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New Species of Slender Salamander, Genus *Batrachoseps*, from the Southern Sierra Nevada of California

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Populations of robust salamanders belonging to the plethodontid salamander genus *Batrachoseps* (subgenus *Plethopsis*) from the southern Sierra Nevada and adjacent regions represent a previously unknown species here described as *Batrachoseps robustus.* The new species is robust, with a short trunk (17–18 trunk vertebrae) and well-developed limbs. It differs from its close geographic neighbor, *Batrachoseps campi*, in lacking patches of dorsal silvery iridophores and in having (typically) a lightly pigmented dorsal stripe, and from *Batrachoseps wrighti* in being more robust, having more trunk vertebrae, and in lacking conspicuous white spots ventrally. This species is widely distributed on the semiarid Kern Plateau of the southeastern Sierra Nevada and extends along the east slopes of the mountains into the lower Owens Valley; it also is found to the south in the isolated Scodie Mountains. It occurs at high elevations, from 1615–2800 m, in areas of low rainfall and high summer temperatures.

THE slender salamanders, *Batrachoseps*, range from the Columbia River in northern Oregon (45°33′N) to the vicinity of El Rosario, Baja California Norte (30°00′N). These salamanders were considered to display mainly intraspecific morphological variation, and for many years only two (Hendrickson, 1954) or three (Stebbins, 1951) species were recognized. Brame and Murray (1968) and Yanev (1980) demonstrated that several to many additional species should be recognized. Some of these represent subdivision of existing taxa based on new information, mainly allozyme and mitochondrial DNA (mtDNA) characters (e.g., Jockusch et al., 1998, 2001), but new discoveries of morphologically distinct forms, such as *Batrachoseps aridus*, *Batrachoseps campi*, and *Batrachoseps gabrieli*, have also led to increases in the number of recognized species. Here we describe a morphologically and genetically distinct species from the southern Sierra Nevada that was discovered many years ago but misidentified as *Batrachoseps stebbinsi* (Richman, 1973). Until recently, we were unsure of the geographic limits of the taxa represented, but now sufficient information is available to justify description of a strikingly distinct and previously unknown species. The new species initially was thought to be restricted to the Kern Plateau region of the southeastern Sierra Nevada, east of the Kern River (as reported and illustrated in Stebbins, 1985). Later, populations were found in the Scodie Mountains, to the southeast, and in Owens Valley. We now think that all of these populations, which display substantial morphological (especially coloration) variation and range in elevation from about 1600 to 2800 m, are conspecific. They occur in relatively extreme environments for terrestrial salamanders, in areas that are exceptionally hot and dry in the summer, and that have a short, unpredictable wet season with little rainfall. Some of them occur at high elevations that are under snow cover for several months each year.

This new species is a member of the genus *Batrachoseps* because it has four toes on the hind limb, a large cranial fontanelle, and an elongated genioglossal muscle. Furthermore, it is a member of the subgenus *Plethopsis* and a relative of both *Batrachoseps* (*Plethopsis*) *wrighti* and *Batrachoseps* (*Plethopsis*) *campi* on the basis of a phylogenetic analysis of sequences of the mitochondrial gene cytochrome *b* (Jackman et al., 1997; Jockusch and Wake, 2002).

Materials and Methods

All specimens used in this study, with the exception of a single specimen mentioned in the text, were collected from the field for this study. Morphological data were taken as in Wake (1996). All measurements are in millimeters, only clearly visible teeth are counted, and standard length (SL) is the distance from the tip of the snout to the posterior angle of the vent. Pertinent morphological measurements are presented in Table 1. We measured 10 adult males and 10 adult females of the new species and of its closest relatives, *B. campi* and *B. wrighti.* Sample sizes for the new species and *B. campi* were too small for us to obtain 20 adults from a single population; thus, we were forced to combine samples from two or more populations. We know that all of these species are variable geo-

TABLE 1. MEASUREMENTS AND TOOTH COUNTS OF THE THREE MEMBERS OF SUBGENUS *Plethopsis*. All $n = 10$ except foot width of *Batrachoseps wrighti* females ($n = 7$) and males ($n = 5$).

Species	Standard length ± SD, range	SL/tail length ± SD, range	SL/head width ± SD, range	SL/hind limb length ± SD, range	Foot width ± SD, range	Limb interval ± SD, range	Premaxillary teeth ± SD, range	Maxillary teeth ± SD, range	Vomerine teeth ± SD, range
B. robustus females	58.2 ± 2.1	1.3 ± 0.1	8.6 ± 0.3	5.4 ± 0.1	3.7 ± 0.4	6.3 ± 0.4	9.9 ± 3.4	53.6 ± 9.3	28.2 ± 7.4
	55.2–61.3	1.1–1.4	8.2–9.2	5.3–5.6	2.9–4.2	6–7	6–15	42–73	20–45
B. robustus males	51.9 ± 4.4	1.2 ± 0.1	7.8 ± 0.3	4.7 ± 0.3	3.3 ± 0.4	4.6 ± 0.7	4.4 ± 1.4	54.0 ± 7.7	23.9 ± 3.4
	43.0–58.9	1.0–1.4	7.1–8.2	4.1–5.0	2.7–3.8	4–6	2–7	38–65	18–28
B. campi females	53.0 ± 4.0	1.3 ± 0.1	7.3 ± 0.3	4.8 ± 0.2	3.4 ± 0.4	4.4 ± 0.7	12.7 ± 2.1	63.7 ± 7.8	21.4 ± 4.4
	46.7–60.7	1.2–1.5	6.7–7.9	4.5–5.1	2.8–4.0	3.0–5.5	10–16	56–74	17–32
B. campi males	44.9 ± 3.8	1.3 ± 0.1	6.8 ± 0.2	4.5 ± 0.3	2.7 ± 0.5	3.4 ± 0.7	6.7 ± 1.3	47.6 ± 11.7	17.7 ± 3.1
	40.7–51.7	1.2–1.4	6.6–7.2	4.2–5.1	2.1–3.3	2.5–4.5	5–9	27–58	13–21
B. wrighti females	45.1 ± 5.9	1.0 ± 0.1	8.4 ± 0.6	5.4 ± 0.6	2.5	6.9 ± 1.0	6.7 ± 2.0	36.9 ± 13.2	22.9 ± 7.0
	38.8–60.1	0.9–1.3	7.6–9.1	4.6–6.2	2.3–2.7	5.5–8.5	3–10	23–66	13–39
B. wrighti males	42.0 ± 2.5	0.9 ± 0.2	8.0 ± 0.3	5.2 ± 0.2	2.4	6.1 ± 0.6	2.9 ± 1.1	24.2 ± 15.4	20.1 ± 7.6
	39.0–47.6	0.7–1.3	7.4–8.4	4.9–5.5	2.3–2.5	5–7	1–5	0–38	10–31

