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(CROSSOPTERYGII: RHIPIDISTIA)  
CONSIDERED IN RELATION TO  
THE ORIGIN OF THE AMPHIBIA

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# A NEW DEVONIAN FISH (CROSSOPTERYGII: RHIPIDISTIA) CONSIDERED IN RELATION TO THE ORIGIN OF THE AMPHIBIA

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## ABSTRACT

*Hyneria lindae*, gen. et sp. nov., is a large rhizodontid rhipidistian fish from the Upper Devonian (Oswayo Formation) of Pennsylvania. It shows a remarkable similarity to the intermediate stages that must have preceded the first true Amphibia. The similarity is due to the parallel evolution of rhizodontid Rhipidistia and the Amphibia from a common stock in the Middle or early Late Devonian.

## INTRODUCTION

The fossil fishes of the suborder Rhipidistia (Osteichthyes, Crossopterygii) have been the subject of intensive research for most of the present century because of their well-established position as the closest known ancestors of Amphibia. Research has been conducted according to a variety of approaches (taxonomic, morphological or functional), but one principal purpose has remained — to test the hypothesis of a direct rhipidistian-tetrapod relationship by the study of resemblances and differences between the two groups. There are certain major obstacles to such a study, the principal ones being that only a relatively small number of rhipidistians are known and that many of the better preserved forms must, in fact, have been contemporaries of the first Amphibia. We must therefore conclude that the rhipidistian-amphibian transition occurred before the Late Devonian. Probably no Late Devonian Rhipidistia should be considered to belong to a lineage directly antecedent to the Amphibia. Such forms must be parallel radiations with the immediate amphibian precursors from a common stock.

The present paper records the existence of a large rhipidistian fish that shows a closer general resemblance to the Amphibia than any other known rhipidistian. This fish is from Upper Devonian (Oswayo Formation) deposits in Pennsylvania and therefore belongs in the list of rhipidistian fishes that are too young to be other than contemporaries of the first tetrapods. However, as will be considered later (under Discussion) the very close resemblance between this fish and the Ichthyostegalia offers some new, if indirect, evidence concerning the relationships of the known rhipidistian families to the first Amphibia.

## TAXONOMIC DIAGNOSIS AND DESCRIPTION

## Superfamily Rhizodontoidea

## Family Rhizodontidae

*Hyneria*<sup>1</sup>, gen. n.

<sup>1</sup> From the village of Hyner, Clinton County, Pennsylvania, near which the specimen was collected.

TYPE SPECIES. *Hyneria lindae*, sp. n.

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DIAGNOSIS. Large fish, estimated total length of only known specimen 250 cm. Proportions of trunk unknown. Skull with heavy dermal bones arranged in typical rhizodontoid pattern. Dermal elements lacking enamel layer, ornamented with a coarse network of anastomosing dentine ridges; isolated tubercles absent. Length of postparietal shield is contained approximately 2.8 times in length of parietal shield. Length of postparietal shield is contained approximately 4.5 times in length of lower jaw. At least one median postrostral element present, with two main lateral post-rostrals, all three elements being overlapped from behind by parietals. Pronounced spiracular notch in lateral margin of postparietal shield. Large ventral ridge under each lateral portion of postparietal shield, passing anteromedially at a right angle to supratemporal-tubular suture. External parietal opening (not preserved), if present, must be situated behind level of centers of ossification of parietals. Vomers triangular in shape but lacking extensive posterior flange. Lower jaw relatively elongate and shallow. Principal gulars narrow and gently curved, lacking marked median angle. Length of principal gular is contained approximately 1.6 times in length of lower jaw. Teeth stout, rhizodontoid, conical with deeply furrowed base. Operculum subrectangular. Cleithrum in form of flat lamina of bone ornamented with anastomosing ridges running parallel to long axis of bone. Clavicle with stout ascending process.

DESCRIPTION. The specimens are illustrated in Figures 3-13. These illustrations will serve in part for a description of the material.

A unique feature of *Hyneria* is the ornamentation of the dermal bones of the skull and the shoulder girdle, isolated denticles being almost completely absent from the surface pattern. On the skull elements, the dentine ridges form an extremely regular pattern of small symmetrical spaces enclosed by tuberculated ridges. On the shoulder girdle, the ridges tend to be more parallel and the enclosed lacunae are therefore elongated (in the direction of the axis of the cleithrum).

