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ARTICLE II.
ON THE INTERCENTRUM OF THE TERRESTRIAL VERTEBRATA.

BY E. D. COPE.

Read before the American Philosophical Society, January 1, 1886.

Since the discovery of the rhachitomous Batrachia, two different views of the homologies of the segments which compose the bodies of their vertebrae have been maintained. According to the one first proposed, that of the writer,* the segments in the accompanying cuts of Trimerorhachis insignis Cope, and Eryops megacephalus Cope, marked \( p \), represent the centrum proper; while those marked \( i \), are pieces which are intercalated between the true vertebrae, and are, therefore, appropriately termed intercentra. According to the second interpretation, that of Professor Gaudry,† the three elements \( p, p, i \) together, constitute a vertebra. It follows that \( i \) cannot then be

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properly termed an intercentrum, so it is named by Gaudry the hypocentrum. The question as to which of these interpretations is correct has an important bearing on the homologies of the corresponding parts in other batrachians and in reptiles; and the phylogenies of these classes cannot be determined until the question is settled. The following pages are devoted to this subject.

I.—THE BATRACHIAN INTERCENTRUM.

That the intercentrum exists is shown by the very frequent occurrence in the Pelycosaurian reptiles of the Permian epoch, of a wedge-shaped bone between the vertebral centra on their inferior side* (Plate I, Fig. 9). Apparently homologous elements occur in the dorsal and cervical regions of Sphenodon,† and in the cervical regions of various other lizards. Similar pieces are found in the dorsal and caudal regions of various Mammalia, for instance, Erinaceus.‡ But in general they are wanting from Mammalia, and are better developed in the Pelycosauria than in any other order of reptiles.

In the Pelycosauria (Clepsydrops, Dimetrodon), the intercentra of the caudal region are continuous with, or form a wedge-shaped common head, of the chevron bones (Plate I, Fig. 9). In the rhachitomous Eryops, in the caudal part of the column, the pieces which correspond with the intercentra of the Pelycosauria in forming the expanded heads of the chevron bones, are those which I have termed intercentra, and which Professor Gaudry has called hypocentra (Plate I, Fig. 1). Here, as in the dorsal region (Cut 2), the intercentra present their lateral angles upwards towards the neural arch. The neural arch rests exclusively on the pleurocentrum, which in turn adheres to the intercentrum behind it by its long side, and to that in front of it by its short side or end. The diapophysis belongs exclusively to the basal part of the neural arch in the dorsal and cervical regions, and its extremity forms a vertical

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† Günther, Transac. Royal Society, 1867, Pl. ii, Fig. 17; Albrecht.
articulation for a single-headed rib. In the cervical region the articular surface for
the rib is continued downwards, forming a shallow groove on the posterior part of the
side of the intercentrum. This groove becomes shorter, and finally disappears from
the intercentra at some distance posterior to the cervical region. In the cervical
region in some of the specimens a groove crosses the inferior side of the inter-
centrum, passing through and dividing into two parts the costal groove. It appears
to be a suture which cuts off a segment from the posterior side of the intercentrum.
This segment is coössified with the intercentrum in most of the cervical vertebrae of
Eryops megacephalus, and disappears so completely from the vertebrae posterior to
this region, that it is impossible to say whether it is primitively absent, or coössified.
The narrower anteroposterior diameter of the intercentra, and the absence of the
lateral costal articular groove would indicate its total absence. This element has
been observed by Fritsch in some Bohemian forms, and has been termed by him the
hypocentrum pleurale.

In the genera described by Dr. Fritsch from the Permian Gaskohle of Bohemia
some conditions have been described by him which differ considerably from those
mentioned above. The figures given by Dr. Fritsch are not entirely consistent
with each other, and appear to have been taken from imperfect specimens. Thus in
Sparagmites lacertinus Fr.,* a neural arch is represented as resting on an intercen-
trum, while the arch next behind it rests on a hypocentrum pleurale, or a divided
pleurocentrum. It is not possible to be certain whether the neural arch stands on the
centrum or intercentrum in the caudal region of Diplovertebron, as in some figures it
covers both (Pl. 52, Fig. 2), and in others only one of these elements (Pl. 50, Fig.
14). In the caudal region of the Diplovertebron punctatum,† the vertebrae have dif-
ferent forms, one being produced inferiorly apparently for a chevron bone, and another
posterior to it, being without prolongation, and without chevron. It is not possible
to be sure from Dr. Fritsch’s descriptions and figures whether the chevron bones are
articulated, or are continua, in these genera.

