10. *On the* Association *of* Dwarf Crocodiles (*Nannosuchus* and *Theriosuchus pusillus*, e. g.) *with the* Diminutive Mammals *of the* Purbeck Shales. By Professor Richard Owen, C.B., F.R.S., F.G.S., &c. (Read November 6, 1878.)

[Plate IX.]

Agreeably with an intimation at the close of the Monograph (No. VIII.) "On the Fossil Reptilia of the Wealden and Purbeck Formations," which appeared in the volume of the Palæontographical Society issued in 1878 (p. 15), I communicated to the Geological Society of London* a paper in which ideas suggested by the subjects of that Monograph on certain relations of Mesozoic and Neozoic Crocodilia to their prey were more fully detailed, and an instructive discussion was thereupon raised agreeably with the writer's design.

To his assumption that the mammalian prey of Neozoic Crocodiles were non-existent in Mesozoic times, an experienced palæontologist objected that such were in existence at those periods, and coexisted with the Teleosaurs and other amphicœlian Crocodiles†.

It had not occurred to me that the mammalian prey of the Neozoic Crocodiles‡, which I had in view, and which were exemplified in my mind and meaning by the Tiger, the Buffalo, and similarly large unguiculate and ungulate species, could be represented or suggested by the extinct mammals from the Purbeck and Stonesfield strata, in the restoration of which, and the vindication of their claims to warm-blooded and mammiferous eminence, no small proportion of past palæontological work had been submitted by me in former days to the Geological Society§.

Subsequent additions to our knowledge of Mesozoic mammals have not revealed any species approaching in size to the Ichneumons‖, which haunt the banks of the Nile, the Indus, or the Ganges. Such Viverrines are disdained by the large Crocodilia of these rivers; at least the vermiform mammals are not known to fall a prey to them, or to call for the exertions, emerged or submerged, which the subduing of the struggles of a tiger or buffalo require. On the contrary, the attitude of the Crocodile to the small mammal is reversed; the Ichneumon is the enemy and destroyer, in relation, at least, to

* February 6, 1878; Quart. Journ. Geol. Soc. vol. xxxiv. p. 421.

† "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."—*Quart. Journ. Geol. Soc.* 1878, vol. xxxiv. p. 428.

‡ "Large species of warm-blooded mammals," *tom. cit.* p. 423. "The advent in Tertiary time of large mammalian quadrupeds browsing or prowling along the shores," &c. p. 426.

§ Trans. of the Geol. Soc. 4to, 2nd series, vol. vi. p. 47, pl. 5; Proc. of Geol. Soc 8vo, 1838, p. 17; Quart. Journ. Geol. Soc. vol. x. p. 426 (1854).

‖ *Herpestes ichneumon*, Cuv., 5 feet in length.

the eggs and newly hatched brood, of the cold-blooded amphibious giant†.

When, therefore, my cogitations had been turned to any possible relations of a Phascolothere* or a Triconodon† to the amphicœlian Crocodilia of the Oolitic or Wealden periods, I thought of the diminutive contemporaneous mammals as reducers of the numbers of such Crocodiles, assuming that the reptiles may have sought the banks or shores to oviposit, and that their eggs and wriggling brood may have tempted the small predatory marsupials, as those of the procœlian Crocodiles do their contemporaneous species of *Herpestes*.

Pursuing, however, my researches on the Crocodilia of the Purbeck series, I have come, as I believe, upon a relation of them to their contemporary diminutive mammals at once most interesting and unsuspected. The Spalacotheres, Peralestes, Stylodons, Triconodons, &c. of the freshwater deposits of the "Feather-bed" may well have been the prey of the Crocodiles of the period; for these Crocodiles were reduced to dimensions which forbade them to disdain such succulent morsels, and, at the same time, they were suitably armed and limbed for the capture of the little marsupials.

The characters of one of these dwarf Crocodiles I now propose briefly to submit to the Geological Society; fuller details and illustrations of this and other small crocodilian genera and species will appear in the forthcoming volume of the Palæontographical Society.