The skull of *Hyneria* has been reconstructed (Figs. 1 and 2) on the assumption that the proportions of the various skull elements (for example, the length of the parietal bone relative to the

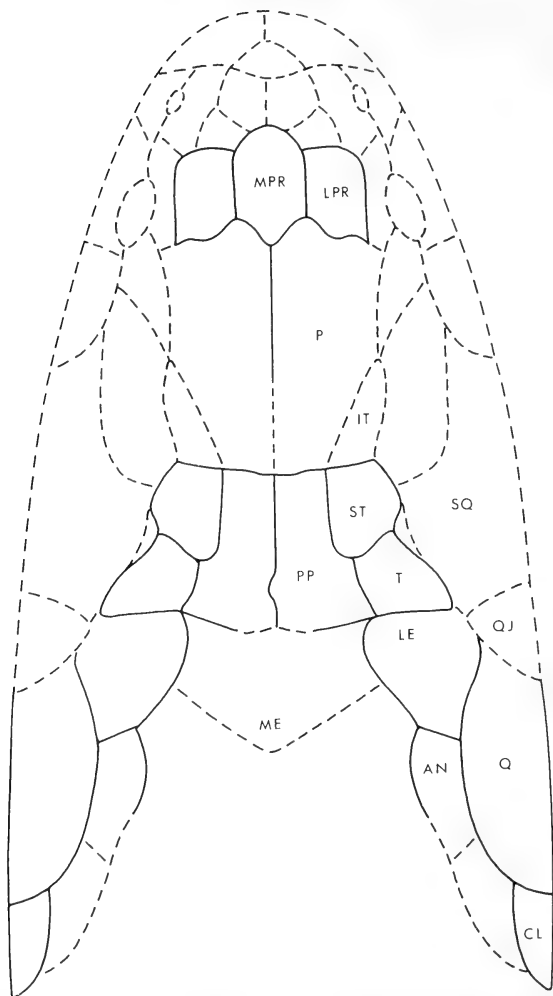


Figure 1. *Hyneria lindae* gen. et sp. n. Reconstruction of skull in dorsal view, approx. 3/10.

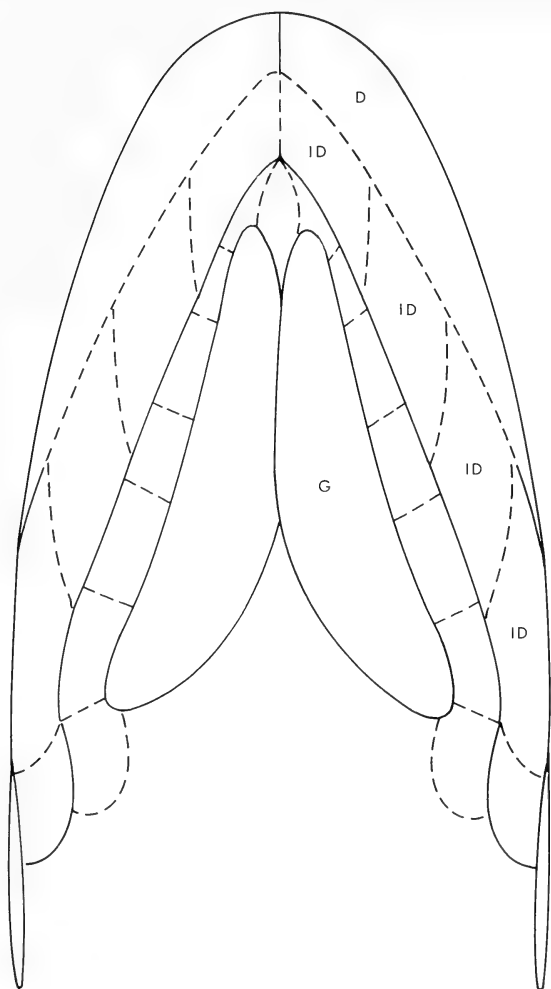


Figure 2. *Hyneria lindae* gen. et sp. n. Reconstruction of skull in ventral view, approx.  $\times 3/10$ .

