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## THE FOSSIL SALAMANDER *PROAMPHIUMA CRETACEA* ESTES (CAUDATA; AMPHIUMIDAE) AND RELATIONSHIPS WITHIN THE AMPHIUMIDAE

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**ABSTRACT**—A revised diagnosis and expanded description are presented for the amphiumid salamander *Proamphiuma cretacea* based on the original topotypic collection of vertebrae and on new atlantes, trunk vertebrae, and caudal vertebrae from the holotype locality. *P. cretacea* is the type and only species in the genus and is reliably known only from the Bug Creek Anthills (late Maastrichtian or early Paleocene in age), in the Hell Creek Formation, Montana, USA. A referred dentary originally believed to be from the same locality is shown to have come from the upper part (late Paleocene in age) of the Ravenscrag Formation of Saskatchewan, Canada, and is re-interpreted as belonging to an indeterminate amphiumid genus and species. Contrary to a recent claim, *P. cretacea* is a diagnosable amphiumid taxon and stands as the geologically oldest member of the family. *Proamphiuma* differs from the type and only other unequivocal amphiumid genus, *Amphiuma* (four species: late Paleocene–Recent, USA), in primitively retaining weaker vertebral crests and processes. *Proamphiuma* differs further from the three extant *Amphiuma* species (conditions unknown for the late Paleocene *A. jepseni*) in three character states that are potentially autapomorphic within the family—indistinct postzygapophyseal process on atlas, vertebral arterial canal closed posteriorly in trunk vertebrae, and spinal foramen present in anterior caudals—plus vertebral plesiomorphies and one vertebral character state of uncertain polarity. The following relationships are hypothesized within the Amphiumidae: *Proamphiuma* (*A. jepseni* (*A. pholeter* (*A. means* + *A. tridactylum*))). This phylogeny and fossil occurrences imply that the characteristic atlanto–cranial joint and elongate trunk and the unique vertebromuscular complex of amphiumids were established by the Cretaceous–Tertiary boundary, while elongation of the snout and associated cranial modifications seen in living amphiumids appeared after the late Paleocene. In terms of its morphology and provenance, *Proamphiuma* remains a good structural ancestor for, if not directly ancestral to, *Amphiuma*.

### INTRODUCTION

The Amphiumidae are a small family of paedomorphic, aquatic salamanders with a limited fossil record. Amphiumids are endemic to North America, where they are known from the Pleistocene–Recent of the southeastern USA, the late Paleocene of Wyoming, USA, and Saskatchewan, Canada, the late Maastrichtian or early Paleocene of Montana, USA, and, possibly, the middle Miocene of Texas, USA (e.g., Salthe, 1973a; Estes, 1981; this study). The three extant species in the type genus *Amphiuma* range in maximum length from about 300–1015 mm (Conant and Collins, 1991) and have an elongate, superficially eel-like body, a single gill slit but no external gills, and tiny fore- and hindlimbs, each with three or fewer toes (Salthe, 1973a; Conant and Collins, 1991; Duellman and Trueb, 1986). Amphiumids are widely regarded as crown-clade salamanders (=Urodela, sensu Milner, 1988; Evans and Milner, 1996) but there is no further consensus on the position of the family, largely because its members exhibit a confusing mixture of derived and paedomorphic character states. Cladistic hypotheses (Edwards, 1976; Hecht and Edwards, 1977; Milner, 1983; Duellman and Trueb, 1986; Sever, 1991; Hedges and Maxson, 1993; Larson and Dimmick, 1993; Hay et al., 1995; Gao and Shubin, 2001) and non-cladistic classifications (e.g., Cope, 1889; Dunn, 1922; Noble, 1931; Regal, 1966; Naylor, 1978a; Estes, 1981) broadly agree in placing amphiumids at a post-cryptobranchid and hynobiid level of organization (however, see Larson, 1991). Many of these schemes have allied amphiumids with ambystomatids, plethodontids, and salamandrids or some combination thereof. Cope's (1889) belief that amphiumids were ancestral to gymnophionans—the latter of which he regarded as a degenerate family of salamanders—has not been seriously entertained since.

Estes (1969) named and described *Proamphiuma cretacea*

based on 17 isolated vertebrae from the Bug Creek Anthills in the Hell Creek Formation, Montana. *P. cretacea* is the geologically oldest amphiumid, and was long regarded as late Maastrichtian in age (Estes, 1969, 1981) or equivalent to the Lancian North American Land Mammal “Age” (NALMA). With the recognition that the Bug Creek assemblage is a mixture of early Paleocene (=Puercan NALMA) fossils and reworked Lancian fossils (Lofgren, 1995), *P. cretacea* is better regarded as late Maastrichtian or early Paleocene in age. Estes' (1969) type description for *Proamphiuma* was brief, and little new information has been presented since: Estes (1981) provided a nearly verbatim rediagnosis and redescription, but listed no new specimens; in their respective Ph.D. dissertations, Naylor (1978a) and Gardner (2000) described a dentary supposedly from the Bug Creek Anthills; and Edwards (1976) reported on the distribution of spinal foramina and identified four caudals among Estes' (1969) topotypic collection. The status of the taxon recently has been challenged by Rieppel and Grande (1998), who argued that the name *P. cretacea* is a nomen dubium. Here I present a revised diagnosis and expanded redescription for *P. cretacea* based on a subset of vertebrae from Estes's (1969) topotypic collection that can reliably be attributed to the species and on additional vertebrae from the holotype locality. I also describe and re-interpret the dentary previously referred to *P. cretacea* as belonging to an indeterminate amphiumid genus and species. The 42 vertebrae now available for *P. cretacea* provide new information on the osteology and taxonomic status of this taxon and permit further insights into the evolutionary history of the Amphiumidae.

Given uncertainty over the higher level affinities of the family, I refrain from placing the Amphiumidae within the monotypic Amphiumoidea (contra Estes, 1981). For reasons discussed below, I restrict membership in the Amphiumidae to *Amphiuma* (four species) and the monotypic *Proamphiuma*. Os-

teological terms generally follow Estes (1981); see also Figures 1 and 2. I use the term “neural spines” for the two ridges that diverge posterolaterally from either side of the posterior end of the neural crest on most amphiumid trunk vertebrae; similar structures on frog vertebrae have been called “paraneural crests” or “paraneural processes” (J.-C. Rage, pers. comm., 2002) but, to my knowledge, these terms have not been used for salamander vertebrae.

**Institutional Abbreviations**—FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MCZ, Museum of Comparative Zoology, Harvard University, Boston, Massachusetts, USA; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Canada.

**Comparative Taxa and Specimens**—This is the first study to compare all three extant species of *Amphiuma* with *Proamphiuma*. Skeletons of *A. pholeter* (UALVP 14487), *A. tridactylum* (UALVP 14364), and *A. means* (FMNH 98657 and 196143), and a middle trunk vertebra dissected from an alcohol-preserved specimen (UALVP 14507) of *A. means* were examined. Figures 3 and 6D–F depict representative vertebrae and dentaries, respectively, from extant species. Comparisons with the late Paleocene species *A. jepseni* relied on Estes’ (1969, 1975, 1981) descriptions and illustrations of the three known specimens.

#### SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866

Order CAUDATA Scopoli, 1777

Crown-order URODELA Duméril, 1806

Family AMPHIUMIDAE Gray, 1825 (amend. Gray, 1850)

**Remarks**—Salthe (1973a) presented a concise review of the early taxonomic and nomenclatural history of the Amphiumidae. Monophyly of the Amphiumidae has never been disputed. The three extant *Amphiuma* species, the late Paleocene *A. jepseni*, and *Proamphiuma* are united by one derived vertebral character state that is unique among salamanders—trunk vertebrae and anterior caudals dorsally bear a pair of postzygapophyseal crests (Estes, 1969, 1981; Naylor, 1978a; see Figs. 1F, G, I, 2, and comments below). Based on specimens of *Amphiuma* and *Proamphiuma* available to him, Edwards (1976) stated these genera were further unique among salamanders he surveyed in having intravertebral exit of the postatlantal spinal nerves restricted to vertebrae in the middle and posterior part of the caudal series. There are two problems with accepting this pattern as autapomorphic for all amphiumids: first, caudals are unknown for *A. jepseni* and, second, a specimen reported below shows that anterior caudals were also pierced by a spinal foramen in *Proamphiuma*. Elongation of the trunk and an increased number of trunk vertebrae constitute a derived, but not unique, condition for the Amphiumidae; although this condition cannot be observed directly for *P. cretacea* or *A. jepseni*, it can reliably be inferred for both species based on the presence of unicipital transverse processes on all but the anteriormost trunk vertebrae. Numerous other character states explicitly or implicitly have been regarded as derived for amphiumids (e.g., Davison, 1895; Salthe, 1973a; Estes, 1981; Duellman and Trueb, 1986; Sever, 1991; Larson and Dimmick, 1993), yet many of these are not unique among salamanders to amphiumids and, more importantly, none can be determined for both fossil taxa. Fusion of the premaxillae, a posteriorly elongate premaxillary pars dorsalis (=“premaxillary spine” of some authors) completely separating the nasals and partly separating the frontals, a posteriorly elongate premaxillary vomerine process separating the nasals and partly bisecting the parasphenoid, absence of a lacrimal, and a single row of vomerine teeth paralleling the premaxillary and maxillary tooth rows all involve characters that can be scored only for species of *Amphiuma*, whereas a

single external gill slit, reduced girdles and limbs, three or fewer toes, columella fused to skull, septomaxilla and ypsiloid cartilage absent, first ceratobranchial and hypobranchial fused, spermatheca present in all but most posterior part of cloacal chamber in females, and cloacal pit, dorsal pelvic, Kingsbury’s, and vent glands present in cloaca of males all involve characters that can be scored only for extant *Amphiuma* species.

Vertebrae are diagnostic for amphiumids and are easily differentiated from those of other salamanders by the following combination of features (Figs. 1–5): notochordal pit retained; atlas with large, hemispherical, slightly laterally compressed, and deeply concave anterior cotyles, prominent and scoop-shaped odontoid process bearing raised, subcircular articular condyle to either side of ventral midline, and robust neural arch with posteriorly short roof bearing low neural and accessory crests; postatlantal vertebrae amphicoelous, with deeply concave cotyles, and all but posteriormost caudals bearing pair of postzygapophyseal crests; trunk vertebrae lacking spinal foramina and bearing subcentral keel, pair of well-developed anterior basapophyses, elongate and moderately high neural crest, and often paired, posteriorly divergent neural spines; and transverse processes weakly bicipitate on anteriormost trunk vertebrae and unicipitate on other trunk vertebrae.