The subjects of the annexed Plate (Pl. IX.), all of the natural size, are selected from numerous evidences of the species, which I propose to name *Theriosuchus*‡ *pusillus*.

These and other Crocodilian evidences of the Purbeck period have been brought to light, or completely exposed, by operations upon the residuary slabs of "Feather-bed" marl which accompanied the Becklesian collection to the British Museum, when the negotiations for the purchase of the whole were concluded.

They are very numerous, chiefly consisting of scattered teeth, scutes, vertebræ, and detached limb-bones, but likewise of a few skulls and mandibles, and, in one or two instances, of considerable portions of naturally connected skeletons. The scattered parts associated with these have served for the ascription to their several species of answerable bones, teeth, and scutes not so associated.

At the first aspect, detecting in the scattered groups of scutes specimens showing the peg (Pl. IX. fig. 10, *a*) and groove (fig. 11, *b*), it seemed as if remains of some young specimens of *Goniopholis* had been brought to light. The condition, however, of two of the skulls, one of which has yielded the subjects of figs. 1, 2, 3, Pl. IX., enabled a comparison to be made which determined their specific and, by

* 'Researches on the Fossil Remains of the Extinct Mammals of Australia,' &c. 4to, 1877, vol. i. p. 16, pl. i. figs. 26, 26*a*.

† *Op. cit.* vol. i. pp. 58, 64, pl. iii. figs. 7, 7*a*, 11–19.

‡ Gr. *θηρίον*, wild beast; *σοῦχος*, Egyptian name of crocodile.

their dentition, generic distinction from both *Goniopholis** and *Petrosuchus*†.

The number of maxillary and mandibular specimens, of which three are figured in Pl. IX. figs. 4, 5 and 7, exemplified a degree of constancy in size which begat a conviction that such was a character of the species; and, diminutive as were the Reptilia in question, their characters were indisputably those of the order Crocodilia. One of them, by the size and shape of certain teeth, came nearer to *Goniopholis*; another, by the same characters, resembled *Petrosuchus*; but the differences were such as could not have been obliterated by growth or age.

Theriosuchus approaches, like *Goniopholis*, nearer to the type of the broad-faced Alligators in the proportion of the antorbital part of the skull (fig. 1, *o*, *n*); but the dentition is more modified than in any other known Crocodile, recent or extinct, and approaches nearer to that which characterizes the Theriodont order of Triassic Reptilia‡.

The premaxillary teeth, five in number in each bone, are small; the three middle ones subequal, the first and fifth smaller; the maxillary teeth are divisible into laniaries (fig. 3, *l*) and carnassials or trenchant molars (ib. *m*). The first maxillary tooth is small, the second and third gain quickly in size, the latter (fig. 5, *a*) assuming the character of a canine; the fourth tooth (ib. *b*, and fig. 6,*b*) is a still larger canine; the fifth (fig. 6, *c*) and sixth (*d*) decrease in size somewhat suddenly, but in length rather than breadth of crown, and terminate the series projecting from the convex part of the alveolar border of the maxillary; the tooth *c* or *d* may be said to terminate the laniary series. Beyond *d* the teeth lose length and slightly gain in breadth; the crown assumes a triangular, laterally compressed or lamellate form, and the enamel is traversed, on the outside, by fine but distinct lines (fig. 6, *e*).

Of these sectorial or carnassial molars, some of the detached specimens of maxillary bones (figs. 4 and 5) indicate as many as eight or nine. The broad base or root of each tooth is not inserted into a separate socket, but is lodged in a recess of the outer alveolar wall; moreover the partitions between these recesses are low or partial, and the teeth appear to have been applied thereto, without being so completely confluent therewith as in the pleurodont mode of fixation of the teeth in certain lizards§. Hence in some of the specimens of the maxillary bone the incisors and canines only are retained, being rooted each in its own complete socket, while the molars have fallen out, and their partially separated recesses are shown as in the figures cited.

