A New Species of *Batrachoseps* (Amphibia: Plethodontidae) from the San Gabriel Mountains, Southern California

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ABSTRACT. A new species of slender salamander, *Batrachoseps gabrieli,* is described based on specimens from two populations that occur in mixed coniferous forest at elevations of about 1,100–1,500 m in the San Gabriel Mountains, Los Angeles County, California. The new taxon is an attenuate species belonging to the morphologically more derived of the two clades in the genus. *B. gabrieli* is distinguished from other attenuate members of the genus by the combination of its relatively broad head, long limbs, wide feet, tapering tail of moderate length, and distinctive color pattern, including markings of bright pigmentation. Within the attenuate clade of *Batrachoseps* the species has no close relatives. In addition to its morphological and ecological distinctiveness, the species differs substantially from all other members of the genus in allozymes and mitochondrial DNA (cytochrome B) sequences. The species is apparently restricted to a small geographic area, and special attention should be given to its preservation.

INTRODUCTION

In the course of a continuing study of geographic variation and systematics of the slender salamanders, genus *Batrachoseps* Bonaparte, 1841, I unexpectedly discovered a strikingly distinct, undescribed species in the San Gabriel Mountains, Los Angeles County, California. The discovery at this late date of a new vertebrate that is both morphologically and ecologically distinctive in such a heavily populated and well-explored region is surprising.

DESCRIPTION OF NEW SPECIES

***Batrachoseps gabrieli,* new species**
San Gabriel Mountain Slender Salamander
Figure 1

HOLOTYPE. MVZ 196449, an adult female collected from under cover on a steep talus slope above Soldier Creek in the upper San Gabriel River drainage, approximately 1 km ESE Crystal Lake, San Gabriel Mountains, Los Angeles County, California. SW Section 28, R9W T3N. 34°18′47″ N, 117°49′57″ W. Approximately 1,550 m elevation. Collected on 28 March 1985 by David B. Wake, Nancy Staub, Samuel S. Sweet, Adonis Tate, Stephen G. Tilley, and Jennifer Tilley.

PARATYPES. MVZ 178631–178646, 195577–195583, 196450–196463, 215938, 215940–215946, 215948, 222957–222961, LACM 143239–143240, (total 53), all from vicinity of type locality, collected between 1982 and 1995. MVZ 178632, 178634, 178639, 178642, 195582–195583 are cleared and stained skeletal preparations.

REFERRED SPECIMENS. MVZ 223570–223571, from Rockbound Canyon, above highway 39, Los Angeles County, California. 34°18′02″ N, 117°49′57″ W. 1,158 elevation. Collected by R.H. Goodman, Jr. and S. Teh, 29 March 1996.

DIAGNOSIS. This member of the attenuate clade of *Batrachoseps* is a slender salamander of moderate size with a relatively broad head, long limbs, large hands and feet, and a markedly tapered tail, distinguished from its geographically nearest neighbors in the genus by these traits and by its color pattern of bright coppery to orange-colored diffuse stripes over the shoulders and in the pelvic region, becoming patches on the tail. It is distinguished from *B. nigriventris* Cope, 1869, by its larger size, its much broader and longer head, its much longer limbs and larger hands and feet, and its tapering tail. It is similar in size to *B. pacificus major,* Camp, 1915, but differs in having a more flattened head that is more sharply differentiated from the neck, much longer limbs, broader hands and feet, and a tapering tail.

DESCRIPTION. *Batrachoseps gabrieli* is a gracile, slender species that is relatively generalized in morphology, being of moderate size (8 adult males range from 39.8–46.3, mean 42.4 mm standard length; 16 adult females from 41.0–50.0, mean 46.1) and having a relatively broad, flattened head that is well demarcated from the neck (standard

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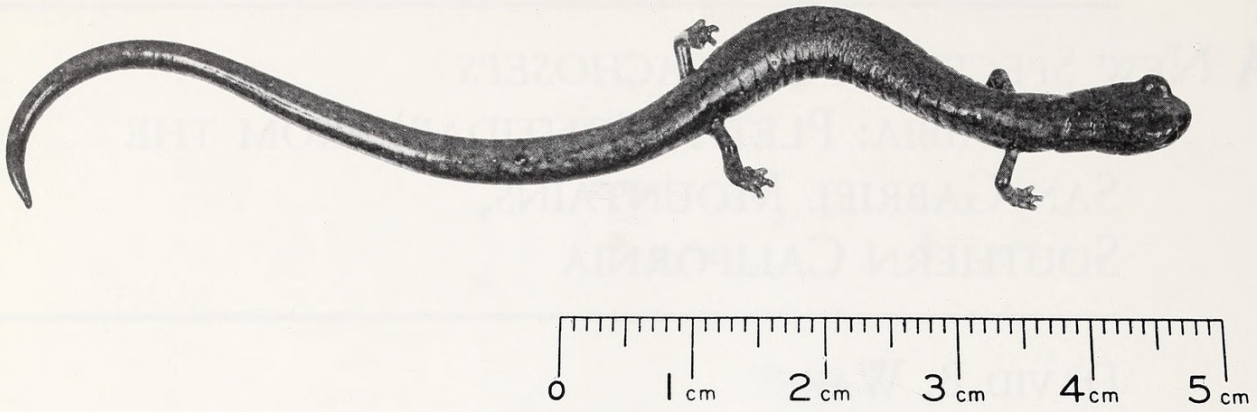

Figure 1. *Batrachoseps gabrieli,* new species. A paratype specimen (MVZ 196454) collected at the type locality on 28 March 1985.

