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Fossil Plethodontid Salamanders from the Latest Miocene of California

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ABSTRACT.—Two salamanders, *Aneides lugubris*, and *Batrachoseps* sp., are reported from the latest Miocene (Hemphillian) upper Mehrten Formation of the western Sierra Nevada foothills of California. A record of *Batrachoseps* sp. is also reported here from the Pinole Tuff of the same age in the San Francisco Bay area of California. These are the second Tertiary records of plethodontid remains and the first from west of the Rocky Mountains. The minimum age of *Aneides lugubris*, and the Sierra Nevada population in particular, is established at approximately five million years. This is consistent with the estimated longevity of this species based on biochemical evidence and modifies a previous biogeographic speculation.

Prior to Peabody's (1959) description of late Miocene trackways of *Batrachoseps* from near Columbia, California, the fossil record of plethodontid salamanders did not extend earlier than the Pleistocene. Since then there has been only one unquestionable plethodontid record from rocks older than the Pleistocene—four vertebrae from the early Miocene of Montana referred to *Plethodon* and *Aneides* (Tihen and Wake, 1981)—but Peabody's footprints remain the only published Tertiary record of plethodontids from west of the Rocky Mountains (Estes, 1981). A large number of vertebrate fossils recently has been collected from the upper part of the Mehrten Formation near Turlock Lake, California. Among them is a small number of plethodontid skeletal elements. A single plethodontid vertebra has also been found in a large collection of vertebrate fossils from the Pinole Tuff of Pinole, California.

The fossils from Turlock Lake were collected from a single locality as part of bulk samples taken by Dennis Garber of Sacramento, California, and by Hugh Wagner during the course of his dissertation work. Wagner separated three salamander vertebrae from the samples, and these were identified by Joseph Tihen as "?*Batrachoseps*." The remaining Turlock Lake salamander elements were separated from the sample by the author.

Identifications were made using a large collection of specimens in the University of California Museum of Vertebrate Zoology. Terminology follows Wake (1963).

ABBREVIATIONS

D—University of California Museum of Vertebrate Zoology, uncatalogued osteological collection. LACMH—Los Angeles County Museum of Natural History, Herpetology Department. LACMVP—Ibid., Vertebrate Paleontology Department. UCMP—University of California Museum of Paleontology, Berkeley. m.y.b.p.—million years before present.

GEOLOGICAL SETTING

The Mehrten Formation is a series of sedimentary rocks derived from andesitic vulcanism in the Sierra Nevada Mountains to the east. Wagner (1981) divided it into four members, and the fossils reported here are from the uppermost, the Modesto Reservoir Member. The locality consists of a loosely consolidated lens of sandstone immediately beneath an undated tuff (tuff T2 of Wagner, 1981). The trackways reported by Peabody (1959) are from a unit

