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## A WELL-PRESERVED FOSSIL AMPHIUMID (LISSAMPHIBIA: CAUDATA) FROM THE EOCENE GREEN RIVER FORMATION OF WYOMING

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**ABSTRACT**—A well-preserved primitive amphiumid skeleton from the Eocene Green River Formation in Wyoming is described as †*Paleoamphiuma tetradactylum*, gen. et sp. nov. This species differs from extant and known fossil amphiumids by the retention of a number of plesiomorphic features: separate ossification of the first hypobranchial and first ceratobranchial; no more than 35 presacral vertebrae; rib-bearers that are directed posterolaterally, taper to a blunt tip, and lack a posteroventral flange; and the presence of four digits in the manus (and probably in pes). Characterized so far only by the absence of derived characters, this new fossil amphiumid is currently a metaspecies.

### INTRODUCTION

The lissamphibian family Amphiumidae (common name “Congo eel”) comprises one extant genus, *Amphiuma*, with three species (Salthe, 1973a–c), *A. means* Garden (in Smith, 1821), *A. pholeter* Neill (1964), and *A. tridactylum* Cuvier (1827). The extant amphiumids document the progressive reduction of digits in manus and pes from three in *A. tridactylum* to two in *A. means*, to one in *A. pholeter* (Neill, 1964:65). The distribution of extant species is restricted to the southeastern United States (the Austroriparian biotic province of Dice, 1943).

The fossil record of amphiumids is very limited (Estes, 1981). A number of isolated vertebrae from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of Montana have been described as †*Proamphiuma cretacea* Estes, 1969. †*Amphiuma jepseni* Estes, 1969, is based on an incomplete skull and associated vertebrae from the upper Paleocene Polecat Bench Formation of Wyoming. †*Amphiuma antica* Holman, 1977, is based on an isolated vertebra from the middle Miocene Fleming Formation of Texas, which cannot be reliably differentiated from vertebrae of living species (Estes, 1981:42). Pleistocene occurrences of amphiumid vertebrae in Texas (Holman, 1965) and Florida (Brattstrom, 1952; Hirschfeld, 1968), have been referred to the extant species *A. means*. The new genus and species described here is documented by the first articulated fossil skeleton belonging in the family.

### ABBREVIATIONS AND MATERIALS

#### Abbreviations

An (l) or (r) following an abbreviation on a figure indicates left or right side, respectively. SVL stands for snout vent length. A taxon name preceded by a dagger (†) is extinct.

**Anatomical**—**ar**, articular; **asc**, atlas centrum; **asn**, atlas neural arch; **bsbr**, basibranchial; **cbr**, ceratobranchial (epibranchial of some authors); **chy**, ceratohyal; **co**, coracoid; **cp**, coronoid process of prearticular; **ds**, dentary symphysis (of left dentary); **dt**, broken bases of dentary teeth; **fr**, frontal; **fe**, femur; **fi**, fibula; **fm**, foramen magnum; **hu**, humerus; **hybr**, hypobranchial (ceratobranchial of some authors); **hybr + cbr**, fused hypobranchial-ceratobranchial; **il**, ilium; **mc**, metacarpal; **mt**, metatarsal; **na**, nasal; **nc**, neural crest; **oc** of **eo**, occipital condyle of exoccipital; **pa**, parietal; **pco**, precoracoid; **pcr**, postzygapophyseal crest; **pmx**, premaxilla; **poz**, postzygapophysis; **pp**, proximal phalanx (*pl.* phalanges); **pra**, prearticular; **prz**, prezygapophysis; **ps**, parasphenoid; **pu-is**, puboischiadic

plate; **q**, quadrate; **ra**, radius; **rb**, rib bearer; **sc**, scapula; **sq**, squamosal; **t**, teeth; **ti**, tibia; **u**, ungual or distal phalanx (**u1–u4** in anterior limb and serially indeterminate in posterior limbs due to preservation); **ul**, ulna.

**Institutional**—FMNH, Field Museum of Natural History, Chicago, Illinois; LSUMZ, Louisiana State University, Museum of Natural Science, Louisiana.

### Comparative Materials

Cleared and stained specimens listed below (prepared following Dingerkus and Uhler, 1977) are indicated by C&S. Dried skeletons are indicated by DS. Snout-ventral length is abbreviated as SVL.

*Amphiuma tridactylum* Cuvier, 1827. Four specimens total: three C&S specimens (LSUMZ 55707, 59344, 59345) ranging from 64 mm to 250 mm SVL; one DS specimen (FMNH 31040) of an estimated 220 mm SVL. All specimens collected from Louisiana.

*Amphiuma means* Garden, 1821. One DS specimen (FMNH 196099; est. 250 mm SVL). From Baton Rouge, Louisiana.

### SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA Linnaeus, 1758  
Subclass LISSAMPHIBIA Haeckel, 1866  
Order CAUDATA Oppel, 1811  
Family AMPHIUMIDAE Gray, 1825  
Genus †*PALEOAMPHIUMA*, gen. nov.

**Type Species**—†*Paleoamphiuma tetradactylum*, gen. et sp. nov. (by monotypy)

**Diagnosis**—As for species.

**Etymology**—*Palaeo* (Greek) ancient or extinct type or form, and *amphiuma* (Greek), referring to the extant genus *Amphiuma*.

†*PALEOAMPHIUMA TETRADACTYLOUM*, sp. nov.  
(Figs. 1–6)

**Holotype**—FMNH PR1810, a nearly complete skeleton, missing most of one forelimb (Fig. 1).

**Type Locality and Horizon**—Locality H of Grande and Buchheim (1994); late early Eocene Fossil Butte Member, Green River Formation, Lincoln County, southwestern Wyoming. Locality H (Grande and Buchheim, 1994), which was near the shore of early Eocene Fossil Lake, is thought to have been freshwater and tropical or subtropical (Grande, 1994). The