whole parietal shield) are similar to those seen in other rhizodontid fishes such as *Eusthenodon wangsjoi* Jarvik (1952). Since the posterior portions of the parietal bone and the rostrum anterior of the median postrostral bone are missing, these parts are necessarily restored only tentatively. However, in no rhizodontoid does the center of ossification of the parietal lie at a level anterior to the midpoint of the bone (in most forms it lies in the posterior half of the bone). Furthermore, there is no indication of the parietal foramen in the preserved portion of the parietal shield (Figs. 11 and 12). A conservative restoration therefore places the center of ossification of each parietal at the midpoint of the length of the bone, as in the genus *Eusthenodon*. The relatively short rostrum is also a conservative restoration, based on the proportions in *Eusthenodon*. A further indicator of the cranial proportions is given by the relative length of the lower jaw. In all known Rhipidistia, there is a more or less constant proportional relationship between the length of the lower jaw and the length of the postparietal and parietal shields (Thomson, 1967a, fig. 10). Assuming that the present fish is typically rhipidistian we may make a conservative estimate of the cranial proportions from the known length of the postparietal shield and the approximate length of the lower jaw. The estimated proportions derived from the two methods give the same ratio of the length of the parietal shield to that of the postparietal shield—approximately 2.8:1. If these estimates are correct they indicate that this fish has the longest parietal shield of any known rhipidistian. In this important feature, therefore, *Hyneria* approaches the early tetrapod condition (e.g., *Ichthyostega*, in which the same ratio is 3.2:1) more closely than any other fish. The separate nature of the postparietal shield (Figs. 9 and 10) in *Hyneria* indicates that the skull in this form was divided by a typical crossopterygian intracranial joint (Thomson, 1967a). The presence of the marked spiracular notch in the postparietal shield also indicates that *Hyneria* is a typical rhipidistian. The functional significance of the ridge under the supratemporal and tabular is not clear at present, but it may have served as an anchor-point preventing relative movement of the dermal skull roof and braincase, in addition to forming the medial margin of the groove for the spiracle.

The shape of the vomer is significant. In all known rhizodontoids (but in no other Rhipidistia; Thomson, 1967b) the vomer has a

marked posterior flange passing along the side of the median tooth-bearing lamina of the parasphenoid, on the undersurface of the ethnosphenoid. The vomer of *Hyneria* has but a short posterior flange; this condition seems easily derivable from the more extreme condition seen, for example, in *Eusthenopteron foordi* (Jarvik, 1942, fig. 56).

The mandible is narrow, elongate and slightly tapered anteriorly. No sign is seen of separate infradentary elements, although these are presumably present and obscured by the external surface ornamentation (as is the case with the parietal shield, compare Figs. 11 and 12). The prearticular is large and a well-marked cavity for the coronoids was present. The tip of the mandible bears a large dentary tusk, as in *Rhizodus*.

The gulars are elongate. The right principal gular shows a smooth medial margin where the left gular overlapped onto it. The right lateral gular series is preserved and its width may be accurately determined (Figs. 2, 5, and 6). However, this series of bones is badly fragmented in the available material and thus it has not been possible to determine the precise number of separate lateral gulars present. The sutures shown in the restoration (Fig. 2) are purely hypothetical, being based on the situation in other rhizodontoid rhipidistians. The lateral gular series overlapped onto the lateral margin of the principal gular of each side, as indicated by the smooth overlap zone seen on the surface of each principal gular (Figs. 2, 5, and 6).

The opercula of *Hyneria* are both slightly incomplete in the specimen (Figs. 7 and 8) but a fairly accurate restoration may be made. Each operculum is somewhat square in shape and considerably shorter along the anteroposterior axis than is the case in most Rhipidistia (anteroposterior length of operculum contained approximately 3.25 times in the length of the lower jaw). The opercula are superficially ornamented in the same style as the other cranial elements. No suboperculum has been found.

