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Vertebrae of Plethodontid Salamanders from the Lower Miocene of Montana

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ABSTRACT—Fossils recovered from the Lower Miocene (Arikareean) Cabbage Patch Formation of southeastern Montana include four vertebrae that can be assigned to the genera *Plethodon* and *Aneides,* family Plethodontidae, although species identification is not possible. Discovery of these fossils corroborates views based on indirect paleobiological evidence that these genera were widely distributed in Central North America in early Tertiary times.

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INTRODUCTION

Very few fossil salamanders of the family Plethodontidae are known from pre-Pleistocene deposits. The oldest are the trackways from the Mio-Pliocene border of California assigned to the genus *Batrachoseps* (Peabody, 1959; Estes, 1970). One modern group of plethodontids, the Tribe Plethdontini (genera *Aneides, Ensatina,* and *Plethodon*), has a disjunct distribution, with species in eastern and western North America and the southern Rocky Mountains. Lowe (1950) and Wake (1966) used paleobotanical evidence as the basis for hypotheses concerning the distributional history of the tribe, and Wake suggested that ancestors of the group probably "occurred all across the continent in early Tertiary." Recovery of vertebrae from the Lower Miocene of Montana which can be assigned to the Tribe Plethodontini lends support to this suggestion. Even though the material is inadequate for precise specific identification, it is worthy of note because of its age and its zoogeographic significance.

MATERIALS AND METHODS

The salamanders reported here are represented by four vertebrae (Montana State University Museum of Paleontology 6504-2003 and 6504-2004, and University of Kansas Museum of Natural History 18296 and 18298). These were collected by field parties of the University of Montana from beds of the Lower Miocene (Arikareean) Cabbage Patch Formation, Granite County, Montana. We have had for comparison a large collection of disarticulated and cleared and stained skeletons of modern species of salamanders (for partial list see Worthington and Wake, 1971, and Edwards, 1976). All of the fossil vertebrae are partially broken. It is impossible to make exact assignments, in part because of our inability to obtain complete measurements, but more importantly because modern species overlap extensively in morphometrics and species identification becomes a statistical problem which our small samples are inadequate to resolve. Vertebrae in salamanders vary regionally within an animal, ontogenetically within populations, and geographically within species (see Worthington and Wake, 1971).

Fossil vertebrae were examined under a binocular dissecting microscope and were compared directly with vertebrae of living species. When it became evident that the vertebrae were similar to those of modern plethodonine genera, the living species were systematically surveyed, and detailed comparisons were made with the species and individuals that were most nearly identical. A detailed variational analysis of the vertebral column of plethodonine salamanders is beyond the scope of the present study. Given the fragmentary nature of our material, it is doubtful that such an analysis would significantly affect our interpretation.

OBSERVATIONS AND DISCUSSION

The vertebrae of salamanders have distinctive patterns of spinal nerve foramina, characteristic of major taxa (Edwards, 1976). All four of the fossil vertebrae have distinct foramina posterior to the rib bearers, and, assuming that the vertebrae represent living families, the only possibilities for familial assignment are the Sirenidae, Plethodontidae, Ambystomatidae (*sensu strictu,* excluding *Dicamptodon* and *Rhyacotriton*), and Salamandridae. The vertebrae of sirenids are very distinctive and differ in many ways from these fossils, particularly in their size, proportions, reduced nature of the rib bearers (cf. Goin and Auffenberg, 1955), and relatively great dorso-ventral dimension. The slender build of the vertebrae, the long, narrow, husk-like centra, and the low neural arch with its weakly developed neural spine all point to plethodontid rather than ambystomatid or salamandrid relationship. There is no sign of mineralized intervertebral cartilages or opisthocoely, and the plethodontid subfamily Desmognathinae is thus eliminated (there are, in addition, other important structural differences from desmognathines). We thus limit our direct comparisons to members of the subfamily Plethodontinae.