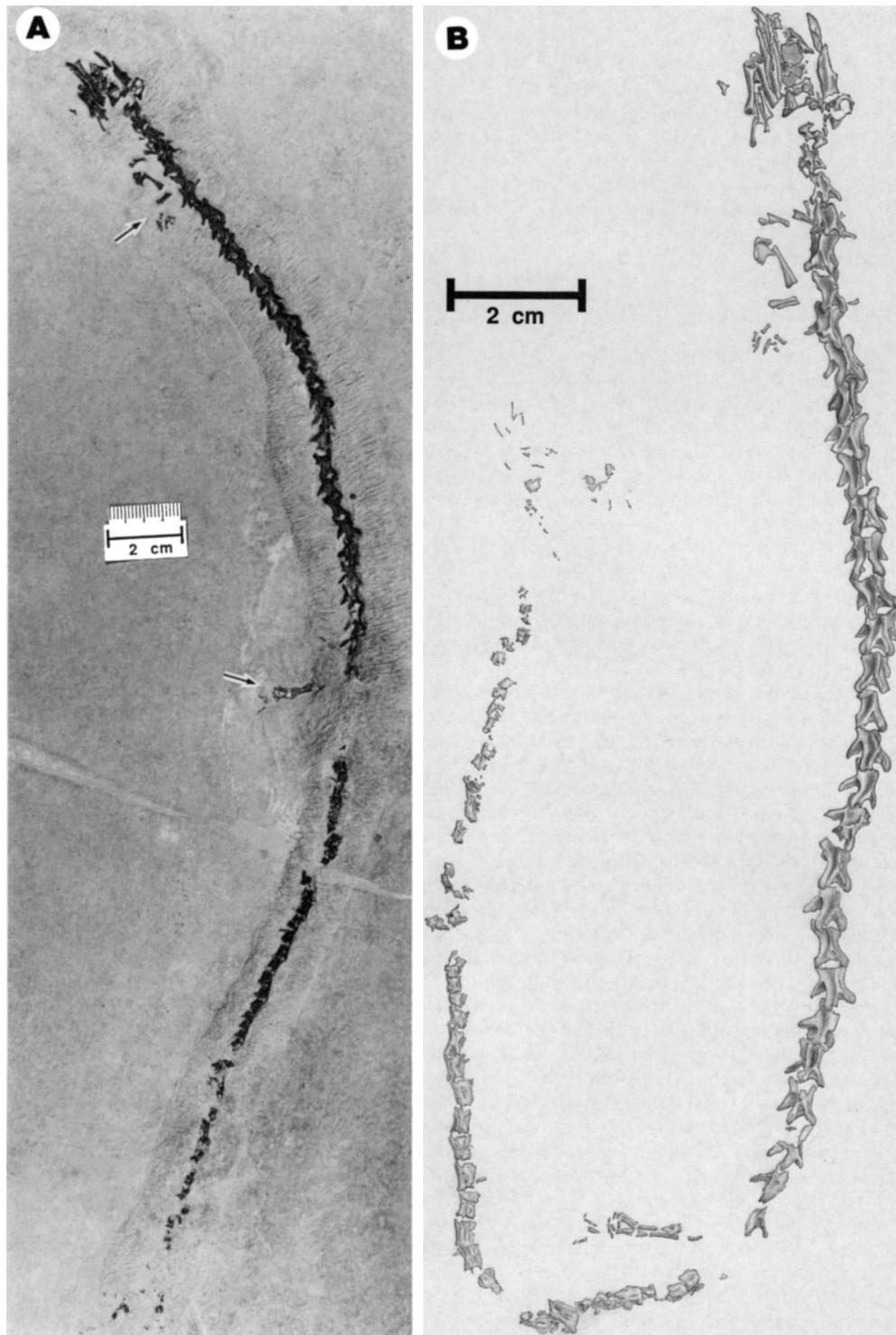


FIGURE 1. †*Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype and only known specimen (FMNH PR1810), from the early Eocene deposits of the Green River Formation of Wyoming. Nearly complete skeleton with disarticulated skull and well-preserved limbs on one side, about 390 mm in total length. **A**, photograph. Arrows point to anterior and posterior limb bones; **B**, line drawing of **A** with body region drawn as bent for the purpose of enlargement.

associated aquatic fauna is one of the world's most diverse Lagerstätten (Grande, 1984, 1994; Grande and Buchheim, 1994).

**Diagnosis**—A fossil representative of Amphiumidae that differs from extant species of *Amphiuma* in having separate first hypobranchial and first ceratobranchial bones; a lesser number

of presacral vertebrae (not exceeding 35); posterior rib-bearers pointing in a posterolateral direction, tapering to a blunt tip distally, and without (postero-) ventral flange; four digits in the manus (and probably also in the pes). These character states are unknown in other fossil species of Amphiumidae.

**Comments**—The holotype is clearly referable to the Amphiumidae on the basis of the elongated trunk, reduced limbs, and the presence of postzygapophyseal crests on the vertebrae. However, †*Paleoamphiuma tetradactylum*, gen. et sp. nov. is here differentiated from the extant species by the absence of shared derived characters diagnostic for the genus *Amphiuma* (see diagnosis above). †*Paleoamphiuma tetradactylum* therefore is currently a metataxon following the convention of Gauthier et al. (1988); also see Archibald (1994).

**Etymology**—*Tetra* (Greek), four, and *dactylum* (Greek *daktylos*), a finger; referring to the presence of four digits in manus.

#### MORPHOLOGICAL DESCRIPTION

The new genus and species is known only by a virtually complete skeleton (FMNH PR1810), approximately 390 mm in total length (Fig. 1). The skull is incompletely preserved but probably measured approximately 20 mm in length. Approximate snout-vent length is 200 mm. The vertebral column is nearly complete except for its posteriormost part, where a gap separates the dorsal from the caudal vertebral column. Even the tail is almost completely preserved.

**Skull**—The skull (Fig. 2) is disarticulated and incompletely preserved. The premaxilla is incompletely exposed (**pmx**, Fig. 2), partially covered by disarticulated elements of the lower jaw. At the tip of the snout, the pars dentalis of the premaxilla is partially preserved. A thin and elongate splint of bone, located behind the pars dentalis of the premaxilla and oriented along the longitudinal axis of the skull, represents the incompletely preserved posterior (nasal) process of the premaxilla, which resembles that of extant *Amphiuma*. As far as we can tell on the specimen, the premaxilla appears to be unpaired, i.e., fused at the midline as in all extant Amphiumidae (e.g., see Carroll and Holmes, 1980:fig. 10). The Paleocene species †*Amphiuma jepseni* is based on an incompletely preserved skull which, when reconstructed, is thought to show a relatively broader snout than is typical for extant species (see Estes, 1969:fig. 4). No maxillary bone is completely exposed on the holotype of †*Paleoamphiuma* to allow the reconstruction of the snout contours. The maxillary bone is relatively stout in extant *Amphiuma*. Its absence in †*Paleoamphiuma* may indicate that it was less well developed in the fossil, in which case the stout maxilla would become a synapomorphy of extant *Amphiuma* (e.g., Carroll and Holmes, 1980:fig. 10). Behind the pars dentalis of the premaxilla, and to the right side of the latter's posterior (nasal) process (in ventral view), the matrix preserves the impression of a broad and roughly rectangular nasal (**na**). In extant *Amphiuma*, the nasal tapers to a blunt tip posteriorly (e.g., Carroll and Holmes, 1980:fig. 10), but this part is not preserved in the holotype of †*Paleoamphiuma*.

