25. *On the INFLUENCE of the ADVENT of a HIGHER FORM of LIFE in modifying the STRUCTURE of an OLDER and LOWER FORM.* By Professor RICHARD OWEN, C.B., F.R.S., F.G.S., &c. (Read February 6, 1878.)

IN tracing the modifications of structure in a series of animals so similar to one another as to be termed a 'natural group,' one is led to consider the relations to such modifications of concomitant changes in external influences during the geological period of the existence of such group. A difference in the density of the parts of the earth's surface habitually trodden by hoofed quadrupeds has been suggested, for example, as a concomitant, if not causal condition in the transmutation of a five-hoofed perissodactyle (*Coryphodon*, e.g.) to a three-hoofed one (*Palæotherium*, e.g.), thence verging in simplification, through *Hipparion*, to the existing single-hoofed Equines*. Thus it has been observed:—"As the surface of the earth consolidated, the larger and more produced mid hoof of the old three-toed pachyderms took a greater share in sustaining the animal's weight; and more blood being required to meet the greater demand of the more active middle toe, it grew; whilst the side toes, losing their share of nourishment, and becoming more and more withdrawn from use, shrank, and so on, according to the hardening of the ground, until only the hidden rudiments of metapodials remained, and one hoof became maximized for all the work"†.

To this it may be objected that demonstration of such progressive gain of hardness and resistance in parts of the earth's surface, trodden by successive Tertiary forms of hoofed beasts, has not yet been had.

There is, however, another series of conditions which is demonstrated, and which may be legitimately taken into consideration in the relation defined at the outset of the present paper. I refer to the changes in the nature of the prey of certain carnivorous animals.

I assume, at least, a legitimacy of inference from negative evidence, that cold-blooded aquatic animals formed the food of Crocodiles in a much greater proportion in the Mesozoic than in the Neozoic period, and that terrestrial air-breathing animals seldom, if ever, were the prey of the Mesozoic Crocodiles, but were, as now, frequently the food of Neozoic ones.

On this assumption I appreciate, with a satisfaction not felt before, the well-marked distinction in certain parts of the structure of procœlian as compared with amphiœlian Crocodiles. The procœlian

* Intermediate conditions are exemplified in the *Eohippus*, *Orohippus*, *Mesohippus*, of Marsh, from North-American Tertiaries. See his 'Introduction and Succession of Vertebrate Life in America.' 8vo. 1877.

† 'Anatomy of Vertebrates,' vol. iii. pp. 792, 793, and cut 614, "Derivation of Equines" (1868).

ball-and-socket articulation of the trunk-vertebræ better adapts that part of the body to be sustained and moved in air than the amphicelian articulation which characterizes the vertebral column of the more aquatic, and probably marine, Crocodiles of the Mesozoic periods.

The presence of prey not in existence at those periods, but which, in later Tertiary and modern times, might tempt a Crocodile to rush on shore in pursuit of a mammalian quadruped, is a phenomenon contemporary at least with the acquisition of the procelian structure in the axial skeleton of such Crocodile.

The extent, the density, the close-fitting articulation of the bony scutal armature of the Mesozoic Crocodilians suggests its use and need in waters tenanted at the same epoch by larger carnivorous marine reptiles,—as, for example, the Ichthyosaurs, Pliosaurus, Polyptychodonts, and Mosasaurs. The Oolitic species of Crocodile (“Crocodile de Caen,” Cuv.; *Teleosaurus cadomensis*, Geoff.) is signalized by Cuvier as “l’espèce la mieux cuirassée de tout le genre”*.

But the *Goniopholis* of the Wealden and Purbeck formations surpassed even the *Teleosaurus cadomensis* and its congeners in this part of its organization.

The great quadrangular dorsal scutes of *Goniopholis* are distinguished by the presence of a conical process continued from one of the angles transversely to the long axis of the scute, like the peg or tooth of a tile, which fits into a depression on the under surface of the opposite angle of the adjoining scute, thus serving to bind together the plates of the imbricated bony armour, and repeating a structure which is characteristic of the large bony and enamelled scales of many extinct ganoid fishes. The hexagonal ventral scutes of *Goniopholis* were firmly joined together by broad sutural borders†.

No knight of old was encased in jointed mail of better proof than these Crocodiles of an older world.