length is 7.5–8.1, mean 7.7 times head width in males; 7.3–8.3, mean 7.8 in females). The species has a relatively large facial region, with a broadly rounded and somewhat flattened snout. Nostrils are small, and there are small nasolabial protuberances associated with the prominent nasolabial groove. Sexually mature males have engorged tissue around the anterior parts of the upper and lower jaws and snout, including somewhat enlarged nasolabial protuberances. No mental hedonic glands are observed in males. Grooving patterns of the head, throat, and neck are typical of the genus. Eyes are relatively large and prominent. Vomerine teeth are in short series, or, more commonly, in patches (19–35, mean 25.7 total in males; 13–29, mean 20.4 in females). Small maxillary teeth are borne in a short, single series that ends under the eye (25–69, mean 46.3 total in males; 30–51, mean 36 in females). Premaxillary teeth are small and relatively numerous (7–13, mean 9.9 in females; 4–10, mean 7.3 in males); those of males are slightly enlarged and far forward in position, piercing the upper lip. Numbers of trunk vertebrae vary from 19–20 (mean 19.5), with one individual having an asymmetrical pelvic articulation and 20.5 trunk vertebrae. Accordingly there are either 18 or 19 costal grooves between the limbs (counting one each in the axilla and the groin). The tail is moderately short compared with other members of this clade (1.14–1.37, mean 1.18 times standard length in females; 1.08–1.36, mean 1.24 in males), and it is narrow at its base; the tail tapers rather strongly to a fine tip. The tail has no discernible basal constriction and is broader than deep basally, becoming round posteriorly. No postiliac gland is evident. Limbs are relatively long and well developed. Limb interval, the number of costal interspaces between adpressed fore- and hind limbs, ranges from 5.5–7.5 (mean 6.5) in females, and from 4–6.5 (mean 5.5) in males. Hind limb length ranges from 4.8–5.8 (mean 5.2) times standard length in females, and from 4.7–5.0 (mean 4.9) in males. The hands and feet are relatively large and well developed for this clade, with well demarcated, stoutly rounded digits and expanded digital tips that bear well-developed subterminal pads. Webbing is insignificant. Fingers and toes in order of decreasing length are 3-2-4-1.

MEASUREMENTS OF THE HOLOTYPE (in mm). Maximum head width 5.9; snout to gular fold (head length) 9.5; head depth at posterior angle of jaw 2.8; eyelid length 2.4, eyelid width 1.5; anterior rim of orbit to snout 1.7; horizontal orbital diameter 2.0; interorbital distance 3.4; snout to forelimb 12.7; distance separating external nares 1.7; snout projection beyond mandible 0.9; snout to posterior angle of vent (standard length) 46.7; snout to anterior angle of vent 42.6; axilla to groin length 26.3; tail length 58.8; tail width at base 3.7; tail depth at base 2.8; forelimb length 7.7; hind limb length 8.0; limb interval 6; width of right hand 2.1; width of right foot 2.8; length of third toe 1.1; body width behind forelimbs 4.4. There are 11 premaxillary, 44 maxillary, and 26 vomerine teeth, and 20 trunk, 3 caudosacral, and 39 tail vertebrae.

COLORATION (in alcohol). This is a dark brownish black salamander that is marked with bright highlights over the shoulder and pelvic region and on the tail. There is not a complete mid-dorsal stripe in any of the specimens; most have a pair of stripes over the shoulder and another pair over the pelvic region, with streaks or patches of color on the dorsum and especially on anterior and middle parts of the dorsal surface of the tail. The venter is a more or less uniform gray-black with some small guanophore patches that are most prominent on the gular region.

COLORATION (in life). Coloration was studied in the holotype. The ground color was black with a complete reticulum of the melanophores. The dorsum and lateral surfaces of the trunk were darker than the ventral surfaces, but the venter was very dark as well. The dorsum was overlain by a layer of dense, coppery iridophores, which intensified and accumulated to form a large spot on the snout in front of the eyes and two short, broad

stripes over the shoulders. The stripes reappeared in the pelvic region and extended as broken stripes, then as blotches, onto the tail. The stripes were intensely orange (when viewed in bright light) in color. The overall impression of the dorsum was of a broad but irregularly bounded coppery-bronze stripe or band, intensified over the shoulders and in the pelvic region. The dorsal proximal parts of the limbs (limb insertions) were an intense coppery-orange. There were a few superficial whitish iridophores evident dorsally, with a few more laterally that extended ventrolaterally beyond the underlying whitish iridophores. The iridophores extended onto the venter where they were found as single cells and small groups of cells on the gular region. They became thinly scattered more posteriorly, and were almost absent in the middle of the abdomen. A scattering of whitish iridophores reappeared in the vent region and extended posteriorly onto the tail. White spots were strongly evident in the throat region. The venter of the tail was mainly black. The iris was dark brown.

There was, in general, great consistency in coloration of the specimens observed, with the pattern being almost constant and differences mainly relating to hue and intensity of color. The animals from Rockbound Canyon appear to be more vividly colored than those from the type locality, with the ground color being a deeper black and the light coloration being brighter and more evident.

OSTEOLOGY. Information concerning osteology is derived from six cleared and stained specimens, and from radiographs of many of the type series. The skull (Fig. 2) is typical of members of the attenuate clade (see below), with a single premaxillary bone, no prefrontal bone, and a large fontanelle. The frontal processes of the premaxillary are long and slender and may either remain separate or fuse to each other between the expanded and anteriorly protruding cartilaginous olfactory capsules, which approach each other closely and apparently squeeze the processes together. Distally the processes separate and broaden to extensively overlap the expanded anterior portions of the frontals. The nasals are large bones that overlap the well-developed septomaxillaries and frontals but fall slightly short of contacting the maxillary frontal processes. The latter do not contact any bones. The frontals are in contact between the eyes and for some distance posteriorly, so the fontanelle, while very large, is not so large as in some of the other attenuate *Batrachoseps* (illustrated in Marlow et al., 1979). The maxillaries are long and slender and bear small teeth in a single series that extends well posterior to the center of the eyeball. The parietals are well separated from each other, and they are narrow, short bones that fall short of the synotic tectum. There are no crests on the otic capsules, but there is a small ridge-like ledge above the articulation zone of the elongate, thin, and slender squamosals. The quadrate is also a relatively small bone, and the suspensorium is weak. The operculum either has no columellar rod, or it is reduced to a barely perceptible projection. The vomers are well articulated to each other and they bear a small preorbital process that varies among individuals. The process supports a row or more frequently a patch of vomerine teeth. The process is less well developed than in members of the robust clade of *Batrachoseps* but more prominent than in other members of the attenuate clade. Paired patches of teeth underlie the large parasphenoid bone. Each patch contains more than 100 tiny teeth. The lower jaw is slender and consists of the elongate dentaries and prearticulars, the latter having only a broad, low coronoid process.