The right frontal and parietal bones (**fr**, **pa**, Fig. 2) are well displayed in ventral view. The shapes and sutural contacts of these dermal skull roofing bones resemble those observed in extant *Amphiuma* (e.g., Carroll and Holmes, 1980:fig. 10). The frontal is an elongated element tapering to a blunt tip anteriorly. The lateral edge of its posterior part is thickened, and carries a distinct, ventrolaterally facing facet which received the anterolateral tip of the parietal in the articulated skull. The medial margin of the frontal is smooth, suggesting that the two frontal bones met in a non-interdigitating suture along the dorsomedial midline of the skull.

The contours of the parietal closely match those observed in extant *Amphiuma* (e.g., Carroll and Holmes, 1980:fig. 10). The lateral edge of the parietal again appears thickened in ventral view. Anteriorly, the parietal extends into a distinct anterolateral process that fits into the aforementioned facet on the posterolateral margin of the frontal. In the articulated skull, the two bones met in a posteromedially trending suture. At about its

midpoint, the lateral margin of the parietal forms a distinct laterally projecting edge that marks the posterodorsal corner of the orbit in the articulated skull. Behind the orbit, the lateral margin of the parietal is slightly concave. The posterior margin of the parietal trends slightly in a posteromedial direction. It met the squamosal and exoccipital in an irregular suture line in the articulated skull.

A scatter of bony flakes along the midline of the skull probably represents fragments of the parasphenoid, again exposed in ventral view (**ps**, Fig. 2). Behind these fragments, the disarticulated and incompletely preserved exoccipitals (**eo**, Fig. 2) can be identified, still defining the contours of the foramen magnum (**fm**, Fig. 2). The right occipital condyle (**oc of eo(r)**, Fig. 2), part of the right exoccipital, is distinct just behind the parasphenoid fragments. A broad, roughly triangular bone, situated behind the parasphenoid fragments, must represent the squamosal (**sq**, Fig. 2), an element participating in the formation of the suspensorium. The mandibular condyle of the left quadrate (**q**, Fig. 2) is well exposed in posterior view at the ventral (distal) end of the left squamosal.

The right occipital condyle, squamosal and quadrate have been subject to more severe disarticulation and dislocation. Although the right occipital condyle is distinct, it is broken off from the rest of the (right) exoccipital. The right squamosal is represented by irregularly shaped bone fragments located behind the (right) parietal, and associated with the rather distinct mandibular condyle of the right quadrate. Between the left occipital condyle (**oc of eo(l)**, Fig. 2), and the remnants of the right quadrate (**q(r)**, Fig. 2) a fragment of the right articular bone is exposed (**ar(r)**, Fig. 2), carrying the facet of the mandibular articulation.

The left lower jaw is exposed in ventromedial view, with an oblique break through it. The break separates the anterior one-third of the dentary and divides the prearticular approximately in half. The anterior tip of the dentary is slightly expanded into a symphyseal facet (**ds**, Fig. 2). The posterior end of the dentary tapers off along the ventral margin of the prearticular (**pra**, Fig. 2). The posterior part of the prearticular expands into an incompletely preserved coronoid process. This coronoid process (**cp**, Fig. 2) appears to be somewhat lower than in extant *Amphiuma*. The prearticular narrows to a pointed tip located closely behind the mandibular symphysis.

**Hyobranchial Skeleton**—A small number of ossified ceratobranchial elements is considered the plesiomorphic character state in adult salamanders (Duellman and Trueb, 1986:463; Larson, 1991:255). Although individuals of extant species of *Amphiuma* have four cartilaginous ceratobranchials, only ceratobranchial 1 ossifies (as seen in an adult-sized cleared and stained specimen of *A. tridactylum* with a snout-vent length of 215 mm [LSUMZ 55707]). This agrees with the condition seen in the only known specimen of †*Paleoamphiuma tetradactylum*, gen. et sp. nov. (FMNH PR1810, an individual that we interpret as an adult-sized specimen based on its body size), which also has only a single ossified ceratobranchial.

In †*Paleoamphiuma*, the first ceratobranchial (**cbr**, Figs. 2, 3A) is an ossification that remains separate from the ossified first hypobranchial (**hybr**, Figs. 2, 3A). This is an important retention of a plesiomorphic feature in the fossil specimen relative to extant amphiumids (see Fig. 3B and C). In lissamphibians, the inferred plesiomorphic condition is for the first hypobranchial and the first ceratobranchial to remain separate (Duellman and Trueb, 1986:463; Larson, 1991:255). In some Lissamphibia, the two elements are fused into a single rod of cartilage, a derived condition (Duellman and Trueb, 1986:463) reported for *Amphiuma* (Baker, 1945:fig. 3.5) and Hynobiidae among salamanders (Larson, 1991:255). In a cleared and stained specimen of *Amphiuma tridactylum* of 64 mm snout-vent length (LSUMZ 59345), the fused element is already fully