The vertebrae are nearly identical in all structural details with those of living members of the genera *Plethodon* and *Aneides.* We eliminated members of the tribe Hemidactyliini (Wake, 1966) in part on the grounds that many members of this group in the appropriate size range have double spinal nerve foramina (Edwards, 1976), and have transverse processes that are more anteriorly placed than in the fossils. Many of the species of the very large tribe Bolitoglossini remain unstudied. Only two bolitoglossine genera, *Hydromantes* and *Batrachoseps,* occur in the United States today. *Hydromantes* has long, cylindrical transverse processes, and differently shaped vertebrae than the fossils. *Batrachoseps* has transverse processes that have a distinct angle along their length, and also have rather different proportions, in addition to being generally smaller. The other bolitoglossines occur in the New World tropics. *Thorius* and *Parvimolge* are eliminated on the basis of their very small size. *Lineatriton* has very elongated vertebrae, very different than those of the fossils. Both *Oedipina* and *Lineatriton* have fused transverse processes. Many species of *Chiropterotriton* and *Pseudoeurycea* can be eliminated on the basis of fused transverse processes, mineralized intervertebral cartilages, or both. Many *Bolitoglossa* also have fused transverse processes. These features differ strongly from our fossil material. We have compared the fossils to all available skeletons of *Bolitoglossa, Pseudoeurycea,* and *Chiropterotriton,* and can readily distinguish them on a variety of criteria.

The only close relative of *Aneides* and *Plethodon* is *Ensatina,* and it has very distinctive vertebrae with different proportions (centra of relatively large diameter) than those of the fossils. We accordingly assign these vertebrae to *Plethodon* and *Aneides.*.

MSUMP 6504-2003 is a midtrunk vertebra that we confidently refer to the genus *Plethodon.* Its centrum is relatively long and narrow. The rib bearers are situated relatively far forward on the vertebra (as compared with number 6504-2004), and the dorsal and ventral rib bearers are connected by a thin web of bone to their tips (on the one side on which the bearers are intact). The impression of the vertebrarterial canal forms a depression along the dorsolateral side of the centrum, and is almost entirely below the ventral rib bearer. This last feature usually distinguishes western species of *Plethodon* from *Aneides.* This vertebra is very similar to the midtrunk vertebrae of such modern western species as *P. dunni* and *P. vehiculum* (Figure 1).

KU 18298 is an anterior caudal vertebra that we assign to *Plethodon.* It has a mid-vertebral spinal foramen and a long, slender centrum. There is a thin keel on one side of the lower part of the centrum. The position of the transverse processes, slightly in front of the midpoint of the vertebra, suggests that this is from about the sixth or seventh vertebral position behind the sacrum. Perhaps it is from the same species as MSUMP 6504-2003.

MSUMP 6504-2004 is a midtrunk vertebra that probably represents a different species than the above. The centrum is noticeably stouter. The rib bearers are situated somewhat farther back on the vertebra, and the dorsal and ventral bearers are completely independent. The vertebrarterial canal passes dorsal to the bulk of the lower rib bearer. All of these features suggest that this specimen is not *Plethodon,* but it may well be assignable to *Aneides,* for it closely resembles the vertebrae of modern western species (Figure 2). The vertebrae of *A. aeneus* of eastern North America have neural arches that are broader and flatter than those of the fossils or other species of *Aneides.* Vertebrae of *A. lugubris* differ in several respects from those of the fossils and from other species (Wake, 1963). With available material we cannot confidently distinguish the remaining species of *Aneides* from one another.

KU 18296 is also a midtrunk vertebra, probably the same species as MSUMP 6504-2004. There is little evidence of a vertebrarterial canal, and there are some subtle differences in position of the rib bearers, but these are differences one expects of regional variation within an individual.

Appropriate measurements of the fossils are presented in Table 1.

