KOWALEVSKY, *Anthracotherium*, p. 274.
[1] R. OWEN, *Anatomy of Vertebrates*, vol I, pp. 223 and 235; vol. II, p. 93; St-GEORGE MIVART, *On the Myology of* Iguana tuberculata (PROC. ZOOL. SOC. LONDON, 1867, p. 768); A. SANDERS, *On the Myology of* Platydactylus japonicus (IBID., 1870, p. 414); St-GEORGE MIVART, *On the Myology of* Chamaeleon parsonii (IBID., p. 851).
[2] It is understood that, in these descriptions, we always take the best characterized type. For the sauropsids, such are the chamaeleon and alligator.
[3] L. DOLLO, *Quatrième Note*, etc., p. 238.

a) No sagittal crest;

b) No mandibular coronoid process;

c) Supratemporal fossae closed;

d) Pterygoids shown appear with the shape of large laminae *perpendicular* to the medial plane of the skull and forming an inclined plane relative to the superior alveolar plane;

e) A mandibular fontanelle.

The first of these two types is observed, more or less indicated, in *lacertilians*; the second in *crocodilians.*

We look now at dinosaurs and compare the skull of *Iguanodon* to that of *Ceratosaurus*, we have [1]:

IGUANODON	CERATOSAURUS
a) A sagittal crest. *b*) Strong mandibular coronoid process. *c*) Supratemporal fossae largely open. *d*) Pterygoids appear with the shape of narrow laminae parallel to the median plane of the skull. *e*) No mandibular fontanelle.	*a*) No sagittal crest. *b*) No mandibular coronoid process. *c*) Supratemporal fossae nearly closed. *d*) Very large pterygoids, extended very far forwards and attached posteriorly onto the internal face of the quadrate. *e*) A mandibular fontanelle.
[1] L. DOLLO, *Quatrième Note*, etc., p. 239.	[1] O. C. MARSH, *Theropoda*, p. 332.

In other terms:

In *Iguanodon*, the mandibular elevators constitute a fairly analogous system to that of lacertilians. In *Ceratosaurus*, in contrast, it reaches farther than that in crocodilians. *Iguanodon* thus masticated chiefly by the aid of its temporal muscles, while *Ceratosaurus* was served principally by its pterygoid muscles.

But *Iguanodon* is a herbivore, *Ceratosaurus* a carnivore. As a consequence, referring to what was said about mammals, observe that: in the act of mastication, a great number of herbivorous dinosaurs utilized the same muscles which are almost solely developed in carnivorous mammals and vice versa.

From whence does this come? I will attempt to show it.

And at first it seems evident that a system of elevators in which one muscle is predominant thus represents a specialization, and it would be tempting to suppose that the temporalis and pterygoids had an equal influence primitively. Whether it was this way in proamniotes: this is something of which I know nothing and which I do not wish to discuss.

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[1] *Diclonius* behaves in general like *Iguanodon* and *Diplodocus* like *Ceratosaurus*.

Nevertheless, concerning amniotes (notably mammals and sauropsids) it appears certain that the forms where the temporalis muscles are stronger are the less modified forms (with regard to the mandibular elevators, that goes in itself). Inversely, the types where the pterygoid muscles dominate are very removed from the basal stock of the group to which they belonged. This point of nature is not surprising, besides; since, if we consider the lower vertebrates, we verify that the role of the dentition was at first more a role of prehension and cutting than true mastication. It is not a question there, in reality, of vertical movement of the jaws. Since then, were some muscles more appropriate for accomplishing this function than the temporalis muscles?

How did they not conserve this dominant position? For the largely different motives below that apply to sauropsids or mammals. I begin with the latter.

I. MAMMALS. - Mastication in these is executed in two ways:

1st - By *grinding*, or vertical jaw movement.

Such are the omnivores;

2nd - By *trituration*, or horizontal jaw movement.

Such are the ruminants and rodents.