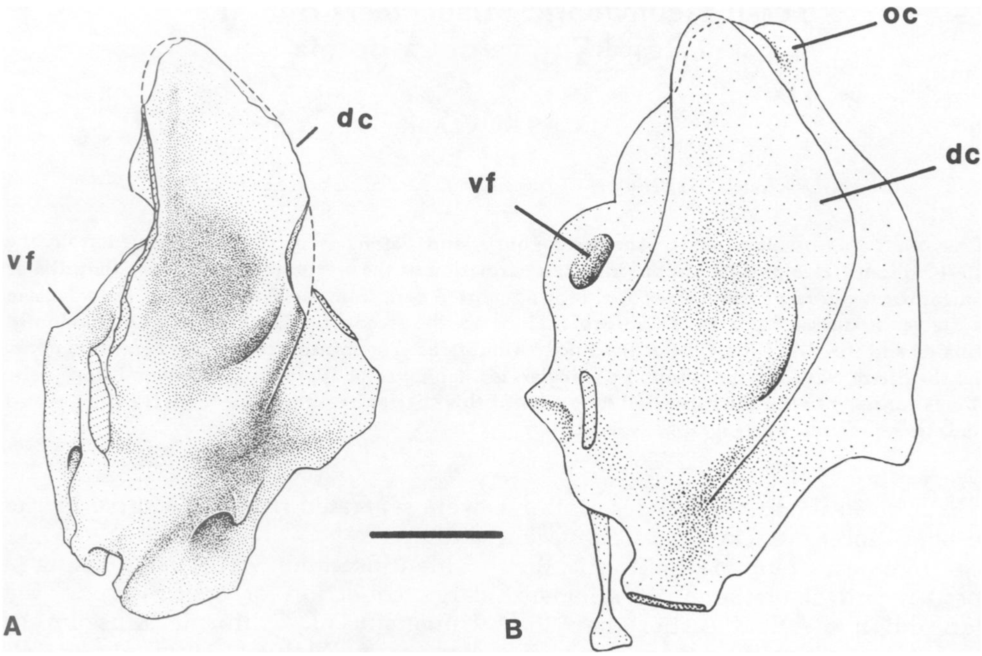

FIG. 1. A. Right occipito-otic complex of fossil *Aneides lugubris* (UCMP 125852a) in lateral view, posterior at top. B. Same, from recent specimen (D1118), a 74.1 mm snout-vent length female. Abbreviations: DC, dorsal crest; OC, occipital condyle; VF, vestibular fenestra. Scale is one mm.

that has usually been included at the base of the Mehrten Formation but this unit will soon be elevated to the status of a formation, the Relief Peak Formation (H. Wagner, pers. comm., 1983).

The Turlock Lake salamander fossils were found associated with the Modesto Reservoir mammalian local fauna. This fauna is biostratigraphically correlated with mammalian faunas of late Hemphillian age, including that of the Pinole Tuff (Stirton, 1939). The latter fauna was collected from tuffaceous silts 0.6 m below the Pinole Tuff (J. H. Hutchison, pers. comm.), which has been radiometrically dated at 5.2 m.y.b.p. (Evernden et al., 1964). The Miocene/Pliocene boundary is established at 5.0 m.y.b.p. (Berggren and Van Couvering, 1974), so the date from the Pinole Tuff indicates a latest Miocene age for the salamanders discussed here. The salamander fossil from the Pinole Tuff was initially identified as a salamander by J. H. Hutchison.

Axelrod (1980) has proposed a slightly younger age (4.0–4.5 m.y.b.p.) for the Modesto Reservoir local fauna based on the paleoecology of the associated Turlock Lake flora. This speculation is based on the inferred annual precipitation indicated for the Turlock Lake flora and the Oakdale flora lower in the same member of the Mehrten Formation. He fitted these inferred precipitation rates to a curve based on a supposed pattern of changes seen in the San Francisco Bay area during the same geological time interval. The Turlock Lake flora fitted the curve at approximately 4 m.y.b.p. However, his analysis is inconclusive because the precise time interval in question (6.0 to 4.0 m.y.b.p.) is not represented in the San Francisco area and the curve is interpolated between these dates. It is therefore simplest at present to place more weight on the biostratigraphic correlations of Wagner (1981) and the radiometric date of Evernden et al. (1964).

Systematic Paleontology

Aneides lugubris (Hallowell, 1849)

Referred Specimen.—UCMP 125852 A–C, a right occipito-otic bone in three pieces. Horizon and Locality: Modesto Reservoir Member (Wagner, 1981) of Mehrten Formation; LACMVP 3917, Cement Goose Pit Island (=UCMP V6878, Turlock Lake site five); Turlock Lake, Stanislaus County, California.

Description and Discussion.—The specimen was accidentally broken into three pieces at the time of removal from the sample. The capsule was nearly complete prior to breakage. No sutures are visible on the bones. 125852 A consists of the lateral part of the bone including most of the otic capsule (Fig. 1A). A large dorsal anteroposterior crest is present, damaged midway along its length. It extends for 3.1 mm along the anterolateral edge of the bone and projects posteriorly beyond the capsule. The height of the crest is slightly less than that of the capsule alone; its greatest height is 0.1 mm. Two anterior processes that articulated with the basal process of the palatoquadrate cartilage are broken distally, and the lateral border of the vestibular fenestra is preserved. The fenestra was 0.6 mm in diameter. Fragment B consists of the occipital condyle, including the calcified cartilage of the joint, and the posterior wall of the capsule including the postotic foramen. Fragment C is an indeterminate part of the ventral wall of the capsule.