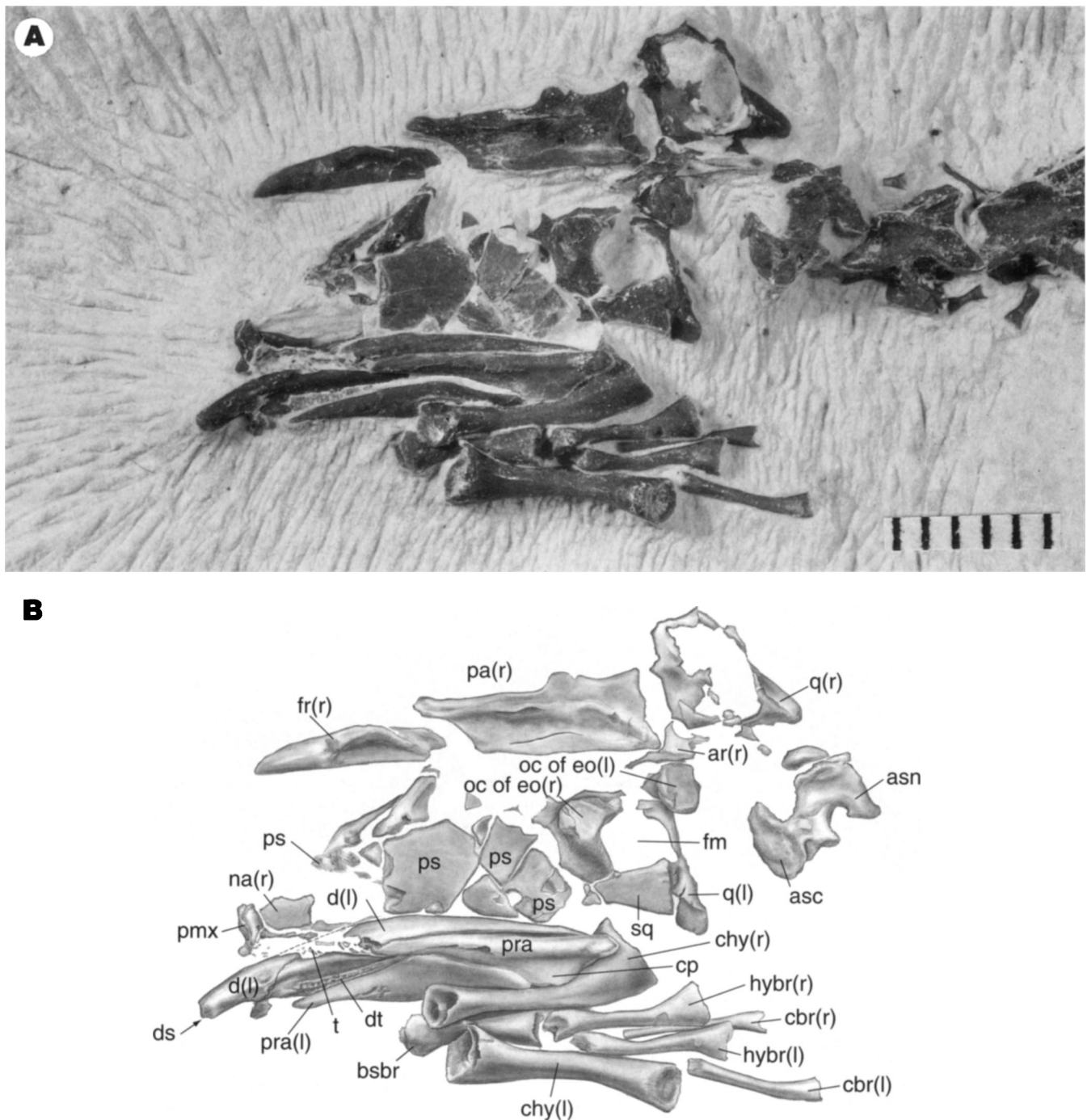


FIGURE 2. †*Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype (FMNH PR1810). Skull from Figure 1. Anterior facing left. **A**, photograph; scale in millimeters; **B**, line drawing of **A**.

ossified and forms the angulated element characteristic for the genus.

**Vertebral Column**—The holotype of †*Paleoamphiuma tetradactylum*, gen. et sp. nov. preserves 71 vertebrae: 31 precaudal vertebrae and 40 caudal vertebrae or vertebral fragments. The tail is certainly incomplete distally. The average total vertebral count for extant amphiumids is about 110, of which approximately 65–70 are precaudals (Baker, 1945). One specimen available to us of *Amphiuma tridactylum* (LSUMZ 55707) has 102 vertebrae, of which 65 are precaudal. The total number of

vertebrae reported for *A. means* is 101, with approximately 64 precaudals and 37 caudals (Davison, 1895). No vertebral counts are available for the third extant species, *A. pholeter*. In summary, the extant amphiumid species have significantly higher precaudal vertebral counts than †*Paleoamphiuma* (e.g., about twice as many precaudal vertebrae).

The only cervical vertebra recognized in salamanders is the atlas (Duellman and Trueb, 1986:325), which in †*Paleoamphiuma* is located immediately behind the disarticulated right occipital condyle (asc, Fig. 2). The atlas is incompletely pre-

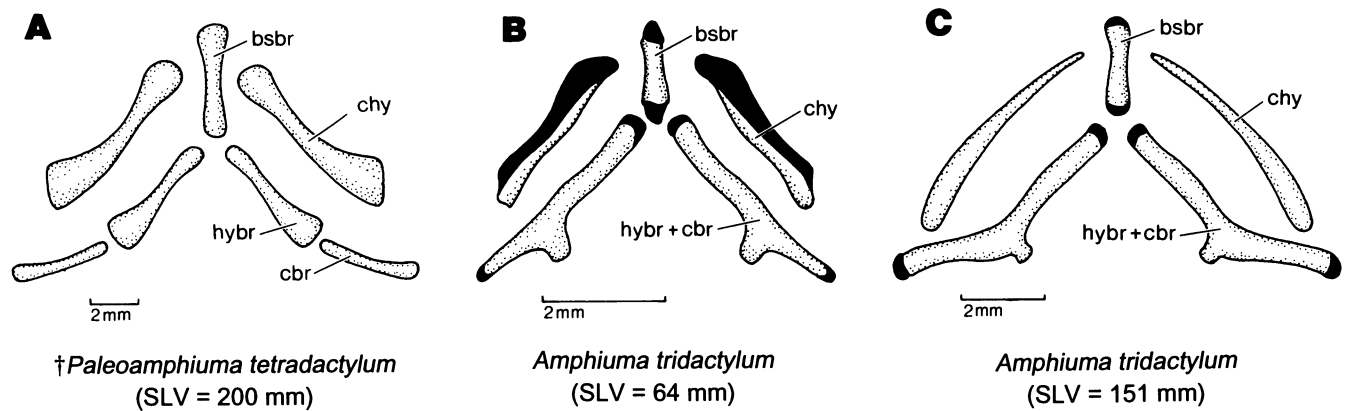


FIGURE 3. Comparison of the hypobranchial skeleton in *†Paleoamphiuma tetradactylum*, gen. et sp. nov. to a typical extant amphiumid, *Amphiuma tridactylum*. Anterior facing up. Note that the hypobranchial and ceratobranchial bones are autogenous in *†Paleoamphiuma tetradactylum*, gen. et sp. nov. In extant *Amphiuma* the hypobranchial is fused to the ceratobranchial even in young juveniles. **A**) *†Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype (FMNH PR1810). Snout-ventral length in figure is an estimate. Branchial arches (see Fig. 2) drawn in position to match **B** and **C**. **B** and **C**, two growth stages of *Amphiuma tridactylum*. Branchial arches drawn from cleared and stained specimens LSUMZ 59345 and 59344, respectively. Stippled regions are bone, and solid black regions are cartilage.

served, but the left atlantal cotyle is distinct, as is the low neural spine (asn, Fig. 2) and the two postzygapophyses that articulate with the first dorsal vertebra. The atlas lacks a rib-bearer as well as associated ribs.

