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GENIC DIFFERENTIATION IN A RELICT DESERT SALAMANDER, *BATRACHOSEPS CAMPI*

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ABSTRACT: The Inyo Mountains salamander (*Batrachoseps campi*) was recently described on the basis of specimens from two populations in the extremely arid mountains of eastern California. Here we report the discovery of 11 additional populations from a series of canyons in the same range. Genic variation in *B. campi* was investigated using starch-gel electrophoresis. A relatively high level of genetic differentiation is demonstrated in the species. Nei genetic distance ranges from .01–.23 (mean = .12) based on 33 electrophoretic loci. Substantial genic subdivision within the species is demonstrated ($\bar{F}_{ST}$ = .470, based on 18 variable loci). No close relationship is postulated between *B. campi* and any other described species of *Batrachoseps*, but the smallest genetic distance recorded (D = .71) is to *Batrachoseps wrighti* from Oregon.

Key words: Amphibia; Caudata; Plethodontidae; *Batrachoseps*; California, Electrophoresis; Genic subdivision; Variation; Allozymes; Relict

THE Inyo Mountains, lying to the north of California's Mojave Desert and in the rain shadow of the highest peaks of the Sierra Nevada, is one of the most arid spots in North America. Hence, the discovery of populations of the lungless, terrestrial salamander *Batrachoseps campi* reported by Marlow et al. (1979) in two canyons on the western slopes of the mountains was most unexpected. Individuals were found in highly localized, mesic microhabitats in and adjacent to permanent springs. For this reason the geographic range of the species in this hostile region was presumed to be extremely limited. However, recent collections of *B. campi* from 11 additional sites in the Inyo Mountains, in drainages extending into the Owens Valley on the west as well as into the even drier Saline Valley to the east, have extended its known range. The range of the species, though greatly extended, is still relatively restricted: 32 km along the length of the Inyo Mountains between Waucoba Mountain and New York Butte, and 10.5–13.5 km east to west across the mountain range.

Only two or three species of *Batrachoseps* were recognized until relatively recently. Starting with the work of Brame and Murray (1968), additional species have been discovered (see summary in Yanev, 1980). The most distinctive of these is *B. campi*, a species that is the most robust in shape and generalized in osteology of the genus, as well as one of the most habitat-restricted species of metamorphosed salamanders. This species has a distinctly peripheral distribution relative to other members of the genus and occurs in extremely arid environments supposedly unoccupied by salamanders elsewhere. The sole exception is a little known congeneric species, *B. aridus*, that is known from a single locality in the desert of southern California. *Batrachoseps campi*, in contrast, has a rather extensive distribution in a completely isolated mountain range. The natural history and local distribution of *B. campi* will be reported in detail elsewhere (K. Berry, in prep.). In this study we present data concerning genic variation in *B. campi* and the relationship of this species to other members of the genus.

As the populations of *B. campi* were successively discovered in a variety of diverse sites, we suspected that the species might be a primarily subterranean form which is widespread in the porous limestone layer known to underlie the Inyo Mountains. If the individuals were widely dispersed in subterranean habitats and surface activity were limited

to suitable outcrop areas, then the pattern of genic variability among the samples would be expected to be similar to that observed in other seemingly continuously distributed taxa of *Batrachoseps* (see Yanev, 1978), or in the many species of eastern *Plethodon* studied by Highton and his associates (e.g. Highton and Webster, 1976). On the other hand, if these populations were isolated from each other by the seemingly uninhabitable desert that separates them at the surface, then a much higher level of differentiation among the samples would be expected. Thus, we examined patterns of genic variability within *B. campi* and the implications of these patterns for the genetic structure of this unique species.

Yanev (1978) compared a single population of *B. campi* with other species of *Batrachoseps*. The results of that study indicated that only *B. wrighti*, from the Cascade Mountains of central and northern Oregon, was a likely relative of *B. campi*. Here we examine the relationship between *B. campi* and its presumed closest relative.