In the lower jaw the foremost tooth is rather larger than those which interlock with the middle premaxillary or 'incisor' teeth above; but not any of the succeeding laniary teeth attain the size

* 'Monograph of Purbeck Reptilia,' Pal. vol. 4to, 1878, pls. i.–iv.
† *Ib. ib.* p. 10, pl. vi.
‡ Quart. Journ. Geol. Soc. 1876, vol. xxxii. p. 99.
§ See 'Odontography,' p. 266.

of the upper canines. The twelfth tooth, counting backwards, assumes the lamellate triangular shape of striate crown characteristic of the superior sectorials; and the inferior ones were lodged, like those above, in a common depression of an outer alveolar wall, developing the ridges dividing such depression into the dental recesses, as shown in fig. 7.

This approximation to a lacertian dental character might seem ground for something more than a family section of the Order Crocodilia. But the quasi-pleurodont attachment of the hinder teeth in *Theriosuchus* is only an extension of the character affecting some of those teeth in existing species of Crocodile*, and successional teeth, or their indications, are in crocodilian relation with the roots of the teeth to be displaced.

In the cranial platform of *Theriosuchus*, fig. 1, the median parietal part of the hind border is less convex, and the two outer parts are more concave, by reason of the further backward production of the mastoids (12), than in the contemporary dwarf Crocodile which I have called *Nannosuchus*. The lateral borders of the sculptured part of the platform are more convex than in *Goniopholis* or *Petrosuchus*. This is owing to the greater proportion of the outer and posterior angles of the platform, which is abruptly depressed below the level of the sculptured surface of the mastoid, and which becomes smooth like the contiguous and lower-placed tympanic. This character, shown in the subject of fig. 1, Plate IX., usefully indicated fragmentary parts of the skull of other individuals of the species. The supratemporal vacuities (T) are relatively larger than in *Goniopholis*. The intervening tract of the parietal (7), more canaliculate than in the larger species, is divided by a mid ridge in two of the cranial specimens, and partially so in the more complete skull, fig. 1. No palpebral ossicle is preserved in the orbit, *o*; the pointed ends of the nasals are produced so as to divide the outer nostril into two (fig. 1, *n*, *n*), as in some specimens of *Crocodilus niger*; were this a character of generic value it might unite *Theriosuchus* with *Halcrosia*, Gray†.

The alveolar part of the maxillary in which the canines are developed makes a corresponding convex extension of its outer border, as in *Goniopholis*. The extent of the 'symphysis mandibulæ' and the angle of divarication of the same are shown in fig. 2.

The matrix being removed from the palatal surface of the skull, fig. 2, exposed the orifice of the Eustachian canal, *e*, the palato-naris, *pn*, the pterygoids, 24, the palatines, 20, portions of the palatal plates of the maxillary, 21, and the pterygo-maxillary vacuities, *y*. The vertebræ, fig. 12, of *Theriosuchus* are amphiplatyan. The humerus, fig. 8, and the femur, fig. 9, have the Crocodilian structure.

* I have noted it in the *Alligator niger*. "No. 765. The right ramus of the lower jaw, from which the posterior part of the inner alveolar wall has been removed, showing the five posterior teeth lodged in a common alveolar groove." Osteological Catalogue, Museum of the Royal College of Surgeons, 4to, vol. i. p. 167 (1853).

† Trans. Zool. Soc. vol. vi. p. 135.

In *Theriosuchus* the breadth and shortness of the antorbital part of the skull, in proportion to the part behind, exceeds that in any modern broad-snouted Crocodile. Even in the young 'Crocodile à deux arrêtes,' figured in plate i. of Cuvier's 'Ossemens Fossiles'*, a transverse line across the fore part of the orbits equally bisects the skull, omitting the mandible. In *Theriosuchus* the same line leaves in advance six thirteenth parts of the length of the skull.