But the inimical contemporaries of these Crocodiles passed away. No representative of Mosasaurian, Plesiosaurian, or Ichthyosaurian families lived after the Secondary epoch. Crocodiles alone, of the larger aquatic Saurians, continued on to the present time, more fortunate than their predecessors in respect to possible hostile fellow-denizens of the deep.

Certain it is that the defensive armour of procelian Crocodiles has degenerated. Bony ventral scutes are exceptional in them‡, and the dorsal ones are fewer, thinner, less closely arranged and less firmly connected with one another. And if this change can be

* ‘Ossements Fossiles,’ 4to, tom. v. pt. 2, p. 139; also Eugène E. Deslongchamps, ‘Notes Paléontologiques,’ 8vo, 1860, pl. xiii.

† “Report on British Fossil Reptiles,” Reports of British Association, 8vo, 1841, p. 70.

‡ Observed by Natterer in certain South-American Alligators. “Beitrag zur näheren Kenntniss der südamerikanischen Alligatoren,” Ann. Wien. Mus. t. ii. (1840) p. 313.

connected with the disappearance of Reptilia, against the attacks of which a better coat of mail may have advantaged the contemporary Mesozoic Crocodilia, it may further be remarked that diminution of weight would favour crocodilian movements in air, and that a loosely jointed armour would less impede the evolutions required to catch a prey on land.

In this relation, also, arising out of the introduction, in Tertiary times, of large many species of warm-blooded mammals frequenting the banks of lakes and rivers tenanted by carnivorous Alligators and Crocodiles, I have been led to ponder upon the well-marked difference in the relative position of the 'palato-nares' (internal or posterior nostrils, figs. 3 & 6 N) which exists between the Secondary and Tertiary Crocodiles.

Figs. 1-3.—*Cranium of Crocodilus*.

1. Lateral view.

2. From above.

3. From below.

O. Orbits.

P. Pterygo-maxillary
apertures.

V. Venous foramen.

T. Temporal apertures.

N. Palatal nostril.

E. Eustachian foramen.

The physiologist discerns in the soft palatal and gular structures, concomitant with the backward position and small size of the 'palato-

nares,' in the existing Crocodiles and Alligators of Asia, Africa, and America, the power of holding submerged a powerful mammiferous quadruped, without permitting the streams of water traversing the great cavity of the mouth during the struggle to get access to the posterior nostrils and wind-pipe of the amphibious assailant.

The valvular mechanism applicable to, or, I may say, possible with, the peculiar position of the posterior nostrils of procœlian Crocodiles, opening vertically behind the bony palate, not horizontally upon that plane, could hardly be adjusted to the relatively larger postpalatine apertures, upon a horizontal plane at some distance from the occiput, with the inner nostril opening at a more advanced position in the mouth—an arrangement which characterizes all amphiœlians.

Figs. 4-6.—*Cranium of Teleosaurus.*

4. Lateral view. 5. From above. 6. From below.

Explanation of letters as under figs. 1-3.

No doubt there were sphincteric structures which would exclude water from the glottis in all the aquatic air-breathing reptiles; but the peculiar and well-developed valvular contrivances to that end in existing crocodiles are conditions of the relative size and position of the posterior nostrils in them, and the repetition of that character in the palato-nares of all known Tertiary crocodiles justifies an in-

ference as to the concomitant valvular structures of the soft parts in those extinct procelian species.

These considerations stimulated or augmented the desire to determine the palatal character of the fossil skulls of those Crocodilia of the newer Mesozoic formations which, in the massive proportions of their jaws, made the nearest approach to the Tertiary and modern kinds. Such demonstration of the structure of the bony palate is accordingly given in the specimens of the Purbeck Crocodiles in the British Museum, which form the subject of my "Monograph on British Fossil Reptilia," in the volume of the Palæontographical Society for 1878.

Although the jaws of *Goniopholis crassidens* and *Goniopholis simus* have proportions adapted to grapple with large and active mammals, the evidence of any such warm-blooded air-breathers coexistent with those Crocodilia is not yet acquired. And the probability of such coexistence is, in my opinion, very small, from the circumstance of the palato-nares being relatively larger and more advanced than in the Crocodiles contemporary with such mammals. The palato-nares in *Goniopholis* open likewise upon a horizontal plane, look directly downward, not obliquely forward, and, moreover, have a different anatomical conformation. Instead of being formed or bounded by the pterygoids exclusively, as in Tertiary Crocodiles, the palatine bones enter into the formation of the anterior third of the circumference of the palato-nares.