The recently discovered populations of *B. campi* that were unknown to Marlow et al. (1979) appear to be indistinguishable from the two originally described populations (French Spring and Long John Canyon, sample numbers 1 and 2 in this study) except in respect to coloration. In both the originally described and the recently discovered populations, the ground color of the salamander is dark brown-black in most individuals. In the two original populations, the only additional color is a scattering of silvery iridophores which, when grouped together, form patches with a slightly greenish hue. These iridophores are concentrated on the upper eyelids and head, and are scarce elsewhere on the animal (see Fig. 1 in Marlow et al., 1979). However, in virtually all individuals of the 11 newly sampled populations, these silvery iridophores form a continuous network covering the entire dorsal surface. In only a few juveniles are there patches on the dorsal surface not entirely covered by the iridophore network (Fig. 1). In larger animals the iridophores may be rather smaller and more punctate causing the animal to appear dark with a greenish cast, or they may be quite dense and reticulate causing the animal to appear light and silvery-green. Both lighter and darker individuals are found in populations from all regions of the range; Fig. 1 shows a darker individual from a northern population and a lighter individual from a southern population.

Materials and Methods

The following specimens were used (number used in electrophoretic study in parentheses; localities mapped in Fig. 2; all *B. campi* localities are in Inyo County, California): 1. French Spring, 1829 m (13); 2. Long John Canyon, 1695 m (7); 3. Barrel Springs, 1950 m (4); 4. Upper Lead Canyon, 2590–2620 m (10); 5. Lower Lead Canyon, 1980 m (12); 6. Upper Addie Canyon, 2440–2530 m (9); 7. Waucoba Canyon, 2200 m (7); 8. Lower Addie Canyon, 2075–2135 m (11); 9. Willow Creek Canyon, 1370 m (1); 10. McElvoy Canyon, 1070 m (9); 11. Keynot Canyon, 1190–1250 m (5); 12. Cove Spring, 1950 m (4); 13. Hunter Canyon, 550–600 m (14). A number of additional canyons were searched, but no other salamander populations were found. The sample of *B. wrighti*, which is not mapped, is from Hidden Lake, Lane County, Oregon (16). All specimens used in the study are preserved and catalogued in the Museum of Vertebrate Zoology.

Samples of liver, spleen, stomach, intestine, and heart were extracted from freshly killed specimens and stored at −76C for later use. Homogenized tissue extracts were pooled from each animal and analyzed by standard techniques of horizontal starch-gel electrophoresis (Ayala et al., 1972; Harris and Hopkinson, 1976; Selander et al., 1971). The following gel/buffer systems were used: Tris maleate pH 7.0 (1:10 dilution of electrode buffer for gel) for Malic enzyme