Dr. Fritsch, however, determines the presence for the first time of the hypocen-
trum pleurale, and describes it in the genera Chelydosaurus and Sphenosaurus.‡ With Gaudry, however, he regards the intercentrum as the true centrum, and then
homologizes the hypocentrum pleurale with the intercentrum of the Pelycosauria.

I have attempted to sustain my interpretation of these homologies§ by reference

* Fauna der Gaskohle der Permiformations Boehmens, Bd. ii, H. 1, Pl. 50, Fig. 16.
† Loc. cit., Pl. 50, Fig. 14. Dr. Fritsch believes the inferior long bone to be a rib.
to the genus Cricotus, type of the order Embolomeri; a form which has not yet been found in Europe, so far as ascertainable. In this genus the chevron bones are continua, while the neural arch is free, as in Eryops. The element which bears the chevron bone being regarded, as in that genus, as the intercentrum, we can affirm (Fig. 3) that the intercentrum is continued upwards to the neural canal, forming a disk, and the pleurocentra are continued downwards and are united below, forming a complete centrum. This explanation looks the more reasonable in view of the existence of the hypocentrum pleurale in the Sphenosauridae, which if combined with the pleurocentra would form a completed centrum. It is, however, uncertain as yet whether this is the make-up of the centrum in Cricotus, because in Eryops the hypocentrum pleurale unites with the intercentrum and not with the pleurocentrum. That my determination of the homologies of the vertebral disks in Cricotus is correct is further evidenced by the structure of the caudal region of Eryops. In *E. erytholiticus* (Pl. I, Fig. 1), the pleurocentra descend further than in the dorsal region, reaching to the inferior face of the column, and separating the intercentra from mutual contact.

Further development of their inferior portion, with truncation of inferior surface, would represent the structure stated by Fritsch to characterize Archegosaurus, and which is still better developed in Cricotus. The chevron bones are always continua in both Eryops and Cricotus. Of the latter genus I possess in my collection many caudal intercentra with chevrons, of all ages, and in none of them is there any sutural articulation visible (Pl. I, Fig. 6).

The correctness of this determination is further confirmed by a study of the dorsal region of Cricotus. In passing along the caudal region towards the sacrum, the chevron-bearing disks or intercentra diminish in anteroposterior diameter both absolutely and relatively, while the centra do not undergo any modification. The neural
arch, from resting by more than half its base on the intercentrum (Fig. 3) gradually transfers itself to the centrum, at the base of the caudal series. It maintains this position throughout the lumbar and dorsal series,* resting freely in an angular fossa of each side of the anterior three-fourths of the superior face of the centrum. It bears the diapophysis with the usual articulation for a single-headed rib (Plate I, Fig. 3). The intercentra even continue to the cervical region, which terminates anteriorly in an intercentrum, which is perhaps the body of the proatlas, the processus dentatus of the atlas of the existing Batrachia, and the occipital condyle (without basioccipital bone) of the Reptilia. † In addition to the preceding reasons for adopting my determination of centrum and intercentrum, it may be added, that in the Cricotus heteroclitus Cope the dorsal intercentra are much narrowed above,‡ some of them so much so as to have a sharp edge, which forms but a narrow bridge above the foramen (Plate I, Figs. 7–8) chordae dorsalis.

