THE AMERICAN NATURALIST

VOL. XXXIV.

January, 1900.

No. 397.

INTERCENTRA AND HYPAPOPHYSES IN THE CERVICAL REGION OF MOSASAURS, LIZARDS, AND SPHENODON.

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IN the course of a recent study of the skeleton of Mosasaurs¹ I was much struck by the uncertainty which prevails in the interpretation of the elements entering into the vertebræ of the neck. The leading American authorities, Cope, Baur, and Williston, differ widely in their descriptions of these parts in different papers. The late Professor Baur himself had a perfectly correct notion of the components of the neck, as I learned from him in conversation; but a clear statement of his views is not to be found in his published writings. Two of the leading German comparative anatomists, Gegenbaur and Wiedersheim, fail entirely to recognize clearly the very interesting structure of the cervical vertebræ. I was thus led to the comparison of the neck vertebræ in different members of the Squamata and Rhyncocephalia, with most interesting results.

It appears that *intercentra* are present in the neck of all

¹ A Complete Mosasaur Skeleton, Osseous and Cartilaginous, *Mem. Amer. Mus. Nat. Hist.*, vol. i, pt. iv. October, 1899.

Mosasaurs, lizards, and Sphenodon, either in a primitive position or secondarily modified to subserve a variety of functions.

The best known modification is in the atlas, where the intercentrum forms the base of the ring. The modifications which have not been so generally recognized are in the axis and the other cervicals, where the intercentra secondarily function as *hypapophyses*, while still remaining more or less distinct from the centra proper.

The primitive relations of the intercentra and pleurocentra (or centra proper) in the axis and atlas are beautifully shown in

FIG. 1. — *Platecarpus coryphaeus* Cope, Coll. American Museum Natural History. Atlas, 1; axis, 2; third cervical, 3. Right neural arch, *n.a.*, in place; left neural arch removed, exposing odontoid (supposed pleurocentrum of atlas), *od.* loosely articulated with axis. Intercentrum of atlas, *i.1*; intercentrum of axis, *i.2*; intercentrum of third cervical, *i.3*; intercentrum of fourth cervical, *i.4*. Intercentra 3 and 4 are secondarily shifted forward upon the hypapophyses of the centra in front.

the accompanying photograph (Fig. 1), taken from the neck of a specimen of *Platecarpus* — one of the Kansas Mosasaurs. But before describing this it will be well to recapitulate.

The prevailing interpretations of the neck components in different types of reptiles are as follows:

1. *Proatlas*. The pair of small dorso-lateral elements in Rhyncocephalia (see Fig. 4, *D*), certain Lacertilia, Crocodilia,

Dinosauria, Pterosauria, Chelonia, are regarded by some authors as vestiges of a "proatlas" or degenerate vertebra between the atlas and the skull. As remarked by Baur, these pieces correspond in position with the "neurapophyses" of a typical vertebra.

2. *Atlas*. The lateral pieces of the atlas proper are by all authors regarded as neural arches or "neurapophyses" (*n.a.* in our figures).

3. *Atlas*. In his early papers Cope—in fact, when he first defined the "intercentrum"—regarded the ventral pieces of atlas and axis as "intercentra" (*i.1* and *i.2* in our figures). The

FIG. 2.—*Chelydosaurus vranii* Fritsch. A rachitomous amphibian vertebra from the Permian of Bohemia, viewed from the *right* side, after Fritsch. Neurapophyses, neural arch, 2 pieces; pleurocentra, on sides of notochord, 2 pieces; hypocentrum pleurale, below notochord, 1 piece; intercentrum arcuale, below notochord, 1 piece.

anterior ventral piece (*i.1*), or lower element of the atlas ring, is, however, described as a "centrum" (*i.e.*, "pleurocentrum") by Baur in his latest paper; by Gegenbaur as possibly an "hypapophysis" (*Vergleichende Anatomie*, 1898, p. 249). In an unpublished lecture chart Baur rightly interprets ventral pieces of both atlas and axis as "intercentra."

4. *Axis*. The odontoid process is regarded as the pleurocentrum or centrum proper of the atlas, which has become secondarily attached to the axis (*od.* in our figures).

5. *Axis*. The posterior ventral piece (*i.2* in our figures) is described as an "intercentrum" by Baur, as the "atlantar hypapophysis" by Williston, in the Mosasaurs.

6. *Cervicals 3-9*. The ventral intermediate pieces (*i.3* to *i.8* in our figures) are spoken of as "intercentra," also as "hypapophyses."

I. RACHITOMOUS PROTOTYPES.

For the origin of these structures we must naturally turn back to extinct forms, and we find two rachitomous prototypes — one composed of six pieces, one of five.