graphically to some extent (e.g., Brame, 1964; Yanev and Wake, 1981); hence caution should be used in using the data in Table 1. We included the type specimens of all three species in the comparison, as well as the largest specimens of each species that we were able to find in collections. We studied 26 allozymes, using standard methods (Yanev and Wake, 1981; Jackman and Wake, 1994). Exact locality information and sample sizes for the electrophoretic study are provided in Table 2. Abbreviations for the proteins studied (Table 3) generally follow Murphy et al. (1996). Genetic distances reported (Table 4) are based on Nei (1978). Genetic distances between haplotypes of the mitochondrial gene cytochrome *b*, given as Kimura (1980) two-parameter distances, are from Jockusch and Wake (2002). Institutional abbreviations are as listed in Leviton et al. (1985). Collection information for museum specimens can be found on the MVZ (http://www.mip.berkeley.edu/mvz/) and CAS (http://www.calacademy.org/) websites.

DESCRIPTION OF NEW SPECIES

Batrachoseps robustus, sp. nov.
Kern Plateau Salamander
Figures 1–3

Holotype.—MVZ 219115, an adult female from 3.4 km south-southeast Sherman Pass Road on USFS rd 22S19, approximately 4.4 km (air) north-northwest Sirretta Peak; approximately 0.9 km (air) southeast Round Meadow on Kern Plateau, Tulare County, California (T22S, R34E, Sect. 31), 2775–2800 m elevation, 35.9604°N, 118.3514°W. Collected by R. Gonzales and R. W. Hansen on 13 July 1991.

Paratypes.—MVZ 219116, 219119–219120, 219122, 219124–219126, 219128–219129, 219131 same data as holotype; MVZ 158288–158300, 1.6 km southeast Osa Meadow, Kern Plateau, Tulare County, CA, 36.1715°N, 118.2939°W; MVZ 158315, 2.9 km northeast Beach Meadows Guard Station, 2.7 km (rd) N Blackrock Rd, Kern Plateau, Tulare Co, CA, 36.1472°N, 118.2692°W; MVZ 158339, 1.6 km (air) N Granite Knob, Kern Plateau, Tulare County, CA, 36.1670°N, 118.2257°W; MVZ 185996–186000, 186002–186005, approximately 8 km (air) west-northwest Chimney Peak, upper part of Long Valley, 1.5 km (rd) south Rockhouse Basin Road on Long Valley Road, Kern Plateau, Tulare County, CA, 35.8832°N, 118.1177°W; MVZ 219134, 219136–219140, Brush Creek Overlook Road (USFS Rd 23S14), approximately 4.8 km south-southeast Burton

TABLE 2. SAMPLES USED FOR ALLOZYME STUDY.

Population	Species	*n*	Locality	MVZ#
1	*B. robustus*	8	Walker Creek	202331–36
2	*B. robustus*	10	Hogback Creek	202362–71
3	*B. robustus*	13	Osa Meadows	158288–300
4	*B. robustus*	3	Blackrock Road	158315–17
5	*B. robustus*	6	Kennedy Meadow	158318–21
6	*B. robustus*	7	Burton Camp	158307–13
7	*B. robustus*	2	Horse Meadow	158338–40
8	*B. robustus*	10	Long Valley	185996–6005
9	*B. robustus*	10	McIver's Spring	158274–77, 79–83, 184900
10	*B. campi*	5	French Spring	167183–87
11	*B. wrighti*	5	Hidden Lake	177846–50

Camp (northeast 1/4 Sect. 11, T23S, R33E), 2375 m, Kern Plateau, Tulare County, CA, 35.9467°N, 118.3850°W; LACM 99469–70, 4 km E Beach Meadows Guard Station (36°8′30″N, 118°15′30″W; Richman, 1973), 2530 m, [Kern Plateau], Tulare County, CA, 36.1417°N, 118°25′83″W; MVZ 202331–202336, Walker Creek, 8.1 km soouth Olancha, Owens Valley, 1740 m, Inyo County, CA, 36.2363°N, 118.0685°W; MVZ 202362–202364, Hogback Creek, 11.3 km south-southwest Olancha (northwest 1/4 Sect 13, T20S, R36E), 1770 m, Inyo County, CA, 36.1899°N, 118.0347°W; MVZ 158275–158277, 169168–169169, vicinity of McIvers (Melvers, on some maps) Spring, Scodie Mtns, 1980–2010 m, Kern County, CA, 35.6215°N, 118.0724°W; MVZ 158279–158281, 3.2 km (air) W McIvers Spring, Scodie Mtns, 2010 m, Kern County, CA, 35.6224°N, 118.1056°W.

Referred material.—MVZ 158304, 158307, 158329, 158331, 158338, 202365–202371, 219114, 219117–18, 219127, 219130, 219132–219133, 219135, 219141–43 219158, 219990, 220813, 222939–222949, 222962, 224862–224863, and 225713, CAS 213163, and CAS 213154. The following cleared-and-stained skeletal preparations are also assigned to the species: MVZ 158274, 158301–158303, 158316–158317, 169171, 172646.