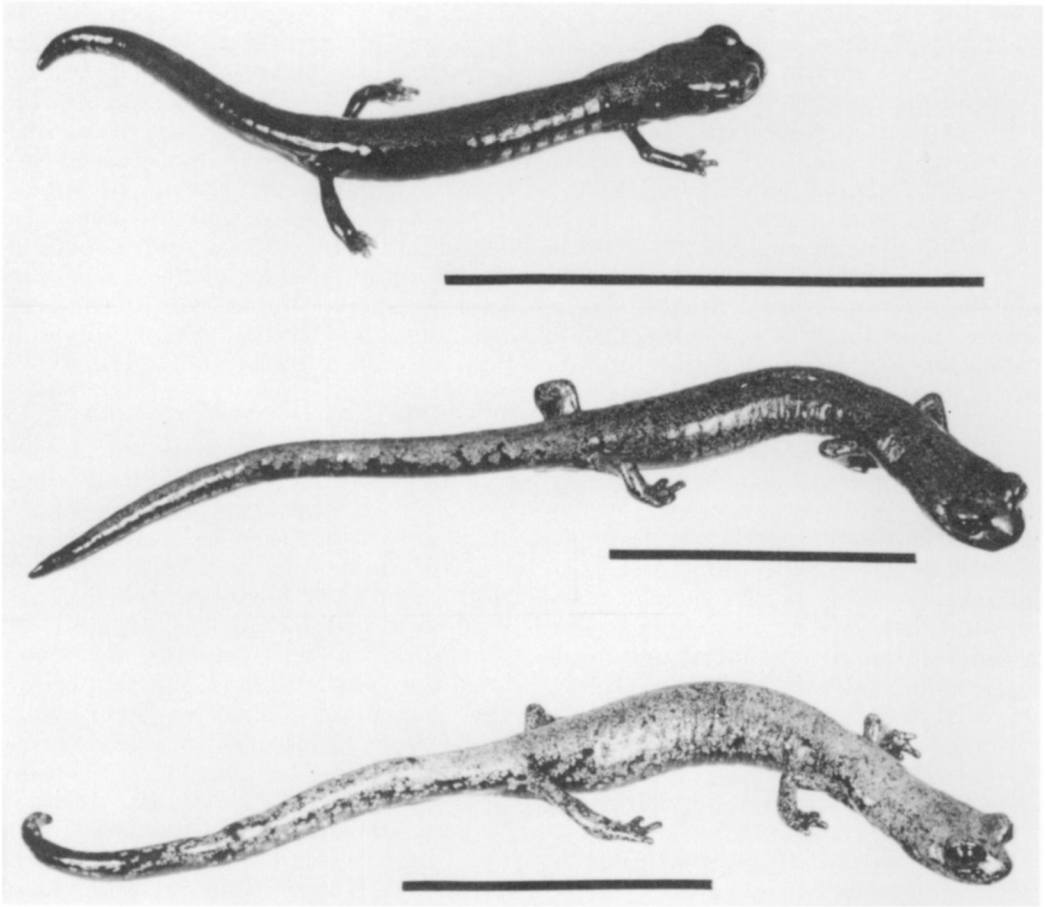

FIG. 1.—Juvenile *Batrachoseps campi* (top) and two adults from Saline Valley drainages of the Inyo Mountains of California. The top two individuals are from Addie Canyon; the lower individual is from McElvoy Canyon. The scale is 25 mm.

(*Me*); Tris citrate pH 8.0 (1:30 dilution for gel, plus NADP) for Glucose-6-phosphate dehydrogenase (*Gd*) and Phosphogluconate dehydrogenase (*Pgd*); Tris citrate pH 8.0 (1:30 dilution for gel) for Phosphoglucomutase (*Pgm*), Aconitase (*Acon*, stained with 1% agar overlay), Isocitrate dehydrogenase (*Icd*, with $MgCl_2$ substituted for $MnCl_2$ in staining solution), Glycerol-3-phosphate dehydrogenase (*Gpd*), Glutamate-oxaloacetate transaminase (*Got*), Malate dehydrogenase (*Mdh*), Sorbitol dehydrogenase (*Sordh*), and Mannose phosphate isomerase (*Mpi*); Borate pH 8.2 (Poulik pH 8.7 for gel) for Peptidases (*Leu-ala* and *Leu-gly-gly*, both stained with 1% agar overlay) and Lactate dehydrogenase (*Ldh*);