The specimen is identical in all respects to the occipito-otic bone of *Aneides lugubris,* which is distinguished by the extreme development of the large dorsal crest. The fusion of the bones in the capsule identify it as a salamander. A crest is developed only rarely in salamander occipito-otics and only in *Aneides* is it found in the precise position seen on this specimen. As discussed by Wake (1963) and Larson et al. (1981), there is a morphocline among the species of *Aneides* in the development of this crest; it is least developed in the most primitive species (*A. aeneus*), well developed in *A. hardii* males, and highly developed in *A. lugubris.* The crest in *A. lugubris* is developed to the extent that this species can be distinguished from the other species of *Aneides* on this character alone.

This is only the second reported occurrence of *A. lugubris* in the fossil record. Hudson and Brattstrom (1977) reported fossils of this species from late Pleistocene deposits near Newport Beach, California. Subfossil remains are also known from deposits near Pacheco, California (UCMP locality V77117) but have not yet been reported in the literature.

Larson et al. (1981) examined the members of the tribe Plethodontini, which includes *Aneides,* using electrophoretic and immunological distance measurements to estimate their times of divergence. The results of these measurements were then compared with a cladistic analysis of morphological characters. The electrophoretic analysis suggests that *A. lugubris* diverged from *A. ferreus* and *A. flavipunctatus* approximately 17 m.y.b.p. whereas the immunological analysis places the same separation at about 23 m.y.b.p. The cladistic analysis also indicates that *A. lugubris* has many autapomorphies that distinguish it from its nearest relatives, so the oldest fossil record of this species indicates the minimum age at which it separated from the other species of the genus. The age of the fossil reported here is consistent with the biochemical estimates of Larson et al. in placing the minimum time of divergence of the *A. lugubris* lineage at approximately 5 m.y.b.p.

This specimen provides further evidence of the conservativeness of morphological evolution in salamanders. A recent critical summary of salamander fossils (Estes, 1981) reports the following fossil records of living species: *Andrias scheuchzeri* in the late Oligocene, *Salamandrina terdigitata* in the early Miocene, *Triturus marmoratus* in the middle Miocene, *Ambystoma maculatum* in the late Miocene, and *Ambystoma opacum* in the late Miocene (ages are following

Berggren and Van Couvering, 1974). Although it is impossible to assess these fossils using a biological species concept, the fact that they cannot be distinguished morphologically from modern species indicates that morphology at least is conserved.

A. lugubris occurs today in two populations (disregarding island populations) separated by the xeric Central Valley. The population on the eastern side of the valley inhabits the Sierra Nevada foothills and occurs in the Turlock Lake area today (Lynch and Wake, 1974). This population has been postulated to have migrated from the eastern San Francisco Bay area no earlier than the Pleistocene in order to explain why it has not spread into the entire range of its preferred habitat (Rosenthal, 1957). The Hemphillian age of the fossil renders this hypothesis chronologically invalid.

The Central Valley was occupied by a sea during the Miocene that effectively isolated the Sierra Nevada Mountains from the west (Cole and Armentrout, 1979). The seaway was drying up at approximately the same time as the fossil was deposited, so it is possible that the fossil represents the earliest immigrants across the developing land connections. An alternative hypothesis, that the Sierra population was once continuous with the western population along the northern end of the Central Valley, is contradicted by chromosomal evidence. The western population can be divided into two geographically separate chromosomal races, and the chromosomes of the Sierra population are similar to those of the southern race, which reaches only as far north as the San Francisco region (S. Sessions, unpublished). Whatever the history of this population before the time of the fossil, the lack of dispersal by *A. lugubris* into the range of its preferred habitat is not explained by the length of time it has occupied the Sierra Nevada foothills. Furthermore, the fossil is from near the southern end of the present range of the population whereas its preferred habitat extends farther south (Rosenthal, 1957), making its lack of dispersal even more pronounced.