The dermal shoulder girdle consists of a typical cleithrum and clavicle (Figs. 7 and 8). The cleithrum is a simple lamina, very similar to that of other Devonian rhizodontoids such as *Eusthenopteron*. The clavicle (Figs. 3-6) shows a marked dorsal process not unlike that seen in the Carboniferous *Rhizodus* and much smaller than in other Devonian forms. No supracleithral elements have been found except for a right lateral extrascapula (Figs. 9 and 10)

which shows obvious overlap areas for a large anocleithrum and for the median extrascapula, the latter apparently also having been a relatively large element (Fig. 1).

The only parts of the trunk that are known are isolated scales, one of which is associated with the cranial fragments. The scales are thicker relative to their diameter than most rhizodontoid scales and there is a prominent thickened rim along the margin of the posterior half of the scale (Fig. 13). Unfortunately, only the inner surface of the scale is shown on any of the available specimens (YPM 4938-4943). A curious feature of the scales is that the free margin is deeply notched. In each of the scales at hand, one of these notches is considerably more marked than the other (Fig. 13). Undoubtedly these notches in the free margin represent emarginations between the dentine ridges that make up the superficial ornamentation of the exposed portion of the outer surface of the scale. However, this notching is not known in other Rhipidistia. The inner surface of the scale is marked with a prominent central boss that seems to be continued posteriorly in the form of a thin ridge that cuts across the growth lines (Fig. 13). The boss itself is contained within the central area of the scale. It is possible that the scales showing this rather unusual structure came from a specialized region of the body, and that their structure is not typical. However, the same shape is seen in all available scales that have a complete margin.

*Hyneria lindae*<sup>2</sup>, sp. n.

SYNONYMY. "rhipidistian" Thomson, 1967a, p. 239

HOLOTYPE. MCZ<sup>3</sup> 9284: disarticulated skull in three blocks.

PARATYPES. YPM<sup>3</sup> 4938, 4939, 4940, 4941, 4942, 4943: isolated scales.

OCCURRENCE. Uppermost Devonian [Oswayo Formation (Ebright, 1952)] of Clinton and McKean counties, Pennsylvania. From two

<sup>2</sup> Name derivation — for my wife, who has assisted me in collecting fossil fishes in many countries.

<sup>3</sup> Abbreviations used: MCZ — Museum of Comparative Zoology, Harvard University  
YPM — Peabody Museum, Yale University



## FIGURES 3-13

### ABBREVIATIONS USED IN FIGURES

AN anocleithrum	MPR median postrostral
CL cleithrum	O operculum
CV clavicle	PA prearticular
D dentary	P parietal
G principal gular	PP postparietal
ID infradentary	PQ palatoquadrate
IT intertemporal	QJ quadratojugal
LE lateral extrascapular	SQ squamosal
LG lateral gular	ST supratemporal
LPR lateral postrostral	T tabular
MD mandible	V vomer
ME median extrascapular	VT vomerine tooth



Figure 3. *Hyneria lindae* gen. et sp. n. Portion of holotype, approx.  $\times 0.4$ .

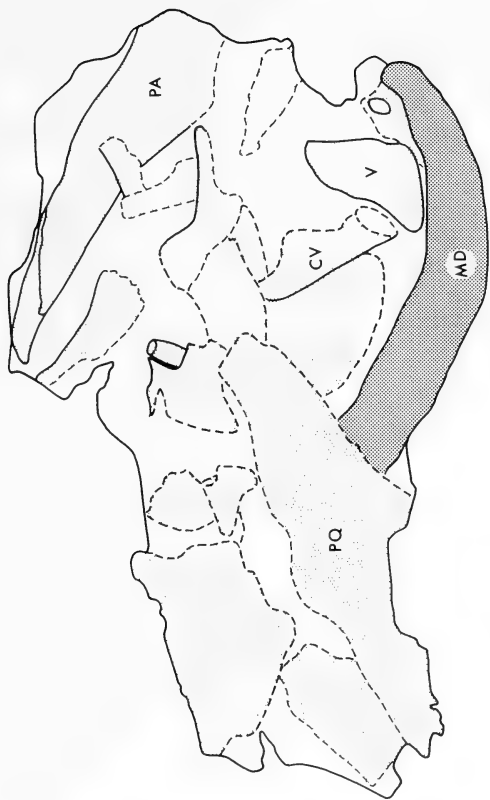


Figure 4. *Hyneria lindae* gen. et sp. n. Diagrammatic view of portion of holotype. In this figure, as in Figures 6, 8 and 10, the heavy shading indicates ornamented dermal bone surfaces.