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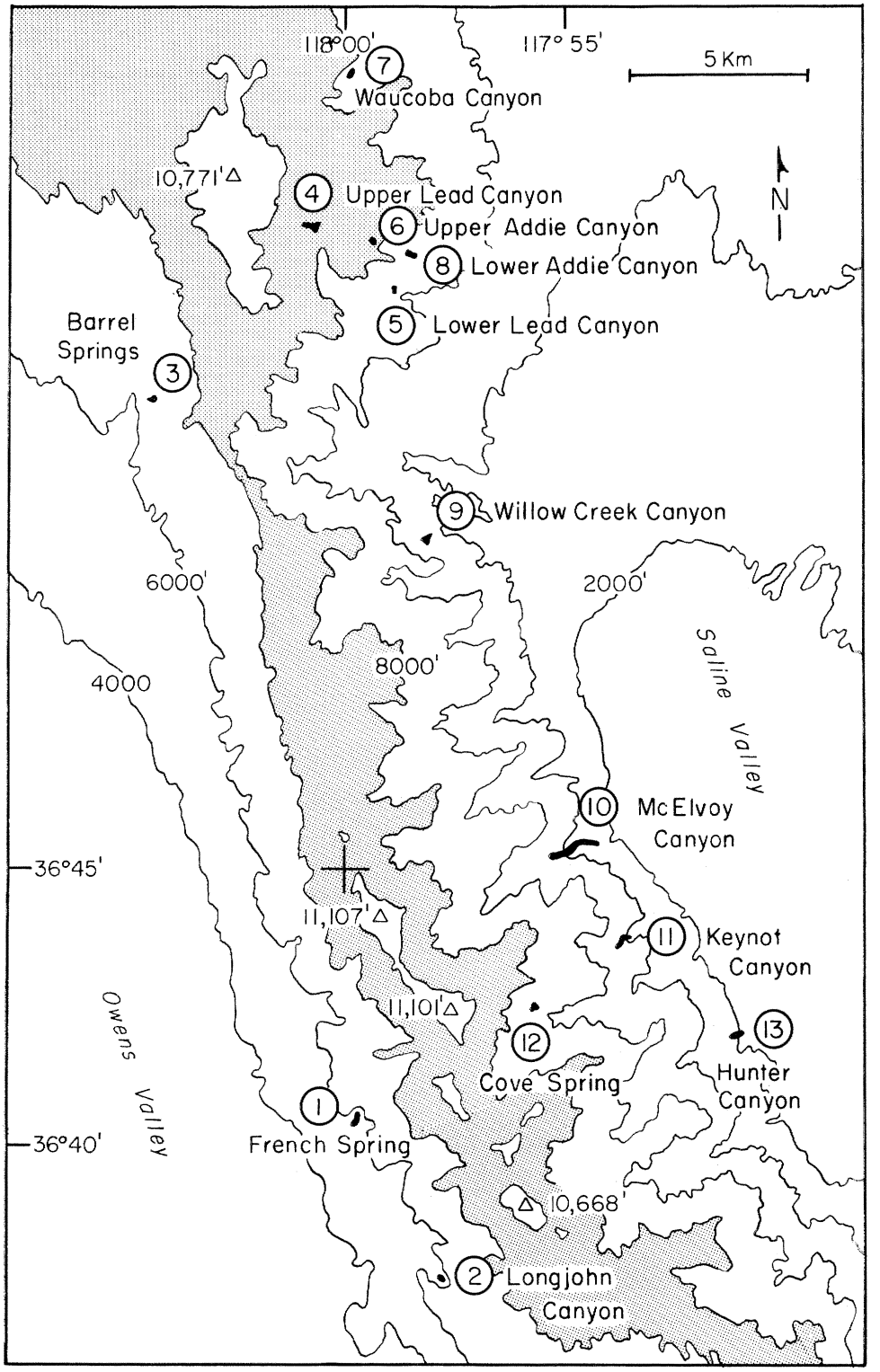
FIG. 2.—The Inyo Mountains and vicinity, Inyo County, California with the 13 known localities of *Batrachoseps campi* indicated as black regions. The stippling designates the area between the 2445 m (8000 ft) and 3060 m (10,000 ft) contour intervals.



Borate pH 8.2 (Tris HCl pH 8.5 for gel) for General protein (*Gp*) and Adenosine deaminase (*Ada*, stained with 1% agar overlay); Phosphate citrate pH 7.0 (1:25 dilution plus NAD for gel) for Aldolase (*Ald*); Lithium hydroxide A + B pH 8.2 (Lithium hydroxide A pH 8.1 for gel) for Superoxide dismutase (*Sod*), Glutamate dehydrogenase (*Glud*, stained with 1% agar overlay), and Esterase (*Est*); Tris citrate pH 7.0 (1:15 dilution plus 15% glycerine for gel) for Glucosephosphate isomerase (*Gpi*, stained with 1% agar overlay), Adenylate kinase (*Ak*, stained with 1% agar overlay), Creatine kinase (*Ck*, stained with 1% agar overlay), Acid phosphatase (*Acp*), and Leucine aminopeptidase (*Lap*).