Batrachoseps sp.

Referred Specimens.—UCMP 125362, a second trunk vertebra; LACMVP 121992, 121993, 121994, and 121996, trunk vertebrae; LACMVP 62020, 121995, and UCMP 82586, caudal vertebrae. Horizons and Localities: UCMP 82586—Pinole Tuff; UCMP locality V3425, Pinole 2. Others—As for *A. lugubris.*

Description and Discussion.—All of the vertebrae are notochordal and amphicoelous (although they were almost certainly opisthocoelous with a cartilaginous condyle as in the living forms; Wake, 1966).

UCMP 125362 is missing the right postzygapophysis and the tip of the left parapophysis but is otherwise complete (Fig. 2A). The dorsal surface is flat except for a low, anteriorly placed neural spine. The prezygapophyses are slightly bipartite, and a spinal nerve foramen occurs both anterior to and posterior to the diapophyses. The diapophyses project sharply posterolaterally along with the parapophyses so that they are at an angle of approximately 45 degrees with the lateral edge of the centrum. Ossifications are present between the ventral longitudinal midline and the ventral surface of the parapophyses, spanning longitudinal bilateral canals. There is an anterior process of the ventral surface of the right parapophysis and a similar process probably extended from the left side prior to breakage. These ventral ossifications have an eroded texture that is probably natural.

Among salamanders, only plethodontid second trunk vertebrae and (variably) salamandrid first trunk vertebrae have both anterior and posterior spinal nerve foramina (Edwards, 1976). The specimen is clearly a plethodontid and not a salamandrid owing to its gracile build, and no salamandrid has poste-

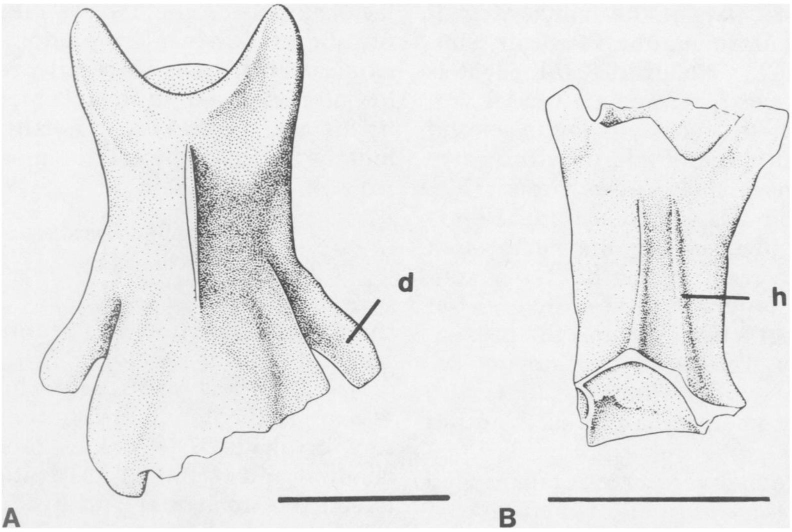

FIG. 2. A. Second trunk vertebra of *Batrachoseps* sp. from the Mehrten Formation (UCMP 125362) in dorsal view, anterior at top. B. Caudal vertebra of *Batrachoseps* sp. from the Pinole Tuff (UCMP 82586) in dorsal view, anterior at top. Abbreviations: D, diapophysis; H, hyperapophysis. Scale is one mm.

riorly deflected para- and diapophyses as in this specimen. The latter character is peculiar to the first two trunk vertebrae of *Batrachoseps* among plethodontids. All other features of the specimen, including the eroded texture to the ventral surface, are characteristic of this genus. However, it is not possible to refer this specimen to a species within the genus.

LACMVP 121992, 121993, 121994, and 121996 are trunk vertebrae with some portion of the laterally directed para- and diapophyses preserved. Specimen 121996 consists otherwise solely of a centrum, but the others retain some portion of the neural arch along with the centrum. Neural spines are absent. The prezygapophyses are slightly flared laterally, but are essentially anterior in orientation. There are small spinal nerve foramina posterior to the para- and diapophyses. The ventral surfaces lack any accessory ossifications and the parapophyses arise as horizontal ridges anteriorly.