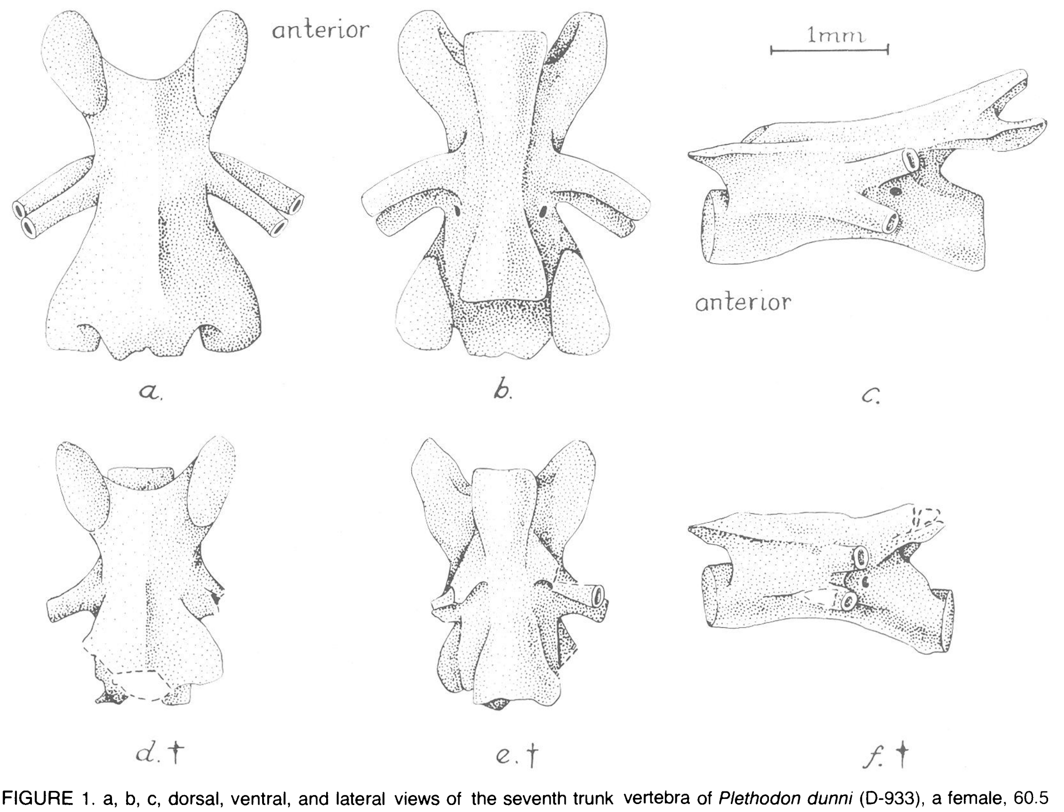

FIGURE 1. a, b, c, dorsal, ventral, and lateral views of the seventh trunk vertebra of *Plethodon dunni* (D-933), a female, 60.5 mm snout-posterior angle of vent, from Wahkeena Falls, Multnomah Co., Oregon. d, e, f, dorsal, ventral, and lateral views of fossil trunk vertebra (MV 6504-2003).