Genetic interpretations of allozyme variation were based on criteria elaborated by Selander et al. (1971) and Harris and Hopkinson (1976). Nei's (1971, 1972) measures of genetic distance (D) and Rogers' (1972) measure of genetic distance (D_R) were used for interpopulational and interspecific comparisons. Estimates of heterozygosity were derived from actual counts. Mean heterozygosity is the number of heterozygous genotypes recorded in the sample divided by the product of the number of individuals and the number of loci surveyed. Estimates of polymorphism are based on the number of loci having two or more variants, divided by the total number of loci. Measures of standardized variance in gene frequency (F_{ST}) are based on Wright (1965) and the modification of Nei (1973) for calculation using multiple alleles.

Results and Discussion

Genic variation in Batrachoseps campi.—We examined 33 electromorphic loci in all individuals of *B. campi*. Fourteen loci showed no intraspecific variation (*Acon-2, Acp, Ada, Ald, Est-1, Gd, Glud, Gp-1, Gp-2, Gpd, Ldh-1, Leu-ala, Pgd, Sod*). In 8 of the 19 polymorphic loci (*Ak, Ck, Est-2, Got-1, Gpi, Icd-1, Ldh-1, Mdh-2*), a single allozyme predominates in all populations, although exact frequencies differ among the populations. The remaining 11 polymorphic loci (*Acon-1, Got-2, Icd-2, Lap, Mdh-1, Me-1, Me-2, Mpi, Leu-gly-gly, Pgm, Sordh*) show important differences among populations, with different allozymes predominating in different populations and geographic groupings of populations (Table 1, Fig. 3).

Adequate samples from most populations permit analysis of geographic differentiation in this species. Population 9 is represented by one specimen (possessing no unique allozymes), and it is necessarily ignored in much of the following analysis. The remaining populations can be grouped as northern (3, 4, 5, 6, 7, 8) or southern (1, 2, 10, 11, 12, 13) using population 9 as a center point, and as western (1, 2, 3) or eastern (4–13), using the crest of the Inyo Mountains as the line of division (the western springs drain into Owens Valley; those in the east drain into Saline Valley). Populations 4, 5, 6, and 8 lie in the same local drainage system; populations 6 and 8 are separated by about 305 m of seemingly uninhabitable terrain.

Considerable north–south differentiation is evident at the loci examined. For example, predominant allozymes for *Icd-2* and *Me-2* differ between the northern and southern populations, and are either fixed or predominate in a majority of the populations in their respective groups (Fig. 3). A lesser degree of north–south differentiation is detected at other loci (*Mpi, Mdh-1, Leu-gly-gly, Me-1*). In contrast, we found little indication of east–west differentiation. Certain allozymes ($Mdh\text{-}1^c$, $Acon\text{-}1^a$, $Got\text{-}2^a$, $Me\text{-}1^a$) are found only in some, but not all, eastern populations, but no allozyme is unique to the western populations.

Even nearby populations show differentiation. Cove Spring (12) and Hunter Canyon (13) are separated by only about 7.2 km. Nonetheless, large differences are evident at several loci. For example, an allozyme of *Icd-2* that is fixed in population 12 was not found in population