Diagnosis.—A large, robust species of *Batrachoseps* (SL of adults averages 51.9 in males, 58.2 in females, Table 1) with a short trunk (17–19 trunk vertebrae), broad head, a relatively short, stout tail, well-developed limbs, and relatively large hands and feet with robust digits. Distinguished from *B. campi* by its narrower head, shorter limbs, and distinctive coloration (often with a dorsal stripe, lacking patches of silvery iridophores but with a complicated dorsal mottling of rusty and gray); from *B. wrighti* by having more trunk vertebrae (mode of 18 rather than 17), a more robust habitus with larger hands and feet, and lacking prominent ventrolateral white spots; from *B. stebbinsi* and *B. simatus* by having generally fewer trunk vertebrae and paired premaxillary bones; from all other species of *Batrachoseps* by its combination of large size, robust habitus, relatively few trunk vertebrae, color pattern and paired premaxillary bones.

Description.—*Batrachoseps robustus,* one of the largest species in the genus (Table 1), has a broad head that is well demarcated from the neck. The facial region of the head is relatively large, and the snout is broad and rather truncated. The head is relatively robust and deep and is not flattened. Nostrils are small, and there are modest nasolabial protuberances associated with the prominent nasolabial groove. Sexually mature males have more pronounced swelling associated with the terminus of the nasolabial grooves that extend beyond the jaw line. No mental glands are found in males. Grooving patterns of the head, throat and neck are typical of the genus. Eyes are relatively large but are not prominent, nor do they protrude noticeably from the side of the head; eyes are either not visible, or barely visible, in ventral view. Vomerine teeth are in moderately long series, or occasionally in patches. Small maxillary teeth are borne in a series of moderate length that ends under the eye. Premaxillary teeth are small and more numerous in females than in males. In some large males, the teeth are somewhat enlarged and are located far forward, where they pierce the upper lip. Of all specimens of known sex that were radiographed or cleared and stained, all females (13) have 18

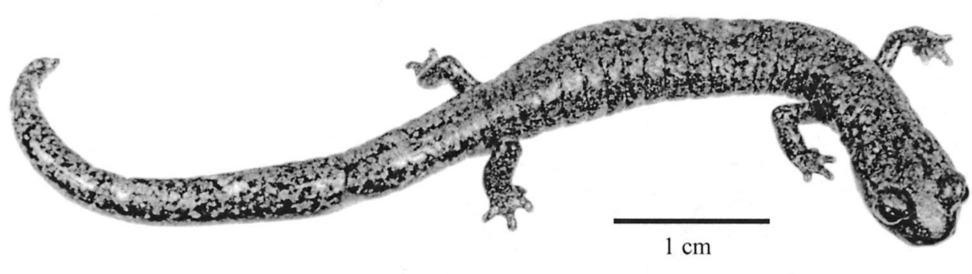

Fig. 1. Holotype. Museum of Vertebrate Zoology (MVZ) 219115, an adult female from the Kern Plateau, Tulare County, California.

trunk vertebrae, but of the eight males studied, two have 19 trunk vertebrae, three 18, two 17, and one was asymmetric (recorded as 17 1/2). There are either 16 or 17 costal grooves between the limbs (counting one each in the axilla and the groin). The tail is short and relatively stout, not tapering much until near the 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. The hands and feet are relatively large and well developed, with well-demarcated, stoutly rounded digits and expanded digital tips that bear well-developed subterminal pads. There are four fingers and four toes. The third toe is markedly longer than the other digits. Webbing is insignificant. Fingers and toes in order of decreasing length are 3-2-4-1.

Measurements of the holotype (in millimeters).—Maximum head width 7.2 (7.8 in life); snout to gular fold (head length) 11.5; head depth at posterior angle of jaw 3.6; eyelid length 3.2, eyelid width 2.1; anterior rim of orbit to snout 2.5; horizontal orbital diameter 2.1; interorbital distance 1.8; snout to forelimb 15.0; distance separating external nares 2.1; snout projection beyond mandible 0.5; snout to posterior angle of vent (standard length) 53.7 (55.2 in life); snout to anterior angle of vent 50.1; axilla to groin length 29.4; tail length 43.5 (45.5 in life); tail width at base 3.5; tail depth at base 3.1; forelimb length 10.5; hind-limb length 11.7; limb interval four costal interspaces; width of right hand 3.0; width of right foot 3.8; length of third toe 1.9; body width behind forelimbs 4.4. There are five premaxillary, 65 maxillary, and 20 vomerine teeth and 19 trunk, two caudosacral, and 30 caudal vertebrae.

Coloration (in life).—Color was recorded in the anesthetized holotype by DBW (25 July 1991). ‘‘Ground color dark brownish black. Dorsal surfaces heavily covered with iridophores that give appearance of a broad dorsal band with irregular and indistinct borders from the eyes onto the anterior part of the tail. Iridophores grouped together and overlain with second level so that white has bronze- to reddish-brown on top of it. Whole band has lively tan-rusty brown appearance, with many irregular gaps where ground color shows. Band becomes very broken up on head, which is a complex mottling—very lively, attractive. Bronze color limited to dorsum with flanks having a heavy guanophore wash that ends rather abruptly at ventrolateral margin. Venter midline unmarked gray-black, but gular region heavily mottled with white iridophores. Dorsal surfaces of limbs heavily marked with iridophores. Iris dark with bronze highlights. Tail irregularly but heavily marked dorsally with iridophores, including bronze color. Large recent scar on tail. Venter of tail unmarked gray-black.’’

Coloration of an anesthetized paratype (MVZ 219140) was recorded the same day. ‘‘Like holotype, but band on dorsum more distinct and bordered by a broken black dorsolateral line produced by gaps in the superficial pigment allowing the very dark black ground color to show through. Black particularly evident on costal grooves. Band much less reddish than holotype and is essentially tan to cream, with only a little bronze. Some cream areas so concentrated that band appears to be spotted or blotched. Sides, venter and limbs and iris like holotype.’’

Variation in coloration.—Batrachoseps robustus displays considerable variation in coloration over its range, both within populations and among geographically separate populations. A general

TABLE 3. ALLELE FREQUENCIES FOR 24 PROTEINS USED IN ALLOZYME STUDY. Populations as in Table 2. In addition, all populations fixed for the same allozyme for SOD and ADA-2.

