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The Status of the Salamander Genera *Scapherpeton* and *Hemitrypus* of Cope

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For a number of years we have been attempting to trace out the fossil history of the family Sirenidae. During the course of this work, we have had occasion to sort through a number of collections of unidentified small fossil material in which we encountered specimens of a large, archaic salamander that is not referable to any modern family. Because some of the specimens seemed to fit Cope's description of *Scapherpeton,* at the earliest opportunity we compared our specimens with the type material, all of which is in the American Museum of Natural History. As we have now seen more material referable to this genus than has heretofore been available to any single worker, we have taken the opportunity to restudy the entire series of specimens. We have also examined material of Cope's genus *Hemitrypus* and include here a redescription of that form.

We are indebted to the American Museum of Natural History and to Dr. Edwin H. Colbert for the loan of material and for the privilege of studying and illustrating the type specimens. To Dr. J. LeRoy Kay of the Carnegie Museum, Dr. Alfred S. Romer of the Museum of Comparative Zoölogy, and Dr. David Dunkle, United States National Museum, we are likewise indebted for the loan of material. Travel associated with this study was made possible by a National Science Foundation grant (N.S.F.-G-5628) held by the junior author.

The following abbreviations are used in this paper:

A.M.N.H., the American Museum of Natural History

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C.M., Carnegie Museum
M.C.Z., Museum of Comparative Zoölogy at Harvard College
U.S.N.M., United States National Museum

SCAPHERPETON COPE

Scapherpeton Cope, 1876, Proc. Acad. Nat. Sci. Philadelphia, vol. 28, p. 353.

TYPE: *Scapherpeton tectum* Cope (1876, p. 355).

A genus of salamanders with heavy, robust, amphicoelous vertebrae. The vertebrae are deeply biconcave and have the foramina for the notochord opposed but apparently not continuous. The foramen chordae is, furthermore, placed high in the glenoid cavity rather than being centrally placed, as it usually is in salamanders. The centrum is laterally compressed and has a strongly developed median ventral keel. With the lateral compression of the vertebra, and the strongly developed median ventral keel, the glenoid cavity is drawn out ventrally so that, in end view, it presents the outline of an inverted teardrop.

The vertebrae of this genus differ from the vertebrae of all known genera of salamanders except *Amphiuma* by the laterally compressed centra. From the Miocene genus *Batrachosauroides* Taylor and Hesse, of the recently described family Batrachosauroididae (Auffenberg, 1958), it differs also in being amphicoelous rather than opisthocoelous, a difference that likewise separates it from an archaic salamander the senior author is describing from the Cretaceous of Wyoming (Auffenberg, in press). From *Amphiuma* it differs in the striking development of the midventral keel, in the lack of well-developed basapophyseal processes on the anterior end of the centrum, and in certain details of the transverse processes and the neural spine. The atlases assigned to *Scapherpeton*, but not proved to belong to it, differ from those of *Amphiuma* in having a wide neural canal that extends laterally over the cotyles and in having the intercotylar process single and obtusely pointed anteriorly rather than partially divided by an anterior median groove.

VARIATION

In the extensive series at hand the observed variation does not exceed that to be expected when it is considered that vertebrae from all parts of the column are probably represented as well as vertebrae from animals of different ages. In even the best preserved of the specimens there is, as is to be expected with specimens of this size and antiquity, a fair amount of erosion and breakage.

The material from the Hell Creek and Lance formations does not

seem on comparison to differ significantly from that of the older Judith River and Belly River formations. Certain specimens from the younger beds do seem to be larger in size, as is shown by the comparative measurements of the type of *Scapherpeton tectum* and a dorsal vertebra (C.M. No. 6467) from the Lance of Niobrara County, Wyoming (see table 1). The type of *S. tectum* is fairly typical in size of the Judith River material, while the Carnegie specimen from the Lance is the largest we have seen. Richard Estes, University of California, is currently studying the herpetofauna of the Lance and has considerable material of this genus. It is hoped that additional vertebrae from this formation will shed some light on this problem. Until Estes finishes his study of this material, we see no justification for recognizing these specimens nomenclatorially.