The first dorsal vertebra is somewhat larger than the atlas, but other than that resembles the successive dorsal vertebrae, all of which are preserved in left dorsolateral view, as far as can be determined (Fig. 1). Amphiumid vertebrae in general are characterized by numerous accessory crests and ridges for the attachment of complex axial musculature (Auffenberg, 1959; Estes, 1981). Prominent among these are the posterior zygapophyseal crests uniquely found in amphiumids (Estes, 1981: 44; see also Davison, 1895:382). These crests are distinct throughout the dorsal region in *†Paleoamphiuma* (pcr, Fig. 4), diverging from the posterior margin of the neural crest (nc, Fig. 4; neural spine of some authors) as they extend towards the tip of the postzygapophyses (poz, Fig. 4). Throughout the vertebral column, the neural and postzygapophyseal crests are broken

along their dorsal margins, however, which results in the appearance of low neural spines as they extend from the anterior margin of the centrum to about its midpoint. In dorsal vertebrae of extant amphiumids, the neural crest is relatively higher and longer than in vertebrae of *†Paleoamphiuma*, although this may be due to incomplete preservation in the holotype of *†Paleoamphiuma*.

Of three cleared and stained specimens of *Amphiuma tridactylum* available to us, the largest (LSUMZ 55707, 215 mm SVL) shows two pairs of transverse rib-bearers on the first dorsal vertebra. Only a single pair of rib-bearers is present on the first dorsal of the rest of our extant *Amphiuma* material, indicating that the double-rib-bearer condition is most likely an anomaly. Each subsequent dorsal in these four skeletons bears a single pair of rib-bearers. A single pair of rib-bearers is also present on each dorsal vertebra in our specimen of *†Paleoamphiuma*. In this specimen the rib-bearers are ankylosed to the centrum with a broad base, point posterolaterally, and end in a

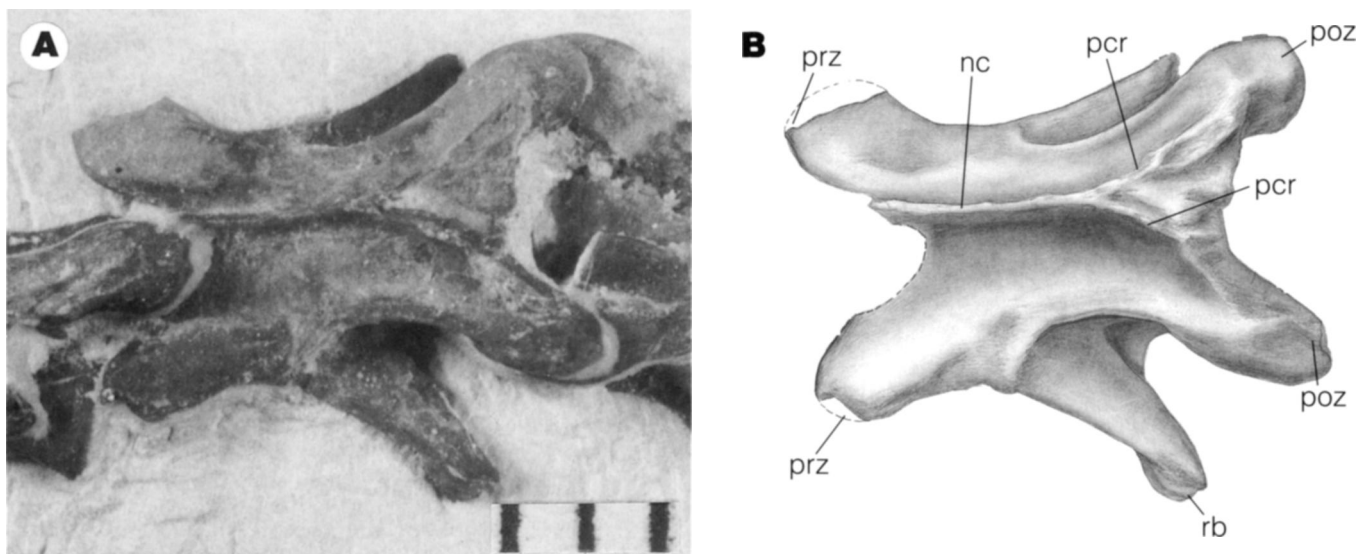


FIGURE 4. *†Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype (FMNH PR1810). Eighth vertebra from specimen in Figure 1. Anterior facing left. **A**, photograph; scale in millimeters; **B**, line drawing of **A**.



blunt tip. The rib-bearers of †*Paleoamphiuma* (**rb**, Fig. 4 and unlabeled in Fig. 1) are relatively narrow but high in the first seven vertebrae (excluding the atlas) and show a sulcate posterior surface distally. The structure and orientation of the first seven pairs of rib-bearers closely resemble those of the first seven to ten pairs of rib-bearers in extant amphiumids. In the extant species, the rib-bearers behind the first seven to ten pairs become broader and more laterally oriented. A deep posterior sulcus separates a dorsal ridge from a (postero-) ventral flange. The posterior rib-bearers of the fossil amphiumid are ankylosed to the vertebral centrum with a distinctly broader base, but they taper distally to a blunt tip, and they continue to trend in a posterolateral direction. Their dorsal surface may appear slightly sulcate in the distal portion, particularly in the posterior dorsal region, but this sulcus is much shallower than in extant species, and a separate (postero-) ventral flange cannot be identified. A distal bifurcation of the rib-bearer is not apparent throughout the dorsal vertebral column in †*Paleoamphiuma*, but may occur in individuals of extant species.

Because none of the dorsal vertebrae are exposed in ventral view, nothing can be said about the structure of the subcentral crest, subcentral foramina, and basapophyses.

The “sacral” region is not differentiated in cleared and stained specimens of *Amphiuma tridactylum* available to us, because the ilium is not directly suspended from the vertebral column. Two “sacral” vertebrae were mentioned by Davison (1895) for *Amphiuma means*, but “Their processes are the same as in the trunk vertebrae” (Davison, 1895:382). The absence of modified sacral vertebrae in amphiumids was also noted by Baker (1945:72). The sacral region of the vertebral column is not preserved in the holotype.

Caudal vertebrae of extant amphiumids are characterized by a strong reduction of the neural spine, posteriorly projecting postzygapophyseal crests, reduced transverse processes, and prominent haemapophyses, which are fused to the centra to form pronounced ventral crests with a posteriorly projecting posteroventral tip. In the holotype of †*Paleoamphiuma*, the caudal vertebrae are generally poorly preserved. In some of the better preserved elements, the posteriorly projecting postzygapophyseal crest is distinct, as are the fused haemapophyses. Isolated bone fragments at the posterior tip of the tail might indicate that posterior haemapophyses have not yet fused with the centrum, although fusion develops early in individuals of extant species (e.g., *Amphiuma tridactylum*, LSUMZ 59345; 64 mm SVL).