Locus	Population										
	1	2	3	4	5	6	7	8	9	10	11
ACOH-1	F	E	E	E	E	C 0.143 E 0.857	E	E	E	E	C
ACOH-2	A	A	A	A	A	A	A	A	A	B	E
PGDH	D 0.75 G 0.25	G	D 0.192 G 0.269 I 0.462 J 0.077	G 0.667 I 0.333	D 0.667 F 0.083 G 0.167 H 0.083	G 0.786 I 0.214	D 0.25 G 0.75	G 0.55 I 0.45	D	F	H
IDH-1	B	B	A 0.077 B 0.923	B	B	A 0.286 B 0.714	B	B	A 0.3 B 0.7	B 0.9 C 0.1	B
IDH-2	A	A	A	A	A	A	A	A	A	C	A
G6PDH	B 0.875 C 0.125	A 0.05 B 0.95	B	B	B	B	B	B	B	B	B
AAT-1	G 0.187 J 0.813	G 0.9 J 0.1	E 0.115 G 0.808 J 0.077	G	E 0.417 G 0.083 J 0.5	G 0.5 J 0.5	E 0.25 J 0.75	G	G 0.25 J 0.75	F	I
AAT-2	B	B	B	B	B	B	B	B	B	A	B
LDH-1	A	A	A	A	A	A	A	A	A	A	D
LDH-2	D	D	D	D	D	D	D	D	D	C 0.2 D 0.8	D
PEP B(Igg)	E	E	E	E	E	E	E	B 0.15 E 0.85	E	G 0.5 H 0.5	E
CK	B	B	A 0.038 B 0.962	B	A0.083 B 0.917	B	B	B	B	B 0.9 C 0.1	B
G3PDH	G	G	G	G	G	G	G	G	F 0.55 G 0.45	E	D
MPI	C	C	C	C	C	C	C	C	C	C 0.9 E 0.1	A 0.2 C 0.8
PGM	C	B 0.6 C 0.4	C	C	C 0.833 D 0.167	C	C	B 0.333 C 0.667	C	C	C
MDHP	C	C 0.5 E 0.5	A 0.154 C 0.846	C	C	C	C	C	B 0.15 C 0.85	C	C
PEP D(I-a)	A 0.063 E 0.938	A 0.05 E 0.95	A 0.038 B 0.462 E 0.462 F 0.038	B 0.5 E 0.5	E 0.917 F 0.083	E	E	E	B 0.05 E 0.95	B 0.1 E 0.9	B 0.6 E 0.4

TABLE 3. CONTINUED

Locus	Population 1	2	3	4	5	6	7	8	9	10	11
ADA-1	D	D	D	D	D	D	D	D	D	E	C
MDH-I	B	B	B	B	B	A 0.143 B 0.857	B	B	B	D	B
MDH-2	F	F	D 0.192 F 0.808	F	F	F	F	C 0.1 F 0.9	F	E	B
GPI	B	B	B 0.654 C 0.346	B 0.5 C 0.5	B 0.917 D 0.083	B	A 0.25 B 0.75	A 0.35 B 0.45 D 0.2	B 0.85 D 0.18	B	B
GLUD	B	B	B	B	B	B	B	B	B 0.9 C 0.1	B	B
IDDH	E	E	C 0.154 E 0.846	C 0.5 E 0.5	E	E	C 0.5 E 0.5	E	E 0.75 G 0.25	E	E
ADH	A	A	A	A 0.833 B 0.167	A 0.917 B 0.083	A	A	A	A	A	A

trend, however, is that animals with light dorsal coloration (e.g., gray or silver) are restricted to the driest portions of the range, such as the Scodie Mountains or the southeastern part of the Kern Plateau. The light-colored dorsal surfaces of these animals may contribute to crypsis on pale-colored substrates. In contrast, salamanders occurring in the most mesic portions of the range, such as the Red Fir forests on the northern portion of the Kern Plateau, are invariably dark-colored. These salamanders closely approximate the reds and browns of downed and decaying Red Fir and Lodgepole Pine logs and associated bark rubble. Color variation was recorded at time of capture for samples from two relatively mesic localities, as follows. (1) north of Poison Meadow, Kern Plateau, 11 July 1991: 20 (SL of living animal), black with brownish iridophores; 20, brownish mottling; 29, 36, red plus brown; 31, few rust-red patches but distinct dorsal band present that overall is brownish-red; 32, prominent rust-red patches; 36, reddish; 40, 46, overall very reddish (''red fir bark red''); 42, silvery gray with faint rust blotching but little rust on tail, dorsal ''band'' indistinct; 44, rust patches all over w/black edging; 45, reddish with black lateral edge line with distinct dorsal band; sides mottled with gray stippling; 50, reddish overall, venter dark chocolate, light spotting ventrally, mostly in gular region; 54, olive gray with few coppery rust-brown patches, more on tail, dorsal ''band'' not distinct. (2) Brush Creek Overlook, Kern Plateau, 12 July 1991: 18, 18, black dorsally; 18, 28, fine rust dorsal flecking, 19, dark with brownish-rust flecking; 42, silvery gray dorsal color; 43, 46, reddish-rust dorsal color.

Osteology.—Information concerning osteology is derived from nine cleared-and-stained specimens (MVZ 158301–158303, 158316–158317, 158274, 169171, 172646, 184900) and from radiographs of many of the type series. The well-developed skull (Fig. 2) is similar to that of *B. campi.* Premaxillary bones of adults are paired, and prefrontal bones are typically present (absent on one side in two individuals). In a juvenile (MVZ 158317, 25.3 SL), there is still a single premaxillary, but tiny paired prefrontals have already developed. The prefrontals vary greatly in size, from tiny spots of bone in some, to bones that are rather large and exceed the septomaxillary in size in others. The bone is never more than about one-quarter the area of the nasal, which is always large and well developed. In two individuals, the nasal is divided on one side (Fig. 2). The nasals overlap the well-developed septomaxillaries and frontals and

TABLE 4. NEI (1978) GENETIC DISTANCE FOR NINE POPULATIONS (SEE TABLE 1) OF *Batrachoseps robustus* AND ONE POPULATION EACH OF *Batrachoseps campi* AND *Batrachoseps wrighti*.