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF THE TYPE AND OF THE LARGEST KNOWN SPECIMEN OF *Scapherpeton tectum*

Measurement	A.M.N.H. No. 5682 (Type)	C.M. No. 6467
Length of centrum along midventral line	8.3	11.7
Width of vertebra at narrowest point	5.5	11.7
Height of vertebra from lowest margin of centrum to line drawn between facets of posterior zygapophyses	8.0	—
Distance from tips of prezygapophyses to tips of postzygapophyses	10.1	—
Width of anterior glenoid cavity	4.2	6.2
Height of anterior glenoid cavity	6.9	6.7
Width of neural canal	1.4	3.0
Height of neural canal	3.2	3.7

In the original description of the genus, Cope recognized no fewer than four species in the material from the Judith River Beds, namely, *tectum, laticolle, excisum,* and *favosum.* If this genus were represented by a recent species on which adequate studies both of ontogenetic and of intraspecific variation could be made, we might be able to determine that some of the observed variation in the material at hand is really deserving of specific designation. In the absence of such studies, however, we believe it is best, on the basis of present material, to recognize only one species in *Scapherpeton.* Cope did not designate a type species,

but he did list *S. tectum* first in the series of the four he proposed. Hay (1902, p. 424), in his catalogue, listed *tectum* as the type. Thus, by both page priority and the action of the first reviser, *tectum* must stand as the type species of the genus *Scapherpeton*, and we assign the names *laticolle*, *excisum*, and *favosum* to the synonymy of *tectum*.

Distribution

At present we have examined specimens of *Scapherpeton* from four localities representing two different ages. We follow Simpson (1937) in his terminology of the stratigraphy, and we consider the Belly River of Alberta as the equivalent of the Judith River of Montana, and the Lance of Wyoming as the equivalent of the Hell Creek of Montana. Thus *Scapherpeton* is represented in the middle portion of the upper Cretaceous in the Judith River and Belly River and also in the Lance and the Hell Creek of the uppermost upper Cretaceous. The following list includes all the catalogued specimens examined by us:

A.M.N.H. No. 5682: One anterior dorsal vertebra (type *Scapherpeton tectum* Cope); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5683: Seven vertebrae (types *Scapherpeton laticolle* Cope); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5684: Two dorsal vertebrae, one caudal vertebra (types *Scapherpeton excisum* Cope); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5685: One vertebra (type *Scapherpeton favosum* Cope); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5791: One atlas (associated with types of *S. laticolle*); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5792: Two partial limb bones (associated with types of *S. laticolle*); Montana, Judith River, Judith River formation.

A.M.N.H. No. 5793: Two atlases; Montana, Judith River, Judith River formation.

A.M.N.H. No. 5794: Five vertebrae and eight vertebral fragments; Montana, Judith River, Judith River formation.

A.M.N.H. No. 5010: Fifteen vertebrae and one atlas; Montana, Hell Creek, Hell Creek formation.

A.M.N.H. No. 5490: Twenty-seven dorsal and caudal vertebrae; Montana, Hell Creek, Hell Creek formation.

A.M.N.H. No. 5365: One dorsal vertebra; Alberta, Red Deer River, Belly River formation.

U.S.N.M. No. 22096: Eight vertebrae and two atlases; Wyoming, Niobrara County, Quarry 1, Lance formation.

U.S.N.M. No. 22097: Three vertebrae; Presumably from Niobrara County, Wyoming.

U.S.N.M. No. 22092: Six fragmentary vertebrae and three atlases; Wyoming, Niobrara County, Lance formation.

U.S.N.M. No. 22093: One fragmentary vertebra; Wyoming, Niobrara County, Lance formation.
U.S.N.M. No. 22094: Eleven vertebrae and one atlas; Wyoming, Niobrara County, Quarry 1, Lance formation.
U.S.N.M. No. 22095: Two vertebrae; Wyoming, Niobrara County, Peterson's Quarry, Lance formation.
C.M. No. 6464: Fifteen vertebrae and one fragment tentatively referred; Wyoming, Niobrara County, Lance formation.
C.M. No. 6466: One dorsal vertebra and five vertebral fragments; Wyoming, Niobrara County, Lance formation.
C.M. No. 6467: Eleven vertebrae and eight atlases; Wyoming, Niobrara County, Lance formation.
M.C.Z. No. 2813: Two dorsal vertebrae; Wyoming, Niobrara County, Lance Creek, Lance formation.