This proportion suggested at first view the immature state of the individual. But of the numerous evidences of *Theriosuchus pusillus*, none were larger than those figured in Plate IX., and several other fragmentary evidences of the species had come from still smaller individuals.

I conclude, therefore, that, as in the case of most species notable for their diminutive size, immature characters of the larger species of the genus are associated with such dwarfishness of the adults.

I estimate the average length of a mature *Theriosuchus* at 18 inches. The length of the skull, taken as that of the mandible, is 3 inches 6 lines. In the articulated skeleton of a modern Crocodile the angle of the lower jaw extends to the third cervical vertebra. In *Alligator lucius* the trunk, from the third cervical to the last sacral vertebra inclusive, is nearly equal to two lengths of the skull; the length of the tail is $2\frac{1}{3}$ lengths of the skull. The trunk of *Theriosuchus*, so defined, includes two lengths of the skull; the tail, as indicated by a portion of skeleton preserved, equalled $2\frac{1}{3}$ lengths of the skull. In the long-jawed Gavials and Teleosaurs the trunk includes about $1\frac{1}{4}$ length of the skull; but the tail is proportionally longer than in the short- and thick-jawed Crocodiles.

The actions and consequences of a *Theriosuchus* submerged with "a warm-blooded animal" of the size of a shrew or rat in its mouth might not excite the physiologist to analyze results and relations to palato-narial arrangements. The case is otherwise with a "large and powerful mammalian quadruped" in that predicament; its amphibious captor would not escape choking by the mere "closure of the external nostrils."

Let any F.G.S., with his head under water, hold his nose and open his mouth, and he will experience some trouble at the glottis.

The exclusion of water from the lungs is truly the important matter; and I fear my allusion to the mechanism for that purpose, which is peculiar to the Neozoic Crocodiles†, was too brief to dispel a possible haziness of conception of such mechanism.

A Crocodile, having seized and submerged a tiger or a buffalo, admits the water into its wide unlabiate mouth by the spaces to which the thickness of the part gripped keeps asunder the upper and the lower jaws. Thus the part of the mouth not occupied by the prey is filled with the fluid in which the mammal is being dragged and drowned.

* Quarto, tome v. 2e partie.

† Quart. Journ. Geol. Soc. vol. xxxiv. p. 423.

Admitting, for Mr. Hulke's argument, that the outer nostrils of a Crocodile, with their dense tegumentary boundary, could, like those of a seal, be shut by the action of a sphincter, exclusion by such narial opening of the watery element would not affect its entry by the mouth forced open by the seized and struggling mammal.

The question is, supposing the water to be stopped out of the anterior aperture, how is it to be excluded from the posterior one of the narial canal and at the same time from the entry of the wind-pipe?

And here comes the point for consideration in the comparison of Mesozoic and Neozoic Crocodiles with relation to their enemies and their prey.

In all the Crocodiles contemporary with "large mammals" there is a double valvular structure at the back of the mouth which prevents the water that may fill and be flowing through the mouth from getting into either the hinder nostril or into the glottis. One valve is fleshy and membranous; it hangs from the hind part of the palate, and answers to our "velum palati:" the other valve is peculiarly Crocodilian, at least in size and shape; it is a broad gristly plate which rises from the root of the tongue, carrying with it a covering of the lingual integument; and, when the palatal valve is applied to it, they form together a complete partition-wall, closing the back of the mouth, between which and the back nostril it is situated; it may be compared to a broad epiglottis, shutting off the glottis from the mouth.

To make this complex mechanical structure available, the back nostril is singularly reduced in size, and such reduction is shown in the skull. The small relative palato-narial orifice in procœlian or Neozoic Crocodilia is truly striking when contrasted with the size of the palato-nares in lizards and in amphicœlian or Mesozoic Crocodilia *.

But this is not the only character or condition of the procœlian palato-naris which renders the adaptation of the valvular machinery available for its purpose. In Neozoic Crocodiles the palato-naris is placed far back—further back than the basihyal—and its plane, instead of being horizontal, is tilted up at the angle, which makes the operation of the two parts, or "folding-doors" of the partition, most effective in closing the oral chamber posteriorly †.