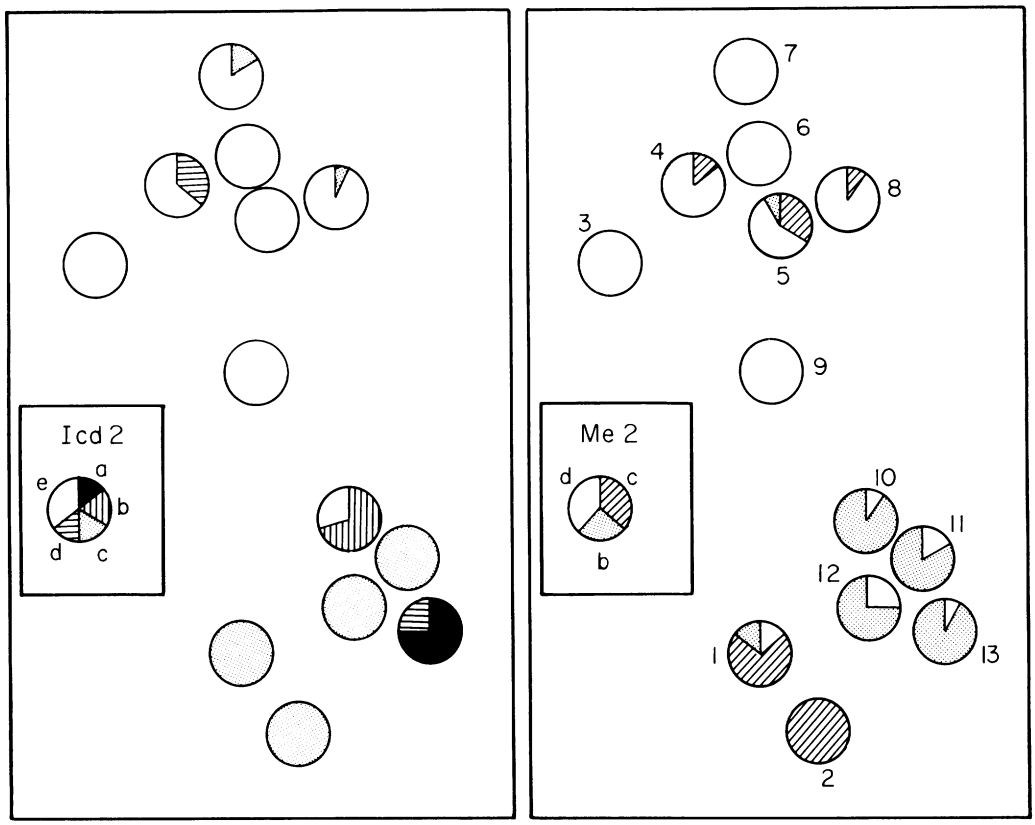


FIG. 3.—Genetic differentiation in *Batrachoseps campi*. Frequency of alleles varies greatly from one population to the next, but some geographic pattern was detected between the northern and southern populational units. The diagrams illustrate the frequencies of the alleles for *Icd-2* and *Me-2* (two of the more variable loci). Numbered localities are the same as in Fig. 2.

13, and the dominant allozymes of *Acon-1* and *Got-2* in population 13 were not found in population 12. Populations 4, 5, 6, and 8 share a common major drainage system, but even in this relatively small area there is evidence of genetic subdivision between populations. Populations 4 and 5 have allozymes of *Pgm* that are in relatively high frequency but which are absent from nearby populations 6 and 8. *Lap* is fixed for alternative allozymes in populations 6 and 8, but these populations are separated only by about 305 m along the same canyon. There is considerable difference between these nearby localities in elevation and exposure, and distinct populations exist on this small scale. These two populations differ at other loci as well (*Icd-2*, *Me-2*), but to a lesser degree.

We analyzed the pattern of presence or absence of specific allozymes in populations with the maximum parsimony Wagner tree method (Farris, 1972). A north–south subdivision of the species is evident here as well (Fig. 4a).

Standardized variance in gene frequency, F_{ST} (Nei, 1973; Wright, 1965), was calculated to evaluate the degree of genetic subdivision of these populations. Here we ignored population 9, because of its small sample size. $\bar{F}_{ST} = .470$ for 18 variable loci sampled in 12 populations. This is greater than the largest $\bar{F}_{ST}$ recorded for any mammal. Patton and Yang (1977) reported $\bar{F}_{ST} = .412$ for the fosso-

TABLE 1.—Allozyme frequencies at variable loci in *Batrachoseps campi* (localities 1–13) and *B. wrighti* (locality 14). The following loci are monomorphic: *Acp, Ada, Ald, Est-1, Gd, Glud, Gp-2, Leu-ala, Sod.* Sample sizes are in parentheses.

