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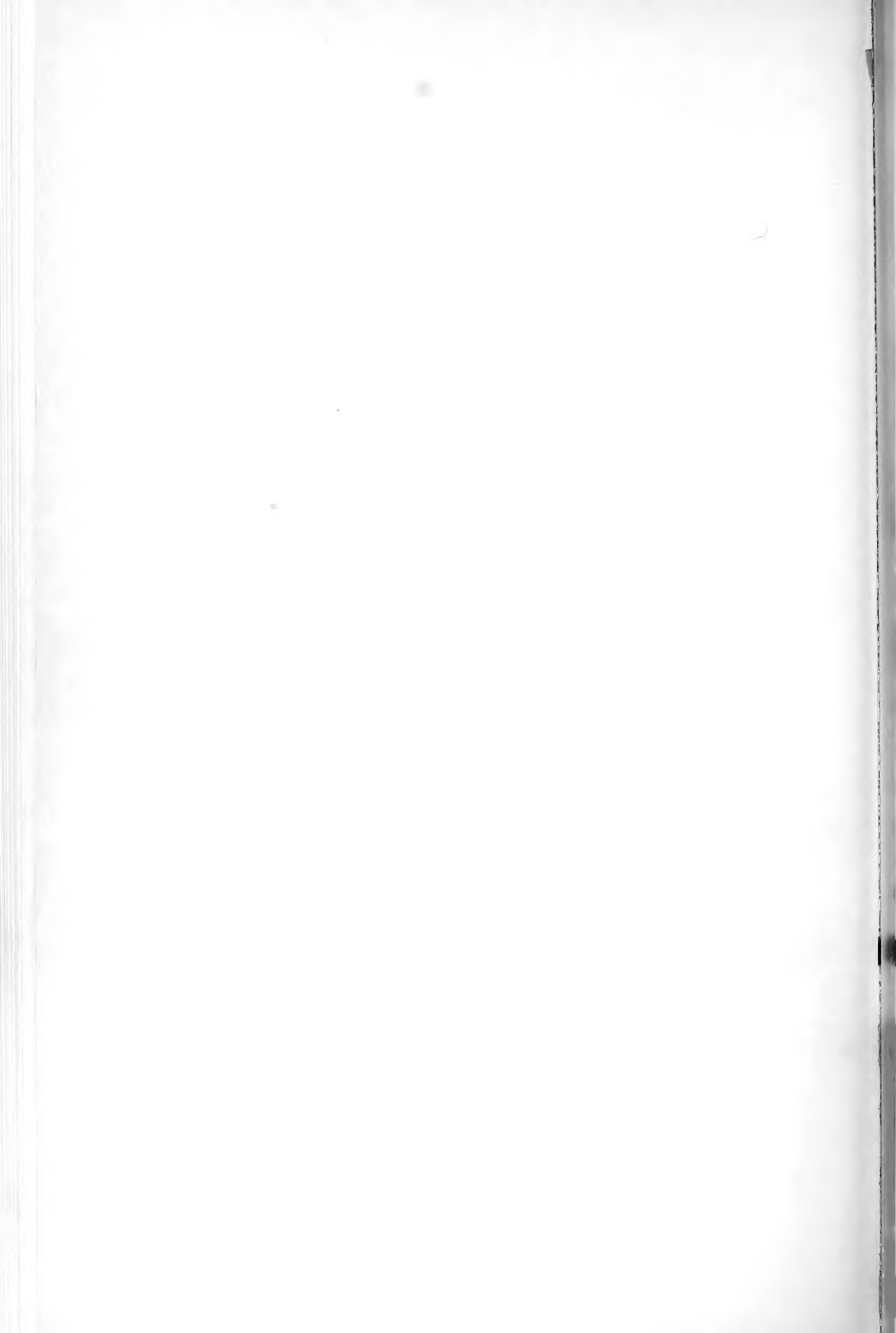
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# VERTEBRAL STRUCTURE IN RHIPIDISTIA (OSTEICHTHYES, CROSSOPTERYGII) WITH DESCRIPTION OF A NEW PERMIAN GENUS

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## ABSTRACT

*Ectosteorhachis nitidus* from the Lower Permian of North America has holospondylous vertebrae, but a new North American genus of osteolepid rhipidistian of the same age has compound vertebrae each comprising a large principal and a small anterior median dorsal accessory centrum. Attempted embryological analysis of vertebral structure in Rhipidistia reveals no evidence of sclerotomic resegmentation and no direct homology with tetrapod vertebrae.