The type genus *Amphiuma* includes four diagnosable species from the late Paleocene and Pleistocene–Recent. The extant species *A. tridactylum*, *A. means*, and *A. pholeter* have, respectively, three, two, and one toe per foot and are limited to the southeastern USA (Salthe, 1973a–c; Means, 1996; Petranks, 1998). Isolated *Amphiuma* vertebrae have been collected from Holocene and Pleistocene sites in Florida, USA (Brattstrom, 1953; Weigel, 1962; Hirschfield, 1969; Meylan, 1995), and from the middle Pleistocene of Texas (Holman, 1965; Slaughter and McClure, 1965); some of these specimens have been referred to *A. means* and others have not been identified to species. The fossil congener *A. jepseni* is known from three incomplete skeletons from the upper Paleocene (equivalent to Tiffanian NALMA) Polecat Bench Formation (=“Fort Union Formation” of some authors) of Wyoming (Estes, 1969, 1975, 1981). Published drawings of the crushed and incomplete to typic skull of *A. jepseni* indicate the species differs from its extant congeners (cf. Estes, 1969:fig. 4 versus Erdman and Cundall, 1984:fig. 2) in having a relatively shorter and broader snout, a relatively shorter maxilla and vomer, with both bones having a correspondingly shorter tooth row, and, evidently, a relatively broader parasphenoid (Estes, 1969, 1981; Naylor, 1978a; contra Rieppel and Grande, 1998). I thus disagree with Rieppel and Grande’s (1998) proposal that the name *A. jepseni* is a nomen dubium. Names of the remaining two nominal species of *Amphiuma* are nomina dubia, as some previous authors have suggested. The name *A. antica* is founded on a poorly preserved trunk vertebra (Holman, 1977:fig. 2) from the middle Miocene (=Barstovian NALMA; Tedford et al., 1987:fig. 6.2) Moscow locality in the Fleming Formation, Texas. Judging from the published illustration, the holotype neither differs significantly from trunk vertebrae of extant congeners (Estes, 1981; Rieppel and Grande, 1998) nor is it clear to me that the specimen can reliably be assigned to the Amphiumidae. Albright (1994:1135) questionably assigned to the Amphiumidae an unfigured, fragmentary trunk vertebra from a stratigraphically lower site (early Miocene or Arikarean NALMA) in the same formation. The holotype parasphenoid (Brunner, 1956: abb. 7, fig. 4) and only specimen of *A. nordica* from the Pleistocene of Germany is likely from a teleost, not an amphiumid (Estes, 1965, 1969, 1981).

Rieppel and Grande (1998) named the new genus and species *Paleoamphiuma tetradactylum* on a skeleton, which was first reported by Grande and Buchheim (1994), from the lower Eocene (=Wasatchian NALMA) Fossil Butte Member of the

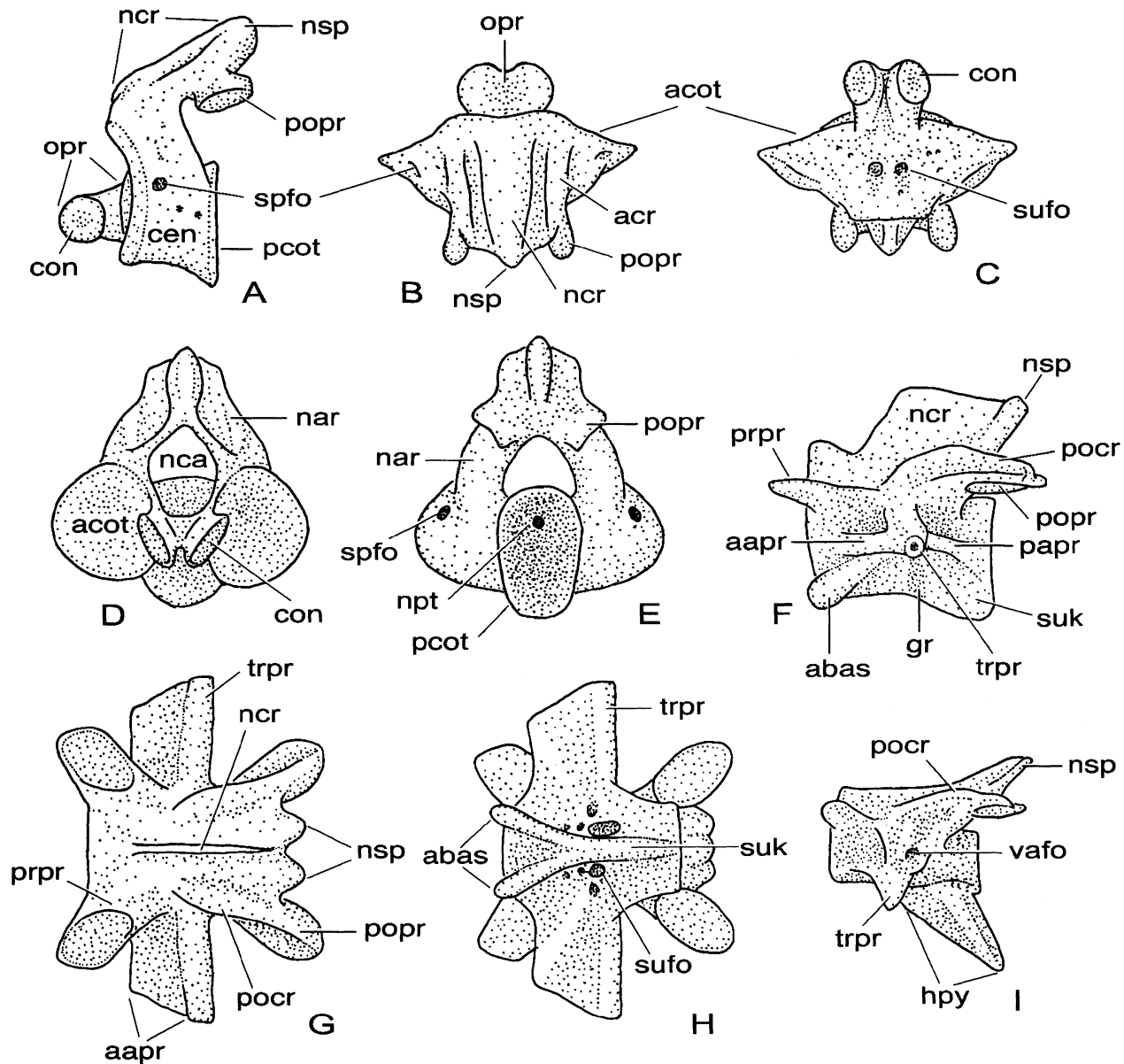


FIGURE 1. Generalized amphiumid vertebrae based on extant *Amphiuma means* and *A. tridactylum*, showing characteristic features and osteological terms. A–E, atlas, in (A) left lateral, (B) dorsal, (C) ventral, (D) anterior, and (E) posterior views; F–H, middle trunk vertebra, in (F) left lateral, (G) dorsal, and (H) ventral views, all with anterior end to left; I, anterior caudal vertebra, in left lateral view. **Osteological abbreviations:** aapr, anterior alar process; abas, anterior basapophysis; acot, anterior cotyle; acr, accessory crest; cen, centrum; con, articular condyle; gr, groove for blood vessel from subcentral foramen; hpy, haemapophysis; nar, neural arch; nca, neural canal; ncr, neural crest; npt, notochordal pit; nsp, neural spine; opr, odontoid process; papr, posterior alar process; pcot, posterior cotyle; pocr, postzygapophyseal crest; popr, postzygapophyseal process; prpr, prezygapophyseal process; spfo, spinal foramen; sufo, subcentral foramen; suk, subcentral keel; trpr, transverse process; vafo, vertebral foramen.

Green River Formation, Wyoming. Rieppel and Grande (1998: 702, 707–708) regarded *Paleoamphiuma* as a primitive amphiumid and listed four features to justify this familial assignment: trunk elongate; limbs reduced; ribs present only in anteriormost part of trunk region; and postzygapophyseal crests on trunk vertebrae. The first three features are not compelling because each occurs in some other salamander families; the first two features also are less pronounced than in extant amphiumids. More critically, I believe that the supposed postzygapophyseal crests were misidentified. Trunk vertebrae of unequivocal amphiumids have a characteristic arrangement of dorsal crests on the neural arch (see Figs. 1–3, 5): the neural crest extends along the midline to the posterior edge of the roof and, to either

side, the unique postzygapophyseal crest extends anteriorly and slightly medially along the postzygapophyseal process onto the roof, before grading into the roof at about the level of the base of the transverse process. At no point does either postzygapophyseal crest contact the neural crest. The former crests are associated with the modified dorsalis trunci epaxial trunk muscles in extant *Amphiuma* (Davison, 1895; Auffenberg, 1959; Naylor, 1978a), and the identical arrangement of postzygapophyseal and neural crests in *A. jepseni* (Estes, 1969:fig. 3c, f) and *Proamphiuma* (Fig. 5) attests to the early establishment and widespread occurrence of this vertebral muscular pattern in amphiumids (Estes, 1969, 1981; Naylor, 1978a). Published figures (Rieppel and Grande, 1998:figs. 1, 2A, 4, 5) of trunk vertebrae