Population	1	2	3	4	5	6	7	8	9	10	11
1	0										
2	0.112	0									
3	0.091	0.055	0								
4	0.11	0.05	0.001	0							
5	0.083	0.102	0.065	0.057	0						
6	0.061	0.035	0.032	0.035	0.064	0					
7	0.056	0.056	0.043	0.035	0.009	0.014	0				
8	0.103	0.03	0.026	0.024	0.09	0.029	0.047	0			
9	0.063	0.103	0.067	0.091	0.052	0.053	0.041	0.087	0		
10	0.548	0.542	0.505	0.54	0.532	0.479	0.496	0.506	0.502	0	
11	0.402	0.459	0.392	0.423	0.447	0.394	0.417	0.435	0.435	0.675	0

contact both the prefrontals and facial processes of the maxillaries. The nasolacrimal duct passes over the prefrontal, and it may be partly incised into the anterodorsal surface of that bone. The duct enters the nasal capsule at the anterior end of the prefrontal, between the nasal and the maxillary. The maxillaries are long and slender and bear small teeth in a single series that extends well posterior to the center of the eyeball. Each maxillary extends about two-thirds to three-quarters of the way through the eye, and the last 20% is typically edentulous and attenuate. There is a sizable dorsal fontanelle lying between the frontals and the parietals, and paired bones do not touch their counterparts. The parietals are well separated from each other; they are moderately broad for this genus. The parietals narrowly fall short of the synotic tectum. There are no crests on the otic capsules, but there is a small ridgelike ledge above the articulation zone of the elongate and slender dorsal portion of the squamosals. The quadrate is a relatively well-developed bone. The operculum bears a well-developed columellar rod. The vomers are well articulated to each other, and each bears a small to large preorbital process that varies among individuals; in some, it

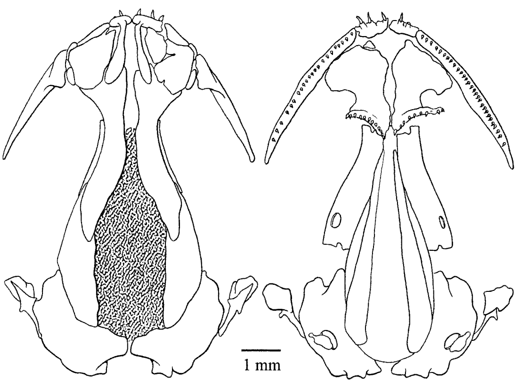

Fig. 2. Dorsal (left) and ventral (right) views of the skull of an adult male *Batrachoseps robustus* (MVZ 158303). Only bones and teeth are shown, apart from the dorsal fontanelle, which is stippled. The nasal bone on the right side is fragmented, and the right vomer also has a small anterior fragment.

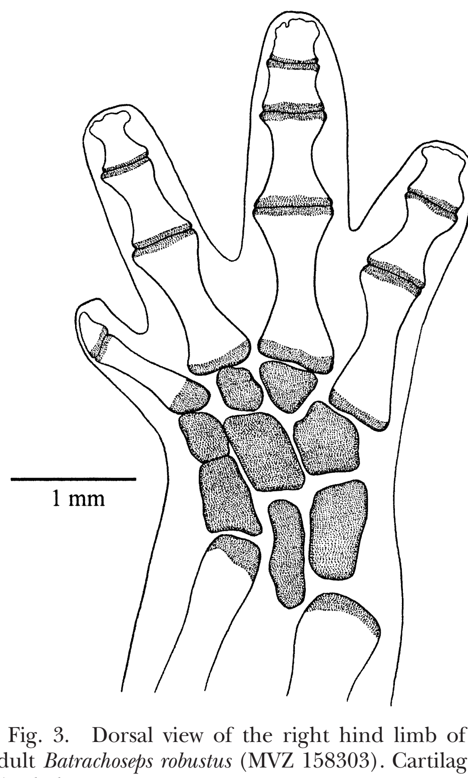

Fig. 3. Dorsal view of the right hind limb of an adult *Batrachoseps robustus* (MVZ 158303). Cartilage is stippled.

reaches nearly to the lateral margin of the body of the vomer and is as well developed as seen in any members of the genus. The process supports a row of vomerine teeth. Paired, relatively narrow patches of teeth underlie the large parasphenoid bone. Each patch contains from about 80 to 120 tiny teeth. The patches are widely separated from each other. The lower jaw is relatively stout and consists of the elongate dentaries and prearticulars, the latter having a broadly expanded, moderately high 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 18 or 19 trunk vertebrae, the last lacking ribs or having very short ribs. There are three caudosacral vertebrae. Tails of most individuals are regenerated, but there are 34 vertebrae in one apparently complete tail and 30 and 31 in two others.

The limbs are long, and the tibial spur is well developed, long and free. Phalangeal formulas are 1-2-3-2 for both hands and feet. The hands and feet are broad and have well-developed digits made up of relatively stout phalanges (Fig. 3). The terminal phalanges are expanded and flattened, often with an irregular surface finish. The mesopodials have the standard arrangement for the genus (illustrated in Marlow et al., 1979). There are eight carpals and eight tarsals, but in one individual, there are only seven carpals as a result of the fusion of the intermedium and centrale.

Habitat and distribution.—Batrachoseps robustus, now known from over 30 sites, occurs in a surprisingly broad range of habitats in a region that appears to be generally unfavorable for amphibians. The elevational range is from 1615 m in Portuguese Canyon on the east slope of the Sierra Nevada to 2804 m at Sherman Pass on the Kern Plateau (Fig. 4). In general, populations are more numerous on the northern and western parts of the Kern Plateau, corresponding to more mesic fir and Jeffrey Pine forests, than in the more isolated and xeric regions to the east and south. With decreasing elevation and precipitation, the occurrence of these salamanders is increasingly restricted to seasonal springs and seeps in otherwise harsh, arid surroundings.

Descriptions of sites at which this species has been collected are based on field notes of RWH, and Figure 5 illustrates habitat conditions.