With this anatomical character, which I am disposed to associate with a fish diet, are combined, in both *Goniopholis* and *Petrosuchus*, upper temporal apertures larger than the orbits and amphiœlian or amphiplatyan vertebræ.

Now all known Tertiary and existing Crocodilia combine with small, posterior, pterygoid palato-nares, upper temporal apertures (fig. 2, τ) less than the orbits (*ibid.* $\circ$); and in some broad-faced kinds the upper temporal apertures are almost obliterated by the progressive increase of the osseous roof of the temporal vacuities. These vacuities, in the recent reptile, are occupied by the temporal muscles, and the power of these biting and holding muscles is in the ratio of the extent of their bony origins.

In the amphiœlian fish-eating Crocodilia, the upper temporal apertures (fig. 5, τ) are larger, and usually much larger, than the orbits ($\circ$); and they are, for the most part, associated with slender jaws and with numerous, small, uniformly sized teeth (fig. 4).

With the palatine modifications which relate to the drowning of air-breathing prey, and with the cranial developments which relate to the grip of such prey, we find, as a rule, in procelian Crocodiles, concomitant modifications in the breadth (fig. 2) and strength of the jaws, in productions of the alveolar borders, and in the size of the teeth (fig. 1). There is also inequality of size, favouring holdfast, as in mammalian Carnivora; and certain teeth of the dental series have accordingly received the name of canines in the Crocodiles with such analogous dentition.

In this comparison and its applications I propose at present to
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conclude with reference to a limb-character distinguishing the *Amphicælia* from the *Procælia*.

In all the Mesozoic Crocodilia of which the skeleton has been sufficiently restored, the fore limbs are shorter in proportion to the hind limbs than they are in the similarly restored Neozoic species*. The difference relates to the more strictly or uniformly aquatic life of the Teleosauroids. This I deduced from the fact that when a Nilotic Crocodile swiftly swims to catch a prey or escape a danger the fore limbs are closely applied to the trunk. The same motionless and unobstructive disposition of the fore limbs has been observed in the marine lizards of the genus *Amblyrhynchus*†.

But the resistance to rapid swimming from fore limbs when so disposed will be the less as the size of such limbs may be diminished.

Thus the Teleosauroids, in their rush after fishes or retreat from Ichthyosaurs, would be favoured by the character of the fore limbs above adduced.

On the other hand their progress on dry land would be more difficult, unless, like the Dinosaurs with similarly stunted fore limbs, they were able, as has been surmised, to run upright on their hind legs, as shown in a photograph of the "Restorations of North-American Dinosaurs and Pythonomorphs" exhibited in the "Central Park of New York." I am, however, disposed to see in the Teleosaurian proportions of the fore limbs in the long-natatory-tailed Iguanodon and Hadrosaur a condition facilitating their locomotion in water.

But, returning to my immediate argument. To what condition, it may be asked, do the augmented size and strength of the fore limbs in Neozoic Crocodiles relate?

The advent in Tertiary time of large mammalian quadrupeds browsing or prowling along the shores of estuaries and banks of rivers haunted by such Crocodiles might, and does, tempt them to make a rush on the dry land to seize such passing prey. In these rushes the fore limbs come into strenuous play as terrestrial locomotive organs.

A Lamarckian might say that the temptation to such locomotion, by the repeated increased exertion and exercise of the fore limbs, would lead in the course of generations to their augmentation of size; and he would set it down as one of the factors in the transmutation of a Teleosaur into an Alligator. His opponent might call for the evidences of the transitional forms.

It is true that, in regard to the general shape of the head, some of the later Mesozoic Crocodilia approach, exceptionally, the more robust proportions which prevail, as a rule, in Neozoic Crocodilia, and that among these latter there are species which exceptionally show the more slender proportions which prevail, as a rule, in the Mesozoic

* 'History of British Fossil Reptiles,' *Crocodilia*, pl. 1, 4to, 1850 (skeletons of *Teleosaurus* and *Gavialis*).