Further, trituration can be produced either by lateral or anteroposterior movement. In the first case are ruminants; in the second, rodents.

Continuing on to the primary prehension and cutting by grinding, it is not necessary to transform the system of mandibular elevators, as can easily be understood. Also, in all ancient ungulates (who were omnivores), a bony structure indicating the strong temporalis muscles is found [1]. It is necessary to see the magnificent sagittal crest which surmounts the skull of *Anoplotherium* [2], this false-ruminant [3], in spite of its didactylism. And that which ornaments the head of *Entelodon*, the equally didactylous false-pig.

But with the end of the Eocene epoch comes the great development of graminates (of Saporta and Marion) and our omnivores - at least those which were not too specialized, since the others (*Anoplotherium*, *Entelodon*, etc.) went extinct without leaving descendants - metamorphose into gramnivores. Limiting the question to the mandibular elevator muscles, the temporalis gradually becomes feeble and the pterygoids substitute for them as the principal agents of mastication simultaneously with the transformation in dietary regime. On the other hand, the appearance of horns, which took place a little later, and their effects such as the extension of the frontals up to the supraoccipital above the parietals [1], still seem to be a favorable circumstance for the decline of temporalis muscles.

In summary, regarding the ungulates, the result of works by W. Kowalevsky is that the advent of graminates brought about a predominance of the pterygoid muscles over the temporalis muscles by means of changing the nutrition.

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[1] W. KOWALEVSKY, *Entelodon*, p. 433.
[2] G. CUVIER, *Ossements fossiles*, pl. CXXXVIII, fig. 1 and 2. Paris, 1836.
[3] False-ruminant and false-pig are terms which appear convenient and easy for us to employ to indicate that *Anoplotherium* and *Entelodon* are Paridigitates: the first, inadaptive selenodont; the second, inadaptive bunodont. On these latter terms, see: W. KOWALEVSKY, *On the Osteology of the Hyopotamidae* (ANNALS AND MAGAZINE OF NATURAL HISTORY, 1873, vol. XII, 4th series, p. 164).
[1] RÜTIMEYER, *Monographie des Genus* Bos, *Linné* in W. KOWALEVSKY, *Entelodon*, p. 431.

I should add that I have noted analogous facts for sirenians. These things are entirely sensible when the dugong and *Halitherium* [2] are compared. As in ungulates, these modifications correspond to an evolution from acementodonty to cementodonty [3].

II. SAUROPSIDS. - The reason by which the pterygoid muscles have precedence over the temporalis muscles in crocodilians has nothing to do with nutrition.

If a teleosaurian and a recent crocodilian are placed side by side, note that [4]:

1st - The teleosaurian has very extended temporal crests, nearly forming a sagittal crest, which are totally lacking in the crocodilian;

2nd - The teleosaurian has enormous supratemporal fossae, which are nearly entirely obliterated in the crocodilian;

3rd - The teleosaurian has very narrow pterygoids, while the same bones are extremely large in the crocodilian.

From which it is concluded that the temporalis muscles were preponderant in the teleosaurian, while the pterygoid muscles dominate in the recent crocodilian. From whence come the transformation?

Teleosaurians are MESOSUCHIA [1]; recent crocodilians, EUSUCHIA. In the evolution of the first towards the second, the pterygoid bones are extended into laminae of large surface area in order to move the choanae back as much as possible towards the occiput [2]. As a result, these offered exceptionally favorable conditions for the development of pterygoid muscles, which profited by acquiring a considerable volume. Inversely, the temporalis muscles, no longer having a similarly vast space for lodging, nor on the other hand similarly important work to effect, become more feeble. Finally, in order to protect a more and more complicated middle ear and bearing extensions in every direction, the cranial vault is compressed and the origin of the temporalis muscles, which is shown by the contour of the supratemporal fossae, was reduced to ridiculous dimensions.