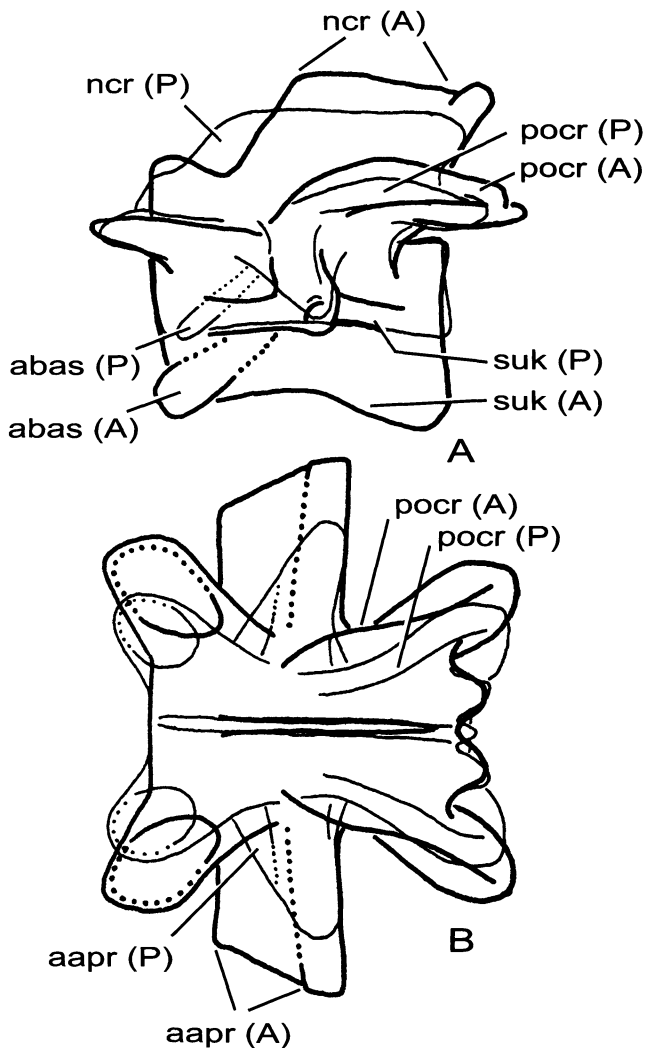


FIGURE 2. Simplified outline drawings of middle trunk vertebra of extant *Amphiuma* (thick line), based on *A. means* and *A. tridactylum*, and of *Proamphiuma cretacea* (thin line), superimposed on one another and at same scale, to show differences in form and proportions of crests and processes. Vertebrae shown in (A) left lateral and (B) dorsal views, both with anterior end to left. Abbreviations for osteological terms follow caption for Figure 1, with suffixes "(A)" and "(P)" denoting structures in, respectively, *Amphiuma* and *Proamphiuma*.

in the holotype of *P. tetradactylum* show a markedly different arrangement of crests, implying a correspondingly different arrangement of trunk musculature. In *Paleoamphiuma*, the neural crest is restricted to about the anterior half of the neural arch, and the supposed "postzygapophyseal crest" arises midway along the dorsal surface of the postzygapophyseal process, extends anteriorly at a more pronounced medial angle towards the midline, and its anterior end joins with the posterior end of the neural crest. The three dorsal crests in *Paleoamphiuma* thus form a posteriorly open "Y" in dorsal view, instead of being separate and approximately parallel as in *Amphiuma* and *Proamphiuma*. In this respect, trunk vertebrae of *Paleoamphiuma* more closely resemble those of sirenid salamanders. The "postzygapophyseal crest" identified by Rieppel and Grande (1998) is probably an aliform crest, which is characteristic of sirenids and some salamandrids. A faint crest noted by one referee (S. E. Evans, pers. comm., 2002) in the approximate position of the postzygapophyseal crest on the left side of one figured trunk vertebra (Rieppel and Grande, 1998:fig. 4A, but

compare with their fig. 2A, 5A) in the holotype skeleton of *P. tetradactylum* differs from unequivocal postzygapophyseal crests in being considerably lower (more so than even in *Proamphiuma*), originating at the base of the postzygapophyseal process (versus extending along length of process), and curving anterolaterally towards the base of the transverse process (versus straighter and extending anteriorly and slightly medially); the structure in question seems better interpreted as the posterior interzygapophyseal ridge, which is also characteristic of sirenids (Estes, 1981; Gardner, 2003). Pending the outcome of a planned collaborative study of the holotype skeleton of *P. tetradactylum*, I exclude this taxon from the Amphiumidae.

#### Genus *PROAMPHIUMA* Estes, 1969

**Type Species**—*Proamphiuma cretacea* Estes, 1969.

**Distribution**—As for the type and only species.

**Diagnosis**—As for the type and only species.

#### *PROAMPHIUMA CRETACEA* Estes, 1969 (Figs. 2, 4, 5)

*Proamphiuma cretacea*; Estes, 1969:2–5, figs. 1, 2.

*Proamphiuma cretacea* (Estes) nomen dubium; Rieppel and Grande, 1998:707.

**Holotype**—MCZ 3504, incomplete trunk vertebra, interpreted as being from the middle trunk region, and missing leading edge of neural crest, distalmost end of left prezygapophyseal process, most of right postzygapophyseal process, part of left postzygapophyseal crest, and most of both transverse processes (Estes, 1969:fig. 1a–e; Fig. 5A, B).

**Holotype Locality, Age, and Horizon**—Bug Creek Anthills, McCone County, Montana, USA; late Maastrichtian or early Paleocene, equivalent to the Lancian NALMA and the Pu0 and Pu1 interval zones of the Puercan NALMA (Lofgren, 1995); upper part of the Hell Creek Formation.

**Referred Specimens**—Atlantes: MCZ 3505, 3637, UALVP 40045, 43813–43816; middle trunk vertebrae: MCZ 3506, 3507, UALVP 43818, 43820–43824, 43827, 43828, 43830–43833, 43837–43839; anterior trunk vertebrae: MCZ 3508, 3509, 3632, UALVP 43817, 43825, 43826, 43834; posterior trunk vertebrae: MCZ 3629, 3631, 3634, 3636, UALVP 43819, 43829, 43835, 43836; caudal vertebrae: MCZ 3630, UALVP 43840. All 41 referred specimens are from the holotype locality.

The above inventory of referred vertebrae excludes four specimens listed by Estes (1969, 1981): MCZ 3627 is a trunk vertebra of the sirenid *Habrosaurus*; MCZ 3635 is a trunk vertebra of the batrachosauroidid *Opisthotriton*; and MCZ 3633 and 3628 are, respectively, a trunk centrum and probable caudal that are not diagnostic beyond Caudata Indeterminate.

**Distribution**—Known only from the holotype locality. See "Remarks" below for unverified records from elsewhere.

**Revised Diagnosis**—Genus and species of Amphiumidae primitively differing from *Amphiuma* in having trunk vertebrae with neural crest relatively lower, subcentral keel relatively shallower, and anterior basapophyses relatively shorter with distal end in line with or behind anterior cotylar rim and in having trunk vertebrae and anterior caudals with postzygapophyseal crests relatively lower (see Fig. 2). Differs further from extant species of *Amphiuma* (conditions uncertain for late Paleocene *A. jepseni*) as follows: more derived in having atlas with indistinct postzygapophyseal processes, trunk vertebrae with vertebral canal closed posteriorly, and anterior caudals pierced by spinal foramen; more primitive in having atlas with ventral rims of anterior and posterior cotyles approximately in line, postatlantal vertebrae with neural crest extending anteriorly almost to leading edge of neural arch roof, and trunk vertebrae with leading edge of neural crest inclined posteriorly at shall-

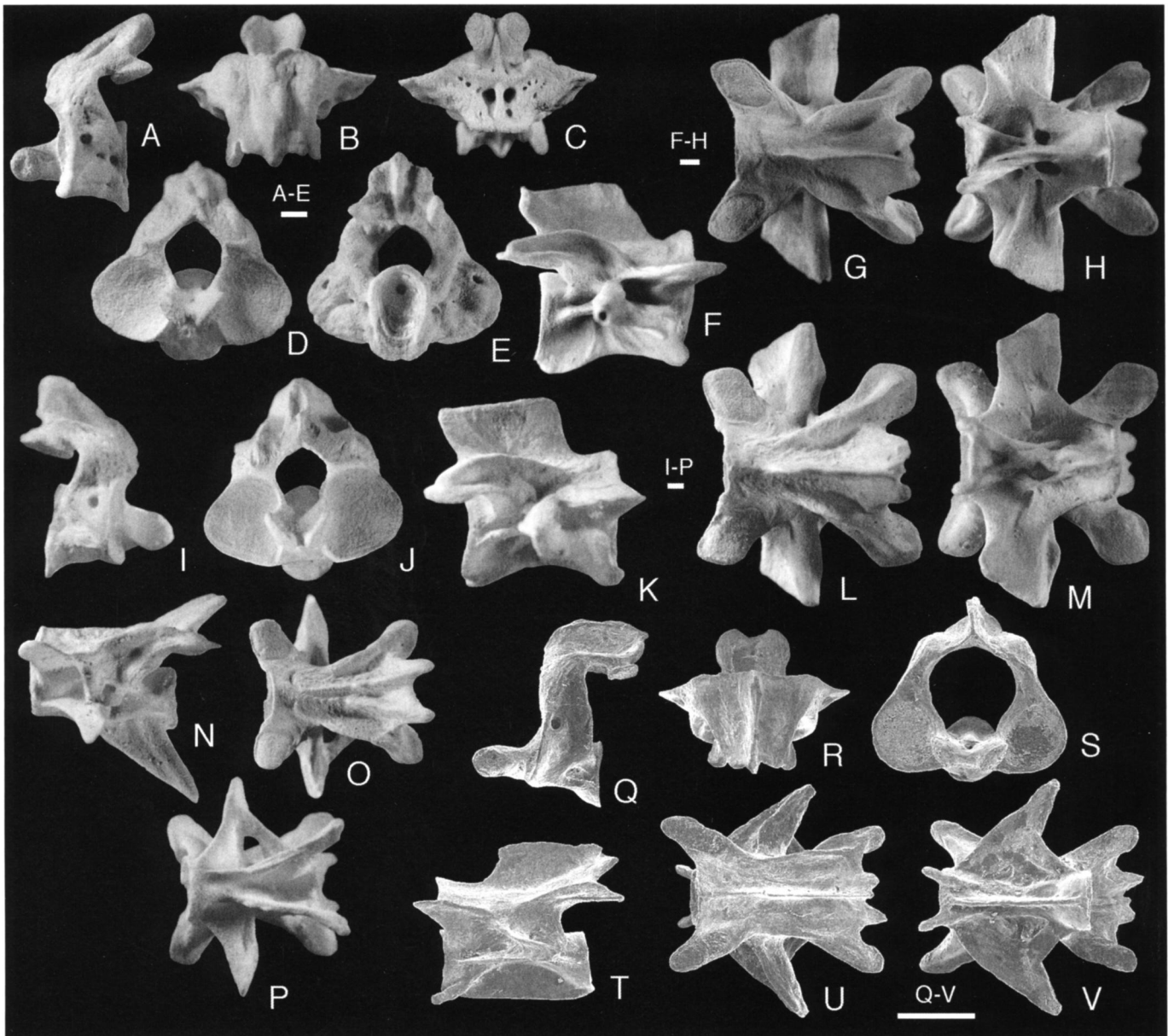


FIGURE 3. Vertebrae of the three extant species of *Amphiuma*; Recent, southeastern U.S.A. *A. means*, type species (A–H): A–E, atlas, FMNH 196143, in (A) left lateral, (B) dorsal, (C) ventral, (D) anterior, and (E) posterior views; F–H, middle trunk vertebra, UALVP 14507, in (F) right lateral view with anterior end to right and in (G) dorsal and (H) ventral views, both with anterior end to left. *A. tridactylum*, UALVP 14364 (I–P): I, J, atlas, in (I) right lateral and (J) anterior views; K–M, middle trunk vertebra, in (K) right lateral view with anterior end to right and in (L) dorsal and (M) ventral views, both with anterior end to left; N–P, first caudal vertebra, in (N) left lateral, (O) dorsal, and (P) ventral views, all with anterior end to left. *A. pholeter*, UALVP 14487 (Q–V): Q–S, atlas, in (Q) left lateral, (R) dorsal, and (S) anterior views; T–V, middle trunk vertebra in (T) left lateral, (U) dorsal, and (V) ventral views, all with anterior end to left. Specimens at different scales; scale bars equal 1 mm.

lower angle; and in one character state of uncertain polarity, namely neural crest on inferred middle trunk vertebrae broadly rounded anteriorly and dorsal edge horizontal in lateral profile.