According to Gaudry, the structure of the dorsal part of the vertebral column in Actinodon and Archegosaurus is identical with that of Eryops§ (Fig. 4). This author represents the neural arch as resting on the pleurocentrum. Fritsch, on the other hand,‖ represents the neural arches as slightly in contact with the intercentra, and

† Amer. Naturalist, 1884, p. 37.
‡ Proceeds. Amer. Philos. Society, 1877, p. 186 (see C. discophorus, which was founded on such intercentra)
‖ Fauna der Goskohle, Tab. 58, fr. 13.
the pleurocentra as between their bases, a condition of things which is probably due to disturbance of the parts before fossilization (Fig. 5). Fritsch also represents the neural arch in Sphenosaurus and Chelydosaurus as resting on the intercentrum, in diagrammatic manner,* and the pleurocentra and hypocentrum pleurale as alternating with them. As Dr. Fritsch does not give profile figures of the original specimens, one cannot judge how much may be due here also to disturbance of the parts. Still more open to this question are the figures of Von Meyer.† The true relation of the parts cannot be learned from these figures and descriptions, and it is probable that the specimens at the disposal of European paleontologists generally are as yet much inferior in the condition of their preservation and in size to those found in Texas.

The vertebrae of the true Stegocephali are, so far as known, undivided and without intercentra, with one exception, and that is the genus Branchiosaurus Fritsch.‡ According to this author, each vertebral body is composed of three parts, a median, an anterior, and a posterior. The median, if separated from the other two parts, would be bi-concave, and it supports the rib. Each of the extremital segments presents a convexity towards the median segment, resembling the epiphysis of a mammal. What the homologues of the three parts may be remains to be ascertained.

II.—THE REPTILIAN INTERCENTRUM.

The Rhynchocephalian genus Sphenodon has been represented by Günther to have cervical and some dorsal intercentra.§ It therefore seemed probable that its structure might throw some light on the homologies of the batrachian and reptilian intercentra. I therefore dissected the vertebral column of a specimen in alcohol kindly presented to me by my friend, Dr. James Hector, chief of the Geological Survey of New Zealand. The attachment of the chevron bones does not, in the figure of Günther, resemble very closely that seen in Clepsydrops, but on examination I found the relations to be structurally and homologically identical with that found in Cricotus. The caudal vertebrae are separated by a rather thick disk of intervertebral cartilage which surrounds the foramen chordæ dorsalis, resembling closely the intercentrum of the Embolomeri. There is an internal annular deposit of phosphate of lime, which, if extended to the entire cartilage, would give us an embolomerous intercentrum like that of Cricotus. This resemblance is a true homology, for the chevron bones spring from this cartilage, although in slight contact with the centrum in front of it (Plate I, Fig. 10).

† Paleontographica, 1858, Vol. vi.
‡ Fauna der Gaskohle, Bd. i, Heft. 1.
§ Transactions of the Royal Society London, 1867, pl. ii, fig. 23.
There can then be no doubt of the homology of the cartilaginous intercentrum of Sphenodon with those of the Pelycosauria, and of the entire centrum of Sphenodon with that of the Pelycosauria. The division of many of the caudal centra of Sphenodon and of many lizards, is evidently not explained by the supposition that one of the parts is an intercentrum. That they are halves of a single centrum is not only rendered probable by the above determination of the intercentrum, but is supported by the modifications presented by the centra themselves. In Sphenodon, instead of gradually losing one of the halves, the latter become, without diminution, more and more consolidated towards the anterior part of the caudal series, and merge into the ordinary type of vertebra, each proximal centrum representing both halves of a distal one (Plate I, Fig. 10).

It is thus probable that each vertebra of a Lacertilian* and of a Pelycosaurian represents one centrum, and that intercentra are present in some types, and absent in others, except as always represented by the chevron bones of the tail. Is this the case with the existing Batrachia?

