ART. XXXVIII.—On the Functions of the "Sacral Brain" in Dinosaurs; by RICHARD SWANN LULL.

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Branca, in a discussion of the fauna of Tendaguru, East Africa,¹ makes a number of thought-inspiring comments upon the huge sauropod dinosaurs which the formation contains. Among other points he is striving to account for the maintenance of their immense bulk upon a possibly meagre diet by assuming digestive powers of extraordinary efficiency. For this he offers the following explanation:

"One may be inclined to look for the ability to take care of food solely in the stomach, intestines, or liver. However, in the dinosaurs we may take into consideration something else, *i. e.*, the 'sacral brain,' if we look upon the swelling of the spinal column in the sacrum as a 'brain.' According to Waldeyer, it is indeed thinkable that the sacral brain in dinosaurs had a certain independence, and cared for the functions of *nourishment*, *digestion*, and procreation [*italics mine*], also that through a particularly strong innervation it had become especially powerful, more powerful than the strongest digestive organs could be without such a sacral brain. In man there appear still to be traces of this, but here the sacral section of the spinal column is completely surpassed by the brain."

What Waldeyer based his argument upon I do not know, but the evidence which I have been able to secure seemingly does not justify such a speculation. This evidence is here presented.

Dinosaurian feeding habits.

Our assumption of feeding habits based upon the character of dinosaurian dentition justifies the following conclusions:

Theropoda.—These are the carnivorous dinosaurs in a strict sense, with teeth which were in the main prehensile and as such confined to the forward portion of the jaws. They must have been used for rending the prey, for in many instances, such as *Allosaurus* or *Megalo-*

¹ W. Branca, Die Riesengrösse sauropoder Dinosaurier vom Tendaguru, ihr Aussterben und die Bedingungen ihrer Entstehung, Archiv für Biologie, 3. Bd., 1. Heft, 1914, pp. 71-78.

saurus, they are sharp-pointed and compressed, with finely serrated cutting edges. In *Tyrannosaurus* they become so thick that the knife-like edge is gone, so that these huge beasts must have dismembered their prey by tearing rather than by cutting it. These latter theropods are analogous to the crocodiles in dental equipment; *Allosaurus*, on the other hand, possessed a more efficient dentition.

The digestive system of the crocodiles shows the highest degree of specialization of any living reptiles, as the stomach is very muscular, with lateral tendinous discs forming an organ very suggestive of the gizzard of the graminivorous birds. In front of this gizzard-like stomach is a capacious portion of the œsophagus, within which is held the excess of food over the rather small capacity of the stomach. The stomach digestion is highly efficient, due not alone to its muscular power, but to the strength of the gastric juice, so that even the bones of the prey are dissolved and not passed through the intestine, as with certain carnivorous birds like the owls. Crocodiles occasionally swallow stones to aid in the trituration of their food, just as do the graminivorous birds.

To what extent the gizzard was developed in the Theropoda is conjectural, but it would seem as though its need were nearly as great with them as with the crocodiles. One aberrant type of theropod, *Struthiomimus*, from the Belly River formation of Canada, has just been the subject of an authoritative paper by Professor Osborn.² This form is now known to have been absolutely toothless, and several theories have been advanced as to its feeding habits—that it was insectivorous, especially ant-eating, or that it fed on small crustaceans or molluscs of the seashore, or that it was ostrich-like in habits, browsing upon leaves and buds which its prehensile limbs drew within the reach of the horn-sheathed mouth. Such an assumption as the last, which bears the weight of Osborn's own opinion, would seem to imply the presence of a more or less efficient gizzard-like stomach functionally comparable to that of the struthious birds.

Sauropoda.—The sauropods are clearly of theropod derivation, but it has been pretty generally assumed that they had forsaken the carnivorous habits of their for-

² H. F. Osborn, Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*, Bull. Amer. Mus. Nat. Hist., vol. xliii, 1917, pp. 733-771.

bears for a vegetative diet, and the tremendous growth of certain plants such as the water hyacinth in the Nile or the waters of New Zealand seems to offer an analogy to what might well have been true of certain aquatic vegetation of the Mesozoic upon which these creatures fed. The teeth were now solely prehensile, sufficiently so for their owners' purpose, but less efficient than those of the Theropoda. The food was in no sense masticated and the inference that a powerful muscular gizzard-like stomach was developed is irresistible, for which the presence of stomach stones, gastroliths, within the ribs of more than one specimen may be taken as added argument.