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The Paleozoic fishes of the suborder Rhipidistia (Order Crossopterygii) are known from a variety of forms of Early Devonian to Early Permian age. They are of special interest because it was from a Devonian rhipidistian stock that the first Amphibia evolved (see, for example, Thomson, 1968) and it is well known that in many features of their structure the Rhipidistia are somewhat intermediate between other osteichthyan fishes and the tetrapods. It is therefore important that rhipidistian structure be known in as great detail as possible in order to interpret better the process of the origin of the tetrapods. A matter of considerable importance in this respect is the structure of the vertebral column. The vertebral column must have been subject to a pronounced change in function when the fishes left the water and began moving on land. The tetrapods rapidly evolved a variety of different patterns of vertebral structure in the new environment (for a recent study, see Parrington, 1968) and the type of vertebral composition is, in fact, a useful taxonomic character among higher categories of fossil Amphibia (Romer, 1964). Thus it is of interest to study the range of vertebral structure in Rhipidistia to see if any indications of the patterns of tetrapod structure and development were already present in these fishes.

The present paper describes and discusses the vertebral structure of two Lower Permian rhipidistian fishes. The description is based largely on new material, particularly of a new fish collected by Vaughn in Utah.

#### MATERIALS

The material studied included the following specimens (for abbreviations, see end of paper): *Ectosteorhachis nitidus* Cope: MCZ 8630, almost complete fish with several vertebrae exposed; MCZ 8930, complete skull and a small postcranial fragment with 4 vertebrae; YPM 5000, almost complete fish lacking posterior trunk and tail, two vertebrae *in situ* exposed by preparation; all material of *Ectosteorhachis* from the Lower Permian, Wichita Group, of North-central Texas (see Romer, 1958).

Specimens on which the new genus and species are based are: YPM 5701, isolated and flattened postparietal shield; YPM 5702, 7 postcranial fragments with scales, 3 with vertebrae in natural

articulation but slightly dislocated; YPM 5703, left gular plate; UCLA VP 1688, disarticulated fragments including one with mandible in natural association. All material of the new genus is from the Lower Permian, Cutler Group, Halgaito Shale of Southeastern Utah. Some of this material was formerly referred to as "*Ectosteorhachis*" by Vaughn (1962).

#### ECTOSTEORHACHIS

The original description (Cope, 1880) of the species *Ectosteorhachis nitidus* Cope includes the following description of the vertebrae: "In *Ectosteorhachis* they are represented by annular ossifications resembling somewhat those of the stegocephalous genus *Cricotus*, but with a larger foramen chordae dorsalis". Cope considered this structure to differ from that of the "completely ossified", "biconcave" vertebrae of *Megalichthys*. Hussakoff (1911) synonymized *Ectosteorhachis* and *Megalichthys*, stating that the vertebrae "in both . . . are narrow rings, but those in Cope's specimen . . . are not well enough preserved to make it absolutely certain that they were complete, and not open, above". In the more recent literature (e.g. Thomson, 1967) the acceptance of a simple ring-shaped vertebral structure in *Ectosteorhachis* has been continued, while this genus is distinguished from *Megalichthys* on other evidence (Thomson, 1964).

Newly available material of *Ectosteorhachis nitidus* from the Wichita Group of north-central Texas includes vertebrae in natural articulation (YPM 5000, MCZ 8930) and also vertebrae from the immediately postcranial region to the level of the first dorsal fin.

Each vertebral unit in all material of *Ectosteorhachis* that we studied consists of a complete, ring-shaped *principal centrum* to which the neural arch is attached (Fig. 1). The principal centrum is slightly wedge-shaped in lateral view, tapering dorsally from a wide base. The notochordal canal is wide and the wall of the principal centrum is correspondingly slim. The posterior portion of the lateral wall of the principal centrum is significantly depressed and the "step" between the raised and depressed surface is developed into a slight ridge that is interpreted as having served for the attachment of the myoseptum (see below). The recessed posterior region does not extend dorsally to the midline but just short of



Fig. 1. *Ectosteorhachis nitidus* Cope. Vertebral centrum in left lateral and posterior view. MCZ 8930.  $\times 5$

this point there is a small facet for the attachment of a rib. This facet separates the main lateral recessed region on either side from a dorsal recessed area that perhaps formed the site of attachment of the neural arch. Immediately in front of this dorsal recessed area there is a short ridge which forms the posterior rim of a transverse groove running directly ventrolaterally from the neural canal; this groove probably carried the ventral spinal nerve (Fig. 1). In front of this groove, on either side of the midline, there is a short anterodorsally directed process that apparently articulated with the rear surface of the neural arch associated with the principal centrum in front. The lateral surface of the principal centrum, anterior to the ridge for the myoseptum, is marked by a series of small foramina (Fig. 1) probably for small blood vessels.

The neural arches are not preserved in material at hand, but their probable association with the principal centra is reconstructed in Figure 2. Ventrally, in the posterior part of the trunk, there is a pair of small haemal processes (hpr, Fig. 2) on the posterior region of each principal centrum; these no doubt became developed into full haemal arches in the tail region.