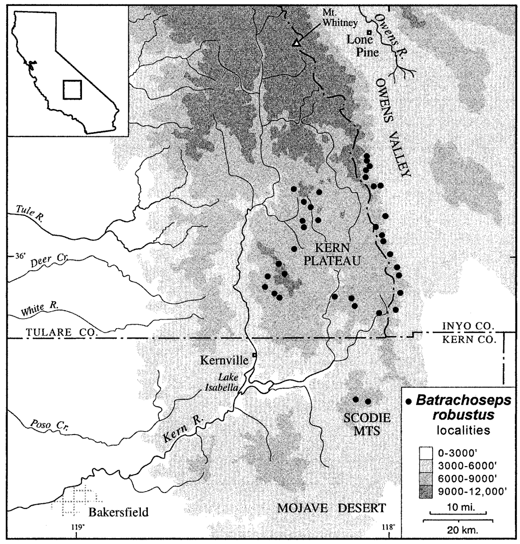

Fig. 4. Distribution of *Batrachoseps robustus* on the Kern Plateau and western margins of the Owens Valley, Inyo County, CA, and in the Scodie Mountains, Kern County, CA.

(1) McIvers Spring, Scodie Mountains, Kern County (elevation 2025 m; Fig. 5A), visited 12 May 1979 and 17 May 1980. This is the southeastern-most locality and appears to be marginal for salamanders. The McIvers Spring drainage is dry Singleleaf Pinyon Pine (*Pinus monophylla*) forest in an area of gentle relief—a plateau of sorts before dropping off into Sage Canyon and down into the Mojave Desert. The soil is very porous and dry. A few Jeffrey Pines (*P. jeffreyi*) grow here, but this species is not extensive, and the trees all appear to be fairly old. Precipitation is estimated to be less than 300 mm per year, with most occurring as winter snowfall. Outflow from McIvers Spring is present for several hundred meters before the surface dries. We found 36 salamanders along the creek during two visits: 24 adults or subadults, and 12 juveniles. All but one of the salamanders were found beneath rocks in sandy soil at the edge of the creek. The soil was moist for 1–2 m on either side of the creek; all salamanders were found within this band of moisture. A single large adult was found under a small log at the base of a large Jeffrey Pine; the ground was covered with pine needles and fallen bark. Other vegetation here includes *Artemisia tridentata, Chrysothamnus nauseosus, Carex* sp., *Taraxacum* sp., *Eriogonum* sp., *Opuntia basilaris, Salix* sp. (patchy), along with a few scattered *Quercus wislizenii* and *Q. kelloggii.* Rock outcrops bordering the creek consist of weathered granite. The total