As a consequence, it is the transformation from MESOSUCHIA to EUSUCHIA which lead to the predominance of the pterygoid muscles over the temporal muscles in crocodilians.

After the preceding discussion, it seems secure that, in mammals as in sauropsids, the preponderant pterygoids are the indication of a specialization of the mandibular elevator muscles. I will apply this to dinosaurs. *Iguanodon* and *Diclonius* would be less modified forms (at least concerning the mandibular elevators, of course); *Ceratosaurus* and *Diplodocus* specialized types. For the latter I believe it is just as possible to indicate the cause of this specialization.

And further, *Diplodocus* has nares which, by their position, recall the blowholes in cetaceans. But how did these arrive to occupy the summit of the head? By a concentration of

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[2] G. R. LEPSIUS, Halitherium Schinzi, *die fossile Sirene des Mainzer Beckens*, p. 120, pl. IX, fig. 92 and 93. Darmstadt, 1882.

[3] G. R. LEPSIUS, *Halitherium Schinzi*, p. 198.

[4] E. E. DESLONGCHAMPS, *Notes paléontologiques*, pl. XIV, fig. 1 and 2 (*Steneosaurus larteti*). Paris and Caen, 1863-69.

[1] T. H. HUXLEY, *On* Stagonolepis Roberstoni, *and on the Evolution of the Crocodilia* (QUART. JOURN. GEOL. SOC. LONDON, 1875, p. 423).

[2] R. OWEN, *On the influence of the Advent of a higher form of Life in modifying the structure of an older and lower form* (IBID., 1878, p. 421).

the postnarial region of the skull. In effect, as is shown by the results from the researches of Mr. P. J. Van Beneden [1], the following curious parallel can be established:

MYSTACOCETES	
Miocene.	*Recent.*
1. Narrow, elongate skull. 2. Nasal bones long, narrow and flat. 3. Considerable distance between the frontal and supraoccipital at the summit of the skull.	1. Relatively short, wide skull. 2. Nasal bones short, wide and convex. 3. Nearly no distance between the frontal and supraoccipital at the summit of the skull.

It is thus produced by a narrowing of all the part located behind the blowholes [2].
Now, comparing the skulls of *Iguanodon* [3] and *Diplodocus*:

IGUANODON	DIPLODOCUS
1. Post-narial region forming about three times the pre-narial region of the skull. 2. Nasal bones long and narrow. 3. Distinct frontals and parietals. 4. Temporal fossae (especially the supratemporal fossa) largely open.	1. Post-narial region forming about one-third of the pre-narial region of the skull. 2. Nasal bones short and wide. 3. Synostosed frontals and parietals. 4. Temporal fossae (especially the supratemporal fossa) very narrow.

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[1] P. GERVAIS and P. J. VAN BENEDEN, *Ostéographie des Cétacés vivants et fossiles*, p. 270. Paris, 1880; W. H. FLOWER, *On Whales, past and present, and their probable origin* (THE NATURE, 1883, July 5, p. 229).

[2] Further, this confirms the embryogenesis: "Eschricht has described, with much care, the changes which the skulls of the *Balaenoidea* undergo in passing from the foetal to the adult condition, justly remarking that the skull of even a large foetus is more different from that of the adult, than the skulls of distinct species of the same genus of Whales are from one another".

"...so that, at length, in that region which, in the youngest foetus, was covered only by the interparietal, three bones - the interparietal, parietal and supraoccipital - are superimposed." (T. H. HUXLEY, *Lectures*, etc., pp. 275 and 276.)

[3] *I. bernissartensis*, Blgr.

As a consequence, in dinosaurs, just as in cetaceans, the transformation from primitive terminal or subterminal nares into blowholes occurred via a concentration of the postnarial region of the skull. But this concentration had as a result (at least in the former) the reduction of the temporal fossae, which entailed weakening of the temporalis muscles. On the other hand, the pterygoid bones had acquired a fairly considerable development, since Mr. Marsh reported that they form "a broad, flat plate [1]". It must therefore be admitted, particularly considering the structure of the mandible, that the pterygoid muscles were dominant in *Diplodocus* and that they owed this dominance to the metamorphosis of the nares into blowholes.