† Darwin, 'Voyage of the 'Beagle,' 'Journal of Researches' &c., 12mo, 1845, p. 386.

Crocodylia. But in the vertebral, the dermoskeletal, and the palato-narial characters there is no known exception to the modifications which severally characterize the amphiœlian and procœlian Crocodiles.

We find, as the Secondary approach the Tertiary periods, that the *Goniopholis*, for example, of the Purbeck and Wealden series shows a nearer approach, in the shortness and breadth of the facial part of the skull, to the majority of the Tertiary and existing Crocodiles than the Oolitic and Triassic amphiœlians exhibit; while the long and narrow jaws, with the series of small, sharp, uniformly-sized teeth, in a straight row, common to Teleo- and Stenœosaurians are now exceptionally manifested by the single genus *Gavialis*, with a very limited geographical range. Such forms and proportions of the jaws and teeth, with some minor dermal modifications affecting scutes and foot-webs, justify the generic status of the Indian Gharrials.

The claims of the American Alligators to generic honour rest on feeble foundations; and in regard to the procœlian Crocodiles of the present day, the work of what our German friends have termed the "Gattungsmacherei," has been most productive. *Tomistoma*, *Oopholis*, *Halcrosia*, *Puleosuchus*, *Rhynchosuchus*, *Rhamphostoma*, *Mecistops*, *Bombifrons*, *Palinia*, *Molinia*, *Caiman*, and *Jaacare* hardly exhaust the multitude of names generic with which herpetology has been encumbered. What is of main importance to know is, that all the Crocodiles bearing the above names have the following characters in common:—the upper temporal apertures smaller than the orbits; the palato-nares small, formed by the pterygoids exclusively, placed far back and on a slope towards the occiput; the vertebræ procœlian.

These Crocodiles vary in respect to the proportions of length to breadth of skull, in the relative length of the nasal bones, in the proportions and course of sutures of the premaxillaries, in the degree of difference of the size of the teeth in the same species, and in the relation of some of the larger lower teeth to the upper jaw when the mouth is shut, also in the number and arrangement of the dermal scutes and in the extent of the toe-webs. And such characters are available, by their observed constancy, in the discrimination of the existing species of Crocodylia.

The connoting of the more essential characters common to the procœlian series, and of those which in like manner were common to the amphiœlian series, has led to the consideration of the concomitant and seemingly influential conditions of such respective organic characters, more especially of the relation of the procœlian modifications to the coming in of the mammalian class, and perhaps to the going out of certain members of the reptilian class: and such considerations are now submitted to the judgment of the Geological Society.

DISCUSSION.

Professor SEELEY gathered that the chief object of Prof. Owen's paper was to show that the modern Crocodiles have been evolved from those of the Secondary rocks, and in consequence of the altered conditions of their struggle for existence which resulted from the development of mammalian life in Tertiary as compared with earlier ages. While admitting the evolution, he thought it had no necessary dependence upon the incoming of mammalian prey. Thus the removal backward of the palato-nares in the modern Crocodiles was a condition that would be gradually and inevitably developed, even if mammals had not existed. In the living Crocodile these nares are surrounded by the pterygoid bones, and to the dorsal surface of those bones enormous muscles are attached, which form great hemispherical masses on each side of the head, and are attached to the inner side of the lower jaw. But in the Secondary Crocodiles this pterygoid region of the palate makes a nearer approach to the condition of the bones and palato-nares in certain lizards. And since in the lizards the internal pterygoid muscle has no such development, owing to the larger size of the temporal muscle, he considered that the gradual increase in size of the pterygoid muscles, consequent on the lateral action of the jaws in tearing food, was the cause of the osseous differences of the palate in this region in the two types, because the tension of the muscles acting on the pterygoid bones at their suture with the palatines would cause those bones to elongate, and as the muscles grew more powerful the palato-nares would thus be carried further and further backward with the bones which embrace them; and similarly, by lateral tension, the pterygoid bones would grow in the line of the median suture and so widen, while they reduced the size of the aperture of the palato-nares. This physiological explanation seemed to be independent of the condition of prey being mammalian.