### Description

None of the 42 vertebrae available for *Proamphiuma creta-cea* is complete. Descriptions below are composites, unless indicated otherwise.

**Atlas** (Estes, 1969:fig. 1f–j; Fig. 4)—The seven referred specimens collectively document the structure of the atlas. The largest specimen (UALVP 43813) is about half again as large

as the smallest (MCZ 3637). The centrum is broad and short, with an intercotylar width of about 2.8–4.1 mm ( $n = 7$ ) and a ventral midline length, including the odontoid process, of about 1.9–2.5 mm ( $n = 6$ ). The paired anterior cotyles are relatively large and extend up about the ventral third to half of the neural arch. Each cotyle is laterally compressed (ratio of maximum height:width about 1.3–1.6) and hemispherical in anterior outline, with the medial edge nearly straight. The anterior cotyle is tilted slightly dorsally and, especially in larger specimens, the articular face of the cotyle is deeply concave. The odontoid process is robust and moderately elongate, accounting for about 0.4 of the total ventral midline length of the bone. The odontoid



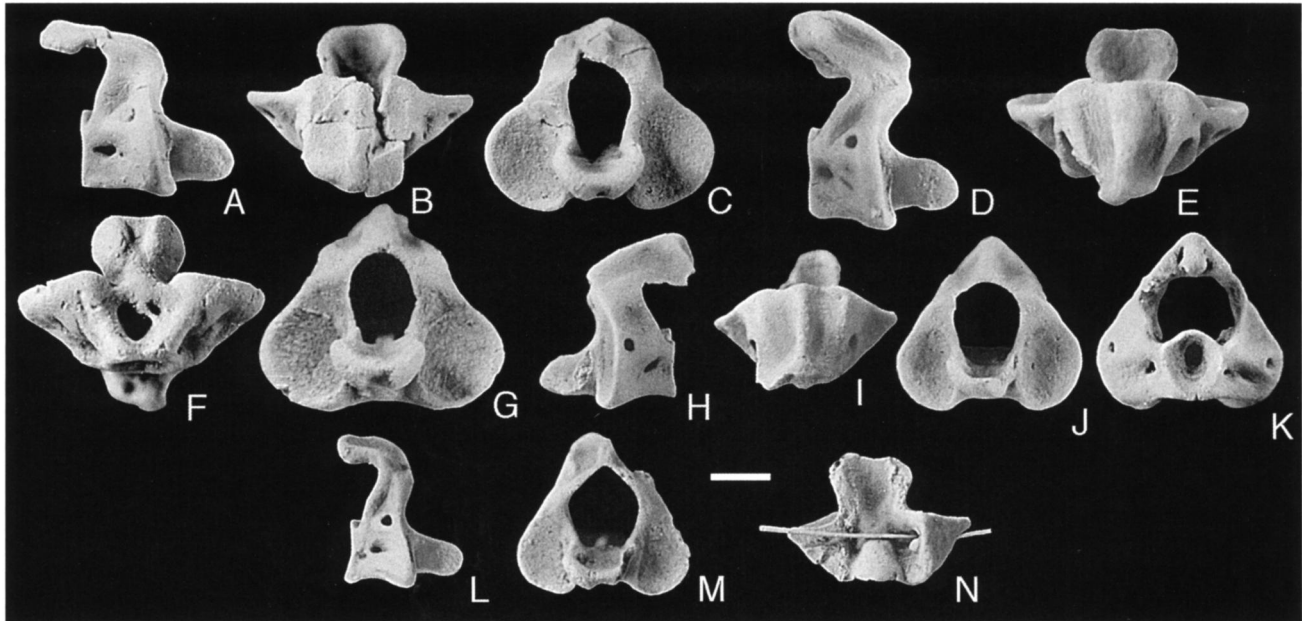


FIGURE 4. Atlantes of *Proamphiuma cretacea*; late Maastrichtian or early Paleocene, Bug Creek Anthills, Hell Creek Formation, Montana, USA. A–C, MCZ 3505, atlas with roof of neural arch fractured, in (A) right lateral, (B) dorsal, and (C) anterior views; D–G, UALVP 43813, largest available atlas, missing lateroposterior edges of neural arch, in (D) right lateral, (E) dorsal, (F) ventral, and (G) anterior views; H–K, UALVP 43814, atlas missing left side of odontoid process and right posterior edge of neural arch, in (H) left lateral, (I) dorsal, (J) anterior, and (K) posterior views; L, M, UALVP 43815, smallest available atlas, missing left edge of odontoid process and posterior part of neural arch on left side, in (L) right lateral and (M) anterior views; N, UALVP 43816, atlantal centrum missing arch and showing hair passing through spinal foramen on right side, in dorsal view. Specimens at same scale; scale bar equals 1 mm.

process is a scoop-like projection that broadens anteriorly and the leading edge is truncate to shallowly concave in dorsal or ventral outline. To either side of the ventral midline, the odontoid process bears a low, shallowly convex condyle that is sub-circular in outline and faces ventrolaterally. In life each of these condyles would have fit into a complementary, concave facet in the medial face of the occipital condyle on the skull, as in extant amphiumids.

In lateral view the ventral rim of the posterior cotyle lies approximately in line with or slightly higher than the ventral rim of the anterior cotyles. In posterior view the posterior cotyle is oval in outline, taller than wide, and tapers ventrally. The inner surface of the cotyle is deeply concave, more so than the anterior cotyles, and is coated with a thin film of calcified cartilage. A small notochordal pit opens in the dorsal half of the posterior cotyle. A low ridge extends along the ventrolateral margin of the centrum between the ventral rims of the anterior and posterior cotyles. Between this pair of ridges the ventral surface of the centrum is pierced by one to three moderate-sized pits or subcentral foramina. The spinal foramen, for exit of the first spinal nerve, is enclosed by bone and opens about midway up the lateral half of the posterior surface of the anterior cotyle. A second foramen opens more ventrally and posteriorly in the lateral wall of the centrum, in front of the rim of the posterior cotyle. No basapophyses or transverse processes are present.

The neural arch is moderately high and robust. The latter condition probably accounts for the high percentage of specimens (five of seven) that retain a substantial portion of the arch. The neural arch on MCZ 3505 is fragmented (Fig. 4B); the arch was depicted as intact in Estes' (1969:fig. 1f–j) drawings of the same specimen. In anterior outline the neural canal is laterally compressed and oval, with the ventral part pinched between the anterior cotyles. With growth the canal becomes relatively broader and increases from about a third to half of the inter-

cotylar width. The neural arch roof is posteriorly short, with the posterior end extending just past the level of the posterior cotyle. The roof is relatively broad and tapers minimally towards the posterior end; damage to the lateroposterior edges of the neural arch on UALVP 43813 (Fig. 4E, F) creates the impression that the arch is more tapered on this specimen. The dorsal surface of the neural arch roof bears a median neural crest and a pair of laterodorsal accessory crests that extend approximately parallel to one another. All three crests are low and the neural crest is subequal in height to or slightly taller than the accessory crests. The neural crest is inclined posteriorly at an angle of about 13° to 28° ( $n = 5$ ) and is steepest on the two largest specimens. The crest terminates posteriorly in a low and blunt neural spine, which wraps around and extends down the posterior face of the neural arch as a vertical ridge (Fig. 4K). To either side of the neural spine, the posterior face of the roof bears a tiny indentation, likely for attachment of a ligament. Where preserved, the postzygapophyseal process is weakly developed and does not project ventrally or laterally any significant distance from the neural arch. The postzygapophyseal facet is flattened and indistinct.

#### Trunk Vertebrae (Estes, 1969:figs. 1a–e, 2; Fig. 5A–U)—

The 33 trunk vertebrae range in ventral midline length from about 2.4–4.6 mm ( $n = 28$ ) and show subtle differences in the form and positions of processes and muscle crests. In extant species of *Amphiuma*, these structures vary continuously along the trunk region (Cope, 1889:pl. 10; Naylor, 1978a; Estes, 1981). For example, vertebrae from the middle part of the trunk series differ from more anterior and posterior trunk vertebrae as follows: neural crest taller (versus lower); paired neural spines low (similar on anterior trunk vertebrae, but taller on posterior trunk vertebrae), moderately elongate (versus shorter on anterior trunk vertebrae and longer on posterior trunk vertebrae), and moderately divergent distally (versus diverge at narrower angle on anterior trunk vertebrae and at broader angle