Figure 5. *Hynertia lindae* gen. et sp. n. Portion of holotype, approx.  $\times 0.4$ .

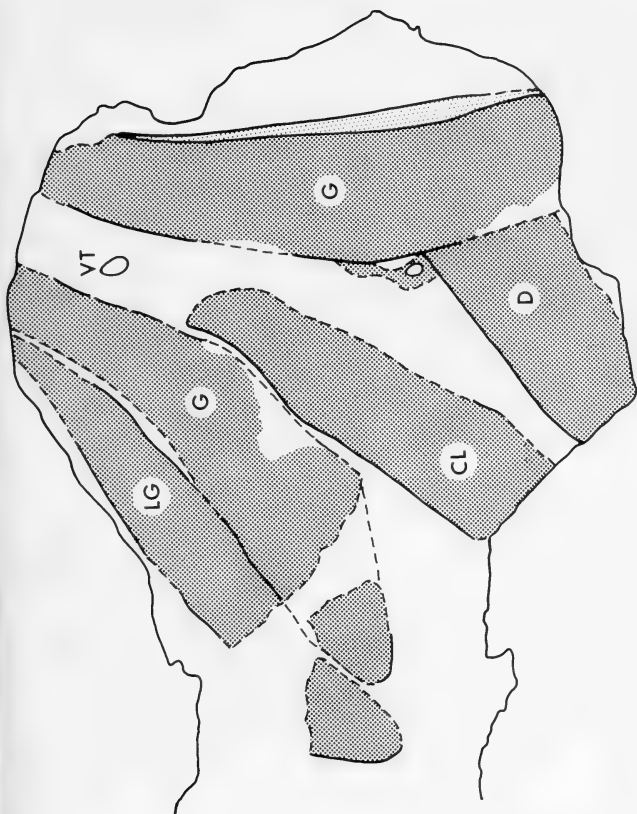


Figure 6. *Hyneria lindae* gen. et sp. n. Diagrammatic view of portion of holotype.



Figure 7. *Hyneria lindae* gen. et sp. n. Portion of holotype, approx.  $\times 0.4$ .

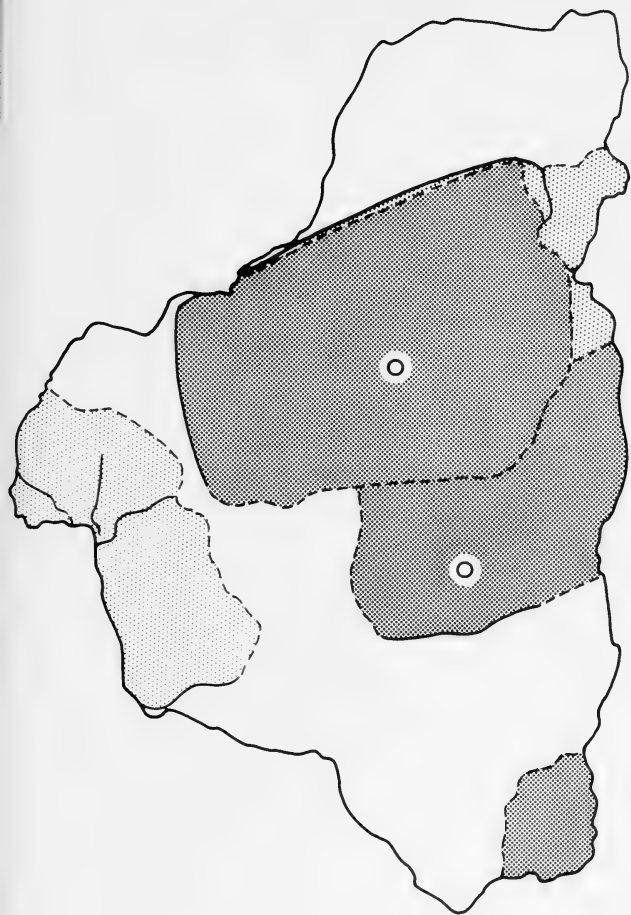


Figure 8. *Hyneria lindae* gen. et sp. n. Diagrammatic view of portion of holotype.