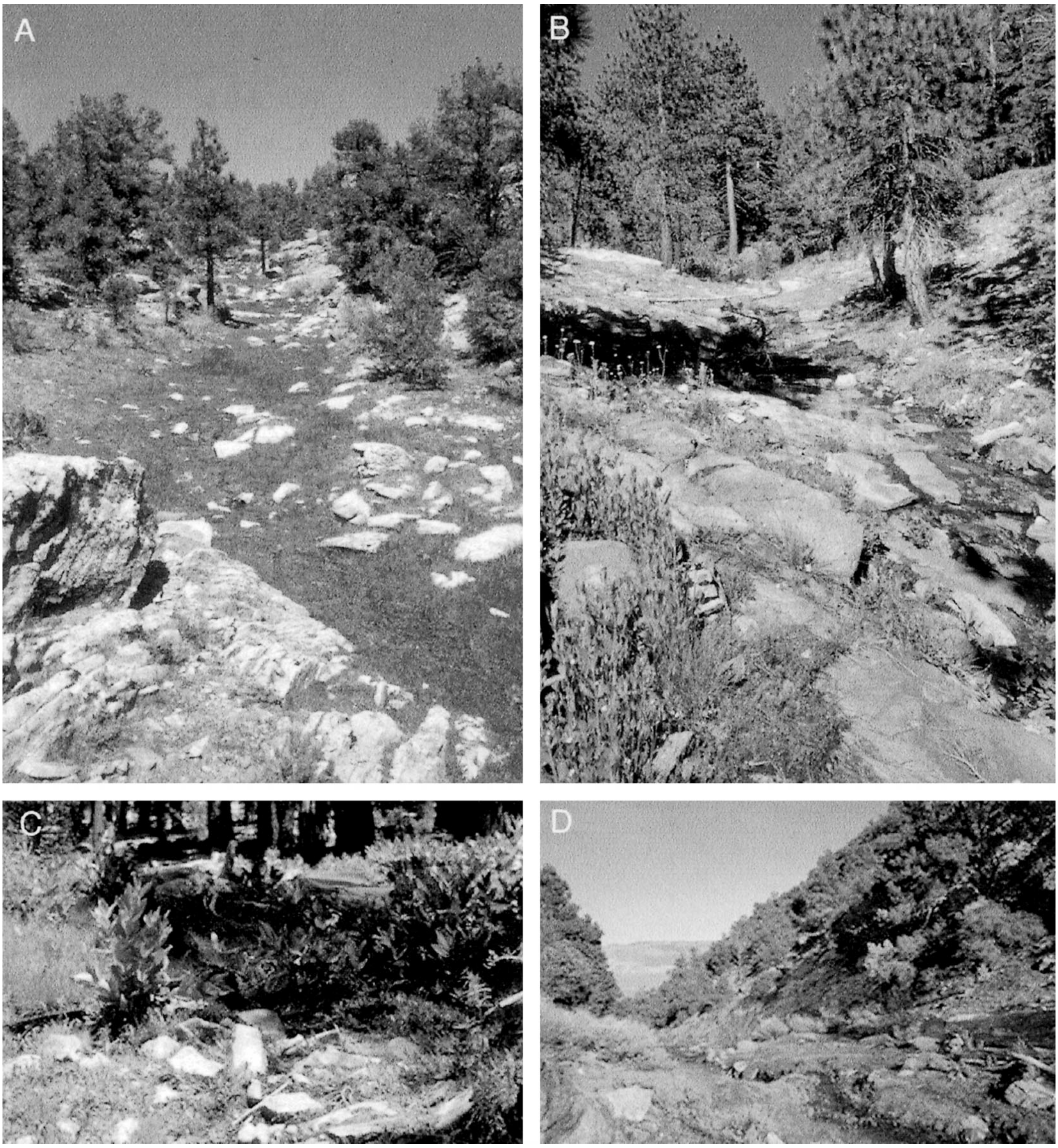

Fig. 5. Habitat of *Batrachoseps robustus.* (A) McIvers Spring, Scodie Mountains, 2025 m, Kern County, CA. Salamanders are apparently restricted to the band of moisture associated with spring runoff, occurring beneath scattered rocks on moist soil. Bordering woodland consists principally of Singleleaf Pinyon Pine (*Pinus monophylla*). 12 May 1979. (B) Vicinity of Brush Creek Overlook, approximately 3 map miles south-southeast Burton Camp, north of Poison Meadow, 2380 m elevation, Tulare County, CA. This site lies on the western edge of the Kern Plateau. Salamanders were found beneath flat rocks at the margins of a seepage. Bordering forest is comprised of Jeffrey Pines (*Pinus jeffreyi*) and White Fir (*Abies concolor*). 10 July 1980. (C) Type locality for *B. robustus,* north-northwest Sirretta Peak, southeast Round Meadow on Kern Plateau, Tulare County, CA. Elevation 2775–2800 m. 13 July 1991. (D) Sage Flat Creek, east slope Sierra Nevada, Inyo County, CA. This site is typical of the eastern slope localities, dominated by Singleleaf Pinyon and Canyon Oaks (*Quercus chrysolepis*), with Bigleaf Sagebrush (*Artemisia tridentata*) common in open areas. Salamanders were found only on or at the base of the shaded, north-facing slope. The arid Owens Valley and the Inyo Mountains are visible in the distance. 25 March 1986.

corridor length over which salamanders were found is no more than 200 m. *Bufo boreas*, *Hyla regilla*, *Sceloporus graciosus*, and *Thamnophis couchii* also were found here.

(2) Brush Creek Overlook, Kern Plateau, Tulare County (elevation 2377 m; Fig. 5B), visited 10 July 1980 and 12 July 1991. Outflow from a small spring courses over a metamorphic rock outcropping with talus before entering a dense White Fir (*Abies concolor*) and Jeffrey Pine forest. Salamanders ($n = 21$ in two visits) were found beneath mostly flat rocks (talus) bordering, but not away from, the spring runoff. Bordering slopes are moderately steep (approximately 35°), with the stream flowing along a gradient of 10–35°. There is little streamside vegetation, except for monkey flowers (*Mimulus* sp.) and currents (*Ribes* sp.).

(3) South of Sherman Pass, Kern Plateau, at type locality, Tulare County (elevation 2774–2804 m; Fig. 5C), visited 13 July 1991. Average annual precipitation is estimated to be > 750 mm, most as winter snowfall, with some summer thundershowers. The habitat here consists of a large seep on a steep (approximately 30°) west-facing slope. Surface flow is present in several areas on the slope, as are scattered rocks and downed logs. The surrounding area is heavily forested and is dominated by Red Fir (*Abies magnifica*) and Lodgepole Pine (*Pinus contorta*). Vegetation within the seep area consists of *Veratrum californicum* and dwarf willows (*Salix* sp.; plants characteristic of wet meadows), and *Dodecatheon* sp. Salamanders (19 adults, 1 subadult) were found both singly and in small groups, under rocks or under or within wet logs. There was little canopy cover at most of the collection sites.

(4) Sage Flat Creek, east slope Sierra Nevada, Inyo County (elevation 1800–1950 m; Fig. 5D), visited 25 March 1986, 15 June 1991, and 6 April 1993, is an example of a relatively open site on the east slope of the Sierra Nevada. It is dominated by Singleleaf Pinyon Pine and Canyon Oaks (*Quercus chrysolepis*), with Bigleaf Sagebrush common in open areas. Salamanders were found under single rocks, within rock rubble and crevices, and under wet logs, exclusively on or at the base of a moderately steep north-facing slope.

Based upon our now considerable field experience with *B. robustus* (> 350 specimens), several patterns emerge concerning its general ecology. Timing and duration of seasonal activity vary according to elevation and available surface moisture. Lower elevation populations (< 2000 m) are probably restricted to a few months of activity in late winter and spring, before surface conditions become warm and dry. Populations occurring at higher elevations are limited in their activity by cold temperatures and snow. We suspect that at higher elevations surface activity is confined to a few months, perhaps May or June to October. Thus, the timing of courtship and egg laying is expected to vary according to local conditions.

Substrate temperatures were recorded for 217 salamanders at point of discovery (under cover) from a Schultheis or Miller and Weber quick-reading thermometer. The mean substrate temperature was 13.5 C, with a range of 5.2–25.0 C. This is well within the range of temperature values for other species of *Batrachoseps* (Feder et al. 1982; RWH, unpubl.).

Near the end of the seasonal activity period at some sites, especially those at lower elevations and xeric environments, we have found only juvenile salamanders (e.g., hatchlings or yearlings). These same sites have produced adults at other times. Although risk of desiccation because of unfavorable surface area-volume relationships is greater for juveniles, we attribute late-season juvenile activity under marginal surface moisture conditions to the need to accumulate fat reserves prior to summer aestivation. Adults, by contrast, do not face the same pressures and, thus, are not required to maintain surface activity during suboptimal periods. All members of *Batrachoseps* are relatively elongate and suited for subterranean existence. However, *B. robustus* has a relatively robust body and a short tail, features that should result in a surface:volume relationship that is beneficial in resisting water loss.

Behavior and life history.—We recorded behavioral responses for 79 individuals as they were discovered under surface cover in the field. The most commonly observed behavior was an attempt to crawl away ($n = 58$; 73.4%), followed by immobility (16.5%), thrashing (5.1%), and coiling (3.8%). When handled, a few individuals released a sticky skin secretion. A single salamander exhibited a rapid coiling and springing response (''watch-spring'' behavior), a trait commonly observed in some attenuate species of *Batrachoseps*. Coiling as a defensive response is widespread in *Batrachoseps*; frequency of deployment varies among species. The apparent rarity of coiling behavior in *B. robustus* is notable.