The hyolingual skeleton is typical of the genus in being entirely cartilaginous, lacking the urohyal, having elongated radii, and having long epibranchials that extend under the skin of the neck and shoulder region as far posteriorly as the forelimb insertion.

There are 19 or 20 trunk vertebrae, the last one lacking ribs. There are two or three caudosacral vertebrae. In other plethodontid genera the last caudosacral is the first one to have a complete haemal arch, but in *Batrachoseps* the arch may be nearly complete on the second as well as the third postsacral, or be complete on one or the other. Tails of adults contain from 37 to 47 vertebrae, but several show evidence of regeneration.

The limbs are long, and the tibial spur is usually well developed and free, but it may be partly fused to the tibia. Phalangeal formulas are 1-2-3-2 for both hands and feet. The hands and feet are relatively broad and have well-developed terminal phalanges that are expanded and flattened (Fig. 3). The mesopodials have the standard arrangement for the genus (illustrated in Marlow et al., 1979). In most individuals the ulnare and intermedium of the carpus are fused or joined, but they may be separate. In one individual the intermedium and centrale are fused in both carpi and both tarsi.

HABITAT AND DISTRIBUTION. *Batrachoseps gabrieli* is known only from the immediate vicinity of the type locality and another nearby locality in the upper San Gabriel River drainage on the southern versant of the San Gabriel Mountain range. The type locality is on the southeast margins of a local flat (Pine Flats), about 1 km SE of a natural lake, Crystal Lake. The type locality is a talus slope on a spur of South Mt. Hawkins (2,372 m maximum elevation), which lies near the southern end of a ridge extending south about 4 km from the crest of the San Gabriel Mountains at Mt. Hawkins. The surrounding mountains form a large semicircular half-ring, open to the southwest, with a crest between 2,200 and 2,600 m. The talus slope faces northwest and is shaded by large Canyon Live Oak (*Quercus chrysolepis*) and Big Cone Spruce (*Pseudotsuga macrocarpa*). Other vegetation on the flat in the immediate vicinity includes Ponderosa Pine (*Pinus ponderosa*), Coulter Pine (*Pinus coulteri*), Jeffrey Pine (*Pinus jeffreyi*), Sugar Pine (*Pinus*

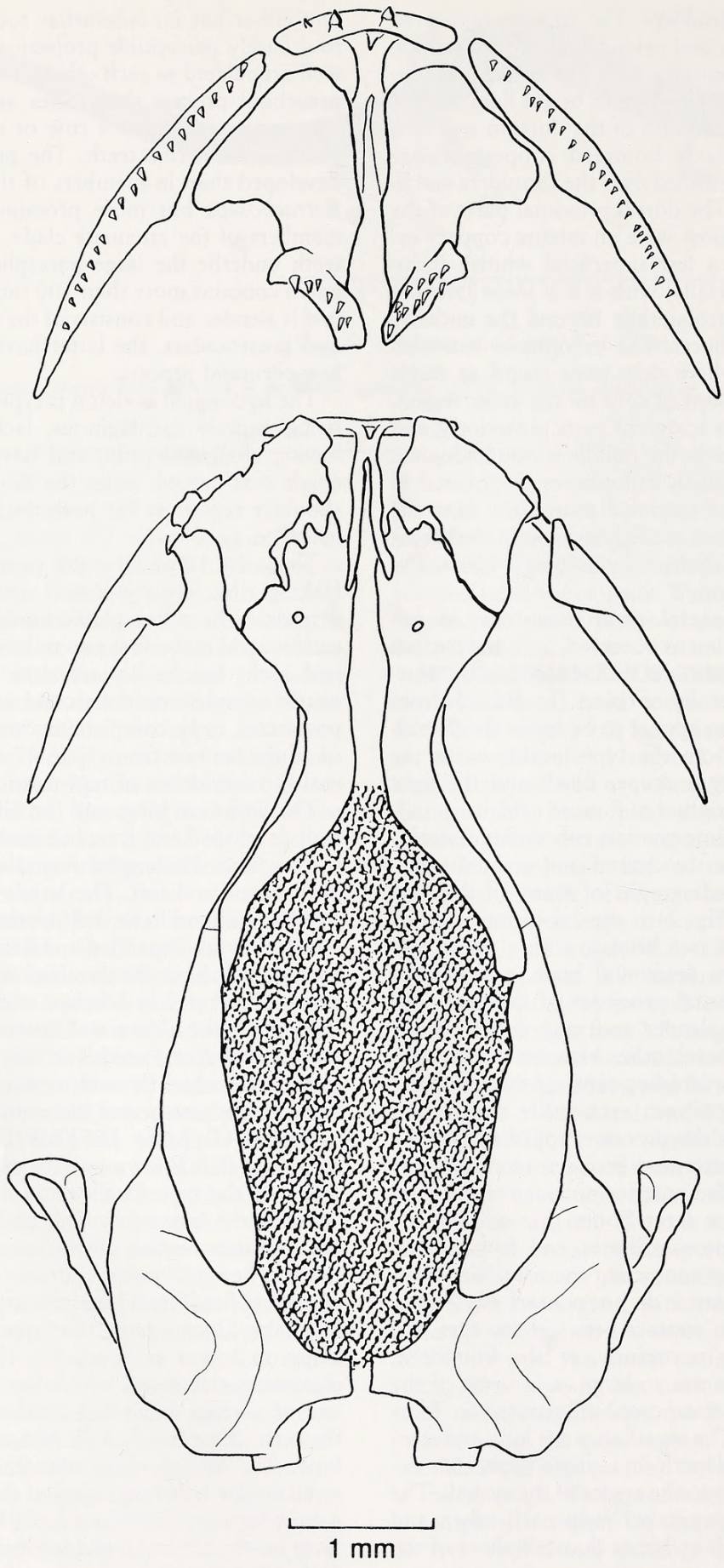

Figure 2. Skull of a specimen (MVZ 178634) of *Batrachoseps gabrieli*. Cartilage not shown. The entire dorsal surface of the skull is shown (below), and a ventral view of the premaxillary, maxillaries, and vomers is shown above. The dorsal fontanelle is shown in stipple.