Predentates.—The predentate dinosaurs, on the other hand, had a differentiated mouth armament. The anterior or prehensile portion was toothless, except in *Hypsilophodon*, but was sheathed with a horny, turtle-like, cropping beak of varying form. The posterior portion of the jaws bore the actual dental battery, consisting of a series of successional teeth which also varied in efficiency and degree of development in accordance with their owners' food, as do those of the ungulate mammals. The Jurassic and early Comanchian forms, such as *Camptosaurus* and *Laosaurus*, were analogous to the browsing ungulates whose brachiodont teeth are fitted to succulent herbage, while the later trachodonts had a dental battery fully as efficient as that of a horse. These dinosaurs chopped their food into short lengths before swallowing, and it may be that the term mastication, which, however, implies a grinding or crushing rather than chopping, may be properly applied to them. Their need of a gizzard-like organ would seem to be less great than in the sauropods.

Stegosaurus, on the other hand, possessed a very imperfect dental battery, as the teeth were both small and relatively few in number—very inadequate apparently for their owner's needs. This genus, however, exhibits a number of characters which, in the Sauropoda, have been taken as indicating an aquatic or at least amphibious life. They are, first, the solid, massive character of the limb bones and the imperfection of their articular ends, those of the stegosaur showing a rugosity fully proportional to those of *Brontosaurus*. The high position of the ribs, bringing the lungs well toward the dorsal side of the body, and the strongly compressed tail

with its high neural spines and well developed chevrons are also suggestive. Add to these a mouth armament no more effective than that of a sauropod, and the association of their remains in a common burial, and the inference of similarity of habitus and food is perhaps justified. Just what effect the tall upstanding armor plates would have upon the navigable powers of *Stegosaurus* is not so clear, but they may have incommoded him under such conditions no more than on land.

It may be fairly assumed, therefore, in view of the wide apparent range of feeding habits on the part of dinosaurs, and their relationship to the crocodiles on the one hand and to the birds on the other, that their digestive system was closely comparable both in the development of its parts and in its innervation to that of these living forms. With the birds, the degree of development of the gizzard varies directly with the consistency of the food. Graminivorous birds possess the strongest muscular layer and the thickest horny lining, while in the series from the insectivorous birds to the birds of prey this condition becomes gradually less marked and the division of labor between the glandular proventriculus and the mechanical gizzard less noticeable (Newton). The assumption of a similar gradation in the development of this organ in the dinosaurs seems also warranted.

Innervation of the alimentary canal.

In the reptiles such as the python, crocodile, or turtle, the *vagus* nerve (Xth cranial) is the principal transmitter of stimuli which *initiate* digestive activity, certain of its fibers being distributed to the muscles and mucous membrane of the fauces, the œsophagus, and the stomach, and it finally terminates at the beginning of the intestine at the pancreas.

Cranial casts of *Tyrannosaurus*³ and of *Stegosaurus* and *Morosaurus*, representing, therefore, the three main dinosaurian groups, all show exits for the IXth to XIth cranial nerves, thus including the *vagus*, relatively larger if anything than in the crocodile. It is fair to assume, therefore, that this nerve was at least as well developed in the dinosaurs and that its distribution and function were comparable.

³H. F. Osborn, *Crania of Tyrannosaurus and Allosaurus*, Mem. Amer. Mus. Nat. Hist., new series, vol. i, pt. 1, 1912, pp. 1-30.

Birds.—The vagus (X) of birds arises behind the glosso-pharyngeal (IX) and is connected therewith as well as with the sympathetic system. After receiving branches from the hypoglossal (XII) and taking up the spinal accessory (XI), the vagus runs down the side of the œsophagus to the ventral side of the proventriculus, where, joining its fellow from the other side, it spreads out to supply the stomach. Other branches, leaving the principal stem of each vagus, supply the liver, heart, and lungs, and, as the recurrent laryngeal branch, also supply the distal portions of the trachea and œsophagus. Some fibres of the vagus often extend beyond the stomach, and are connected with the sympathetic nerves of the trunk, supplying parts of the intestinal canal. (Newton.)

The approximate agreement in the innervation of both birds and crocodiles is further argument for dinosaurian innervation.