In Figure 2 a reconstruction of the soft structures associated with the vertebrae in *Ectosteorhachis* is given. It will be noted that it is necessary to restore a considerable amount of cartilage between each principal centrum.

## A NEW PERMIAN RHIPIDISTIAN

The material from southeastern Utah represents a fish different than *Ectosteorhachis* although in previous studies it had been tentatively assigned to that genus (Vaughn, 1962). It is only the second known genus of rhipidistian of unequivocal Permian age. A formal diagnosis of this new fish is given below, followed by a complete description of the vertebral structure.

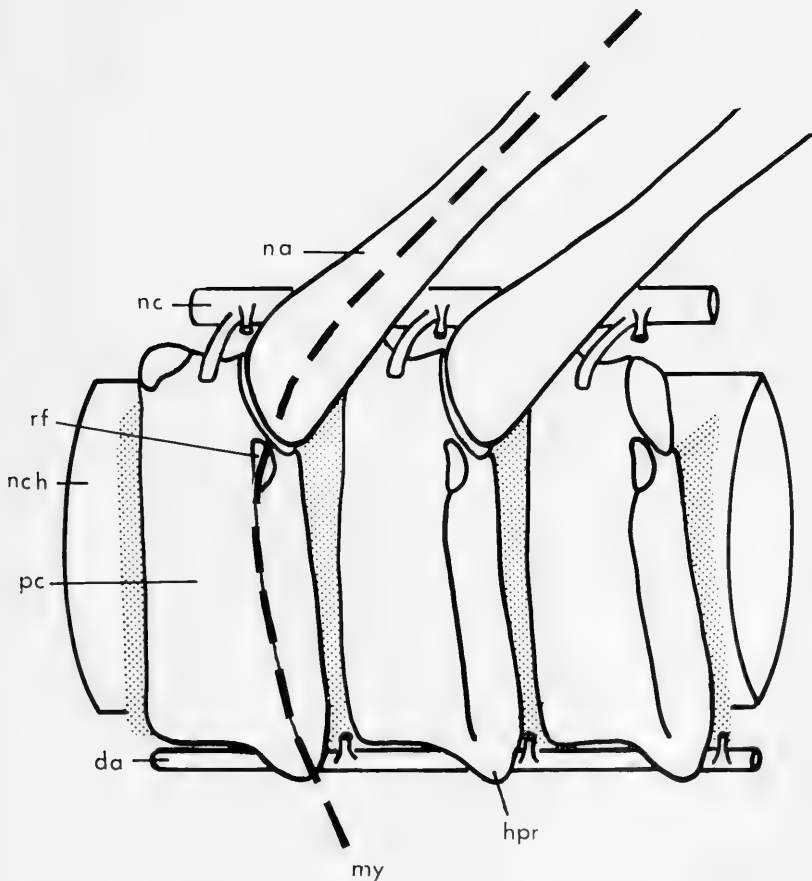
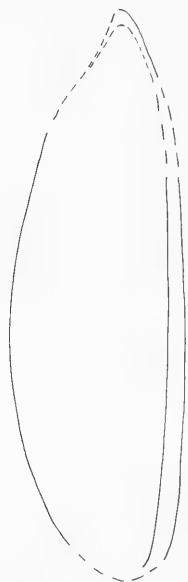


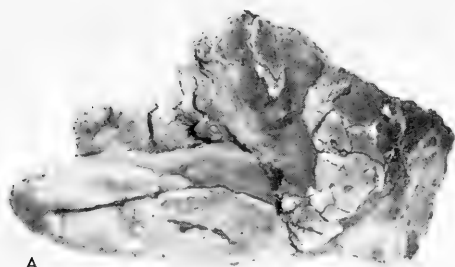
Fig. 2. *Ectosteorhachis nitidus* Cope. Reconstruction of three vertebrae and associated soft parts in left lateral view. The stippling represents cartilage.

## FAMILY OSTEOLEPIDAE

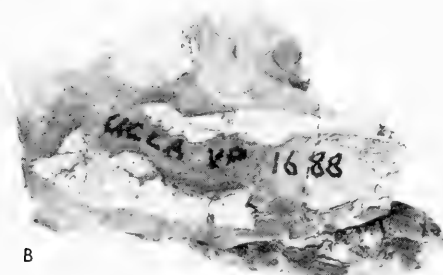
*Lohsania* gen. n.TYPE SPECIES. *Lohsania utahensis* sp. n.DERIVATION OF NAME. *Lohsania* (feminine) from the Navajo words for fish (*loh*) and old (*sani*).Fig. 3. *Lohsania utahensis* gen. et. sp. nov. Left gular plate.  $\times 1.2$ 

DIAGNOSIS. Osteolepid rhipidistian of medium size, estimated maximum total length 60 cm. Postparietal shield essentially as in *Ectosteorhachis*; gular bone more narrow and elongate than in *Ectosteorhachis*, maximum width contained 3.3 times in greatest length (as opposed to 2.3 times in *Ectosteorhachis*). Each vertebral unit composed of a principal centrum that is incomplete dorsally and a crescentic anterior accessory centrum lying in the dorsal midline. Neural arch attached primarily to the accessory centrum. Posterior recessed area of lateral wall of principal centrum lacking (in available material).