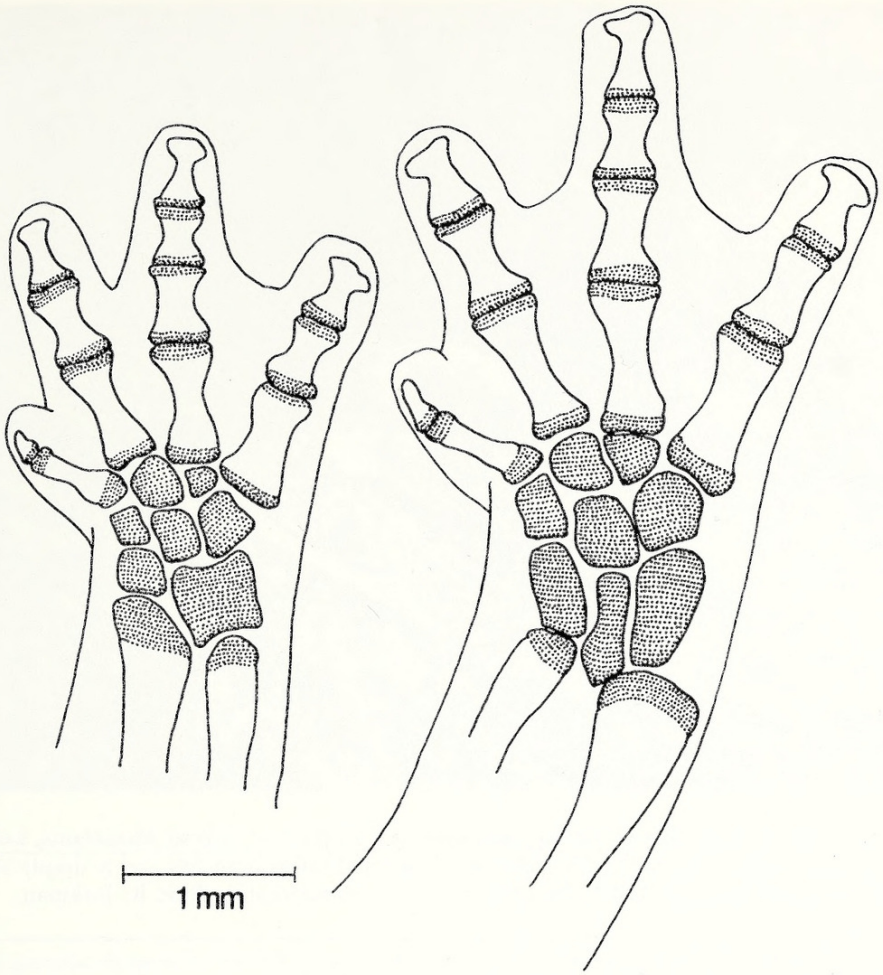

Figure 3. Right forelimb and right hind limb of a skeletal preparation of a specimen (MVZ 195583) of *Batrachoseps gabrieli*. Cartilage is stippled.

lambertiana), and White Fir (*Abies concolor*). Incense Cedar (*Calocedrus decurrens*), Black Oak (*Quercus kelloggii*), California Laurel (*Umbellularia californica*), and Oregon Big-Leaf Maple (*Acer macrophyllum*), as well as Western Sword Fern (*Polystichum munitum*) occur on the talus slope. Although this is a rich and diverse woodland, there are many openings in the forest where native bunch grasses and *Yucca whipplei* are common. Soldier Creek rises from springs at the base of the talus slope and has a strong winter flow but is dry at the type locality throughout most of the year.

All but a few salamanders were found on the steep talus slope, under large (ca 0.5 m long) rocks, rotting logs, or downed tree limbs and bark (Fig. 4). The salamanders were occasionally found under dried old fronds at the base of large ferns. A few were found on soil along Soldier Creek at the base of the talus slope, in sympatry with *Ensatina eschscholtzii eschscholtzii,* the only other salamander known to occur in the area. *Batrachoseps nigriventris* occurs at lower elevations (1,200 m) less than 1 km to the SW at Falling Springs, along Soldier Creek. *Aneides lugubris* has been taken a short distance below the type locality (2.6 km by air) at Coldbrook Camp (1,000 m), where both *Ensatina* and *B. nigriventris* are also found.

The activity of these salamanders near the surface is probably limited to a few winter and early spring months. At this elevation snow is present nearly every winter and may persist for one or two months. Salamanders have been observed in February and March when scattered snow banks were present. On 28 March 1985, when salamanders were abundant, the air temperature was 3.5° C. One small rock (10 × 20 cm) well set into the slope but resting on a surface of smaller talus rocks had a cavity beneath it that sheltered three adult salamanders. The soil temperature at this spot was 4.2° C. Summer and fall drought probably drives the animals deep into the talus slope.

Two specimens were collected on 29 March 1996, at a second locality, Rockbound Canyon, about a km to the S of the type locality, but at a lower elevation (1,158 m). One animal was found under a rock about 10 m from a small flowing stream, while the other was found under a log about 15 m from the stream. The species occurs in sympatry with *B. nigriventris* at this locality, and

Figure 4. The habitat at the type locality of *Batrachoseps gabrieli,* in the San Gabriel Mountains, Los Angeles County, California. The steep talus slope is covered with rocks, leaf litter, and fallen branches and is deeply shaded for most of the year. Photograph taken 19 February 1989. The collector in the photograph is Todd R. Jackman.

both species have been taken under the same log, but separated by an interval of one week.

BEHAVIOR. No salamanders have been observed active on the surface, but they have been found under some rather superficial cover. When salamanders are first uncovered they form a tight coil that then slowly relaxes. When coiled the animals appear to be stout and brightly colored dorsally, but shiny black when the coil is turned over. The species is alert and active; it rests in an s-shaped posture with its limbs outspread and it springs or leaps readily. The head is held above the substrate, and the eyes in life are strongly protuberant.