Certain of the spinal nerves (dorso-lumbar) communicate with the sympathetic system and thence with the alimentary canal, but their function, in so far as it has been observed, principally in man and certain mammals, is *inhibitory*, and hence the reverse of a stimulus to digestion. Such sacral nerves as do pass to the alimentary canal are distributed to the hinder portion only, beyond the glandular or digestive part. They are stimulating, not inhibitory nerves, but their function is merely the elimination of faecal matter and is in no other sense digestive.

The stomach in the mammal at least is largely automatic in its movements, as is the heart, and while its activity may be initiated or inhibited by impulses from the vagus or sympathetic nerves, the stimuli which cause the rhythmic movement originate in the muscles themselves, for this movement will continue after the severance of all nerve connection with the cerebro-spinal or sympathetic centers. The reptilian heart is notorious for its automatic contraction after its excision from the body, and in all probability the heart and stomach of a dinosaur were fully as automatic.

All of this seems to show that we have no right in assuming for the dinosaur an innervation or functioning of the alimentary canal at variance with the standardized type of the living amniotic vertebrates.

The spinal canal of *Stegosaurus ungulatus* has been studied in detail by the author, who finds not only a sacral dilatation but a *brachial* one as well; that is, from vertebræ VIII to XIII, the maximum width, that of 38 mm., as compared with the average of 25 mm., is attained by vertebra XI, which is exactly opposite the shoulder articulations in the Yale mounted specimen. There is also a corresponding heightening of the canal, although this is a less constant feature, for further back (XV and XVII) there is evidence of a ligament or other delimiting structure below the bony roof of the neural arch itself. Brachial and sacral dilatations of the neural canal are most marked in the turtles among existing reptiles, owing to the immobility of the trunk and the consequent reduction of its musculature and associated nerves, the two enlargements being necessary where the nerves depart to the limbs. That this is the whole significance of these two enlargements in *Stegosaurus* and also in other dinosaurs I have no doubt, and the relative size of each dilatation bears an approximate ratio to that of the limbs innervated, plus in the hinder pair the huge caudofemoral and other muscles which actuated the tail.

I still feel, despite the contention of the German writers, that the "sacral brain"—which should not be called by such a term—possessed no unusual function whatever, but only the normal one of transmission and reflex action in an unusual degree, and that to invoke any new and unknown function as a reason for its relatively immense size, especially one connected with digestive efficiency, is not justified by the evidence at hand.

Branca further says:⁴ "We may also think of these animals as sluggish in habit, in consequence of which much less food was required than is the case in an active animal." On the other hand, in warm-blooded animals the largest species occur in cooler climates, because large animals have "a relatively smaller radiating surface than smaller ones, a factor of the greatest importance in the regulation of body warmth." To the first statement I can take no exception. The second, however, gives food for thought. In the first place, is it an invariable rule that the largest species of warm-blooded animals occur in cooler climates? The present-day distribution

⁴ Loc. cit.

of the elephant, hippopotamus, and rhinoceros does not bear this out, and even in the Pleistocene the largest elephants, such as *Elephas imperator*, were southern forms compared with the smaller, cold-adapted *E. primigenius*. With marine creatures Branca's statement seems more nearly true, for the walrus and huge sea-elephants are both adapted to cold waters, and the same is true of the right whales, *Balæna mysticetus* and *B. australis*. The sperm whale, on the other hand, is tropical or subtropical, not occurring, except accidentally, in the polar regions (Flower and Lydekker), while the great rorquals (Balænoptera) are found in all seas except the Arctic and probably the Antarctic also. Of the deer, perhaps the largest living form is the Alaskan moose, while no bears in existence can compare in magnitude with the great Kadiak bear of the same region. But this argument loses weight if the dinosaurs were not warm-blooded, and though the supposition that they were has been advanced, it is not susceptible of proof. It is within the range of possibility that the temperature of the more agile dinosaurs rose appreciably during the time of their activity, as in many of the so-called cold-blooded (poikilothermous) creatures today, but whether or no any dinosaurs had a mechanism for even a partial maintenance of temperature is unknown. If their bodily heat varied with that of the surrounding air, the greater bulk and hence relatively smaller radiating surface would render them less susceptible to rapid temperature changes, and thus prolong their time of activity by tiding over a brief drop in temperature, but would hardly be available in an extended cooler period. That increase of size in dinosaurs was an adaptation for the conservation of energy, and in this way reduced the relative amount of nourishment necessary for their maintenance, seems hardly probable.