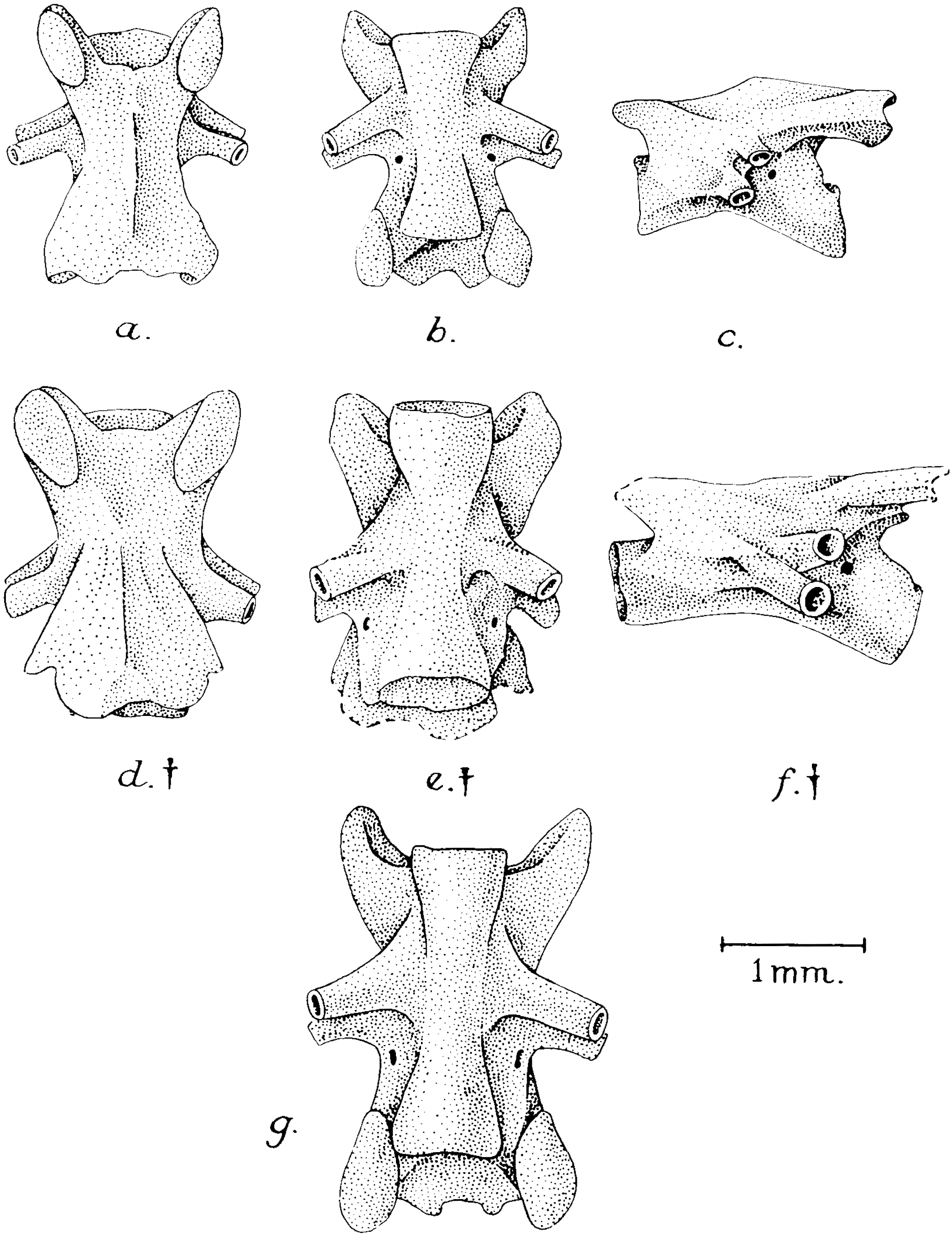

FIGURE 2. a, b, c, dorsal, ventral, and lateral views of the seventh trunk vertebra of *Aneides ferreus* (D-1218), a male, 43.1 mm snout-posterior angle of vent, from Sixes River Road, Curry Co., Oregon. d, e, f, dorsal, ventral, and lateral views of fossil trunk vertebra (MV 6504-2004). g, ventral view of seventh trunk vertebra of *Aneides flavipunctatus* (D-910), a male, 56.4 mm snout-posterior angle of vent, from Holy City, Santa Clara Co., California.

TABLE 1. Selected measurements (mm) of fossil vertebrae, made under binocular dissecting microscope with ocular micrometer.

Measurement	*Plethodon* sp. MSUMP 6504-2003	*Plethodon* sp. KU 18298	*Aneides* sp. MSUMP 6504-2004	*Aneides* sp. KU 18296
Centrum length	2.0	1.5	2.1	1.9
Centrum width	.7	b	.8	.7
Zygapophyseal length	2.3	1.9	2.3	2.5
Anterior zygapophyseal width	1.0	b	1.6	1.6
Posterior zygapophyseal width	b	b	1.4[a]	1.5[a]
Total width, including rib bearers	1.9[c]	b	1.8	b
Total height, from ventral border of centrum	.9	b	1.3	.9

[a]slight breakage, major estimation involved in recorded measurement.
[b]vertebra too fragmentary to measure.
[c]left side broken, value given is twice the distance from end of left rib bearer to midline.

The position of the transverse processes in all three fossil trunk vertebrae is more anteriorly placed than in any living species of *Aneides* or *Plethodon.* Nevertheless, the difference is slight, and in all other respects the fossils strongly resemble the modern genera.

Another salamander, *Taricha (Paleotaricha) miocenica,* is known from the same beds (Tihen, 1974). While our assignments of the few vertebrae available to us must remain tentative, it is of interest that all of the salamanders have apparent western, rather than eastern, affinities.

The discovery of fossils assignable to *Plethodon* and *Aneides* in rocks of this age and geographic position is to be expected, based on paleogeographical and phylogenetic evidence (Lowe, 1950; Wake, 1966). Wake (1966) suggested that no interchange between the plethodontid salamander faunas of eastern and western North America was likely to have taken place more recently than Miocene times. Recently obtained biochemical evidence (Maxson et al., 1979; Larson et al., 1981) suggests that division of both *Plethodon* and *Aneides* into eastern and western groups predated the age of the fossils reported here, and the assignment of these fossils to the western rather than the eastern groups in both genera makes biogeographical sense. Discovery that both genera were in existence in western United States in early Miocene times is also consistent with paleogeographical, morphological, and biochemical evidence, all of which suggests that lineage divergence in the tribe Plethodontini was mainly an early Tertiary event.

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