Relationships

While none of the writers on this genus except Hay has questioned that it is a salamander, there has been no consensus on its relationship to the other caudates. Cope, in the original description, indicated that he thought it, possibly with *Hemitrypus*, represented a family different from any now living, but he did not propose a name for such a family. Hay (1902, p. 424) listed the two as salamander genera *incertae sedis* and in his second catalogue (1929, pp. 820–821) listed them with some "supposed microsaurian genera whose relationships are uncertain." Romer (1945, p. 592) referred them with question to the Ambystomatidae. Herre (1950, p. 23), on the other hand, placed them in his suborder Palaeurodeloidea, but gave them no family assignment.

We agree with Cope that *Scapherpeton* is not a member of any living family, and we further believe it should not be assigned to either the Batrachosauroididae or the family of the undescribed opisthocoel from Wyoming mentioned in the diagnosis. We therefore propose that the following family be erected for its reception.

SCAPHERPETONIDAE, NEW FAMILY

A family of salamanders erected for the genus *Scapherpeton* and at present known only from the Cretaceous of North America.

This family has amphicoelous vertebrae and differs from all others, except the Amphiumidae, in having the centrum laterally compressed and attenuated ventrally so that in end view the shape of the glenoid cavity resembles an inverted teardrop. The foramen chordae is, furthermore, in the upper one-fourth of the glenoid cavity instead of being centrally placed as it usually is in salamanders. In this respect likewise it is approached by the Amphiumidae. From the Amphiumidae it

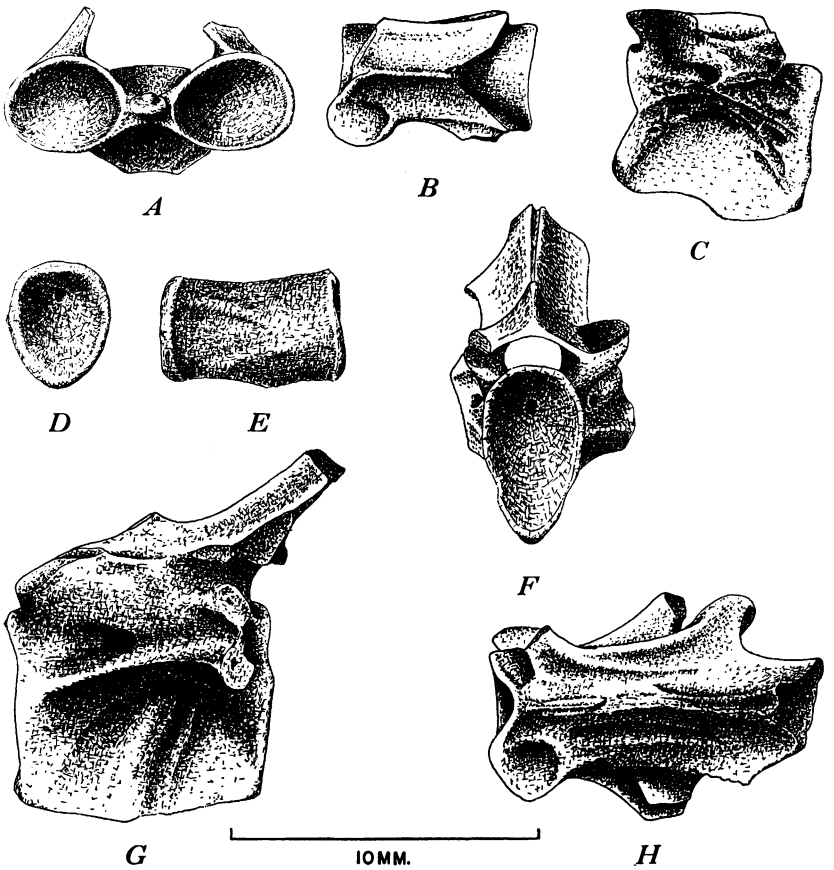

FIG. 1. A. Anterior view of atlas of *Scapherpeton*, C.M. No. 6467. B, C. *Scapherpeton laticolle*, type, A.M.N.H. No. 5683. B. Dorsal view. C. Lateral view. D, E. Centrum of *Hemitrypus jordanianus*, type, A.M.N.H. No. 5686. D. End view. E. Lateral view. F–H. *Scapherpeton tectum*, type, A.M.N.H. No. 5682. F. Anterior view. G. Lateral view. H. Dorsal view. Four times natural size.