Ribs are poorly ossified in *Amphiuma*, even in adults. Baker (1945) reports ossified ribs associated with the first three dorsal vertebrae. This is the condition seen in a cleared and stained specimen of *A. tridactylum* (LSUMZ 55707; 215 mm SVL). In the macerated skeleton of an adult *A. means* (FMNH 196099), ossified ribs are associated with the first four dorsal vertebrae. In the holotype of †*Paleoamphiuma*, ribs are associated with at least the first two, but certainly not beyond the first five dorsal vertebrae. The ribs appear to be slightly better ossified than in our extant amphiumid specimens.

**Pectoral Girdle and Forelimb**—Scattered elements of both forelimbs are preserved on the holotype of †*P. tetradactylum* (Fig. 5). One limb, presumably the left, is nearly complete, and preserved in a partially articulated fashion; elements of the other limb are partially buried under the vertebral column.

The right scapula is well exposed (**sc**, Fig. 5). It is 3.2 mm long, and as in individuals of extant *Amphiuma*, it is a slightly curved, rod-shaped ossification. To the left and ventral to the expanded basal portion of the scapula lies a flake of bone that appears to be part of the coracoid ossification (**co**, Fig. 5). If correctly identified, this latter bone indicates that the scapula and coracoid remain separate in †*Paleoamphiuma*; these elements are fused to each other in extant adult-sized salamanders

that are not neotenic (e.g., Duellman and Trueb, 1986:336). Close to the proximal head of the humerus are two rectangular and overlapping flakes of bone that may represent the coracoid and procoracoid portions of the coracoid ossification. The associated left scapula is evidently not preserved. The left humerus (**hu**, Fig. 5) again is well exposed and 6.6 mm long. The humerus has a slightly constricted diaphysis, a weakly expanded proximal head, and a distinctly expanded distal end. The preaxial part of the humerus, supporting the cartilaginous radial condyle in the living animal, projects more distinctly than the postaxial margin supporting the ulnar condyle. Of the two zeugopodial elements, the radius (**ra**, Fig. 5) is the more strongly developed bone with a length of 4.3 mm. It has a slightly constricted shaft and a distinctly expanded distal end. Behind the radius lies the slender ulna (**ul**, Fig. 5), which is not expanded distally. No carpal elements are preserved; but this is probably because they remained cartilaginous as in extant adult amphiumids.

The autopodium is partially disarticulated (Fig. 5). However, the inferred second digit shows perfect alignment of three elements: a proximal metacarpal (**mc2**, Fig. 5), an intermediate proximal phalanx (**pp2**, Fig. 5), and a distal (terminal) ungual (**u2**, Fig. 5). Just behind this digit are the ungual and the articulated proximal phalanx (**u3** and **pp3**, Fig. 5) of the third digit, elements which could have been associated with a disarticulated metacarpal (**mc3?**, Fig. 5) that has been dislocated posteriorly. The possibility cannot be ruled out, however, that the posteriorly dislocated metacarpal may have been associated with digit 4, rather than digit 3. On the left side of digits 2 and 3, two additional elements are preserved: metacarpal 1 and ungual 1 (**mc1** and **u1**, Fig. 5). On the right side of digit 3 two additional elements may represent metacarpal 4 and ungual 4 (**mc4?** and **u4**, Fig. 5). In case we have misidentified mc3 and it really represents mc4, then our mc4 would in fact be pp4. Either way, the manus of the holotype of †*Paleoamphiuma tetradactylum*, gen. et sp. nov. is interpreted as having four digits, which is characteristic of salamanders in general, but not of extant Amphiumidae. The phalangeal formula for †*Paleoamphiuma* is either 1-2-2-1 or 1-2-2-2 (because of disarticulation of the limb in the holotype, we cannot distinguish which it is). Either possibility contrasts with Caudata in general (which usually have 1-2-3-2 or 2-2-3-3; Duellman and Trueb, 1986:337), as well as with *Amphiuma* in particular, where the phalangeal formula is 2-2-1 for *A. tridactylum* (with three digits: Stroudermayer, 1949); 2-2 for *A. means* (with two digits: Stroudermayer, 1949); and is unknown here for *A. pholeter* (with one digit: Neill, 1964). Either of the two possible phalangeal counts for †*Paleoamphiuma* indicates that it retains a preaxial digit that is absent (assumed lost) in *Amphiuma*. The digit retained in †*Paleoamphiuma* would be digit one under the assumption that the fifth digit is the one lost in all Caudata (Duellman and Trueb, 1986:337).

In a specimen of *Amphiuma tridactylum* with a snout-vent length of 215 mm (LSUMZ 55707), the pectoral girdle remains incompletely ossified. The scapula forms a small, rod-like ossification, slightly expanded ventrally, and extending dorsally into a cartilaginous suprascapular portion. Ventrally, the scapula is connected to the coracoid which remains unossified but which displays a distinct anterior procoracoid portion. When ossified in adult salamanders, the coracoid is fused to the scapula (Duellman and Trueb, 1986:336). Long bones of the much reduced forelimb retain unossified articular heads. The humerus is longer than the zeugopodial elements, among which the ulna is more strongly developed than the radius. The distal part of the ossified ulna is markedly expanded, and carries a large cartilaginous articular head which fits in between the two proximal carpal cartilages. The carpus comprises three cartilages, the large ulnare-intermedium, the smaller radiale, and a single dis-