What the modifications of the soft soluble parts of the hyoid and

* This, indeed, deceived De Blainville and Bronn as to the homology of the palato-nares in *Teleosaurus*; see 'Abhandlungen über die Gavialartigen Reptilien der Lias-Formation,' fol. 1841, pp. 12, 16, 24.

† See my "Anatomy of the Sharp-nosed Crocodile (*Croc. acutus*, Cuv.)," in the Proceedings of the Committee of Science &c. of the Zoological Society of London, October 25, 1831, part i. p. 139—in which, after comparison with the Egyptian Crocodile (*Croc. suchus*, Geof.), I "explained the uses of the apparent closure of the fauces, in which, on looking into the mouth, no orifice or passage for the food was perceptible; and remarked on the necessity for so

palate may have been in amphicœlian Crocodiles we may never know; but the large relative size, the forward position, and the horizontal plane of the bony openings oppose the application thereto of any such special and complex valvular structures as anatomy has revealed in existing Crocodiles.

If the submergence of the Crocodile with its "large mammalian" prey should continue so long as to render it needful for the reptile to "take a fresh breath," it can protrude its prominent snout from the surface and inhale a current of air which will traverse the long "meatus" and enter the glottis by the chamber common to nose and windpipe, which is shut out from the mouth by the modifications of a "velum palati" and "epiglottis" above explained. The same effect results from the "uninterrupted tube" in the procœlian Crocodiles as in that of the Cetacea. A teleologist must admit that "the contrivance is admirable;" it is equally effectual in both cases, and a Paley might expatiate upon the diversity of means by which the end is attained.

But we have no ground for inferring such means from the structure of the bony palate in the fossilized skulls of the amphicœlians; nor does our present knowledge of mammalian life in the Mesozoic periods encourage any belief that it was needed.

EXPLANATION OF PLATE IX.

Fig. 1. Upper view of skull of *Theriosuchus pusillus*.
Fig. 2. Under view of the same skull.
Fig. 3. Side view of the same skull.
Fig. 4. Left maxillary, inner side view, young individual, of *Theriosuchus*.
Fig. 5. Right maxillary, outer side view, of full-grown individual.
Fig. 6. Crowns of large canine and three following teeth, magnified.
Fig. 7. Dentary bone and fragments of mandible, inner side view.
Fig. 8. Portions of humerus, ulna, and radius.
Fig. 9. Femur.
Fig. 10. Outer surface of medio-dorsal scutes.
Fig. 11. Inner surface of ditto.
Fig. 12. Two dorsal vertebræ, under view.

All the figures, save 6, are of the natural size.

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complete a safeguard of the larynx in an animal breathing air, but destroying its living prey by submersion in water."

Geoffroy St.-Hilaire, 'Description des Reptiles de l'Egypte,' p. 236.

Hunter had left a preparation demonstrating the same structure, which is described in the 'Catalogue of the Physiological Series in the Museum of the Royal College of Surgeons,' 4to, 1832, vol. iii. p. 72, Prep. No. 1466.