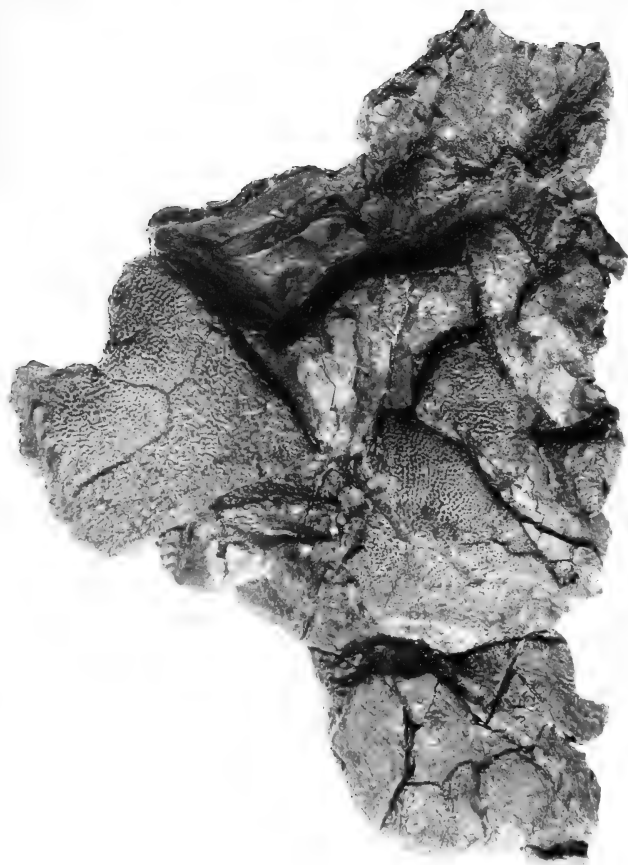


Figure 9. *Hyneria lindae* gen. et sp. n. Portion of holotype  
approx.  $\times 0.4$ .



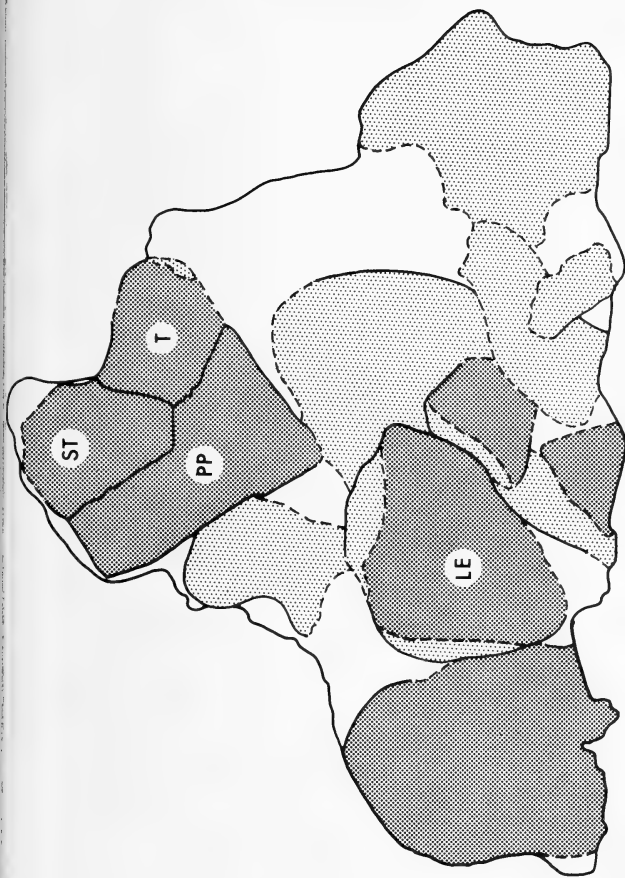


Figure 10. *Hyneria lindae* gen. et sp. n. Diagrammatic view of portion of holotype.