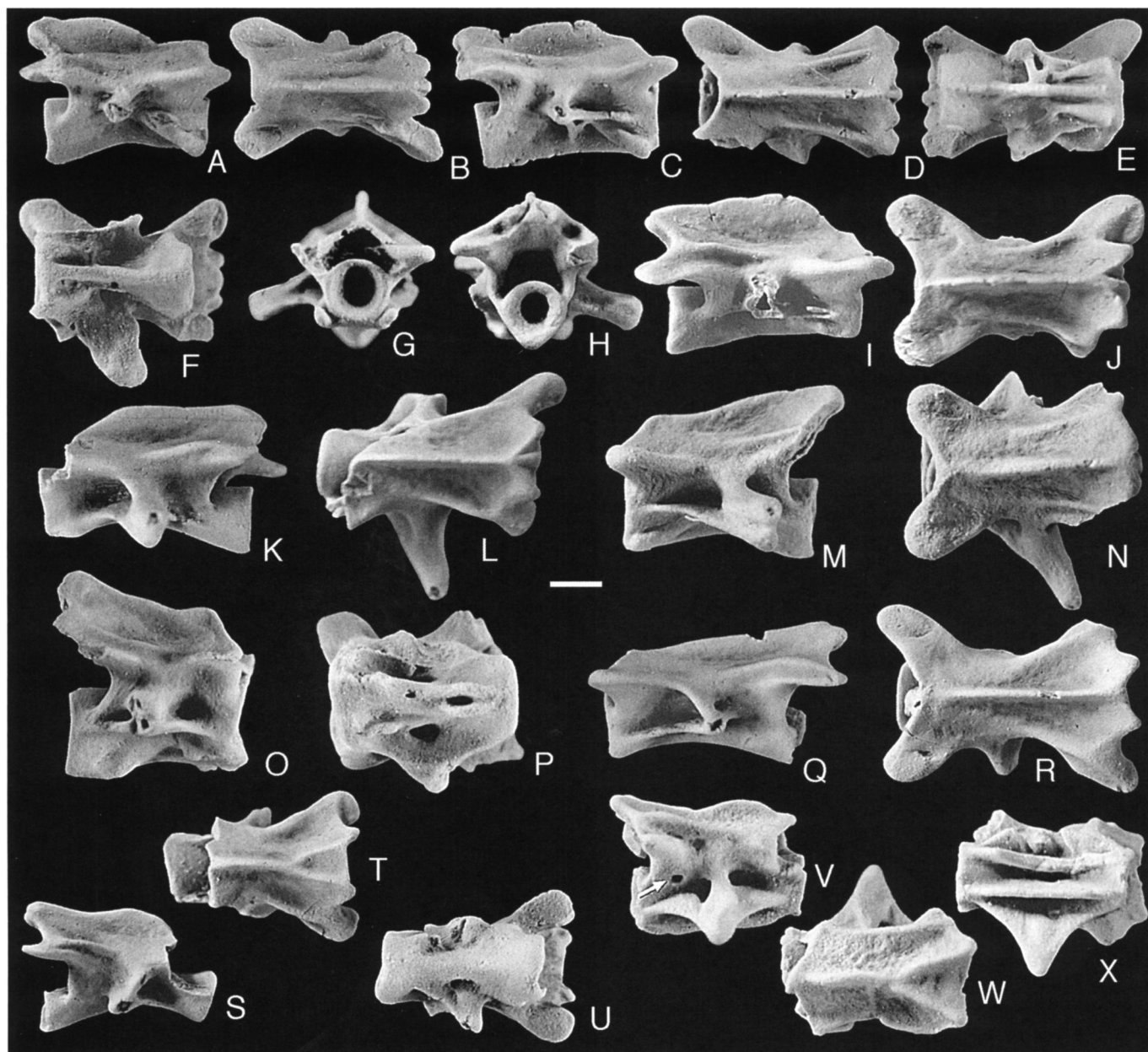


FIGURE 5. Postatlantal vertebrae of *Proamphiuma cretacea*; late Maastrichtian or early Paleocene, Bug Creek Anthills, Hell Creek Formation, Montana, USA. Inferred middle trunk vertebrae (A–L): A, B, MCZ 3504, holotype, in (A) right lateral view with anterior end to right and (B) dorsal view with anterior end to left; C–E, UALVP 43818, in (C) right lateral view with anterior end to right, (D) dorsal view with anterior end to left, and (E) ventral view with anterior end to right; F–H, UALVP 43830, in (F) ventral view with anterior end to left and in (G) anterior and (H) posterior views; I, J, UALVP 43831, in (I) right lateral view with anterior end to right and (J) dorsal view with anterior end to left; K, L, UALVP 43839, in (K) left lateral and (L) dorsal views, both with anterior end to left. Inferred anterior trunk vertebrae (M–P): M, N, MCZ 3509, in (M) left lateral and (N) dorsal views, both with anterior end to left; O, P, MCZ 3508, in (O) right lateral view with anterior end to right and (P) ventral view with anterior end to left. Inferred posterior trunk vertebrae (Q–U): Q, R, MCZ 3629, in (Q) left lateral and (R) dorsal views, both with anterior end to left; S–U, UALVP 43835, in (S) right lateral view with anterior end to right and in (T) dorsal and (U) ventral views, both with anterior end to left. Anterior caudal vertebra (V–X): UALVP 43840, in (V) right lateral view with anterior end to right and arrow pointing to spinal foramen and in (W) dorsal and (X) ventral views, both with anterior end to left. Specimens at same scale; scale bar equals 1 mm.

on posterior trunk vertebrae); postzygapophyseal crests taller and located close to dorsolateral edge of neural arch (versus lower and located closer to midline in anterior trunk vertebrae, but immediately adjacent to or on laterodorsal edge in posterior trunk vertebrae); and subcentral keel moderately deep (versus deeper on anterior trunk vertebrae and shallower on posterior trunk vertebrae). Assuming that similar variation occurred in *Proamphiuma cretacea*, the above listed criteria suggest that 18

of the trunk vertebrae at hand for the species are from the middle part of the trunk region. My description focuses on these specimens because I interpret the holotype as a middle trunk vertebra and because vertebrae from this region are representative for the trunk series.

The most nearly complete and informative of the inferred middle trunk vertebrae at hand are the holotype MCZ 3504 (Estes, 1969:fig. 1a–e; Fig. 5A, B) and the referred specimens



MCZ 3506 (Estes, 1969:fig. 2c), MCZ 3507 (Estes, 1969:fig. 2a), UALVP 43818, 43830, 43831, and 43839 (Fig. 5C–L), and UALVP 43827 (not figured). The centrum is amphicoelous and constricted medially midway along its length. Both cotyles are deeply concave, the inner walls are coated with a thin film of calcified cartilage, and the notochordal pit is relatively large and opens in about the center of each cotyle. The anterior cotyle is circular in outline, whereas the posterior cotyle tends to be slightly compressed laterally and oval in outline, with the narrow end directed ventrally. The subcentral keel spans between the anterior and posterior cotyles, and varies from a narrow flange on some specimens to a broader, shallower, less pronounced ridge on others. The ventral edge of the keel is concave dorsally in lateral profile and lies approximately in line with or, more commonly, well dorsal to the ventral rims of the cotyles. Although absent on the holotype (Estes, 1969:fig. 1e), a prominent subcentral foramen typically opens to either side of the ventral midline, between the subcentral keel and the base of the transverse process. The lateral face of the subcentral keel is variably indented midway along its length by a faint vertical groove that, in life, carried a blood vessel from the subcentral foramen. The paired anterior basapophyses are small, narrow, ridge- or prong-like structures, each of which arises from about the midpoint of the centrum and extends anteroventrally and slightly laterally. The anterior end of the basapophysis is blunt and occasionally projects slightly beyond the rim of the anterior centrum, but more typically lies in line with or just behind the rim. From about the midpoint of the vertebra, a stout and unicapital transverse process projects laterally and slightly ventroposteriorly. Where intact, the transverse process is blunt distally. The distal end of the process on two specimens (MCZ 3506 and UALVP 43839) has a pair of tiny indentations that, in life, presumably were finished in cartilage. Three alar processes (=“laminae” of Estes, 1969, 1981) are associated with the transverse process. The largest is the anterior alar process—this is a triangular flange that extends between the lateral wall of the centrum in front of the transverse process and the anteroventral edge of the transverse process. Estes’ (1969:4, 1981:44) statement, “ventral lamina [=“alar processes” here] of rib-bearer [=“transverse process” here] present but apparently not well developed anteriorly,” is true only in comparison to trunk vertebrae of extant *Amphiuma means* and *A. tridactylum*; in these species the anterior alar process is a prominent rectangular flange that extends along the length of the transverse process (Figs. 1G, H, 2B, 3G, H, L, M). The posterior alar process is smaller and is best developed on UALVP 43830 (Fig. 5F) as a posteriorly narrow flange that extends along the proximal part of the posteroventral edge of the transverse process. The dorsal alar process is a low, indistinct ridge that runs along the proximal half of the dorsoanterior surface of the transverse process. The vertebralarterial canal opens anteriorly through a small vertebralarterial foramen in the base of the transverse process. No vertebralarterial foramen is present posteriorly, which indicates that the vertebralarterial canal is closed posteriorly and does not extend through the base of the transverse process. Spinal foramina are absent.

The neural canal is broad and low, and the roof is shallowly convex dorsally. In dorsal outline the roof of the neural arch is elongate and hourglass-shaped, with the lateral edge weakly constricted medially above the base of the transverse process. No interzygapophyseal ridges are present. The pre- and postzygapophyseal processes are relatively elongate and narrow. Prezygapophyseal processes taper distally to a gently rounded tip and project anterolaterally at about 35°–45° from the midline. Postzygapophyseal processes project posterolaterally at complementary angles, but typically are more blunt distally. The prezygapophyseal facet is elliptical in dorsal outline and faces dorsally or dorsomedially, whereas the postzygapophyseal facet

is more oval, with the distal end broader, and faces ventrally or ventrolaterally. The postzygapophyseal crest is a low and mediolaterally narrow ridge that extends anteromedially along the dorsal surface of the postzygapophyseal process and carries onto the dorsolateral surface of the neural arch, then grades anteriorly into the roof of the arch at about the level of the base of the transverse process. The neural crest is mediolaterally narrow and extends from just behind the leading edge of the neural arch roof to the posterior margin of the arch. The lateral profile of the neural crest varies, presumably with the position along the trunk series as in extant amphiumids. Where most prominently developed, as on MCZ 3507 (Estes, 1969:fig. 2a) and UALVP 43827 (not figured), 43831 (Fig. 5I), and 43839 (Fig. 5K), the crest is an elongate and moderately high blade. The leading edge of the neural crest rises steeply in a broad curve and the dorsal edge of the crest continues posteriorly in an essentially horizontal plane. On UALVP 43818 (Fig. 5C), however, the neural crest is relatively lower anteriorly and ascends posteriorward at a shallower angle to its full height. The neural spines are a pair of low, posteriorly divergent ridges. Each ridge arises from the lateral surface of the neural crest, near the posterior end of the latter, and extends lateroposteriorly for a short distance along the dorsoposterior edge of the neural arch roof. In dorsal view the posterior ends of the neural crest and the paired neural spines may form a tripartite prong that often projects slightly past the posterior edge of the neural arch. The posterior face of the neural arch is indented, to either side of the midline, by a small depression that is enclosed medially by the end of the neural crest and laterally by the end of the neural spine.