differs in lacking basapophyseal processes on the anterior end of the centrum and in having the neural spine extending forward to the anterior margin of the roof of the neural arch. Furthermore, the transverse process differs from that of *Amphiuma* in being placed more posteriorly on the vertebra and in being more laterally compressed, conditions that more nearly approach those found in *Cryptobranchus*. The processes are, however, smaller and less well developed than in the latter genus. The extent to which the neural spine is produced in a

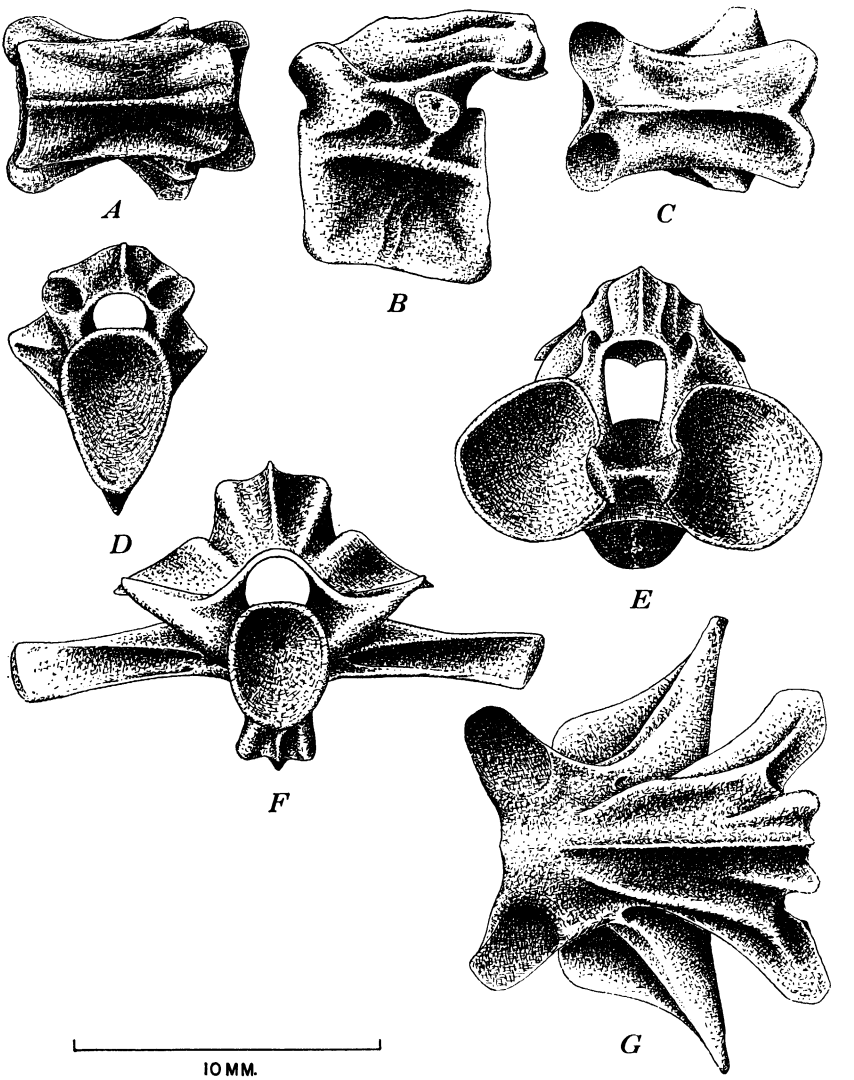

FIG. 2. A–D. *Scapherpeton*, A.M.N.H. No. 5010. A. Ventral view. B. Lateral view. C. Dorsal view. D. Anterior view. E–G. *Amphiuma means*. E. Anterior view of atlas. F. Anterior view of dorsal vertebra. G. Dorsal view of dorsal vertebra. Four times natural size.

posterior direction, as exemplified by the type of *tectum* and indicated in some of the other specimens, seems to be unique among salamanders (fig. 1). In this respect it is most closely approached by *Cryptobranchus*.