We have found recently hatched young most commonly during May and June (with some in March, April, and July), but this likely reflects our field activity schedules and ability to gain access to high-elevation sites following snow melt. Hatchlings tend to aggregate in groups of 2–5 and occur under smaller pieces of cover than are used by subadults and adults.

On 3 May 1993, five gravid females were collected on the Kern Plateau (Long Valley Road near Rockhouse Basin Road). Given the extremely dry conditions, we were surprised to find any salamanders. None responded immediately following hormone injection (Jockusch, 1996). This suggests that these animals were not physiologically ready for oviposition. Three of these individuals responded by laying eggs following a second injection about a month later; each laid three eggs while retaining 1–3 eggs. Apparently clutch size is small and egg and hatchling size relatively large. Perhaps oviposition occurs in connection with summer rains, which normally occur in the high mountains in this area but are unpredictable. Two eggs hatched after 96 and 103 days of development at 13 C. This is substantially slower development than in members of the subgenus *Batrachoseps* (range from 65–85 days, with variation both across populations and species), but faster than the development of *B. wrighti* (average of 126 days) at the same temperature (E. Jockusch, pers. comm.). The smallest female observed to be gravid (MVZ 219143) is 44 SL.

Etymology.—The species name is derived from the Latin word *robustus*, with reference to its size and robust habitus.

Discussion

A single specimen of this species, identified as *B. stebbinsi*, was reported nearly three decades ago (Richman, 1973). This misidentification occurred because external dimensions of *B. robustus* and *B. stebbinsi* are very similar (compare our Table 1 with Brame and Murray, 1968). We first realized that the two were not conspecific when we observed plesiomorphic osteology in a single cleared-and-stained specimen from the Kern Plateau. Subsequent biochemical studies (Jackman et al., 1997; Jockusch and Wake, 2002; unpubl. allozyme data) demonstrated the distinctiveness of the two species, which belong to two different clades. Once we understood that *B. robustus* is a member of the clade now recognized as the subgenus *Plethopsis*, we focused attention on differentiation within that group, using starch-gel electrophoresis to survey allozymes in nine populations of *B. robustus* and one each of *B. campi* and *B. wrighti* (Table 2).

Substantial allozymic differentiation is found within *B. robustus* but less than that encountered in *B. campi* (Yanev and Wake, 1981). Fifteen of the 26 proteins studied were polymorphic. Direct count heterozygosity ranges from 0.038 (Hogback; n = 10) to 0.109 (Osa Meadow; n = 13). Genetic distances (D; Nei, 1972) range from 0.016 to 0.124 (mean 0.066). The Scodie Mountains are geographically isolated from the rest of the range. However, the range of genetic distances between the population from this region and those in the remainder of the range is small (0.055–0.108, mean 0.077), suggesting that isolation is relatively recent. The two populations sampled from the Owens Valley (Walker Creek and Hogback Creek) are well differentiated from each other (0.115), with each being most similar to the Kern Plateau population located most closely to them to the west (Walker Creek to Burton Camp, 0.065; Hogback Creek to Burton Camp, 0.039, and to Chimney Peak 0.034). The nine populations are well differentiated from both *B. wrighti* and *B. campi* but are more similar to the former. The value of D = 0.397–0.463 (mean 0.428) to *B. wrighti* and 0.485–0.556 (mean 0.525) to *B. campi*; between *B. wrighti* to *B. campi* D = 0.681. There are seven fixed differences between *B. robustus* and *B. wrighti*, and another locus is nearly fixed; eight fixed differences with another nearly fixed difference distinguish *B. robustus* from *B. campi*; *B. wrighti* and *B. campi* differ by 12 fixed differences. Genetic distances to members of the subgenus *Batrachoseps* are all in excess of D = 1.0, with more than 10 fixed differences (unpubl. data).

The mitochondrial DNA gene cytochrome *b* of *Batrachoseps* was studied by Jackman et al. (1997), who sequenced 555 base pairs, and by Jockusch and Wake (2002), who studied 278 individuals and sequences up to 784 bp in length. Samples of three populations of *B. robustus* were included: Scodie Mountains, Kern County, Ninemile Canyon, Inyo County, and topotypic material. Maximum sequence divergence was 3.7% (between Scodie Mountains and the type locality), compared with 1.8% within *B. wrighti* and 4.2% within *B. campi*. Maximum parsimony analysis with all characters and types of change weighted equally suggests a sister-group relationship between *B. robustus* and *B. wrighti* (bootstrap support: 65%), but other methods are unable to distinguish between *B. campi* and *B. wrighti* as possible sister taxa (Jockusch and Wake, 2002).

The subgenus *Batrachoseps* has three osteological synapomorphies: fused premaxillary bones throughout life, prefrontal bones absent, and no preorbital process of the vomer. The new species is plesiomorphic with respect to all three characters, as are *B. campi* and *B. wrighti*. There are no osteological synapomorphies of *Plethopsis*, but DNA sequences and allozymes support its status as a clade.

Jockusch and Wake (2002) concluded that the subgenus *Plethopsis* contains three distinctive and well-differentiated species whose phylogenetic relationships are unresolved. The diversification of the group is relatively old, and missing taxa would likely have a major influence on resolution of relationships if they were known and available. Despite the close proximity of *B. campi* and *B. robustus* (43 km), these species are diverged from each other, with respect both to allozymes and mtDNA, to roughly similar degrees as they are diverged from the geographically remote (nearly 900 km) and ecologically very different (mesic, heavily forested habitats) *B. wrighti*. The three species of *Plethopsis* are all peripheral in distribution to the more species rich subgenus *Batrachoseps*, which ranges from northwestern Baja California to southwestern Oregon, south and west of the range of *Plethopsis*.

Some species of the subgenus *Batrachoseps* come close to the range of *B. robustus*, but we know of no sympatry with any other salamander with the exception of a small zone of overlap with a population of *Hydromantes* sp. on the west side of the Owens Valley. A population of *B. relictus* occurs on the western margin of the Kern Plateau, 1.6 km from the nearest *B. robustus* and well within the elevational range of the latter, and several species occur in Kern Canyon, the Greenhorn Mountains, and the southern Piute Mountains (this is the closest approach of *B. stebbinsi*).

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