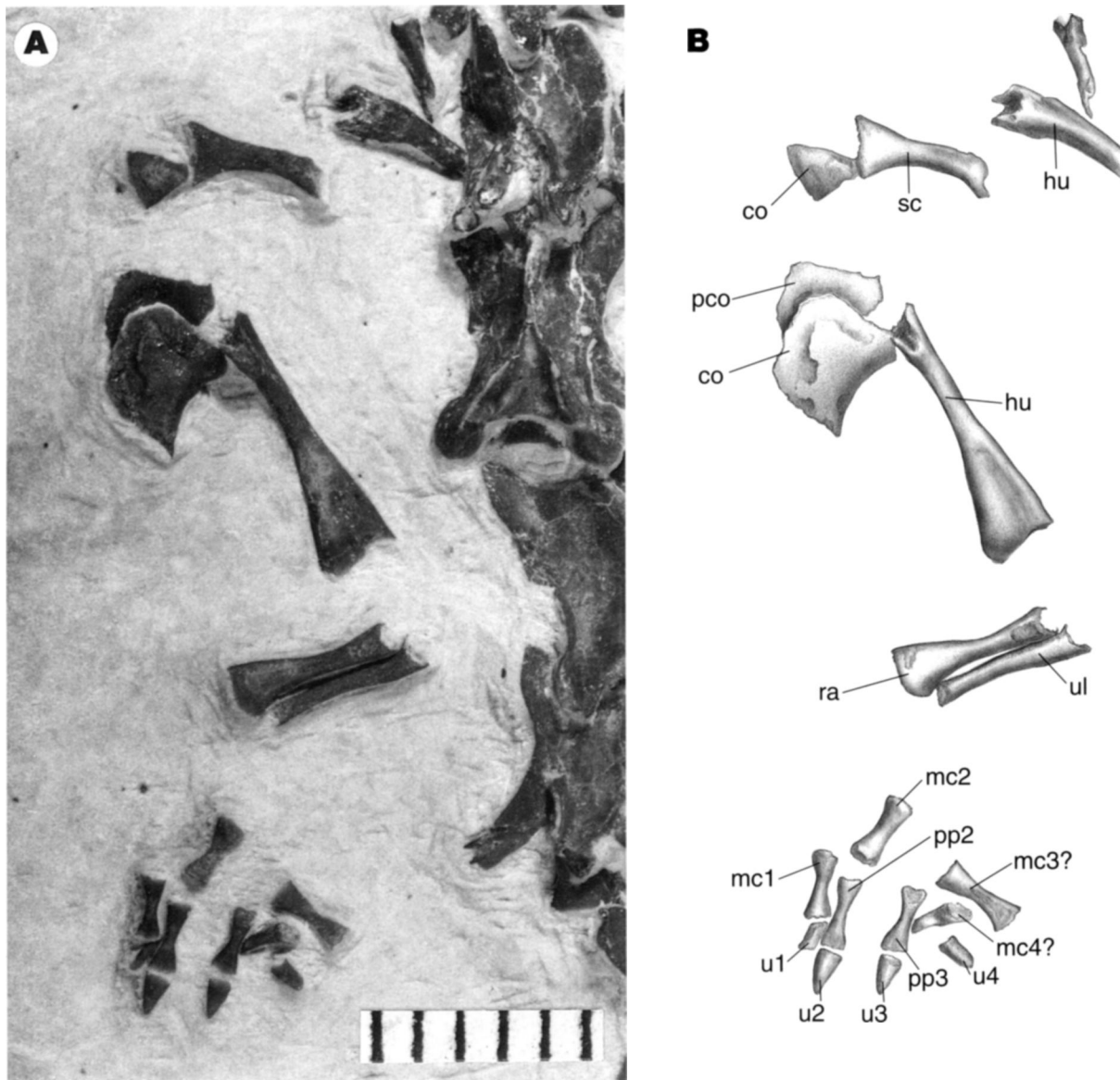


FIGURE 5. †*Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype (FMNH PR1810). Pectoral girdle from Figure 1. **A**, photograph; scale in millimeters; **B**, line drawing (vertebral elements omitted).

tal carpal. The metacarpals and phalanges are all ossified; the phalangeal count is 2-2-1 (Stroudermayer, 1949).

**Pelvic Girdle and Hindlimb**—Both hindlimbs have been flipped to the same side of the body in the specimen of †*Paleoamphiuma*, and lie closely juxtaposed one behind the other (Fig. 6). Disarticulation of the feet prevents a precise phalangeal count.

The one preserved ilium (**il**, Fig. 6) is a tiny rod-shaped ossification extending upwards from an expanded base and slightly angulated in its middle part. To the left of (distal to) the ilium and proximal to the distal end of the broken anterior femur lies a partially crumbled bony plate which represents the ossified puboischiadic plate (**pu-is**, Fig. 6). Its exact contours can no longer be established. The more posterior of the two femora (**fe**, Fig. 6) is complete and measures 5.9 mm in length. It is an essentially straight bone with a slightly constricted shaft and a weakly expanded distal end. Both zeugopodia are incompletely preserved, but the anterior one shows the tibia (**ti**, Fig.

6) to be more strongly developed than the fibula (**fi**, Fig. 6). The fibula measures 3.6 mm in length.

Among the mixed elements representing the two feet, there are a total of four unguals (**u**, Fig. 6), each of which is associated with a proximal phalanx. Two of the unguals are also associated with a corresponding metatarsal. It appears that the foot of the anteriorly located leg has been flipped backwards and now overlaps the distal ends of the zeugopodial elements. The phalanges of the posterior limb point straight laterally instead. We thus identify two metatarsals associated with three proximal phalanges and two distal (terminal) unguals distributed among three digits as belonging to the anteriorly located foot. The foot of the posteriorly located limb is represented by two metatarsals, two proximal phalanges, and two distal unguals. As far as preserved, the pedal ossifications indicate the presence of three digits with two phalanges each. Since salamanders generally have a single phalanx in the first toe, we assume that the pes of †*Paleoamphiuma* included four digits