In the formation of the atlas, *Scapherpeton* is rather typical of salamanders. There are two well-developed cotyles, and the central portion of the atlas is somewhat flattened so that each cotyle is generally wider than high. Also the intercotylar process is rather short and is median and unpaired and much narrower than the neural canal. In this respect *Scapherpeton* differs strikingly from *Amphiuma* which has the intercotylar process partially divided on the median line so that it appears as a paired structure, and has this process much wider than the neural canal, which in the atlas of *Amphiuma* is very narrow and about twice as high as wide. The dorsal portion of the neural arch is broken in all the *Scapherpeton* atlases at hand, but it is obvious that the neural canal is proportionately much wider than in *Amphiuma*, for it extends laterally to above the cotyles while in *Amphiuma* the neural canal is entirely between the cotyles. In this respect *Scapherpeton* is more like *Cryptobranchus*.

HEMITRYPUS COPE

Hemitrypus COPE, 1876, Proc. Acad. Nat. Sci. Philadelphia, vol. 28, p. 358.

TYPE: *Hemitrypus jordanianus* Cope (1876, p. 358).

The single vertebra from the Judith River formation on which Cope based this genus has been fractured beyond repair. The neural arch is represented by three fragments. The largest of these has a portion of a posterior zygapophysis present, but it is so broken as to be entirely useless so far as identification is concerned. The centrum is in fair condition. It is similar to that of *Scapherpeton* and to that of *Amphiuma* in having the foramen chordae placed high in the centrum, but it differs from that of *Scapherpeton* in lacking a strong midventral keel. Although the centrum is heavily eroded, faint ridges on the ventral and anterior margin of the centrum may represent basapophyseal accessory processes, another character that would tend to separate it from *Scapherpeton*.

Fortunately, fairly complete material referable to this genus in the United States National Museum is available, allowing a redescription of the genus and a comparison with other forms. The most complete middorsal element is described below.

U.S.N.M. No. 22252, a middorsal element in fairly good condition and only slightly eroded. The centrum is without the large midventral keel of that of some genera, rounded in end view, only slightly compressed laterally. The foramina chordae are located in the upper third of the centrum and apparently are not continuous. The transverse processes are located posteriorly, the two lateral articular surfaces sepa-

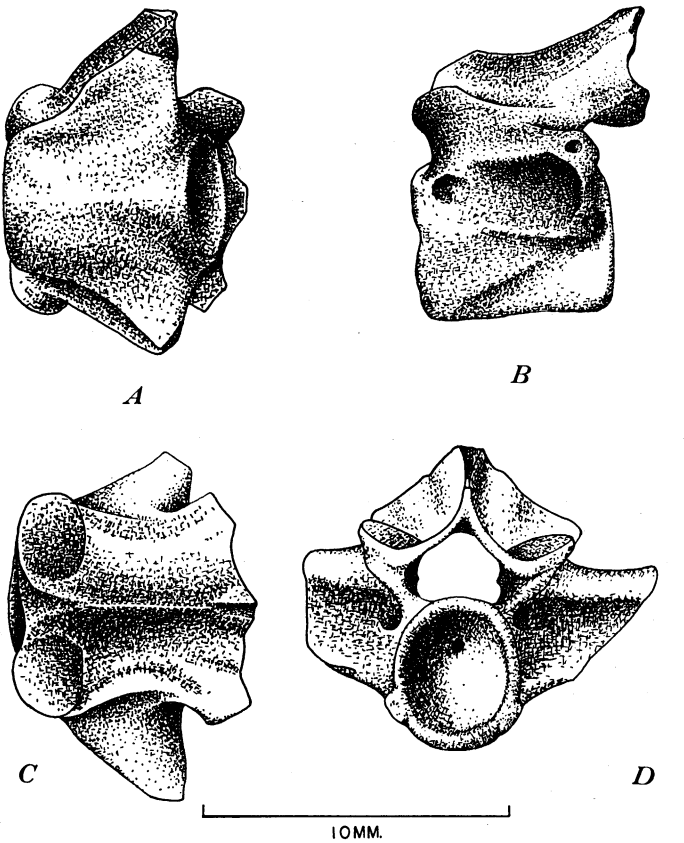

FIG. 3. *Hemitrypus jordanianus*, U.S.N.M. No. 22253. A. Ventral view. B. Lateral view. C. Dorsal view. D. Anterior view. Four times natural size.