With these preliminaries, it is now possible to explain the concordances (supratemporal fossae nearly closed, absence of mandibular coronoid process, large and flat pterygoid bones, etc.) existing between *Ceratosaurus* and *Diplodocus*, concordances which separate them from *Iguanodon* and *Diclonius.* They proceed simply from the fact that in these forms the mandibular elevator muscles retained a relatively primitive form, while in the others they were strongly specialized.

One point remains, however. I want to speak about the prelacrimal fossa [2]. Its distribution in the four genera must occupy us, done as follows:

PRELACRIMAL FOSSA

Not		very developed
absent	very reduced	1. *Ceratosaurus*
		2. *Diplodocus*
1. *Diclonius*	1. *Iguanodon*	

What interpretation can be admitted to this prelacrimal fossa? As this is also known in pterosaurs and birds, some authors have supposed that it was a structure tending to make the skull lighter, more delicate. If this was its only purpose, I can hardly understand its presence in *Ceratosaurus*. Indeed, this latter demands rather a solid, massive skull:

1st - To resist the energetic actions which might be exerted on the jaws of this powerful carnivore;

2nd - To support the weight of the horn, which surmounts its nose.

Besides, was there no reason to investigate whether the great extension of the aforementioned fossa had anything to do with the development of the pterygoid muscles? And, in reality, it can be observed that:

1st - Among the four dinosaurs considered, it is weak or absent when the pterygoids are weak. In contrast, it is large when the aforementioned muscles are predominant;

2nd - According to Mr. Professor Wiedersheim [1], whose assertion I can confirm, a dissection demonstrated to me his exact observation that the pterygoid muscles in birds insert on the anterior border of the prelacrimal fossa. Would it be impossible that, in the case where the aforementioned muscles acquired a significant volume and searched for a supplementary support

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[1] O. C. MARSH, *Diplodocidae*, p. 164.

[2] Mr. Marsh calls it the "*antorbital foramen*" (*Diplodocidae*, p. 161) and tells us that it exists only in the *Sauropoda* and *Theropoda* (*Theropoda*, p. 330). However Mr. Huxley has noted its presence in *Hypsilophodon* [T. H. HUXLEY, *On* Hypsilophodon Foxii, *a new Dinosaurian from the Wealden of the Isle of Wight* (QUART. JOURN. GEOL. SOC. LONDON, 1870, p. 6, pl. I, fig. 1*a*)] and I have also noted it, albeit very reduced, in *Iguanodon* (L. DOLLO, *Quatrième Note*, etc., p. 240, pl. IX, fig. 1*i*).

[1] R. WIEDERSHEIM, *Lehrbuch der vergleichenden Anatomie*, vol. I, p. 265. Jena, 1882.

on the maxilla, as the masseter of rodents, the prelacrimal fossa was enlarged to admit their passage, just as the infraorbital foramen? The examination of the anterior border of the prelacrimal fossa of *Ceratosaurus* and *Diplodocus* could be instructive in this regard.

In closing, I am happy to be able to thank my excellent friend, Mr. P. Pelseneer, doctor of natural sciences, who was willing to make several preparations and outlines for me. I equally thank Mr. Professor Albrecht and am obliged to express my profound gratitude for having taken to me the wood imprints in the text of his work.

EXPLANATION OF PLATE VI.