DESCRIPTION. *Lohsania* is readily assigned to the osteolepid Rhipidistia because of the typical structure of the scales and



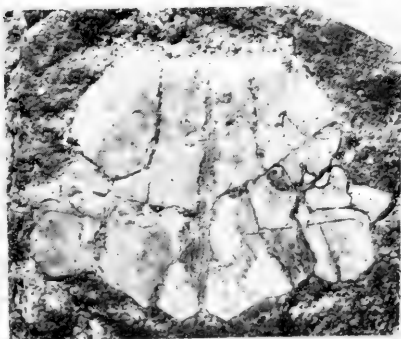
A



B



C



D

Fig. 4. A and B. *Lohsania utahensis* gen. et sp. nov. Mandibles and associated elements in left and right lateral view. UCLA VP 1688.  $\times 0.8$

C. *Ectosteorhachis nitidus* Cope. Postparietal shield in dorsal view. MCZ 8930.  $\times 0.8$

D. *Lohsania utahensis* gen. et sp. nov. Postparietal shield in dorsal view. YPM 5701.  $\times 1.5$



Fig. 5. *Lohsania utahensis* gen. et sp. nov. Five vertebrae in right lateral view, slightly displaced. Holotype YPM 5702.  $\times 2$



Fig. 6. *Lohsania utahensis* gen. et sp. nov. Two incomplete vertebrae in right lateral view, slightly displaced. Holotype YPM 5702.  $\times 2.8$



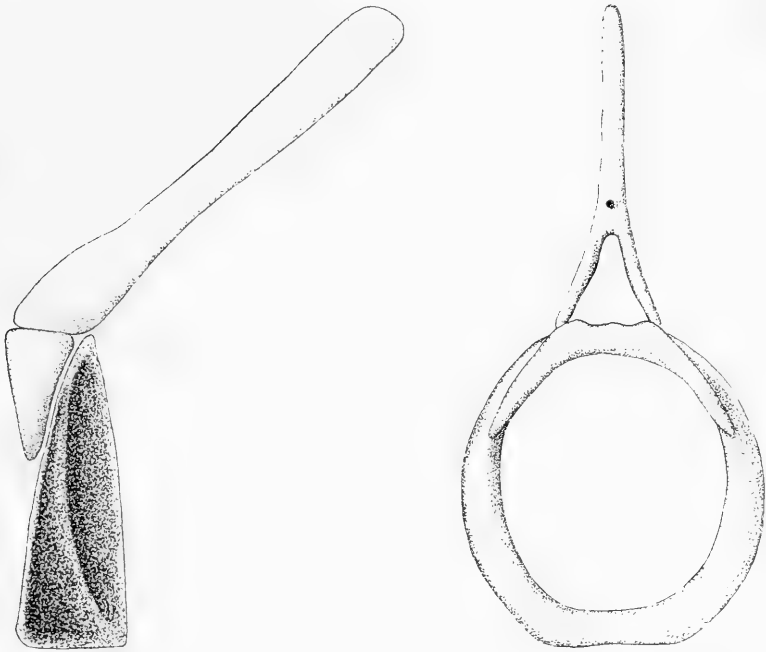


Fig. 7. *Lohsania utahensis* gen. et sp. nov. Vertebra in left lateral and anterior view. YPM 5702.  $\times 3.2$

dermal bones. We have been unable to distinguish the scales from those of *Ectosteorhachis* in either gross or micro-structure. The postparietal shield of the dermal skull roof, illustrated in Figure 4 along with the same region in *Ectosterorhachis*, was not found in direct association with vertebrae of the characteristic *Lohsania*-type, but is confidently assigned to this taxon. The main points of difference are in the somewhat slightly broader anterior margin and the shape of the posterior margin.

A single vertebral unit in *Lohsania* (Figs. 5 and 6) consists of three separate elements — a principal and an *accessory centrum* and a neural arch. The principal centrum in the available material is relatively undifferentiated. However, we consider a poorly defined ridge (Figure 7) running slightly diagonally across the posterior part of the lateral face of the principal centrum to mark the line of attachment of the myoseptum (Figure 8). The recessed area posterior to this ridge, seen in *Ectosteorhachis* and