rated by a constricted vertical lamina. The upper articular surface is larger than the ventral one. The buttress of the lower process is strongly developed and continued downward and anteriorly to the anterior edge of the centrum at an angle of about 45 degrees. The posterior buttress is not nearly so well developed, extending almost straight back to the edge of the glenoid cavity. The anterior buttress is vertically compressed, forming a small horizontal shelf extending anteriorly to about the middle of the base of the prezygapophyseal buttress. A large nutritive foramen is located between the two buttresses both anteriorly and posteriorly. The neural arch is emarginate from above, flattened dorsally. The neural spine is partly broken, but apparently high and thin, extending from a V-shaped notch at the anterior

edge of the arch to the posterior raised portion of the arch. The prezygapophyseal articular surfaces are oval, directed laterally, their anterior edges at right angles to the main axis of the centrum. From the front the articular surfaces are at a much greater angle to the perpendicular than they are in *Scapherpeton*. From the front the lateral portions of the neural canal are flattened dorsally, while the roof is drawn up into an acute point medially. The floor of the canal is strongly convex.

U.S.N.M. No. 22253 seems to be a more anterior vertebra of a larger specimen. In the main it is essentially the same as the one described above, except that the centrum is much shorter and wider. The transverse processes are better preserved, each showing a deep groove anteriorly between the upper and lower buttresses. The anterior ends of the lower buttresses at the edge of the centrum are provided with small eroded areas, suggesting the former presence of small basapophyseal processes. Faint ridges on the type vertebra seem to represent small basapophyseal processes. *Scapherpeton* seems to lack these ridges.

In the absence of more complete fossil skeletons of *Hemitrypus*, it is impossible for us to make a definite familial assignment of this genus. Isolated vertebrae referred to this genus are not nearly so distinctive as are those of *Scapherpeton*. There is a very slight possibility that individual elements referred to *Hemitrypus* may represent a particular part of the vertebral column of *Scapherpeton*, but such variation along the column is more than would normally be expected on the basis of modern urodeles. For the present we prefer to recognize *Hemitrypus* as a distinct genus. In certain respects the vertebrae of *Hemitrypus* are approached reasonably closely by those of some of the modern families of salamanders. While it is possible that the form may belong to the Scapherpetonidae, our considered opinion is that on the basis of the evidence before us it is, for the present, best simply to consider it a salamander *incertae sedis*. Figure 3 illustrates one of the better specimens referred to this genus.

According to our present knowledge of the temporal distribution of salamanders, the Sirenidae have the longest time span, occurring as they do from the lower Cretaceous to the present. At least two other families are known from the Cretaceous, but both of these represent archaic stocks that are not known to have lasted into the Cenozoic. These are the Scapherpetonidae, as herein defined, and an as yet undescribed family of opisthocoelous forms from Wyoming. Possibly the Scapherpetonidae may eventually be connected with the Amphiumidae, but so far we have seen no evidence of a connecting link. In

Florida, where *Amphiuma* is at present extremely abundant, its fossil history is brief indeed. It is abundant in only a few late Pleistocene deposits, but no sign of it has been seen in earlier formations, although several of these older deposits contain other urodele remains.

At present, four modern families are known from the Paleocene, if the European *Wolterstorffiella* is indeed a hynobiid and if the footprints from Montana called *Ambystomichnus* are correctly assigned to the Ambystomatidae. Two additional European forms from this epoch are *Koalliella* (a salamandrid) and *Geyeriella*, which may be a plethodontid.

The Proteidae are known as fossils from the Eocene of Europe.

In the Miocene, the family Cryptobranchidae is represented by *Megalobatrachus*. This is the only period from which the recently described family Batrachosauroididae is known. The single genus in this family is probably but the vestige of a more widespread, earlier, archaic stock.

The Amphiumidae, as mentioned above, appear in the Pleistocene.

Not enough data are available at the present time to allow a definite assignment of the three fossil families to a proper position in the phylogenetic sequence. We believe, however, that the opisthocoelous form from Wyoming and the Batrachosauroididae show definite affinities to the Salamandridae, and that the Scapherpetonidae show tendencies towards the Amphiumidae.

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