ETYMOLOGY. The species is named for the mountain range in which it is found. I recommend that the species name be pronounced gha-bree-el-ee.

DISCUSSION

There are two distinctive clades within *Batrachoseps.* Because of the relatively robust morphology of the body and limbs of the members, I refer to one of these as the robust clade; it includes only *B. wrighti* (Bishop, 1937) (central and northern Cascade Range, Oregon) and *B. campi* Marlow, Brode and Wake, 1979 (Inyo Mountains, California). I refer to the other as the attenuate clade; it includes the remaining species (seven currently recognized, including the new species, with approximately 8–10 to be described; Marlow et al., 1979; Yanev, 1980). *B. gabrieli* is a member of the more speciose, attenuate clade based on the osteological data reported herein.

Members of the attenuate clade of *Batrachoseps* are similar in osteology, and study of six skeletons of the new species reveals no especially distinctive features, although the feet are broad and well developed and the digits are stout, with especially well-developed and distally expanded terminal digits. The vomers of the new species have short but distinct, tooth-bearing preorbital processes. There is a single premaxillary bone, and prefrontal bones are absent. As is typical in this genus, there are 2 or 3 (usual condition in this species) caudosacral vertebrae. The dorsal fontanelle of the skull is broadly open, again a characteristic of the genus. Most species of *Batrachoseps* have a columellar rod of the operculum of moderate size, but none has been found in *B. gabrieli*; this may prove to be a useful derived trait, but its distribution has yet to be determined and it is difficult to observe.

The genus *Batrachoseps* is currently under study in my laboratory, and several manuscripts are in preparation that will extensively revise current taxonomy. The point of departure for this revision is the allozyme study by Yanev (1978, 1980), which compared 105 populations. Yanev (1980) presented

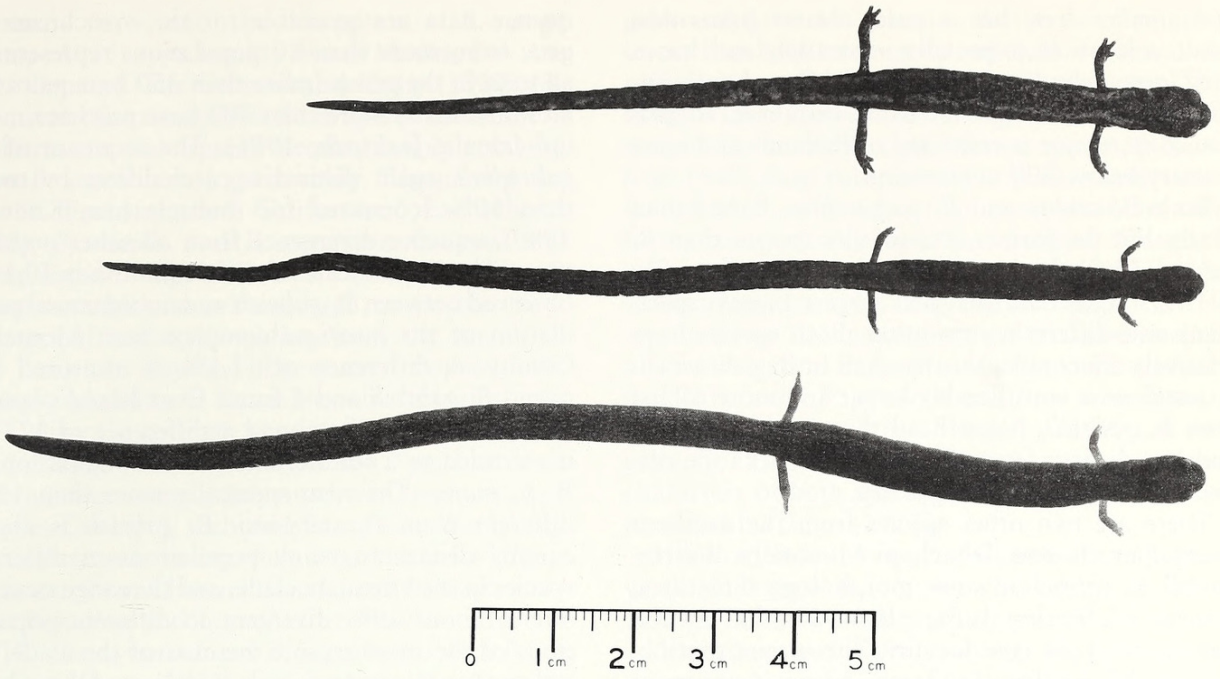

Figure 5. Photograph of three species of *Batrachoseps* that occur in close proximity in the mountains and adjacent lowlands of southern California, to show relative proportions. Top, *Batrachoseps gabrieli* (from type locality); middle, *B. nigriventris* (from Coldspring Camp, Los Angeles County); bottom, *B. major* (from lower Ortega Highway, Orange County).

a phenogram of genetic distances for 18 "taxonomic units" but recognized only seven species, one of which was indicated as "sp. nov." in her figures 1 and 2, but which was named *Batrachoseps campi* (Marlow et al., 1979) by the time Yanev's paper was published. Yanev had no samples of an eighth species, *Batrachoseps aridus* Brame, 1970, which she predicted (correctly, based on new but unpublished allozyme and mtDNA data from my laboratory) would be found to be a close genetic relative of her superspecies complex *Batrachoseps pacificus* (Cope, 1865) (and not close to *B. stebbinsi* Brame and Murray, 1968, which Brame, 1970, thought was the closest relative of *B. aridus*). Yanev showed that the coastal attenuate taxa replace one another in a series of parapatrically distributed units having almost non-overlapping ranges that extend from southwestern Oregon to northwestern Baja California. Work in progress in my laboratory (using data from allozymes, mtDNA sequences, and morphology) will document even more extensive taxonomic diversity than Yanev (1980) reported.