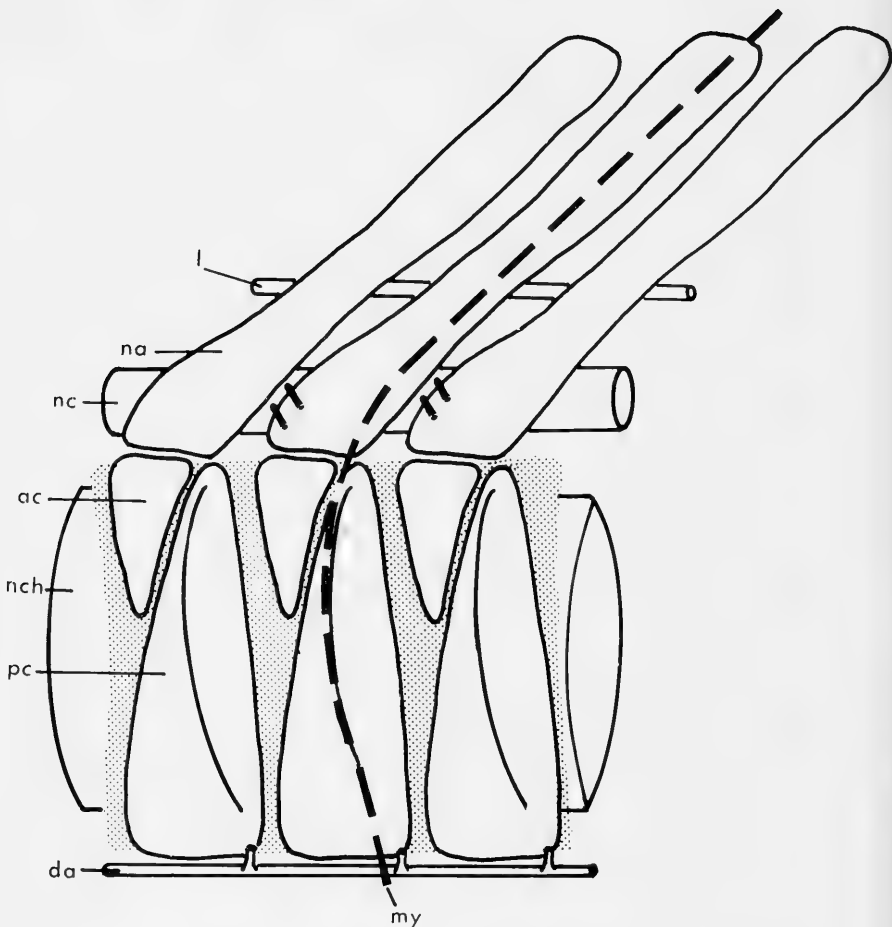


Fig. 8. *Lohsania utahensis* gen. et sp. nov. Reconstruction of three vertebrae and associated soft parts in left lateral view. The stippling indicates cartilage.

other rhipidistians, is lacking. This absence may be associated with the presence of an accessory centrum in *Lohsania* (see below). Also lacking are grooves for the intersegmental arteries or spinal nerves; this may be due to the imperfect nature of the preservation. In lateral view the principal centrum (Figure 7) tapers markedly toward the dorsum. A unique feature of the vertebrae of *Lohsania* is the presence of a median accessory central element

in the dorsal midline. This element is associated with the anterior face of each principal centrum, as is demonstrated by the constant close association of each accessory element with the principal centrum behind even in material (such as YPM 5702, Fig. 4) where considerable displacement of the vertebrae has taken place. This constant relationship must be a natural phenomenon. The accessory centrum is crescentic in shape, and the lateral wings curving down between the principal centra taper sharply on either side. The accessory element bears on its dorsal surface a pair of parallel, anteroposteriorly directed ridges (Figure 7) which mark the attachment of the neural arch. In two vertebrae from our material (part of YPM 5702) the accessory centrum seems to be fused to the principal centrum. Possibly this is related to the relative position along the column.

The neural arch is illustrated in Figures 5, 6 and 7. The base of each arch seems to be associated primarily with the accessory element but there was also a slight connection with the tips of the principal centrum. There is a very small, but clearly defined, canal for the dorsal ligament (Fig. 6). This canal was presumably oriented horizontally and this allows us to restore precisely the posterior slope of the neural arches.

Figure 8 is a tentative restoration of the soft structure associated with the vertebral column in *Lohsania*.

### *Lohsania utahensis* sp. n.

*Ectosteorhachis* aff. *E. nitidus* Vaughn, 1962, p. 533.

HOLOTYPE. YPM 5702, fragments of trunk in partial articulation (Figs. 5 and 6).

PARATYPES. YPM 5701, postparietal shield (Fig. 4); YPM 5703, left gular bone (Figure 3); UCLA VP 1688, partially disarticulated fragments including mandibles (Fig. 4).

OCCURRENCE. All specimens from the Halgaito Shale, Cutler Group, Lower Permian of San Juan County, Utah; probably of Wolfcampian age (see Vaughn, 1962). YPM 5702 — NW  $\frac{1}{4}$ , NE  $\frac{1}{4}$  sec. 34, T. 40 S., R. 19 E. YPM 5701 — NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$  sec. 29, T. 40 S., R. 19 E. YPM 5703 — NW  $\frac{1}{4}$  sec. 3, T. 41 S., R. 17E. UCLA VP 1688 — NW  $\frac{1}{4}$ , NE  $\frac{1}{4}$  sec. 34, T. 40 S., R. 19 E.