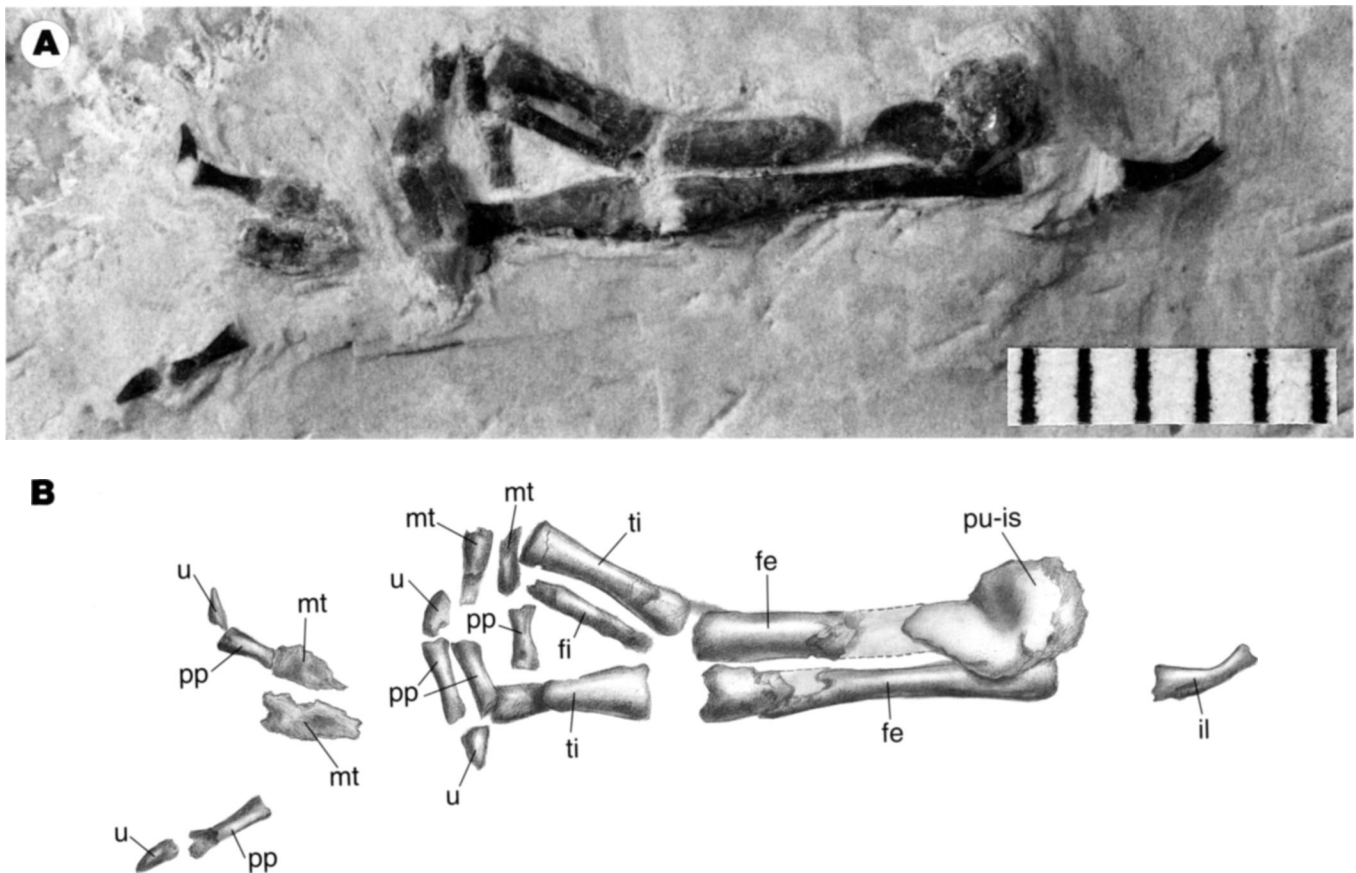


FIGURE 6. †*Paleoamphiuma tetradactylum*, gen. et sp. nov., holotype (FMNH PR1810). Pelvic girdle from Figure 1. Parts of both limbs are mixed together and some elements are missing, so an exact count of phalanges is not possible. **A**, photograph; scale in millimeters; **B**, line drawing.

with a phalangeal formula of 1-2-2-2, thus mirroring the structure of the forelimb.

In a cleared and stained specimen of *Amphiuma tridactylum* with a snout-vent length of 215 mm (LSUMZ 55707), the pelvic girdle again remains incompletely ossified. Ossification is restricted to the reduced dorsal wing of the ilium which takes on the shape of a slender and curved rod with an expanded base, and to a small rounded spot within the pubis. The long bones in the hindlimb carry cartilaginous articular heads, the fibula is more strongly developed than the tibia, tarsal cartilages again remain unossified, and the phalangeal formula again is 2-2-1 (Stroudermayer, 1949).

#### DISCUSSION

†*Proamphiuma cretacea* from the Upper Cretaceous of Montana was based on vertebrae which were described by Estes (1969, 1981) as closely resembling those of extant species of *Amphiuma*. The major morphological differences between †*P. cretacea* and extant *Amphiuma* were described as a more pronounced constriction of the centrum and less prominent development of the neural spine, various vertebral crests, and the basapophyses. Relatively narrow vertebrae are also shared by †*Amphiuma jepseni* Estes, 1969, from the Paleocene of Wyoming, although the neural spine and vertebral crests as well as the basapophyses in this taxon are equally developed as in extant forms. Comparing the illustrated vertebrae of †*P. cretacea* and †*A. jepseni* with macerated and cleared and stained skele-

tions of extant *Amphiuma* does not reveal more significant constriction of the centrum in the fossil species. On the other hand, the rounded snout said by Estes (1969, 1981) to be diagnostic of †*P. jepseni* depends on the reconstruction of an incompletely preserved and disarticulated skull (see Estes, 1969:fig. 4). In our opinion the materials available for these two fossil species are too fragmentary to allow differential diagnosis of a separate genus and two separate species. We therefore consider the names †*Proamphiuma cretacea* Estes, 1969, and †*Amphiuma jepseni* Estes, 1969, to be *nomina dubia* (sensu Grande and Bemis, 1998:19). We also consider †*Amphiuma antica* Holman, 1977, based on a single incomplete and broken vertebra to be a *nomen dubium*. The validity of this latter taxon was already questioned by Estes (1981:42).

By contrast, the fossil amphiumid described above from the Eocene of Wyoming is clearly distinguished from extant species by the retention of a number of plesiomorphic features—i.e., by the absence of a number of synapomorphies shared by *A. means* and *A. tridactylum* (and, by implication, *A. pholeter*). Although the relationships of amphiumids with other salamanders remain largely unresolved, recent phylogenetic analyses (Larson and Dimmick, 1993; and references therein) consider plethodontid salamanders to be the sister group of the Amphiumidae. Plethodontids will therefore be used in the polarization of characters discussed below.

The inclusion of †*Paleoamphiuma* in the Amphiumidae is justified on the basis of an increased number of precaudal ver-

tebrae, the reduction of ossified rib rudiments to no more than the four anteriormost dorsal vertebrae, by the significant size reduction of the limbs, and by the presence of postzygapophyseal crests on the vertebrae. The fossil taxon differs from the extant species by a series of plesiomorphic traits. The first hypobranchial and the first ceratobranchial remain separate in †*Paleoamphiuma*, whereas these two elements are fused into a single element in *Amphiuma* (Fig. 3). As preserved in the holotype, the precaudal vertebral column includes 31 vertebrae in †*Paleoamphiuma*, and may have included as many as 32 or 33, but certainly no more than 35 elements. In extant species of *Amphiuma*, the precaudal vertebral column never comprises less than 60 vertebrae. In †*Paleoamphiuma* the posterior rib-bearers point in a posterolateral direction, taper to a blunt tip distally, and a (postero-) ventral flange is absent. In *Amphiuma* the posterior rib-bearers point straight laterally, do not taper distally, and a (postero-) ventral flange is distinct. The fossil amphiumid retains four digits in the manus (and probably also in the pes), whereas extant species of *Amphiuma* have reduced the number of digits from three (*A. tridactylum*) to two (*A. means*) or to one (*A. pholeter*). There is also the suggestion that the ventral parts of the limb girdles (coracoid plate in the pectoral girdle; puboischiadic plate in the pelvic girdle) show a greater degree of ossification in †*Paleoamphiuma* than is typical for extant species of *Amphiuma*, and that scapular and coracoid ossifications remained separate, whereas these elements co-ossify in extant salamanders.

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