Several allopatric and parapatric populations of varying degrees of morphological distinctiveness were considered by Yanev (1980) to be semispecies; she chose to recognize these taxonomically as subspecies of a widespread superspecies, *B. pacificus*. I recognize four species of *Batrachoseps* in southern California below the region of the Santa Paula River: *B. aridus, B. gabrieli, B. nigriventris,* and *B. pacificus*. There are two morphologically and biochemically distinct taxa of the *pacificus* superspecies in southern California, *B. p. pacificus* and *B. p. major.* Three taxa occur in the San Gabriel River drainage of the San Gabriel Mountains: *B. gabrieli, B. p. major,* and *B. nigriventris,* and the latter two occur in sympatry at several localities on the southern California mainland (Brame, 1970). The other taxa are more restricted in distribution. *B. aridus* has been found in two canyons on the north and east margins of the Santa Rosa Mountains in the Colorado Desert, and *B. p. pacificus* occurs on the northern Channel Islands. *B. p. major* is found on the southern Channel Islands as well as on the mainland, and *B. nigriventris* occurs in sympatry with *B. p. pacificus* on Santa Cruz Island. Distribution of southern California *Batrachoseps* has been summarized and mapped by Brame and Murray (1968), Brame (1970) (their *B. attenuatus* (Eschscholtz, 1833) in southern California is present-day *B. nigriventris*), and Stebbins (1985).

The most slender, narrow-headed, and short-limbed of these five taxa is *B. nigriventris,* a species associated with upland habitats, mesic habitats, or both, in southern California. This species occurs in sympatry with *B. gabrieli.* The two species differ sharply in morphology, with *B. gabrieli* having a much broader head, longer limbs, larger hands and feet, a shorter, more tapering tail, and a distinctive color pattern (Fig. 5). The species overlap in numbers of trunk vertebrae, but *B. gabrieli* usually has one or two fewer than *B. nigriventris.*

While *B. p. major* has a relatively broad head and gets larger than *B. gabrieli,* it has shorter limbs

and smaller feet, has a pale, almost patternless adult coloration (especially ventrally), and has a very long, cylindrical tail (Fig. 5). *B. gabrieli* usually has one to two fewer trunk vertebrae. In general, *B. p. major* is restricted to flatlands and open country below 700 m elevation.

Both *B. aridus* and *B. p. pacificus* have broad heads, but the former is a smaller species than *B. gabrieli* (the holotype of *B. aridus,* at 48.4 mm SL, is 18% larger than the next largest known specimen) and differs in coloration. Both species have relatively short tails, shorter than in *B. gabrieli. B. p. pacificus* is considerably larger and more robust than *B. gabrieli,* has a head that is less flattened and less distinct from the neck, and lacks the distinctive coloration of *B. gabrieli.*

There are two other species from the southern Sierra Nevada and Tehachapi Mountains that resemble *B. gabrieli* in some morphological features, the closest locality being about 100 km to the northwest of the type locality. The species that occurs at this locality (Ft. Tejon, where it occurs in sympatry with topotypic *B. nigriventris*) is assigned tentatively to *B. stebbinsi.* It is a talus-dweller and resembles *B. gabrieli* in proportions and even in some aspects of its color pattern (patches of bright pigmentation on the tail). It is larger and more robust, however, and has longer limbs and a larger, more rounded head. The two species have equivalent numbers of trunk vertebrae, but *B. stebbinsi* has a shorter tail. The other species, *B. simatus* Brame and Murray, 1968, from the lower Kern River Canyon, attains larger size than *B. gabrieli* and has 21–22 trunk vertebrae. It has a broad, flattened head, like *B. gabrieli,* but has longer limbs and a more gracile appearance. While it has a tapering tail of similar relative length to that of *B. gabrieli,* it lacks the distinctive color pattern of the latter.

Much unpublished allozyme and mtDNA sequence data exist for *Batrachoseps,* and they will be published in detail elsewhere by me and others. Here only some results relevant to the new taxon are presented. *Batrachoseps gabrieli* is highly differentiated genetically from all other taxa, such that it is not possible to infer what its sister taxon might be. Nei's genetic distances (D_N) derived from allozyme studies (for details of methods see Yanev and Wake, 1981; Nei, 1972) are all large. The lowest value of D_N to any other taxon is $D_N = 0.65$, which is measured to different populations of *B. p. major* and to the Ft. Tejon population tentatively assigned to *B. stebbinsi.* There are fixed differences separating the taxa at 12 of the 26 allozymic loci sampled. Smallest D_N to other taxa are: *B. nigriventris* 0.70, *B. p. pacificus* 0.71, *B. aridus* 0.86, *B. simatus* 0.94.

With respect to mtDNA sequences, differentiation is also great, with no obvious close relatives, although it falls within a *pacificus* complex (including the *B. pacificus* superspecies of Yanev, 1980, and *B. aridus*; Jockusch, 1996). Unpublished sequence data are available for the cytochrome B gene from more than 80 populations representing all taxa in the genus (more than 350 base pairs for all individuals, more than 700 base pairs for most individuals; Jockusch, 1996). The sequence of *B. gabrieli* is again distinctive, and differs by more than 10% (corrected for multiple hits; Kimura, 1980) sequence divergence from all other populations. The lowest level of differentiation is 10.1%, observed between *B. gabrieli* and an unnamed population of the *pacificus* complex from Monterey County. A difference of 11.1% is measured between *B. gabrieli* and a Santa Cruz Island population of *B. p. pacificus,* and a difference of 12.0% is recorded to a southern California population of *B. p. major.* The new species is more than 15% different from *B. stebbinsi. B. gabrieli* is about equally distant to many populations of different species in the attenuate clade, and the range extends out to about 20% divergent to different populations of the most remote member of the clade, *B. attenuatus.* Divergence from members of the robust clade is even greater and ranges from 23.6–36.5%.