The characteristics displayed by these four specimens are all found in *Batrachoseps*, but they are also seen in other genera of bolitoglossine plethodontids. None of these other genera occurs in California, however, and taken with the association of this material with unquestionable *Batrachoseps* material it is referred to that genus.

LACMVP 62020 is a complete anterior caudal vertebra (but not a caudosacral vertebra). Paired hyperapophyses extend anteriorly and slightly medially from small processes immediately dorsal to the postzygapophyses and meet medially at the anterior edge of the neural arch. The transverse processes are anteriorly placed and laterally directed, arising from horizontal longitudinal grooved ridges that gradually expand anteriorly. The hemal arch extends posteroventrally only as far as the posterior edge of the centrum and has a low longitudinal hypapophysis on its anteroventral surface. The tiny spinal nerve foramina are centrally located posterodorsal to the transverse processes. LACMVP 121995 is an intermediate caudal vertebra missing the left prezygapophysis and transverse process as well as the distal part of the hemal arch. It is slightly narrower but is basically similar to LACMVP 62020. UCMP 82586 is a posterior or intermediate caudal vertebra with the postzygapophyses and hemal arch missing and only the bases of the transverse processes present (Fig. 2B). It is similar to LACMVP 62020 except that the bases of the hemal arch extend the entire length of the centrum, the hyperapophyses converge but do not meet anteriorly, and the prezygapophyses are stouter and are not deflected as strongly laterally. It is also noticeably smaller than all of the other specimens.

These caudal vertebrae compare well with *Batrachoseps* in all of their characters. The convergence of the hyperapophyses is seen only in *Batrachoseps* and it is the only non-tropical plethodontid with anteriorly placed transverse processes (D. B. Wake, pers. comm.).

The great size of the Turlock Lake specimens relative to living *Batrachoseps* is worthy of note. Peabody (1959) noted that the *Batrachoseps* trackways from the lower part of the Mehrten Formation were made by a relatively large individual. The fossils reported here fall within the known size range of the genus but at the highest end; the trunk vertebrae have centra ranging in length from 2.2 to 2.6 mm. Their size is comparable to that of the largest available skeleton known to D. B. Wake, LACMH 36167, a specimen of *B. pacificus* with a snout-vent length of approximately 63 mm. Although the morphology of the specimens does not allow them to be identified to species, the great size of the Turlock Lake specimens suggests that they could be *B. pacificus*. It should be noted that *B. stebbinsi* (Brame and Murray, 1968) and *B. campi* (Marlow et al., 1979) reach a similar size.

These specimens represent the first published fossil remains of the plethodontid tribe Bolitoglossini. Although it is the largest tribe in the family both in numbers and in taxonomic diversity it is not surprising that it lacks a fossil record. Bolitoglossines are predominantly tropical, and fossils are rarely preserved or later exposed in tropical environments. *Batrachoseps* is the northernmost member of this tribe and the most primitive (Wake, 1966).

Family Plethodontidae,
Incertae Sedis

Referred Specimen.—LACMVP 121997, the proximal portion of a femur. Horizon and Locality: As for *A. lugubris.*

Description and Discussion.—The femur was approximately 6 mm in length before breakage. The sickle-shaped trochanter and rounded excavation between the trochanter and head of this specimen are characteristic of both salamandrids and plethodontids, and the anteroposterior narrowness of its head indicates that it is a plethodontid (Hecht and Estes, 1960). Femora of this type from the late Cretaceous were referred by Estes (1964) to *Prodesmodon*, but vertebrae referred to this genus lack a plethodontid spinal nerve foramen pattern (Edwards, 1976). Estes (1981) suggested that these femora may not belong to this taxon; it is therefore unclear whether this type of femur is restricted to the Plethodontidae. The occurrence of LACMVP 121997 with unquestionable plethodontid remains is sufficient reason to ignore this possible exception.

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