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Symbols common to all figures:

a Submaxillary foramen.
b Prelacrimal fossa.
c External nares.
d Orbit.

e Upper temporal fossa.
f Lateral temporal fossa.
g Sagittal crest.
h Mandibular coronoid process.
i Temporalis muscle.
k Internal pterygoid muscle.
l External pterygoid muscle.
m Mandibular fontanelle.
n Nasal-prefrontal fontanelle.
o Parietal foramen.
p Foramen magnum.
q Masseter.
r Ray of transverse fibers of infraorbital hole.
s Lamina of left atlasntal.neurapophysis.
t Left postzygapophysis of proatlas articulating with left prezygapophysis of atlas.
u Left atlantal neurapophysis.
v Right atlantal neurapophysis.
x Left atlantal postzygapophysis.
y Right atlantal postzygapophysis.

z Atlantal pesudocenter.
a' Lamina of right neurapophysis of proatlas.
b' Right postzygapophysis of proatlas.
c' Indentation for exit of 1st cervical nerve (*n. suboccipitalis*, Winslow).
d' Hole for exit of second cervical nerve.
e' Atlantal-axoidial hypapophysis.
f' Hypapophysis between axis and 3rd cervical vertebra.
g' Hypapophysis between 3rd and 4th cervical vertebrae.
h' Hypapophysis between 4th and 5th cervical vertebrae.
i' Hypapophysis between 5th and 6th cervical vertebrae.
k' Left diapophysis of 4th cervical vertebra.
l' Head of left 4th cervical rib.
m' Rudimentary tuberculum of left 5th cervical rib.
n' Capitulum-tuberculum of left 5th cervical rib.
o' Paradiapophysis of 5th cervical vertebra.
p' Left diapophysis of atlas.
V0 Proatlas.
V1 Atlas.
V2 Axis.

V3 3rd cervical vertebra.
V4 4th cervical vertebra.
V5 5th cervical vertebra.

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FIG. 1. - Left profile of a skull of *Diplodocus* (after Mr. Marsh). Scale: 1/4.
FIG. 2. - Left profile of a skull of *Diclonius* (after Mr. Cope). Scale: 1/10.
FIG. 3. - Left profile of a skull of *Iguanodon mantelli*. Approximate scale: 1/5.
FIG. 4. - Left profile of a chamaeleon skull with the mandibular elevator muscles.
FIG. 5. - Left profile of an alligator skull with the mandibular elevator muscles.
FIG. 6. - Left profile of a skull of *Ceratosaurus* (after Mr. Marsh). Scale: 1/6.
FIG. 7. - View from above of a chamaeleon skull with the mandibular elevator muscles.
FIG. 8. - Occipital view of a chamaeleon skull with the mandibular elevator muscles.
FIG. 9. - Occipital view of an alligator skull with the mandibular elevator muscles.
FIG. 10. - View from above of an alligator skull with the mandibular elevator muscles.
FIG. 11. - Left profile of the atlas and proatlas of *Iguanodon mantelli*, Ow. Scale: 1/2.
FIG. 12. - Left profile of a skull of *Hystrix cristatus*, to show the ray of fibers of the masseter which traverse the infraorbital hole (in part after Mr. Flower).
FIG. 13. - Left profile of the proatlas and first 5 cervical vertebrae of *Hatteria punctata*, Gray (after Mr. Albrecht). Scale: 5/1.
FIG. 14. - Dorsal view of the proatlas and atlas of *Iguanodon mantelli*, Ow. Scale: 1/2.
FIG. 15. - View from above of a skull of *Diplodocus* (after Mr. Marsh). Scale: 1/4.
FIG. 16. - View from above of a skull of *Ceratosaurus* (after Mr. Marsh). Scale: 1/6.
FIG. 17. - View from above of a skull of *Diclonius* (after Mr. Cope). Scale: 1/10.
FIG. 18. - View from above of a skull of *Iguanodon mantelli*, Ow. Approximate scale: 1/5.

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EXPLANATION OF PLATE VII.

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Iguanodon mantelli, Owen. Individual T from the series of the Musée. - Restoration and mounting by Mr. L. F. De Pauw, Head of Workshops. - Approximate scale: 1/20.

IGUANODON MANTELLI, OWEN.

RESTORATION AND MOUNTING BY MR. L. F. DE PAUW.