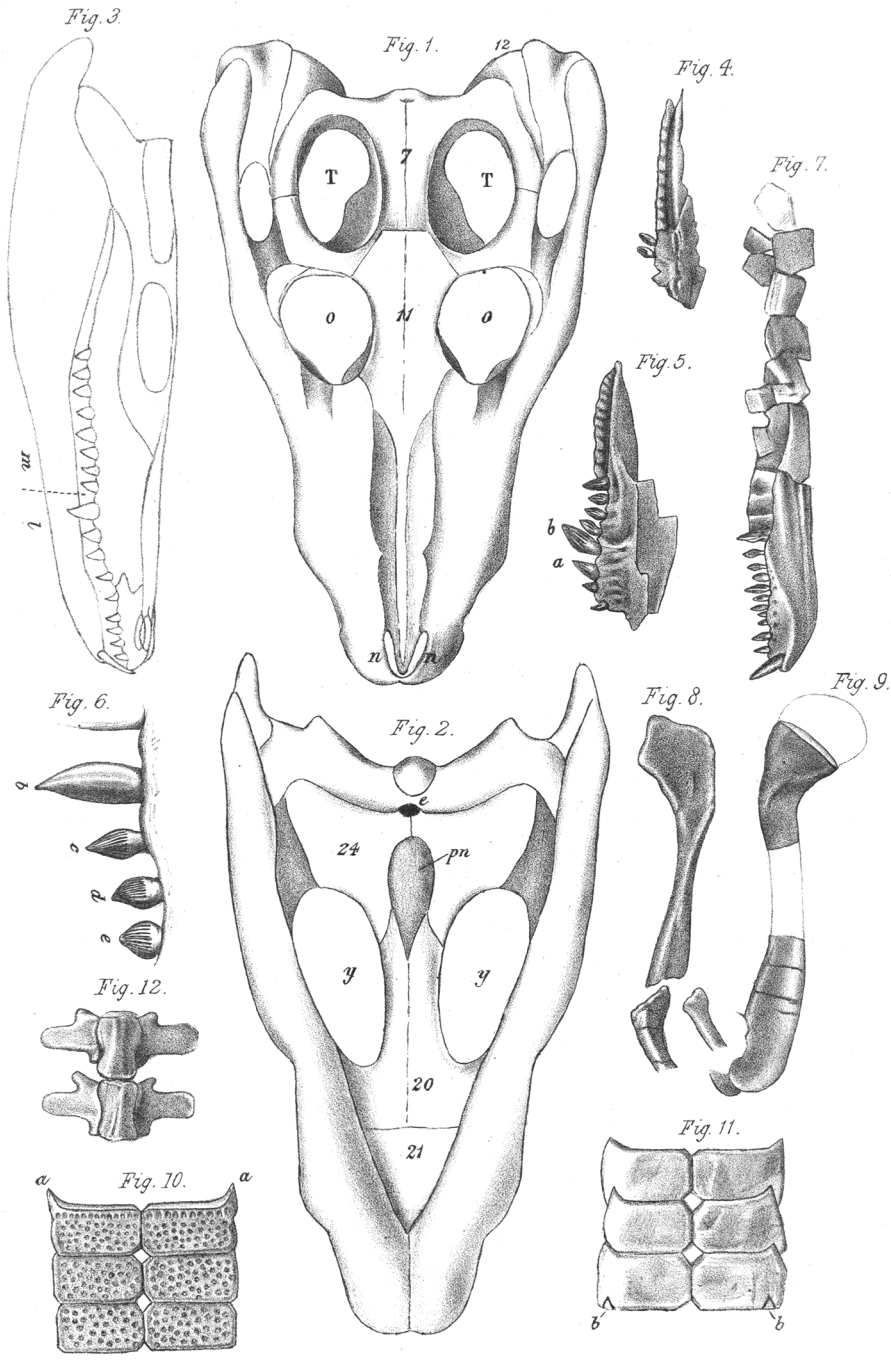
See also Cuvier, 'Leçons d'Anat. Comparée,' 8vo, tome iv. (1805), p. 284. "Les ouvertures internes des narines sont très en arrière dans cet animal, contre l'ordinaire des autres reptiles," which other reptiles include the Crocodiles not procœlian or Neozoic.

Discussion.

Mr. Hulke remarked on the resemblance of the under and upper sides of the skull described to that of *Goniopholis*.

Prof. Seeley demurred to the nomenclature employed by the author in describing teeth, and especially to his statement that in this and other Crocodilians there were several canines.

Prof. Owen stated that he had used the term *canine* in reference to the relative size and form of the teeth of Crocodiles, and not to their position in the jaws.



A.S.Foord lith. Hanhart imp.

DWARF CROCODILES.