DIAGNOSIS. As for the genus, above.

## COMPARISON AND DISCUSSION

At the present time, the vertebral structure of *Ectosteorhachis* and *Lohsania* may only be compared in detail with that of one other rhipidistian fish, *Eusthenopteron foordi* Whiteaves (family Rhizodontidae; Upper Devonian) as described by Jarvik (1952). As shown in Figure 9 each vertebral unit in *Eusthenopteron* consists of a neural arch and a principal centrum which are basically very similar to those of *Lohsania*, and a set of "accessory elements" that are not at all similar to the single accessory element in *Lohsania*.

The principal centrum of *Eusthenopteron* is extremely similar to that of *Lohsania*, but it is important to note that the latter lacks the extensive posterior recessed lateral surface. All three forms possess a myoseptal ridge. This ridge, in *Eusthenopteron* and *Ectosteorhachis* bears a facet for the articulation of a rib, although the facet in *Ectosteorhachis* is much smaller. The posterior recessed area on the principal centrum in *Ectosteorhachis* is developed in the same way in *Eusthenopteron* (Fig. 9). The groove for the spinal nerves in *Ectosteorhachis* is not seen in any other form but a pair of notches in the accessory elements in *Eusthenopteron* possibly mark the passage of these elements.

The accessory elements in *Eusthenopteron* are a pair of small subcircular elements interposed between the neural arches (Fig. 9). They are also seen, somewhat imperfectly, in the Middle Devonian genus *Glyptolepis* (family Holoptychidae) from Scotland (specimen OS3.11/2, Museum of Zoology, Cambridge University). The most striking feature of these elements is that they are not associated with the notochord itself. In slightly disassociated specimens in which the various elements of the vertebra become separated one from another (for example, the specimen of *Glyptolepis* noted above), the accessory elements are shown to be mechanically associated with the neural arches, while the accessory elements in *Lohsania* are shown to be associated with the principal centra behind them. The accessory elements in *Eusthenopteron* are therefore not completely homologous with the accessory elements in *Lohsania*. The accessory elements in *Eusthenopteron* have been termed "interdorsals" (Jarvik 1952), "pleurocentra" (Romer, 1964), or "intercalaries" (Schaeffer, 1967). That they are not true interdorsals and particularly that

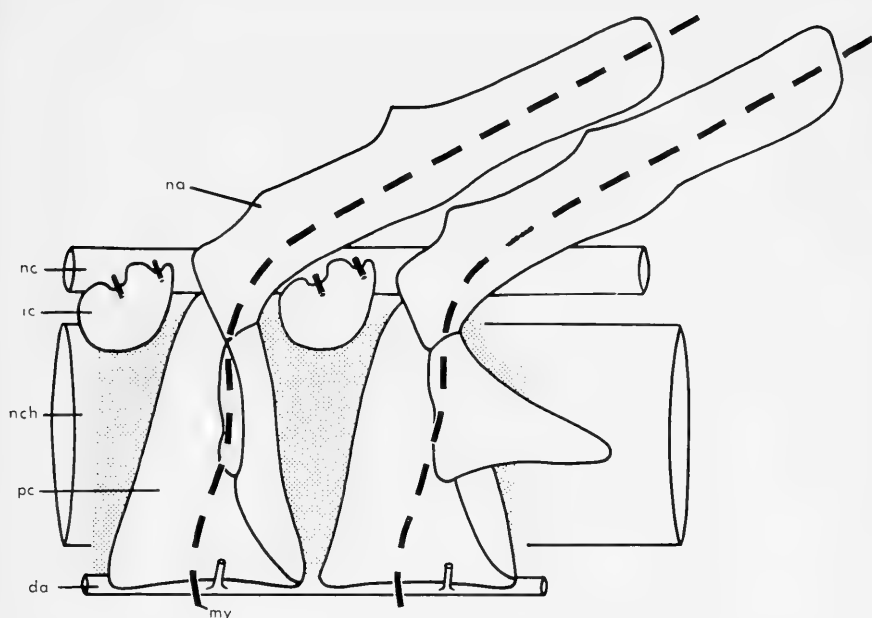


Fig. 9. *Eusthenopteron foordi* Whiteaves. Reconstruction of two vertebrae and associated soft parts in left lateral view. The stippling represents cartilage.

they are not homologous with the pleurocentra of tetrapods (see below) is demonstrated by the fact that they are not fully associated with the notochordal sheath and thus are not true central elements. Schaeffer's interpretation that they are intercalaries, homologous with the intercalaries found between the neural arches in certain actinopterygian fishes (e.g. *Amia*), seems the most accurate and is accepted here. The accessory elements of *Lohsania*, on the other hand, are fully associated with the notochordal sheath.