![Fig. 6. — *Eryops megacephalus.* Vertebral column represented in Fig. 1, from below; one-fourth natural size. From Permian epoch of Texas.](image)

In an important memoir, Hoffman† presents us with the results of his investigations into the homologies of the ribs of the terrestrial Vertebrata. He finds that in all of them, excepting the Batrachia, the primitive ribs are processes of the intervertebral, and not of the vertebral cartilage. The intervertebral cartilage in reptiles with ball and socket joints divides, each half uniting with its adjacent body, the one to form the ball, and the other the concave extremity of a vertebra. In the Mammalia the halves form the epiphyses respectively. In this class the head of the rib justifies this origin, remaining as it does articulated in a fossa which is equally excavated from two adjacent epiphyses. I have shown that the head of the rib in the Pelycosauria is articulated with the undivided intercentrum.‡ The structure in this order is in confirmation of the doctrine that the element I have called intercentrum is such in fact. The passage of time has seen in the Reptilia in general, the same modification in the mode of attachment of ribs as occurs in the vertebral column of the Mammalia, etc., in pass-

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* Baur shows that in the Lacertilian genera *Uroplatus* and *Gecko*, intercentra are present throughout the dorsal, lumbar, and sacral regions. *American Naturalist*, 1886, p. 174.

† Niederländisches Archiv. f. Zoologie, 1878, p. 199.

ing from the front to the back. The intercentral articulation is lost, and finally the head of the rib disappears. Only the tubercular attachment to the diapophysis remains, in the Streptostylica, and this is a simple one.

In the modern Batrachia the rib articulation is that of a double-headed rib to a double-headed diapophysis which originates from the neural arch. There is nothing in the history of the class to show that, as in the case of the reptiles, the head has been transferred or lost. In recent Batrachia, elements resembling the intercentra of Pelycosauria are unknown. The origin of the ribs of fishes and Batrachia have been shown by Gøtte to be in the connective tissue of the interspaces of the myocommata, which are opposite the middles of the vertebral centra. It follows that there is at no time connection of the ribs with the lines of separation of the vertebral bodies.

If the intercentra become the functional centra in the Sphenosauridae, it is likely that they are such in the Stegocephali, and in the modern Batrachia.* It follows, then, that Batrachia, excepting Rhachitomi and Embolomeri, have no centra, but intercentra only. This view is confirmed by three facts, two of them already mentioned:

I. There are no intercentrum-like bodies in existing Batrachia.

II. The ribs which originate from intercentral cartilage and intercentra in reptiles, originate from the principal vertebral bodies in Batrachia.

III. The chevron bones are continua with intercentra in Reptilia, and with the caudal vertebral bodies of Batrachia.

With regard to the last proposition I may add, that I have examined young *Necturus maculatus*, of four inches in length; of larvae of *Gyrinophilus porphyriticus*, of three inches; of *Spelerpes ruber* of two and a half inches; of *Amblystoma punctatum*, of 35mm; and of *Spelerpes bilineatus*, of 25mm† length. In none of these is the least trace of articulation of either chevron bone or of neural arch in any part of the column to be discovered (Plate I, Fig. 11).

Researches into the embryology of the Urodela and Anura have not yet brought to light any traces of the rhachitomous structure; which is probably a case of inexact parallelism, coenogeny or falsification of the embryonic record—a phenomenon which is not uncommon. There can be no doubt, however, that the entire record was presented in the embryonic history of Permian land Vertebrata, and for a long period subsequently, but that the rhachitomous stage has been, with the true centrum, lost from the batrachian line at least.

As I have shown, in the Embolomeri the intercentra tend towards reduction in the dorsal region, while the centra are predominant. If the tendency of the evolution

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* American Naturalist, 1886, p. 77.
† For these specimens I am greatly indebted to the Smithsonian Institution and the Secretary, Prof. Baird.
of the Batrachia has been to the extinction of the centrum, the line of the Embolomeri tends in the opposite direction, or towards the type of the Reptilia. Although the general characters of the skull of Cricotus are Batrachian, the presence of a free pro-atlas (Fig. 3, a b) adds to the evidence of reptilian affinity.* It is probable then that we have in the Embolomeri that order of Batrachia from which the Reptilia were derived, through intermediate forms not yet discovered.† It is also evident that the Sphenosauridae cannot be referred to this order as I have proposed, but that they constitute a family of Rhachitomi.

We have thus clearly shadowed forth in the Permian Vertebrata the ancestry of the existing true Fishes,‡ Batrachia, Reptilia, and Mammalia.§

III.—ALTERNATIVE EXPLANATIONS.