Figure 11. *Hyneria lindae* gen. et sp. n. Portion of holotype, parietal shield in dorsal view,  $\times 0.8$ .



Figure 12. *Hyneria lindae* gen. et sp. n. Portion of holotype, parietal shield in ventral view,  $\times 0.8$ .

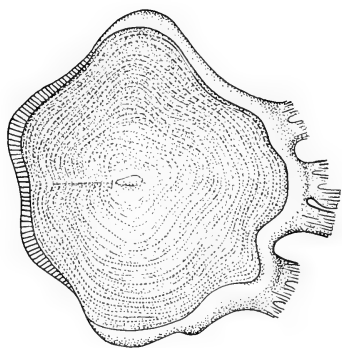


Figure 13. *Hynieria lindae* gen. et sp. n. Reconstruction of scale in internal view,  $\times 2$ .

localities: 1) holotype and paratypes from a large road cut on the north side of U.S. highway 120, between the villages of North Bend and Hyner, Clinton County, Pennsylvania, and 2) fragments of a shoulder girdle which are cautiously referred to the same taxon from a locality on the east side of Route 46, 0.6 miles north of the McKean/Cameron County line, near Emporium, Pennsylvania.

DIAGNOSIS AND DESCRIPTION. As for the genus.

#### COMPARISONS

*Hyneria* clearly belongs in the rhipidistian superfamily Rhizodontoidea, as is indicated by the structure of the scales, by the absence of enamel on the dermal bones and scales, and by the pattern of ornamentation on the dermal bones. At the present time, the Rhizodontoidea are classified into two groups, comprising on the one hand the genus *Rhizodopsis* (Family Rhizodopsidae) and on the other, the genera *Tristicopterus*, *Eusthenopteron*, *Platycephalichthys*, *Eusthenodon*, and *Rhizodus* (which probably includes *Strepsodus*). The genus *Sauripterus* is questionably included in this second group (see below) which normally forms the single family Rhizodontidae. *Hyneria* naturally falls with the rhizodontids. Of these, with the possible exception of *Rhizodus* (the skull of which is unknown), *Hyneria* is the most advanced form. In fact, it is remarkable that the Devonian genera in the family Rhizodontidae may be arranged in a temporal sequence which also corresponds to a direct sequence of structural modification. Within the group we may see a rapid achievement of a diphyccercal tail (incompletely symmetrical in *Tristicopterus*), progressive elongation of the snout region of the skull (Fig. 14), and progressive modification of the dermal bone ornamentation from a pattern of more or less isolated denticles (*Tristicopterus*) to a pattern with the denticles arranged in short rows forming ridges (*Eusthenopteron* and *Platycephalichthys*), to the uniting of these ridges into a coarse incomplete network (*Eusthenodon*), to a complete regular network of ridges with no separate tubercles (*Hyneria*). The Carboniferous genus *Rhizodus* has a pattern of ornamentation in which some separate tubercles may be retained as in *Eusthenopteron* (more evident in *R. ornatus* than *R. hibberti*). *Hyneria* clearly differs from each of the above-mentioned