It is always difficult to attempt to decide the homology of a particular bony element solely from fossil material. This is particularly true when it comes to the homology of the vertebrae. Despite this difficulty, problems that require consideration are the questions of vertebral homology and of a possible resegmentation of the vertebral column in Rhipidistia. It is now well accepted (Williams, 1959; Panchen, 1967; and Schaeffer, 1967) that the vertebrae of tetrapods undergo an ontogenetic resegmentation of the original, segmentally arranged sclerotomic material that be-

comes involved in the organization of the adult vertebra within the perichordal tube. This occurs through the separation of the cranial and caudal halves of sclerotome segments and their subsequent recombination such that the adult vertebra is formed from the caudal half of the sclerotomic material of one segment and the cranial half of the sclerotomic material from the segment immediately behind. Thus a new intervertebral separation develops in an originally intrasegmental position. Such sclerotomic resegmentation does not occur in living fishes (at least not in exactly the same form; cf. *Lepisosteus* in Schaeffer, 1967). The homology of the vertebral elements of the Rhipidistia is of primary interest in this respect, because of the almost intermediate position that they occupy between fishes and tetrapods.

The Gadovian system of vertebral homology involving the interpretation of vertebral components as being induced by a series of embryonic elements, has been subjected to considerable re-examination in recent years (Williams, 1959; Schaeffer, 1967). While this system is evidently not applicable to most tetrapods, in fishes such as *Amia* (Schaeffer, 1967) it is possible to distinguish in the very early developmental stages a series of segmentally arranged anlagen which induce the development of the final osseous centrum. We cannot, of course, observe any part of such a process in fossil forms in cases in which the adult centrum is holospondylous. However, where the adult vertebra is composed of more than one element the strong likelihood exists that each element is induced by a separate anlage and we may attempt such an analysis in order to try to shed more light on the problem of vertebral homology.

In considering the fossil Rhipidistia, we have as guides to the homology of the vertebral elements the position of the intersegmental artery, the position of the myoseptum, and the position of the haemal process on the principal centrum. In all forms that we know about, the myoseptum is located in the normal embryologically "primitive" position in the posterior half of the principal centrum, with the intervertebral artery behind it. The myoseptum passes directly up onto the neural arch in all forms (with the possible exception of *Lohsvania*). In the case of the holospondylous *Ectosteorhachis* (Fig. 10A), we may see that the portions of the vertebrae that might normally be considered to be derived from anlagen in the embryonic caudal sclerotome-half, namely, the

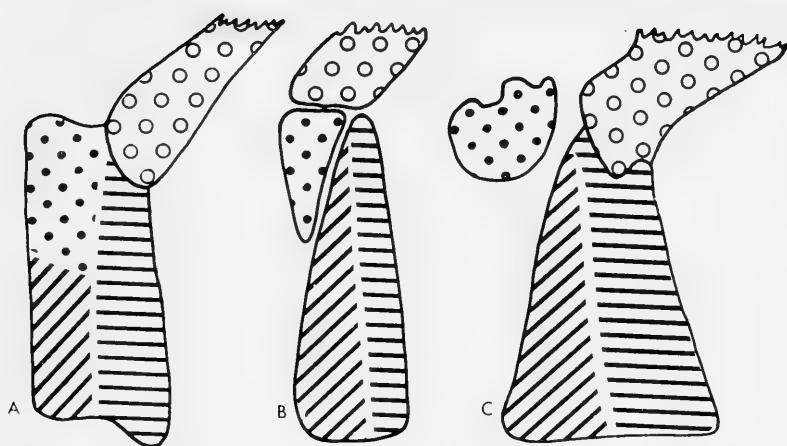


Fig. 10. Hypothetical analysis of the embryonic derivation of the vertebral units in (A) *Ectosteorhachis*, (B) *Lohsania* and (C) *Eusthenopteron*. Portions indicated with open circles are thought to be induced by the basidorsal, closed circles induced by the interdorsal, horizontal lines by the basiventral and diagonal lines by the interventral.

neural arch (induced by the so-called basidorsal) and the haemal arch (induced by the basiventral), are in the same posterior position in the adult. In continuing this rather academic analysis in Gadovian terms, we may identify the anterodorsal portion of the principal centrum (including the groove for the spinal nerve and the anterodorsal articular process) as having been induced by an interdorsal and the remaining anteroventral portion of the centrum as having been induced by an interventral (Figure 10A). It will be seen that there is no indication here of vertebral resegmentation.

The situation in *Lohsania* (Figure 10B) is exactly comparable, except that in this case the accessory centrum (in a position suggesting induction by the interdorsal) is formed as a separate element and, presumably for mechanical reasons involved with the function of the vertebral column, the principal centrum is narrow dorsally. The neural arch nonetheless retains its posterior position.