I may here consider other possible ways of interpreting the homologies of the segments of the rhachitomous vertebral column, as follows: Let us first suppose with Gaudry and Fritsch that the segments called intercentra in the figures and plates accompanying this paper, are the true centra, and that the chevron bones are not continua, but are originally separate, and have become coëssified with the elements with which we find them now continuous. It will follow that the larger bodies of the vertebral column of Cricotus, which in the dorsal region support the neural arch, are intercentra, and that the centra are in that genus in process of extinction. The same will be true of the so-called dorsal, and part or all of the so-called caudal vertebrae of Sphenodon, and of the Pelycosauroidea. We thus have the Reptilia in the position which I have assigned to the Batrachia, the terms centrum and intercentrum being merely reversed. As, however, these names were first applied to the Pelycosaurian reptiles by me, and as it will require less change of nomenclature to retain these names for the bodies as they appear in Mammalia and Reptilia, it will be better to maintain the proposition that the Batrachia have lost their centra, and retain only intercentra.

Another alternative is to regard the hypocentrum pleurale as the intercentrum with the chevron bone. It will be remembered that the hypocentrum pleurale is described by Dr. Fritsch as lying below the pleurocentra. This is of course on the anterior side of the "hypocentrum." It looks reasonable to suppose that in the completion of the body of which the pleurocentrum is a part, the hypocentrum pleurale should be included. Such might be supposed to be the case in the centrum of Cricotus, and of the Pely-

* The proatlantal centrum is thoroughly coëssified in all the salamander larvae above referred to.
† I have suggested this view in the American Naturalist, 1884, p. 37; 1885, p. 77.
‡ Additional specimens of Didymodus display very distinctly the sutures I have described, which Mr. Garman thinks to be accidental.
§ A second posterior foot of Clepsydrus displays perfectly the mammalian characters I have ascribed to it.
cosauria. But on this point we have as yet no evidence. On the other hand in the rhachitomous Eryops, where the centrum is not completed, we have seen that in the cervical region the hypocentrum pleurale probably unites with the intercentrum in front of it. Let us suppose this to have been the case throughout the vertebral column. The interpretations would be as follows:

In the caudal region of Eryops the hypocentrum pleurale would bear the chevron bone, and the present intercentrum would become the centrum. We would then have in the caudal region of Archeosaursus and Cricotus, the remarkable state of affairs of two true centra present, one of which has an intercentrum coössified with it, and the other supports the neural arch. The same would be the interpretation of the dorsal structure in Cricotus. As there is no direct evidence of such structure in the vertebral regions mentioned, nor in the caudal region of the Pelycosauria, its assumption appears to me to be the least probable alternative before us. Under this interpretation we have to regard the pleurocentrum as either vanishing, or becoming coössified with the intercentrum (m., hypocentrum) in the vertebral centra of existing Batrachia, which would then consist of four elements each, viz., two pleurocentra, hypocentrum pleurale, and intercentrum (hypocentrum), in the caudal region at least. Of this no evidence can be obtained from embryos of a length of 25 mm and over. In Reptilia the centrum would consist of pleurocentrum and intercentrum (hypocentrum) combined, a division of which we have no evidence in the embryology of the vertebral column in these animals. In the divided caudal centra of the lizards one might see intercentrum (hypocentrum) and pleurocentrum, but this supposition is not necessary to account for this structure. I have observed above, that the evidence furnished by the vertebrae themselves is in favor of this division having arisen in the middle of a true centrum. The chief objection to this interpretation of the reptilian centrum is, however, to be found in the column of Cricotus, where we find the large bodies which bear the chevron bones, in the process of extinction, leaving behind bodies which are homologous with the centra of the Pelycosaurian reptile. And this is equally true, whether we regard the hypocentrum or the hypocentrum pleurale as the intercentrum, for it is the pleurocentra which remain, to be the true centra of Cricotus.