Seven vertebrae are interpreted as being from the anterior part of the trunk series (see Fig. 5M–P) based on their relatively deeper subcentral keel, lower and more medially placed postzygapophyseal crests, less elongate and less divergent neural spines, lower neural crest, and, for some, an anteroposteriorly shorter centrum. Several specimens have a prominent vertical groove extending from the subcentral foramen down the lateral face of the subcentral keel. No specimen has either the anteriorly open notch or enclosed foramen, for exit of the second spinal nerve, that variably occurs in the wall of the neural arch on the first trunk vertebra in some individuals of extant *Amphiuma* species (Edwards, 1976, pers. obs.). In extant species of *Amphiuma*, the transverse processes are consistently weakly bicipitate on the first two to five trunk vertebrae. Weakly bicipital transverse processes preserved on three of the anterior trunk vertebrae available for *Proamphiuma cretacea* (MCZ 3509, Fig. 5M, N; MCZ 3508, Fig. 5O, P; MCZ 3632, unfigured) indicate that these specimens came from the anteriormost part of the trunk series. MCZ 3508 also has a prominent elliptical pit that opens ventrally along the posterior part of the subcentral keel. A similar pit occurs on anterior trunk vertebrae in two extant amphiumid skeletons available to me: in the fourth trunk vertebra of a specimen of *A. means* (FMNH 196143) and in the fifth and sixth trunk vertebrae of a specimen of *A. tridactylum* (UALVP 14364). Although not obvious in figures published here, MCZ 3508 also is pathologic—the anterior cotyle is distorted and the anterior part of the subcentral keel is twisted to the left.

The eight inferred posterior trunk vertebrae (see Fig. 5Q–U) are transitional into the caudal region (see below) in having the subcentral keel further reduced in depth, the neural crest and, often, the postzygapophyseal crests relatively lower, the postzygapophyseal crests located more laterally, and the posterior ends of the neural spines shifted more laterally. MCZ 3629 (Fig. 5Q, R) is typical for most specimens from this region in having weak anterior basapophyses, an elongate and low neural crest, and anteroposteriorly short neural spines. By contrast, on UALVP 43835 (Fig. 5S–U) the anterior basapophyses are ab-

sent, the neural crest is restricted to the anterior half of the neural arch, and the neural spines extend more anteriorly and the posterior end of each is displaced farther laterally; this combination of features suggests that UALVP 43835 is from the posteriormost end of the trunk series.

**Caudal Vertebrae (Fig. 5V–X).**—Caudals have not previously been described or figured for *Proamphiuma cretacea*. The two specimens at hand are UALVP 43840 and MCZ 3630; the latter was identified as a caudal by Edwards (1976:308) and, originally, as a trunk vertebra by Estes (1969). Both specimens are associated with trunk vertebrae of *Proamphiuma* based on provenance, size, and overall structure and are identified as caudals based on the presence of paired haemapophyses (versus trunk vertebrae having a median, subcentral keel) and a spinal foramen piercing the wall of the neural arch (versus trunk vertebrae lacking the spinal foramen). Both vertebrae resemble anterior caudals of the sirenid *Habrosaurus*, which is also represented at the Bug Creek Anthills (Estes et al., 1969; Bryant, 1989; Gardner, 2003), but differ from the latter as follows: postzygapophyseal crest present, albeit low; divergent neural spines lower than aliform crests (which occur at approximately the same position on caudals of *Habrosaurus*) and posterior end of neural spines not turned up; interzygapophyseal ridges absent; no deep fossae in lateral wall of vertebrae, either in front of or behind transverse process; and spinal foramen lying more posteriorly, slightly more than half of the distance posteriorly between base of transverse process and rim of posterior cotyle. Edwards (1976) identified three more putative caudals among Estes' (1969) original collection for *Proamphiuma*: two of these (MCZ 3627 and 3635) are neither from the caudal region nor referable to *Proamphiuma*; the third specimen (MCZ 3628) is likely a caudal, but it cannot be referred to any salamander genus (see above, "Referred Specimens").

The more nearly complete caudal is UALVP 43840 (Fig. 5V–X). This specimen is missing the transverse process and the ventral edge of the haemapophysis on the left side as well as most of each zygapophyseal process. The centrum is amphicoelous and about 3.0 mm in ventral midline length. The anterior and posterior cotyles are subcircular in outline, deeply concave, lined with calcified cartilage, and the notochordal pit opens in the center of the cotyle. The intact haemapophysis on the right side is a shallow, mediolaterally narrow flange that extends between the anterior and posterior cotyles and is free distally. A unicipital transverse process projects lateroventrally from about the midpoint of the centrum on the right side. The base of the process is pierced by a narrow vertebral arterial canal that opens anteriorly and posteriorly. The dorsal alar process resembles that on the trunk vertebrae, but the anterior and posterior alar processes form a broad and laterally pointed, triangular plate. Basapophyses are lacking. A tiny spinal foramen pierces the wall of the neural arch, slightly more than half the distance posteriorly between the base of the transverse process and the rim of the posterior cotyle. The neural and postzygapophyseal crests and the neural spines resemble those on the most posterior trunk vertebrae. Based on comparisons with extant *Amphiuma* species, the combination of shallow and flange-like haemapophyses, prominent transverse process with wing-like anterior and posterior alar processes, and low and widely divergent neural spines argue for UALVP 43840 having come from the anteriormost part of the caudal series. This interpretation is important because in extant *Amphiuma* species intra-vertebral exit of spinal nerves is confined to more posterior caudals (Edwards, 1976).

MCZ 3630 (unfigured) lacks the distal parts of the paired haemapophyses, both transverse processes, and much of the neural arch. Although the distal ends of the haemapophyses are broken, when intact these processes would have differed from those on UALVP 43840 in being deeper and in projecting ven-

troposteriorly and slightly laterally. These features suggest that MCZ 3630 occupied a more posterior position along the caudal series.

## Remarks

Despite the new specimens reported here, *Proamphiuma* remains one of the most poorly represented salamanders in the Bug Creek Anthills assemblage (Estes et al., 1969; Bryant, 1989; this study). *Proamphiuma* is known from just two collections of vertebrae—one in the MCZ (Estes, 1969, 1981; Estes et al., 1969) and one in the UALVP (this study). Atlantes from these collections indicate at least seven individuals of different sizes (cf. Fig. 4D versus L) are represented. Although sufficient numbers of vertebrae are available to document much of the vertebral morphology for the genus, skull elements remain unknown. Given that many institutions besides the MCZ and UALVP have collected from the Bug Creek Anthills and that extant amphiumids have robust and distinctive skull elements, it is likely that skull bones eventually will be recognized for *Proamphiuma*.

There are no reliable occurrences of *Proamphiuma* from outside of the holotype locality. Holman's (1977:394) statement that *Proamphiuma* "is known from the late Paleocene of Wyoming" is incorrect and refers, instead, to *Amphiuma jepseni*. Based on a personal communication from J. G. Armstrong, Naylor (1978a:507) reported *Proamphiuma* from the late Campanian–early Maastrichtian (=Edmontonian NALMA) Fruitland Formation of New Mexico; however, no mention of the genus appears in Armstrong-Ziegler's (1980) subsequent descriptive paper or in faunal lists (Armstrong-Ziegler, 1978; Hunt and Lucas, 1992, 1993) of lower vertebrates from the unit. Fox (1976:8) recorded *Proamphiuma* in a preliminary faunal list for the middle Campanian (=Judithian NALMA) Dinosaur Park Formation (=“upper Oldman Formation” of Fox and contemporary authors), Alberta, Canada, based on specimens in the collection of the UALVP. I have not seen any specimens in the UALVP collection—other than those reported above from the Bug Creek Anthills—that can be referred to *Proamphiuma*. Denton and O'Neill (1998:492) suggested that fragmentary elements from the Marshalltown Formation (Campanian) of New Jersey may pertain to *Proamphiuma*, but this record cannot be substantiated until the specimens in question are described and figured.

The 42 vertebrae reported here for *Proamphiuma* are small, yet solidly ossified, and bear well-developed crests and processes. Despite their small size, these specimens thus appear to be from relatively mature individuals. When scaled against skeletons from extant amphiumids and assuming similar vertebral counts, the largest vertebrae at hand for *Proamphiuma* suggest a total body length in the range of 30 cm. This is approximately the maximum size attained by extant individuals of *Amphiuma pholeter* (Means, 1996). By contrast, extant individuals of *A. means* and *A. tridactylum* are considerably larger, each with record total body lengths of just over 100 cm (Conant and Collins, 1991). Extant species of *Amphiuma* are nocturnal, secretive burrowers that inhabit shallow, sluggish waters (Baker, 1945; Salthe, 1973b, c; Means, 1996; Petranks, 1998). By analogy, *Proamphiuma* probably pursued a similar lifestyle.

## Genus and Species Indeterminate (Fig. 6A–C)

*Proamphiuma cretacea* Estes; Naylor, 1978a:507–508, fig. 98; Gardner, 2000:345, 352, fig. 9-4A–C.

**Specimen**—UALVP 14316, incomplete left dentary (Fig. 6A–C).

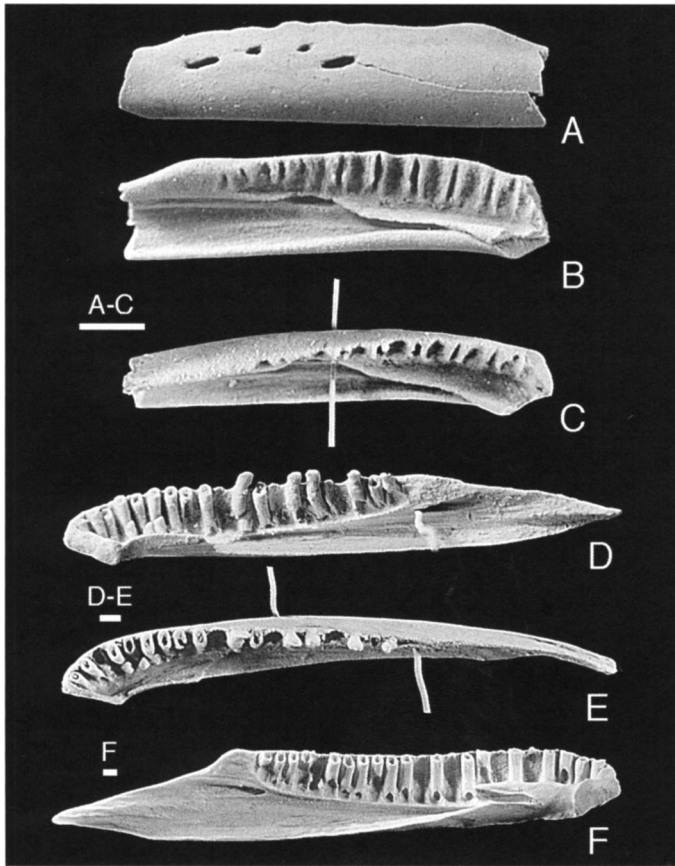


FIGURE 6. Dentaries of select amphiurids. Genus and species indeterminate (A–C); late Paleocene, Roche Percée, Ravenscrag Formation, Saskatchewan, Canada: UALVP 14316, left dentary missing symphyseal end and posterior part of area for attachment of postdentary bones, in (A) labial and (B) lingual views and (C) occlusal view showing hair passing transversely between posterior opening for mandibular canal in lingual face and posteriormost external nutritive foramen in labial face. Extant species of *Amphiuma* (D–F); Recent, southeastern U.S.A.: D, E, *Amphiuma means* type species, FMNH 98657, right dentary with anterior teeth lacking crowns, in (D) lingual and (E) occlusal views, showing wire passing obliquely (distolingually–mesiolabially) between posterior opening for mandibular canal in lingual face and posteriormost external nutritive foramen in labial face; F, *A. tridactylum*, UALVP 14364, left dentary lacking tooth crowns, in lingual view. Specimens at different scales; scale bars equal 1 mm.