The conclusion from the genetic data is that *B. gabrieli* is strikingly distinct relative to all congeneric taxa and populations. Various methods have been used to calibrate a "molecular clock" for allozymes. Yanev (1980), following Sarich (1977), used a calibration of $D_N = 1$ being equivalent to about 20 million years of divergence. Calibrations are most appropriate when based on independent geological events and inferred vicariant events (e.g., as in Good and Wake, 1992). Yanev showed a relatively good correspondence between inferred vicariant events (based on geological dating) and her molecular clock estimates. If we use her calibration we obtain a divergence time of *B. gabrieli* from other extant members of the genus of about 13 million years. If we use a more conservative estimate based on comparisons from several plethodontid genera of allozymic data with albumin immunological distances (Maxson and Maxson, 1979), we obtain a time of about 9 million years; this is approximately what would be obtained from use of the independent calibration for a non-plethodontid salamander, *Rhyacotriton* (Good and Wake, 1992). Another calibration for the salamandrid genus *Taricha* (Tan, 1993) yields a slightly shorter time. So, under any time estimation scheme currently available, *B. gabrieli* represents a lineage that has been separated from other lineages within the genus for a very long time, perhaps for 8 to 13 million years.

TAXONOMIC COMMENTS. The *Batrachoseps* of southern California have long confused taxonomists, and the resultant taxonomic history is complex. Cope (1865) described *B. pacificus* (type locality listed as Santa Barbara, considered to be an error by Van Denburgh, 1905, who assumed the type specimen was obtained from the northern Channel Islands). Later Cope (1869) described *B. nigriventris* (type locality Ft. Tejon, Kern County). The California species of the genus were ignored

for many years, until the description of *B. major* (Camp, 1915; type locality Sierra Madre, Los Angeles County). The Grinnell and Camp (1917) distributional list recognized three species in southern California: a wide-spread slender, mainly northern form *B. attenuatus* (type locality "Umgebung der Bai St. Francisco auf Californien" Eschscholtz 1833), *B. major,* and *B. pacificus.* Grinnell and Camp listed *B. nigriventris* as a synonym of *B. attenuatus,* which was considered to be the most widespread taxon, extending from the region of San Francisco Bay and the western slopes of the central and southern Sierra Nevada through southern California and into northwestern Baja California (although they carefully noted "south at least to mountains immediately north of Claremont, Los Angeles County"), including Santa Catalina Island. *B. pacificus* was known only from the three largest of the northern Channel Islands, and *B. major* only from Pasadena and Sierra Madre. Fowler and Dunn (1917) also synonymized *B. nigriventris* with *B. attenuatus.* Dunn (1922) described two more insular species, *B. leucopus* Dunn, 1922 (type locality Los Coronados, North Island) and *B. catalinae* Dunn, 1922 (type locality Santa Catalina Island). Storer (1925) recognized four species: *B. pacificus* from the northern Channel Islands, *B. catalinae* from Santa Catalina Island (which he believed was a valid species), *B. major* from Los Angeles and Riverside counties, and *B. attenuatus,* which was listed from Ft. Tejon, the Santa Monica Mountains, and the mountains north of Claremont. Storer also included specimens from the Sierra San Pedro Martir in northern Baja California, Mexico, in *B. attenuatus,* and noted that the species had been recorded, but not confirmed, from La Paz, Baja California. Storer made no comment concerning *B. leucopus,* presumably because it occurred only in Mexico and was not part of the California fauna.

In his famous monograph on plethodontid salamanders, Dunn (1926) reduced all taxa of *Batrachoseps* to subspecies of *B. attenuatus,* commenting that "the forms of *Batrachoseps* present rather a problem to the systematist, the question being how many forms to recognize and on what characters. There is apparently no overlapping of ranges and the species is one with a number of more or less emphasized local races, and with very indefinite and variable characters" (p. 230). Dunn placed salamanders from San Diego Co. and the Sierra San Pedro Martir Mountains of northern Baja California in *B. a. leucopus.* His *B. a. attenuatus* occurred as far south as the Santa Monica and San Gabriel mountains, while *B. a. major* occurred in Los Angeles, Riverside, and Orange counties. Finally, *B. a. catalinae* was restricted to Santa Catalina Island.

Slevin (1928) followed Dunn (1926) in most respects, but he synonymized *B. a. catalinae* with *B. a. attenuatus,* extended the range of the latter southward to Laguna Beach, Orange Co., and eastward to San Bernardino, San Bernardino Co., and considered *B. a. major* to be restricted to Los Angeles and Riverside counties. At the time few specimens had been examined, and field work was insufficient to resolve the taxonomic problems. This situation was corrected by Campbell (1931), whose revised taxonomy recognized two species, *B. pacificus* (with three subspecies: *pacificus, major, catalinae*) and *B. attenuatus* (with two southern California subspecies: *attenuatus, leucopus*). Campbell was familiar with the organisms in the field, and he studied large samples of preserved specimens. He reported two instances of sympatry: 1) between *B. a. attenuatus* and *B. pacificus* on Santa Cruz Island, and 2) between *B. p. major* and *B. a. attenuatus* in South Pasadena and the Monterey Hills, Los Angeles Co. His *B. a. leucopus* was said to express characters of both species, and the range was that recorded by Dunn (1926).

Hilton (1945) overlooked Campbell's important work and regressed to the taxonomy of Slevin (1928). Hilton's work is characteristically erratic, adding some useful observations, but in some respects confusing matters. For example, he reports that *B. a. major* occurs at higher elevations than his *B. a. attenuatus,* while the reverse is true.