Among the primitive Amphibia (Stegocephalia) we find types in which every vertebra is composed of six pieces, as figured by

FIG. 3. — *Discosaurus* Credner. A rachitomous amphibian vertebra from the Permian of Saxony, viewed from the left side, after Credner. Neurapophyses, neural arch, 2 pieces; pleurocentra, lateral, 2 pieces; intercentra, median ventral, 1 piece.

Fritsch, Fig. 2 (*Chelydosaurus vranii*). It is possible, therefore, that the "proatlas" may represent, not a separate vertebra, but part of the atlas of a persistent rachitomous type.¹ This is improbable.

¹ According to this hypothesis, for which at present little can be said, the homologies would be as follows:

<i>Atlas Components.</i>	<i>Secondary.</i>
Primitive neurapophysis	= proatlas.
Primitive pleurocentrum	= neural arch.
Primitive intercentrum	= base of atlas ring.
Primitive hypocentrum pleurale	= odontoid process.

The demonstration of a vestigial, anterior, cervical nerve belonging to the degenerate "proatlas" vertebra would be fatal to the above hypothesis.

A likelier rachitinous prototype is that afforded by *Disco-saurus* Credner, another *Stegocephalian*, in which it is seen (Fig. 3) that the intercentrum is in front of its corresponding pleurocentrum or centrum. Such a vertebra consists of five pieces. If from such an atlas prototype the pleurocentrum (*pl.*) were to be transformed into the odontoid process, the first result

FIG. 4. — Typical cervical vertebrae of Mosasaurs, lizards, and Sphenodon. *A.* *Platecarpus*, a Mosasaur, with left neural arch of atlas removed. *B.* *Varanus*, a monitor lizard, with intercentra secondarily shifted to tips of hypapophyses. *C.* *Cyclurus*, a lizard, with intercentra in *primitive position*, excepting *i.2*, which has been shifted backwards and coalesced with hypapophysis of axis. *D.* *Sphenodon*, a Rhynchocephalian, with all intercentra in *primitive position*, excepting *i.2*, which is coalesced with axis, as in *Cyclurus*.

would be to bring the atlas and axis intercentra together without change of form. This is exactly what we find in *Platecarpus*, one of the Kansas Mosasaurs (Fig. 1). The photograph represents a condition in which the intercentra 1 and 2 are alike in their wedge-shaped form, and are still entirely free from the other elements of the atlas and axis (see also Fig. 4).

2. CONDITIONS IN THE MOSASAURS, LIZARDS, AND SPHENODON.

The modifications of the primitive type, in which each centrum has an intercentrum below and in front of it, are well illustrated in the accompanying diagrams (Fig. 4).

The condition of the Platecarpus axis and atlas is even more primitive than that of Sphenodon; but Sphenodon is more primitive than Platecarpus in the vertebræ behind the axis.

A. In Platecarpus both atlas and axis intercentra free and wedge-shaped. Intercentra 3-7 shifted forward secondarily upon the short hypapophyses of centra 2-6.

D. In Sphenodon a "proatlas"; intercentrum 1 of atlas loosely connected with neurapophysis of atlas; intercentrum 2 of axis completely coalesced with axis; intercentra 3-7 in their primitive position.

B. In Varanus intercentrum 1 broadly connected with atlas neurapophysis; intercentrum 2, forming an anterior hypapophysis upon axis, loosely connected in young, suturally united in adults; intercentra 3+ forming tips of the long hypapophyses of centra 2+. (This hypapophysial connection of the intercentra is an advance upon that initiated in Platecarpus.)

C. In Cyclurus intercentrum 1 broadly united with atlas ring; intercentrum 2 completely coalesced with axis; intercentra 3 and 4 in primitive position, but expanding to function as hypapophyses; intercentra 5 and 6 small, in primitive position.

The secondary modifications have, therefore, been of four kinds:

1. Conversion of the atlas intercentrum 1 into the basal piece of the atlas ring by loss of its wedge-shape and broadening of its contact with the neurapophyses (*e.g.*, Varanus, Cyclurus).

2. Lateral or complete union of the axis intercentrum 2 with the anterior portion of the axis centrum (*e.g.*, Cyclurus, Sphenodon).

3. Secondary conversion of the intercentra 2+ into hypapophyses (*e.g.*, axis of *B*, *C*, *D*; axis and third cervical of Cyclurus).

4. Shifting of the intercentra 3-7 forward upon the hypapophyses of the preceding vertebræ (*e.g.*, Varanus, Platecarpus).

This history of the atlas and axis complex in the Mosasaurs, lizards, and Sphenodon may, in conclusion, briefly be summarized as follows :

1. The intercentrum of the atlas fuses with the neural arches of the atlas to form the basal portion of the ring.
2. The intercentrum of the axis fuses with the centrum of the axis to form a kind of hypapophysis.
3. The intercentra of the remaining cervicals 3-7 either remain primitive in position, or are shifted forward upon the hypapophyses of the next vertebra in front.

AMERICAN MUSEUM OF NATURAL HISTORY,
December 7, 1899.