Thus on either of the assumptions just mentioned, the development of the dorsal part of the vertebral column in Cricotus is in an opposite direction to that stated by Fritsch to characterize the Sphenosauridae. This is the main point to be proven. If further I have shown that the larger dorsal bodies of Cricotus are homologous with the centra of the Pelycosauria and Lacertilia, the proposition remains proven that the inferior vertebral bodies of the Rhachitomi and the entire vertebral bodies of existing Batrachia, are intercentra and not centra.
1. ERYOPS ERYTHROLITICUS %.
2-6. CRICOTUS HYPANTRICUS %.
7-8. C. HETEROCLLITUS %.
9. CLEPSYDROPS NATALIS %.
10. SYPHONON DON GUENTHERI.
11. SPELERPES BILINEATUS %.

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In order that the result shall be otherwise, it will be necessary to make the extreme assumption, that in Cricotus the two vertebral bodies represent hypocentrum pleurale (bearing chevron), and hypocentrum, the pleurocentrum having disappeared. The reader can judge which of the alternatives is the more probable, the disappearance of the insignificant hypocentrum pleurale, which only exists in distinct form in the Sphenosauridae, or of the large pleurocentra which are so well developed in the Rhachitomi, and which in the caudal region of that order are almost identical with the bodies marked ce in Cricotus (Fig. 3). On this hypothesis we are led to the reductio ad absurdum, that the bodies which do not support the chevron bones in the caudal region of Eryops (Pl. I, Fig. 1 c), are not homologous with the bodies which do not support the chevron bones in the caudal region of Cricotus (Pl. I, Fig. 2 c–5) with which they are identical in position and connections.

Explanation of Plate I.

Figs. 1–6, two-thirds natural size; Figs. 7–10, natural size; Fig. 11, five times nat. size.

Fig. 1.—Eryops erythroliticus Cope (Epicordylus olim), proximal caudal vertebrae. The first intercentrum is the last one without chevron bone. From the Permian of Texas.

Fig. 2.—Cricotus hypantricus Cope, portions of the vertebral column of one individual, selected from the cervical (a), dorsal (b), and caudal (c), regions; left side. From the Permian of Texas.

Fig. 3.—The centrum of the anterior dorsal vertebra of 2b, from front, showing the hypantrum and hypantrapophyses. (Proceedings Amer. Philos. Soc., 1884, p. 29.)

Fig. 4.—Another dorsal centrum without neural arch, from front; a, from behind; b, from above, showing facet or neural arch.

Fig. 5.—Intercentrum from cervical region, showing rib attachment, from front; a, from behind; b, from the side; c, from above.

Fig. 6.—An intercentrum from the caudal region; a, from above.

Figs. 7 and 8, dorsal interccentra of Cricotus heteroclitus Cope, from Illinois; collection of W. F. E. Gurley.

Fig. 7.—Lateral view.

Fig. 8.—Front view of another intercentrum, the superior part broken away; a, lateral view.

Fig. 9.—Clepsydrops natalis Cope, a portion of the caudal region, showing ribs and chevron bones, from the side; fig. 9a from below, showing one free intercentrum, out of its place (i). From the Permian of Texas.

Fig. 10.—Sphenodon guentheri Buller; from New Zealand, caudal vertebrae, lateral view; a, an intercentrum with chevron bone from front. The reticulated portions are osseous tissue.

Fig. 11.—Spelerpes bilineata Green, larva, vertebrae, five times natural size, linear. 11a, Three cervical vertebrae, including atlas and connate centrum of proatlas; 11b, a dorsal vertebra; 11c, two sacral and two anterior caudal vertebrae; 11d, second caudal vertebra from behind. The caudal vertebrae show the continuity of the chevron bones. Specimen from the collection of Professor S. F. Baird.

Letters.

pra, proatlas, centrum.

i, intercentrum.

p, pleurocentrum.

c, centrum.

ch, chevron bone.

r, rib.

d, diapophysis.

pa, parapophysis.

poz, postzygapophysis.

ha, hypantrum.

hap, hypantrapophysis.

nc, notochordal foramen.

f, foramina.

si, sacral intercentrum.

se, sacral centrum.