Dr. MERYON was sorry that the author had not gone to the full length in regard to evolution, and, referring to the backward position of the palato-nares, said that this was a provision adapted to their holding their prey under water to drown it. He also referred at some length to the influence of the nervous system in inducing changes.

Mr. HULKE observed that with respect to Prof. Owen's idea that warm-blooded animals were not preyed on by the Mesosuchian Crocodiles, it could not be doubted that such did actually exist contemporaneously with them, and that they might become an easy prey when fording rivers or lakes, as at the present time. He thought that the inference drawn from the strong scutal armour of the Mesosuchia, that these lived in presence of stronger and larger animals, and so stronger armour was necessary for their defence, was not justified by the facts of to-day. The Jacquari of Tropical America, as an example, is similarly armoured, yet has no larger and stronger adversaries. In referring to the suggestion that the backward position of the palato-nares was an adaptation to exclude the entrance of

water into them whilst struggling with a drowning prey, he thought this exclusion was brought about mainly by the closure of the exterior nostrils, since if these were closed, the nasal passage being filled with air and not a vacuum, water could not enter the posterior nares by the mouth. It was, however, the exclusion of water from the glottis and not from the posterior nares which is important. The narial passages and trachea do not form a continuous, but an interrupted tube, without the admirable contrivance which Cetaceans have of a conical larynx, which can be raised and plugged into the palato-nares; for the upper opening in Crocodiles is a simple slit, not particularly prominent, and not capable of such exact adjustment to the palato-nares as in Whales.

Mr. HICKS asked if, with the cessation of the existing circumstances, the acquired structural modifications would cease and the Crocodile go back to its primitive form.

Sir PHILIP GREY-EGERTON observed that in the beginning of the paper the author noticed the modifications of structure of mammals adapted to the surface of the earth, the splay-footed ones moving better over the soft surface; but it must not be overlooked that with these coexisted narrow-footed forms. He thought that the author should have shown that the splay-footed ones alone existed then.

Prof. OWEN, in reply to Dr. Meryon, said that he was gratified to find that his paper had called forth the remarks to which he had listened with pleasure from his old and esteemed friend. It would be seen, however, that his paper was teleological rather than evolutionist, indicative of how the structures characterizing the Neozoic Crocodilia would operate in giving them advantage in the capture of terrestrial prey. No doubt a reference had been made to the Lamarckian view of the conditions under which such modifications of structure might be acquired, and the requirements, by an objector, of the intermediate stages of the change from the amphiœlian to proœlian types was referred to. Instances of that character were few, but might be cited. The Mesozoic *Goniopholis*, *e. g.*, with broad thick jaws, wavy alveolar tract, and large and unequal teeth, combined these Neozoic characters with the Mesozoic large, horizontal, advanced palato-nares. The existing Gavial retains the long narrow jaws, straight alveolar tract, numerous small and similar-sized teeth, with the small, sub-vertical, posteriorly placed palato-nares characteristic of Neozoic Crocodiles. Considering the enormous lapse of time between the Wealden and Eocene periods, it may reasonably be expected that many more of these "missing links" will be found; and one object in our allusion to them in this paper, honoured by Dr. Meryon's remarks, was the additional stimulus it held out to palæontologists and intelligent collectors of fossils to researches which might be rewarded by such discoveries.

With regard to that part of Mr. Hulke's objection bearing on the scutal characters of Mesozoic and Neozoic Crocodiles, it is true that, as Natterer has pointed out, the ventral as well as the dorsal scutes of the Jacuari are ossified; but those scutes are less firmly connected together; they are united neither by the peg-and-groove

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mechanism, nor by thick sutural margins; and the advantages of diminished weight and increased freedom of inflection of the trunk are still possessed unexceptionally by the procelian Crocodiles.

Prof. OWEN remarked, in reply to Sir Philip Grey-Egerton, that the objection that other quadrupeds besides hoofed ones trod the Tertiary earth no doubt would apply to the quotation introductory to his paper, but that was made merely to exemplify the meaning of the title. "A change of characters concomitant with change of density in the earth's surface" was analogous to "a change of characters concomitant with the introduction of new forms on that surface." But the difference between the quotation and the subject-matter of the paper was that the changes of density were hypothetical and unproven, whereas the coming-in of large mammalian quadrupeds at the Tertiary period was an accepted fact.