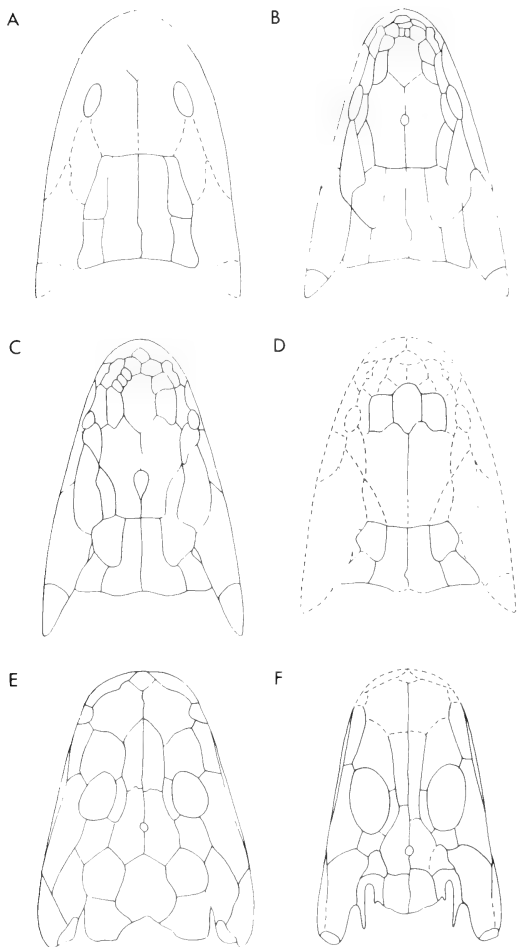


Figure 14. Dorsal view of the skull in: A. *Tristicopterus alatus*, B. *Eusthenopteron foordi*, C. *Eusthenodon wangsjoii*, D. *Hyneria lindae*, E. *Ichthyostega* sp., F. *Acanthostega gunneri*, showing progressive elongation of parietal shield. After Jarvik (1952) and original.

genera. However, since *Rhizodus* is rather poorly known it may be well to emphasize that in respect to those features of its structure that are known, such as the shoulder girdle and operculum (Smith-Woodward, 1891), this genus seems quite separate from *Hyneria*. The possibility also exists that another very poorly-known rhipidistian, the genus *Sauripteris* from the Upper Devonian of Pennsylvania, is related to the material described above. However, the shoulder girdle again seems rather different, apparently having a different structure of the clavicle.

#### ENVIRONMENT OF DEPOSITION

Study of the total fauna of the deposits from which *Hyneria* was collected will be deferred to a later date. We may note here that in addition to the large rhipidistian fish, very numerous small fragments of an antiarch similar to *Bothriolepis* (the presence of which helps to confirm the Upper Devonian correlation of the beds) and spines of "*Xenacanthus*" are found. The antiarch remains are highly fragmented, although very well preserved.

Thin sections of the matrix in which the fossil materials are preserved have been studied by Dr. D. C. Rhoads of Yale University, to whom I am grateful for the following observations. The deposits were laid down in quiet freshwater, probably in a flood plain between distributary channels. There is evidence of reworking of the sediment by burrowing organisms. Frequently the small bone fragments are seen to be displaced to a high angle with respect to the bedding by these burrowings. The red color is in the ferruginous cementing material. There were no great concentrations of organic matter in the deposit other than the bone fragments. The environment was strongly oxidizing. From this I conclude that the small bone fragments were probably carried into the region by flood waters (but from no great distance) and then accumulated temporarily in pools where larger fishes later became stranded.

#### DISCUSSION

As noted in the Introduction, there are many drawbacks to present discussion of rhipidistian-tetrapod relationships. If the *Ichthyostegalia* were not known, then the sequence of structural evolution seen within the rhizodontid Rhipidistia, culminating in

the genus *Hyneria* as described here, would seem a natural stage in the evolution of tetrapods. However, *Hyneria* cannot have evolved before the middle Late Devonian, while the advanced nature of the Late Devonian Ichthyostegalia shows that any structural stages in their evolution corresponding to the rhizodontid sequence must have occurred much earlier.

However, the fact of the close resemblance between the known Rhizodontidae and our analysis of what the ancestors of the first Amphibia must have been (see, for example, Thomson, 1966, 1967a, 1967b), in terms of both structure alone and the pattern of structural evolution, suggests a strong genetic relationship between the two groups. It also seems logical to assume that the rate of evolution in the immediately pre-tetrapod line(s) must have been far greater than in more "normal" Rhipidistia since a major series of adaptive changes was occurring. Possibly the best interpretation of the out-of-phase evolution of rhizodontid Rhipidistia and ichthyostegal Amphibia is that they arose in the Middle Devonian from the same ancestral stock with a large number of features in common. Thereafter both lineages showed similar adaptations in terms of such features as the feeding mechanism (elongation of the snout), but with evolution proceeding much faster in the lineage leading to the Ichthyostegalia.

#### ACKNOWLEDGMENTS

I am grateful to Professor A. S. Romer of Harvard University for the generous loan of material described in this paper and to Dr. D. C. Rhoads of Yale University for valuable interpretations of the lithology. The drawings were prepared by Miss Ward Whittington. The study has been supported financially by National Science Foundation grant GB-4814.



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