In our opinion, the construction in *Eusthenopteron* may also be considered to follow the same pattern, with the exception that the interdorsal anlage, instead of inducing a central element (as in *Lohsania*) or a portion of the principal centrum (as in *Ecto-*

*steorhachis*), has induced the formation of an intercalary element (Figure 10C). Even so, it will be noted that the element induced by the interdorsal also has an association with the spinal nerves.

The condition in *Megalichthys* and other holospondylous forms such as *Rhizodus* and *Rhizodopsis* is presumably the same as in *Ectosteorhachis*. Dr. S. M. Andrews (as quoted in Schaeffer, 1957) has discovered the existence of a diplospondylous condition in *Osteolepis*. While the above interpretations are completely tentative and will be liable to modification upon full publication of Dr. Andrew's results, it may be noted that a full diplospondylous condition could be derived in the scheme given above by simple separation of elements induced in the cranial and caudal halves of a *nonresegmented* unit, that is, by separation of a unit induced by the combined interdorsal and interventral instead of one induced by the interdorsal alone.

The structure of neither *Lohsania* nor *Eusthenopteron* seems to be directly comparable to that of any tetrapods except the Ichthyostegalia, although it is possible that the embryonic rudiments that induce rhipidistian structures induce different structures which, through resegmentation, make up the vertebrae of tetrapods. The extremely close similarity of structure between *Eusthenopteron* and *Ichthyostega*, with intercalary elements rather than true accessory centra, must reflect a very close similarity in the function of the vertebral column in these forms. However, in view of our conclusion that the intercalary elements of *Eusthenopteron* bear no close relationship to the pleurocentra of tetrapods such as the Rhachitomi, we must note that a similar view must apply to the intercalaries (the so-called pleurocentra) of *Ichthyostega*. In fact, from the evidence of the vertebral column we are inclined to separate the Ichthyostegalia from all other tetrapods and furthermore we consider it unlikely that the ichthyostegals gave rise to any known later Temnospondyli.

The above scheme of vertebral homology is entirely compatible with our knowledge of the structure and development of the vertebrae of "primitive" actinopterygian fishes, such as *Amia* (Goodrich, 1930; Schaeffer, 1967). And insofar as the standard Gadovian terminology is applicable to such forms as *Amia*, we feel justified in using it as a tool for the interpretation of rhipidistian vertebrae, especially since there is no sign of resegmentation or the sort of modification of embryonic structure seen in



*Lepisosteus* in these fishes. That the structure of the Rhipidistia is more closely comparable with that of other osteichthyan fishes rather than with that of tetrapods is perhaps not surprising, and there is, in fact, a remarkable resemblance between the vertebrae of *Lohsania* and those of the amioid *Osteorhachis* (Goodrich, 1930, p. 39). Our inability to identify particular tetrapod patterns in Rhipidistia serves only to emphasize the conclusion (see, for example, Thomson, 1967; in press) that the characteristic amphibian patterns must have evolved on the "tetrapod side" of the fish-amphibian transition. The holospondylous and apsidospondylous conditions in Rhipidistia may well have evolved in accordance with the same mechanical situations to which the Amphibia responded (aquatic and semi-terrestrial locomotion, respectively: Thomson, 1967; Parrington, 1968) but resegmentation of the vertebral components seems to have been a particular tetrapod characteristic and it led to the development of the new vertebral patterns characteristic of the tetrapod radiations. It is particularly interesting that while non-resegmented holospondylous Rhipidistia are known, presumably every instance of holospondyly in tetrapods (if resegmentation has occurred) is secondary and not inherited directly from a rhipidistian ancestor.

#### CONCLUSIONS

We have described the vertebral structure in two late Paleozoic rhipidistian fishes. From our study of these forms and of *Eusthenopteron*, we conclude that there is no evidence of resegmentation of the vertebrae in the Rhipidistia. Furthermore, we conclude that the type of vertebral structure seen in *Eusthenopteron* and *Ichthyostega* bears no direct relationship to that seen in the mainline of tetrapod evolution, that is, the accessory elements in the adults of rhipidistians and ichthyostegals are not true pleurocentra.

#### ACKNOWLEDGEMENTS

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#### ABBREVIATIONS

- MCZ — Museum of Comparative Zoology, Harvard University  
 YPM — Peabody Museum, Yale University  
 UCLA VP — University of California, Los Angeles, Department  
     of Zoology collections  
 ac — accessory centrum  
 c lig — canal for dorsal ligament  
 da — dorsal ligament  
 ic — intercalary  
 hpr — haemal process  
 l — dorsal ligament  
 my — myoseptum  
 na — neural arch  
 nc — nerve cord  
 nch — notochord  
 pc — principal centrum  
 rf — facet for rib articulation

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