**Locality, Age, and Horizon**—Unrecorded Roche Percée locality, southeastern Saskatchewan, Canada; late Paleocene, equivalent to Ti4 interval zone of the Tiffanian NALMA (Krause, 1978; Fox, 1990); upper part of Ravenscrag Formation.

**Description**—UALVP 14316 is an incomplete left dentary that is about 6.5 mm long in preserved length, and lacks both the symphyseal end and the posterior part of the area for attachment of the postdentary bones. No teeth are preserved, but the posterior 10 or 11 tooth positions are present. Comparisons with dentaries of living amphiurids suggest that UALVP 14316 probably is missing the first three or four tooth positions, for an estimated count of 13–15 loci, and that when complete the bone may have been relatively shorter than in extant amphiurids. UALVP 14316 resembles dentaries of extant *Amphiuma* species (Fig. 5D–F) and *A. jepseni* (Estes, 1969:figs. 3a, b, 5) and differs from dentaries described for other Paleocene salamanders in the following combination of features: bone robust, moderately elongate, and weakly tapered anteriorly in lingual or labial view; labial surface broadly convex labially

and perforated by prominent external nutritive foramina; dorsal edge twisted lingually towards posterior end of bone in dorsal view; dental parapet relatively tall and, judging by preserved walls of pedicels, evidently bore highly pleurodont and relatively large, widely spaced teeth; dorsal edge behind tooth row developed into low dorsal process that, in life, contributed to coronoid process of postdentary bones; and subdental shelf developed as horizontal shelf anteriorly, with posterolingual edge notched to receive anterior end of angular, and absent more posteriorly. The four external nutritive foramina are aligned in a dorsally convex row on the labial surface. The posteriormost foramen lies at about the level of the fourth locus from the posterior end of the tooth row and directly opposite from the posterior opening for the mandibular canal in the lingual face of the bone. The latter opening lies anterior to the level of the posterior end of the tooth row.

**Remarks**—UALVP 14316 was first reported by Naylor (1978a), who believed the specimen came from the Bug Creek Anthills. Based on this presumed provenance, plus the specimen's small size and amphiurid-like structure, Naylor (1978a) and Gardner (2000) referred UALVP 14316 to *Proamphiuma cretacea*. Subsequent examination of the original accession record indicates, however, that UALVP 14316 was collected from one of the geologically younger (late Paleocene in age) Roche Percée localities in the Ravenscrag Formation of southeastern Saskatchewan, Canada. Assignment of UALVP 14316 to *P. cretacea* is no longer tenable, because that identification relied heavily on the assumption that the specimen came from the holotype locality for *P. cretacea*.

The structure of UALVP 14316 is still consistent with it being from an amphiurid, but the specimen cannot be identified below this level. UALVP 14316 differs from dentaries of extant *Amphiuma* species in two characters describing the relative position of the posterior opening for the mandibular canal in the lingual surface of the bone (cf. Fig. 6A–C versus D–F): (1) posterior opening for mandibular canal lies directly across or opposite from posteriormost external nutritive foramen in labial surface, as demonstrated by the transverse path of a hair pushed through these openings in Figure 6C (versus opening for mandibular canal well behind level of posteriormost external nutritive foramen, as demonstrated by the path of a wire pushed through these openings in Fig. 6E) and (2) posterior opening for mandibular canal lies anterior to level of posterior end of tooth row (versus opening in line with or behind level of posterior end of tooth row). For the former character, outgroup comparisons with the basal urodeles *Cryptobranchus* and *Hynobius* suggest that UALVP 14316 exhibits the primitive state relative to extant *Amphiuma* species. Polarities for states of the latter character are equivocal, because the pattern seen in UALVP 14316 occurs in *Hynobius* and the pattern seen in extant species of *Amphiuma* occurs in *Cryptobranchus*. UALVP 14316 cannot be compared in detail with or referred to the paracontemporaneous *Amphiuma jepseni*, from the Polecat Bench Formation of Wyoming, because the three dentaries known for *A. jepseni* are too fragmentary and obscured by matrix (Estes, 1969:figs. 3a, b, 5) to show the position of the posterior opening for the mandibular canal or, apparently, any other potentially informative characters.

UALVP 14316 is the first record for the Amphiuridae in the Ravenscrag Formation and the only reliable record for the family in Canada. The Roche Percée localities in the upper part of the Ravenscrag Formation have produced a moderately diverse assemblage of paedomorphic salamanders. Besides the indeterminate amphiurid reported here, described components of this assemblage include: the earliest proteid, *Necturus krausei* (Naylor, 1978b); the cryptobranchid, *Cryptobranchus saskatchewanensis* (Naylor, 1981); and the gigantic scapherpetontid *Piceoerpeton willwoodense* (Naylor and Krause, 1981). A *Sca-*

*pherpeton*-like scapherpetontid and the batrachosauroidid *Opisthotriton* have also been reported (e.g., Naylor, 1978b, 1981), but no specimens have been described or figured.

## DISCUSSION

### Taxonomic Status of *Proamphiuma*

Vertebrae reported above from the Bug Creek Anthills are characteristic for amphiumids. Variation among these 42 specimens is no greater than the variation seen within extant amphiumid species, supporting the argument that the specimens pertain to a single taxon—namely *Proamphiuma cretacea*. Examination of these specimens and comparisons with representative material from the three extant species of *Amphiuma* indicate that some of the vertebral characters used by Estes (1969, 1981) are not appropriate for differentiating amphiumid genera, as Rieppel and Grande (1998) suggested. Nevertheless, some of the differences listed by Estes (1969, 1981) remain valid and additional differences are also evident.

Estes (1969, 1981) believed that *Proamphiuma* differed from extant *Amphiuma* in seven vertebral characters: subcentral keel and postzygapophyseal crests (i.e., “muscle crests” of Estes), basapophyses, and neural crest (=“neural spine” of Estes) all less prominent; neural arch on atlas directed more nearly posteriorly; and trunk vertebrae both narrower and more constricted medially. I consider the first four characters diagnostically reliable (see below), but the last three are not appropriate for differentiating amphiumid genera. The angle at which the atlantal neural arch is inclined posteriorly, as measured along the dorsal edge of the neural crest in lateral view, is more variable within *Proamphiuma* than Estes (1969, 1981) suspected and overlaps substantially with extant species of *Amphiuma*. Among atlantes now available for *Proamphiuma* (e.g., Fig. 4A, D, H, L) the angle described by the dorsal edge of the arch ranges from about 13° to 28° ( $n = 5$ ) and is steepest on the two largest specimens (UALVP 40045 and 43813), suggesting that the arch becomes steeper with growth. In specimens at hand for *Amphiuma* the atlantal neural arch is similarly steep in *A. means* (28°–31°;  $n = 2$ ) and *A. tridactylum* (33°;  $n = 1$ ), but it is essentially horizontal in the one individual of *A. pholeter* (cf. Fig. 3A and I versus Q, respectively). The shape and proportions of trunk vertebrae differ among amphiumids only at the specific level. Trunk vertebrae available for *P. cretacea* and *A. pholeter* and figured (Estes, 1969:fig. 3c–f) from the holotype of *A. jepseni* differ from those of *A. means* and *A. tridactylum* in being less constricted or waisted medially in dorsal outline (contra Estes, 1969) and in being relatively narrower (Fig. 2).

Vertebrae known for *Proamphiuma* differ from those of extant *Amphiuma* species as follows (see Figs. 2–5): (1) neural crest on trunk vertebrae relatively lower; (2) subcentral keel on trunk vertebrae relatively shallower; (3) anterior basapophyses on trunk vertebrae relatively shorter, with anterior end typically in line with or behind rim of anterior cotyle (versus anterior end of basapophyses projecting beyond anterior cotyle); (4) postzygapophyseal crests on postatlantal vertebrae relatively lower; (5) postzygapophyseal processes on atlas shallow and indistinct (versus prominent and project ventrally); (6) vertebral canal in trunk vertebrae closed posteriorly (versus open posteriorly); (7) anterior caudals pierced by spinal foramen (versus spinal foramen absent from first two caudals, present in ninth and all subsequent caudals, and with intervening transitional zone of two to seven caudals; Edwards, 1976); (8) ventral rims of posterior and anterior cotyles on atlas approximately in line in lateral view (versus posterior cotyle expanded ventrally, with ventral rim well below level of anterior cotyles); (9) neural crest on postatlantal vertebrae extending anteriorly almost to leading edge of roof (versus anterior end of crest located more posteriorly, approximately in line with posterior

edge of prezygapophyseal facets); (10) leading edge of neural crest on trunk vertebrae inclined posterodorsally at a shallower angle in lateral view (versus inclined more dorsoposteriorly at a steeper angle); and (11) neural crest on inferred middle trunk vertebrae broadly rounded anteriorly and dorsal edge horizontal in lateral profile (versus neural crest on all trunk vertebrae more nearly resembling a posteriorly tilted square, with anterior and dorsal edges meeting at a sharp, nearly right-angled junction). Considering that postzygapophyseal crests are autapomorphic for amphiumids, the relatively lower postzygapophyseal crests (character 4) in *Proamphiuma* probably represent the primitive amphiumid condition. Outgroup comparisons with the basal urodeles *Hynobius* and *Cryptobranchius* suggest that, relative to extant *Amphiuma* species, *Proamphiuma* exhibits the primitive state for six more characters (1–3 and 8–10) and the derived state for characters 5–7. Polarities for states describing the different profiles of the neural crest (character 11) in *Amphiuma* and *Proamphiuma* are equivocal because neither pattern occurs in *Hynobius* or *Cryptobranchius*.