Lowe and Zweifel (1951) and Stebbins (1951) agreed that there were two species in southern California and reported three sites at which they occur in sympatry, the two reported by Campbell (1931) and a third near Irvine Park, Orange Co. However, these authors thought they detected evidence of an intermixing or introgression southeast of Redlands in San Bernardino Co. Stebbins (1951) treated *major* and *catalinae* as subspecies of *pacificus,* and *leucopus* as a subspecies of *attenuatus.*

A monographic study by Hendrickson (1954) was regressive. He simplified taxonomy by recognizing a single species in southern California, *B. attenuatus,* with two subspecies, *pacificus* (including *major*) and *attenuatus.* While he accepted that there was some sympatry, he felt that there was substantial intergradation and treated the population reported by Lowe and Zweifel (1951) and Stebbins (1951) from near Redlands as a hybrid swarm. Hendrickson referred to a taxonomically awkward category of "intermediate" populations, which encompassed *leucopus, catalinae,* and, in part, *major.*

Savage and Brame undertook a detailed study of southern California *Batrachoseps* in the 1950s and produced a still unpublished manuscript that has influenced subsequent taxonomy. Peabody and Savage (1958), citing the above manuscript, returned to the Campbell (1931) taxonomy, except that *leucopus* was considered to be a subspecies of *pacificus* instead of *attenuatus,* and *catalinae* was not recognized as distinct and was placed in the species *B. pacificus.* Brame and Murray (1968) showed that *major* and *pacificus* were morphologically distinct and recognized them as separate species. Their *B. pacificus* was restricted to the northern Channel Islands, while *B. major* (including *leucopus* and *catalinae*) was said to occur on the mainland south

of the Santa Monica and San Gabriel mountains, and on the southern islands: Santa Catalina, Los Coronados, and Todos Santos. They also reaffirmed the distinctiveness of *B. attenuatus* and *B. major,* but referred the Santa Cruz Island population formerly assigned to *B. attenuatus* to a new species, *B. relictus* Brame and Murray, 1968 (type locality in Kern River Canyon, Kern County). The *Batrachoseps* in the Sierra San Pedro Martir also were assigned to *B. relictus.* Later Brame (1970) described *B. aridus* (type locality Hidden Palm Canyon, Riverside County).

Starting in the 1970s, genetic (allozymic) studies of the genus were undertaken by Yanev, and these remain largely unpublished. However, a general summary of her findings, published in 1980, has influenced present taxonomy (see especially Stebbins, 1985). She showed that *B. nigriventris* is distinct from *B. attenuatus* (which does not extend below central California), and she assigned the Santa Cruz Island population considered by Brame and Murray as *B. relictus* to *B. nigriventris.* She reduced *relictus* and *major* (of Brame and Murray, 1968) to subspecies of *B. pacificus.*

At present I recognize the following taxa of *Batrachoseps* in southern California and adjacent Mexico:

1. *B. p. pacificus* occurs on San Miguel, Santa Rosa, Santa Cruz, and the Anacapa Islands (but not on Santa Barbara Island, as sometimes indicated).

2. *B. p. major* (including *catalinae* and *leucopus,* which I consider to be subjective junior synonyms) occurs on the mainland and on the following southern islands: Islas Todos Santos, Islas Coronados, and Santa Catalina. I tentatively include the populations in the Sierra San Pedro Martir (assigned to *B. relictus* by Brame and Murray, 1968, and identified as an unnamed new subspecies by Yanev, 1980) in this taxon (as did Stebbins, 1985). *B. p. major* is widespread in the open lowland areas of southern California. These areas are now heavily populated, with accompanying habitat destruction, and the once common salamanders are difficult to find in much of the region. *B. p. major* occurs well to the east, near Cabazon and in Palm Springs, relatively near to the type locality of *B. aridus* (Cornett, 1981). As shown by Brame and Murray (1968), the two subspecies of *B. pacificus* are morphologically distinct (*B. p. pacificus* has a broader head, longer limbs, a shorter tail, and is more similar to *B. gabrieli* in appearance than is the more cylindrical, elongate, and paler *B. p. major*). However, pending completion of studies in progress, I continue to use the taxonomy of Yanev (1980).

3. *B. nigriventris* occurs on Santa Cruz Island and in upland and more mesic coastal zones, and in the San Gabriel Mountains. The map presented by Brame (1970) for *B. attenuatus* shows most of the currently known range of *B. nigriventris* in southern California. It is the slender, dark-bellied, short-limbed species of upland regions, and it occurs in sympatry with *B. p. major* at various places in Los Angeles and Orange counties, including the Baldwin Hills, the Palos Verdes region, the Monterey Hills, the Puente Hills, and the Chino Hills. It also occurs in the San Joaquin Hills and along the coast as far south as Aliso Creek, Orange Co., and we recently found it in Tenaja Canyon, extreme southwestern Riverside Co., the southeastern limit of its known distribution.

4. *B. aridus* is found only in two isolated desert canyons, the type locality in Hidden Palm Canyon and in Guadelupe Canyon. This species is distinguished from *B. pacificus major,* which is the closest geographical neighbor, by its smaller size, broader head, and much shorter tail, and by its distinctive color pattern (brightly colored flecks which form poorly bounded patches, well displayed in the illustration in Brame and Hansen, 1994).

5. *B. gabrieli* is known only from the two localities reported herein in the San Gabriel Mountains.

CONCLUDING REMARKS. I was surprised to discover that the population on which this species is based was highly differentiated genetically from all other populations with which it was compared. Apparently this species is restricted to the general vicinity of the type locality. A number of apparently suitable microhabitats in the San Gabriel Mountains have been searched unsuccessfully. Given this limited distribution and deep differentiation, I infer that the species is a relic that requires special protection. The habitat is restricted and fragile, and special efforts should be taken to protect the area. The known habitat, two small areas of about one hectare in extent, are vulnerable. The type locality lies on the margins of a once developed recreation area in the vicinity of several large springs. The old development has been totally removed except for some nearby stone foundation remnants, but the area has been subject to disturbance from casual human use. The type locality is in the Crystal Lake Recreation Area of Angeles National Forest, and I urge administrators of the forest and the California Resources Agency to give special protection to the region.

I believe that the genus *Batrachoseps* is tropical in origin and that it has moved to the northwest from its origins in association with the complex movements of the crust of this planet over a period of many years (Hendrickson, 1986; Wake, 1987). This new population was discovered by chance, and it is possible that more undiscovered populations exist in southern California. I urge that special attention be given to careful exploration of southern California and adjacent Mexico for additional populations of this genus.

Batrachoseps is comprised of a large number of genetically differentiated groups, and the current taxonomy is inadequate to express the extent of the evolutionary diversification of the lineage. The new species described herein adds another entity to this complex group. Work in progress in my laboratory will explore the evolutionary history of this lineage.

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