Comparisons with the late Paleocene *Amphiuma jepseni* are difficult because no atlantes or caudal vertebrae have been reported for the species and the sole trunk vertebra figured by Estes (1969:fig. 3c–f) is broken anteriorly in such a manner that neither the anterior extent nor profile of the neural crest can be determined with confidence. Judging by Estes’ (1969, 1981) descriptions and figures, trunk vertebrae of *A. jepseni* resemble those of extant congeners and differ from *Proamphiuma* in having a more prominent neural crest, postzygapophyseal crests, subcentral keel, and basapophyses. At present these are the only character states supporting membership of *A. jepseni* within *Amphiuma*. The skull of *A. jepseni* as figured by Estes (1969:fig. 4) is relatively short and broad. Considering that extant *Amphiuma* species are unusual—but not unique—among living salamanders in having a narrow and elongate skull, the relatively shorter and broader skull in *A. jepseni* is probably primitive.

The use of vertebral characters to differentiate *Proamphiuma cretacea* from species of *Amphiuma* admittedly is complicated by at least two factors. First, many of the characters describe relative or qualitative differences in the size or form of structures. Although these differences are difficult to quantify in a meaningful manner, they become obvious when representative vertebrae of the two genera are compared at the same scale (Fig. 2). Second, many of the characters clearly vary intraspecifically with overall element size, regionally along the trunk and caudal series, or both. This intraspecific variation is minor, however, compared to the more pronounced differences seen in the same characters between *Proamphiuma* and *Amphiuma*.

In summary, *Proamphiuma cretacea* primitively differs from the four accepted species of *Amphiuma* in four characters describing the lesser development of vertebral crests and processes. *P. cretacea* differs further from the three extant species of *Amphiuma* (conditions unknown for *A. jepseni*) in three derived character states (one each from the atlas and trunk and caudal vertebrae) that may be autapomorphic within the family, depending on the condition in *A. jepseni*, in three plesiomorphies (one each from the post-atlantal vertebrae, atlas, and trunk vertebrae), and in one trunk vertebral character state of uncertain polarity. I believe this suite of differences is sufficiently extensive to warrant the continued recognition of *P. cretacea* as a diagnosable amphiumid taxon (contra Rieppel and Grande, 1998).

### Relationships Within the Amphiumidae

The only cladistic study of relationships among amphiumids is Karlin and Means’ (1994) electrophoretic analysis of 24 loci for the three extant species of *Amphiuma*. A more comprehen-

sive analysis of relationships among the five recognized amphiumid species is premature until specimens described by Estes (1969, 1975, 1981) for *A. jepseni* are critically re-examined and, ideally, skull elements are available for *Proamphiuma* and better agreement is reached on the immediate outgroups of the Amphiumidae. Nevertheless, sufficient information now exists to propose the following nested set of relationships within the family: *Proamphiuma* (*A. jepseni* (*A. pholeter* (*A. means* + *A. tridactylum*))). This hypothesized pattern can be tested in the future by a rigorous cladistic analysis.

Vertebrae of *Proamphiuma* exhibit the full complement of basapophyses, crests, and processes that are characteristic for amphiumids (Estes, 1969, 1981; Naylor, 1978a), including the unique postzygapophyseal crests on the trunk vertebrae that are associated with the modified dorsalis trunci epaxial trunk musculature in extant amphiumids. Weaker development of these vertebral structures in *Proamphiuma*, compared to *Amphiuma*, implies that the associated vertebral musculature was present, but less differentiated (Estes, 1969, 1981; Naylor, 1978a). Atlantes in *Proamphiuma* and extant *Amphiuma* species also resemble one another in the structure of the neural arch, odontoid process, and anterior cotyles—a combination that implies a similar pattern of atlanto-cranial articulation and associated musculature (Naylor, 1978a); see Erdman and Cundall (1984) for information on the atlanto-cranial complex in living amphiumids. *Proamphiuma* exhibits two more characteristic amphiumid vertebral features that have not previously been identified for the genus: (1) an elongate body and increased number of trunk vertebrae can be inferred from the presence of unicipital transverse processes on all but the anteriormost trunk vertebrae and (2) deeply concave anterior cotyles on the atlas indicate that the complementary occipital condyles on the skull were stalked (i.e., posteriorly elongate). In extant amphiumids these conditions seem to be associated with burrowing and feeding, respectively. Elongation of the body is a common trend in fishes, amphibians, and reptiles, and facilitates movement through crevices and similarly confined spaces (Gans, 1975). Extant amphiumids have increased the number of precaudals to about 65–70 vertebrae (Baker, 1945; Rieppel and Grande, 1998; pers. obs., 1999) and are accomplished burrowers (Baker, 1945; Knepton, 1954; Salthe, 1973b, c). Manipulation of extant amphiumid skeletons shows that stalked occipital condyles on the skull and deep anterior cotyles on the atlas allow the skull to rotate dorsoventrally in a wide arc about the atlanto-cranial joint. Erdman and Cundall's (1984) functional study of feeding in *A. tridactylum* demonstrated that rapid anterodorsal displacement of this joint aids in snapping the mouth closed during the latter part of the feeding strike.

*Proamphiuma* and *Amphiuma* are the only two amphiumid genera that I recognize and, by default, are sister-taxa. Given that *Proamphiuma* shares no apomorphies with any amphiumid taxon, other than those character states that are primitive for the family, for the purpose of deciphering the evolutionary history of the Amphiumidae it is more informative to view *Proamphiuma* as the basalmost member of the family. In terms of its provenance and known morphology *Proamphiuma* is a good structural ancestor for *Amphiuma*, if not directly ancestral to the latter (Estes, 1969, 1981; Naylor, 1978a). *Proamphiuma* also provides a minimum date of latest Cretaceous or early Paleocene for the origin of the Amphiumidae and the recovery of specimens from present day Montana is consistent with the view (Naylor, 1978a; Milner, 1983; Duellman and Trueb, 1986) that amphiumids are endemic to North America.

The four species of *Amphiuma* are united by four vertebral synapomorphies presumably related to enhanced development and performance of the associated trunk muscles: neural and postzygapophyseal crests both relatively high, subcentral keel relatively deep, and anterior basapophyses relatively more elon-

gate and extending beyond rim of anterior cotyle. The three extant species form a less inclusive clade that is supported by the shared presence of an elongate, narrow snout and corresponding cranial modifications—e.g., dentary elongate; maxilla, vomer, and their respective tooth rows posteriorly elongate; and parasphenoid narrow. The tapered snout and elongate jaws in extant species of *Amphiuma* aid in borrowing through loose substrate, moving through narrow burrows, and, in combination with the posteriorly elongate mouth opening, permit the consumption of larger, more diverse, and more active prey (Erdman and Cundall, 1984). These observations imply that the short-snouted *A. jepseni* may have been a less active burrower, perhaps resembling the extant *A. pholeter*, which reportedly favors soft, mucky bottom sediments (Means, 1996), and that it preyed upon smaller, less active prey.

The extant species of *Amphiuma* form a morphocline in which limbs become relatively shorter and the number of toes reduced from three in *A. tridactylum*, to two in *A. means*, and to one in *A. pholeter* (Neill, 1964), yet Karlin and Means' (1994) electrophoretic analysis identified the first two species as each other's closest relatives. Two putative trunk vertebral synapomorphies also support a sister-pair relationship between *A. tridactylum* and *A. means*: (1) anterior alar process more rectangular in ventral or dorsal outline and uniformly broad anteroposteriorly along length of transverse process (process primitively triangular in outline, broadest medially, and narrowing laterally along transverse process) and (2) neural arch relatively wide and strongly constricted medially in dorsal view (arch primitively narrower and less constricted medially). The implications of this arrangement are two-fold. First, limb length and toe counts were reduced independently in *A. means* and *A. pholeter*. Second, rather than being typical or representative amphiumids as phylogenetic analyses (Larson and Dimmick, 1993; Hay et al., 1995) and functional studies (Erdman and Cundall, 1984; Reilly and Lauder, 1992) routinely assume, *A. tridactylum* and *A. means* may instead be the most "advanced" members of the family. As such, *A. pholeter* may be a better candidate for a representative (i.e., "primitive") living member of the genus and family.

The phylogeny I have proposed here and the temporal occurrences of amphiumid species imply that the characteristic atlanto-cranial joint and elongate trunk and the unique vertebramuscular complex of the family were established by the Cretaceous-Tertiary boundary. *Amphiuma jepseni* provides a minimum date of post-late Paleocene for elongation of the snout and associated cranial modifications seen in living amphiumids. The sequence in which other hallmark amphiumid attributes—e.g., girdles and limbs reduced; number of toes reduced; premaxillae fused and having vomerine process and pars dorsalis posteriorly elongate—arose and the levels at which these are apomorphic cannot yet be deciphered from the fossil record. Such inferences must await the discovery of additional amphiumid fossils from appropriate horizons.

## CONCLUSIONS

(1) *Proamphiuma cretacea* is reliably known only from the Bug Creek Anthills (late Maastrichtian or early Paleocene in age), Hell Creek Formation, Montana, USA. Four of the 17 topotypic vertebrae originally listed for *P. cretacea* cannot be referred to the taxon. Additional specimens reported here from the holotype locality include atlantes, trunk vertebrae, and a caudal that triple the number of available vertebral specimens.

(2) A dentary previously thought to be from the Bug Creek Anthills and referred to *Proamphiuma cretacea* is shown to be from a geologically younger (late Palaeocene) locality in the Ravenscrag Formation of Saskatchewan, Canada, and is re-in-



terpreted as belonging to an indeterminate amphiumid genus and species.

(3) *Proamphiuma cretacea* is a diagnosable amphiumid taxon, the geologically oldest member of the family, and the type and only species in the genus. *Proamphiuma* differs primitively from the Cenozoic *Amphiuma* in four character states describing lesser development of vertebral processes and crests, and differs further from the three extant species of *Amphiuma* (conditions unknown based on published reports of the late Paleocene *A. jepseni*) in a suite of 11 vertebral apomorphies, pleiomorphies, and character states of uncertain polarities.

(4) The following relationships are hypothesized among the five amphiumid species accepted here: *Proamphiuma cretacea* (*Amphiuma jepseni* (*A. pholeter* (*A. means* + *A. tridactylum*))). *Proamphiuma* is a good structural ancestor for, if not the actual ancestor of, *Amphiuma*. This phylogeny and fossil evidence imply that the characteristic atlanto-cranial joint and elongate trunk and the unique vertebromuscular complex of amphiumids arose before elongation of the snout and associated cranial modifications typical of living amphiumids. As currently known, the fossil record remains too limited to indicate the sequence in which other important amphiumid features arose and the levels at which these are apomorphic.

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