Locus	Locality													
	1 (13)	2 (7)	3 (4)	4 (10)	5 (12)	6 (9)	7 (7)	8 (11)	9 (1)	10 (9)	11 (5)	12 (4)	13 (14)	14 (16)
Acon-1	*b*	*b*	*b*	*b*	*a* [.25] *b* [.75]	*b*	*b*	*b*	*b*	*a*	*a* [.20] *b* [.80]	*b*	*a* [.96] *b* [.04]	*c*
Acon-2	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*b*
Ak	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a* [.53] *b* [.47]	*b* [.66] *c* [.34]
Ck	*a* [.23] *b* [.77]	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b* [.97] *c* [.03]
Est-2	*d*	*d*	*d*	*d*	*c* [.13] *d* [.87]	*b* [.06] *d* [.94]	*d*	*d*	*d*	*d*	*d*	*d*	*d*	*a* [.07] *d* [.93]
Got-1	*b*	*b*	*b*	*b*	*a* [.08] *b* [.92]	*a* [.06] *b* [.94]	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*a*
Got-2	*c*	*c*	*c*	*a* [.44] *c* [.56]	*a* [.42] *c* [.58]	*a* [.28] *c* [.72]	*c*	*a* [.45] *c* [.55]	*a*	*a* [.33] *c* [.67]	*a* [.50] *c* [.50]	*c*	*a* [.57] *c* [.43]	*b*
Gp-1	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*a*
Gpd	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*b*
Gpi	*b*	*b*	*b*	*a* [.20] *b* [.80]	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*
Icd-1	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a* [.36] *c* [.64]	*b*
Icd-2	*c*	*c*	*e*	*e*	*e*	*e*	*c* [.14] *e* [.86]	*c* [.05] *e* [.95]	*e*	*b* [.67] *e* [.33]	*c*	*c*	*a* [.65] *d* [.35]	*e*

Lap	*a* [.82] *c* [.18]	*a*	*a* [.75] *c* [.25]	*a* [.90] *c* [.10]	*a* [.67] *c* [.33]	*a*	*a*	*c*	*c*	*a* [.88] *c* [.12]	*c*	*c*	*a* [.35] *c* [.65]	*b*	
Ldh-1	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b* [.50] *c* [.50]	*b*	*b*	*b*	*b*	*a*	
Ldh-2	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a* [.63] *b* [.37]	
Mdh-1	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*a*	*c*	*a* [.83] *c* [.17]	*a* [.90] *c* [.10]	*a* [.88] *c* [.12]	*a* [.04] *c* [.96]	*b* [.94] *d* [.06]	
Mdh-2	*b*	*b*	*a* [.25] *b* [.75]	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b* [.90] *c* [.10]	*b* [.88] *c* [.12]	*b*	*d*	
Me-1	*b*	*b*	*b*	*a* [.50] *b* [.50]	*a* [.75] *b* [.25]	*a* [.28] *b* [.72]	*b*	*a* [.45] *b* [.55]	*b*	*b*	*a* [.30] *b* [.70]	*b*	*b*	*b*	
Me-2	*b* [.14] *c* [.72] *d* [.14]	*c*	*d*	*c* [.15] *d* [.85]	*b* [.09] *c* [.33] *d* [.58]	*d*	*d*	*c* [.09] *d* [.91]	*d*	*b* [.90] *d* [.10]	*b* [.80] *d* [.20]	*b* [.75] *d* [.25]	*b* [.93] *d* [.07]	*a*	
Mpi	*a* [.18] *c* [.82]	*c*	*c*	*a* [.80] *c* [.20]	*a* [.88] *c* [.12]	*a* [.78] *c* [.22]	*a* [.71] *c* [.29]	*a* [.59] *c* [.41]	*c*	*c*	*c*	*c*	*c*	*b*	
Leu-gly-gly	*a* [.59] *b* [.41]	*a*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*c* [.25] *b* [.75]	*a*	*b*	
Pgd	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*a*	
Pgm	*a* [.05] *b* [.95]	*b*	*b*	*a* [.30] *b* [.70]	*a* [.30] *b* [.62] *c* [.08]	*a* [.06] *b* [.94]	*b*	*b*	*a*	*b*	*b*	*b*	*b*	*b*	
Sordh	*a* [.14] *b* [.86]	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*a* [.83] *b* [.17]	*a* [.90] *b* [.10]	*a* [.75] *b* [.25]	*b*	*c* [.75] *d* [.25]	

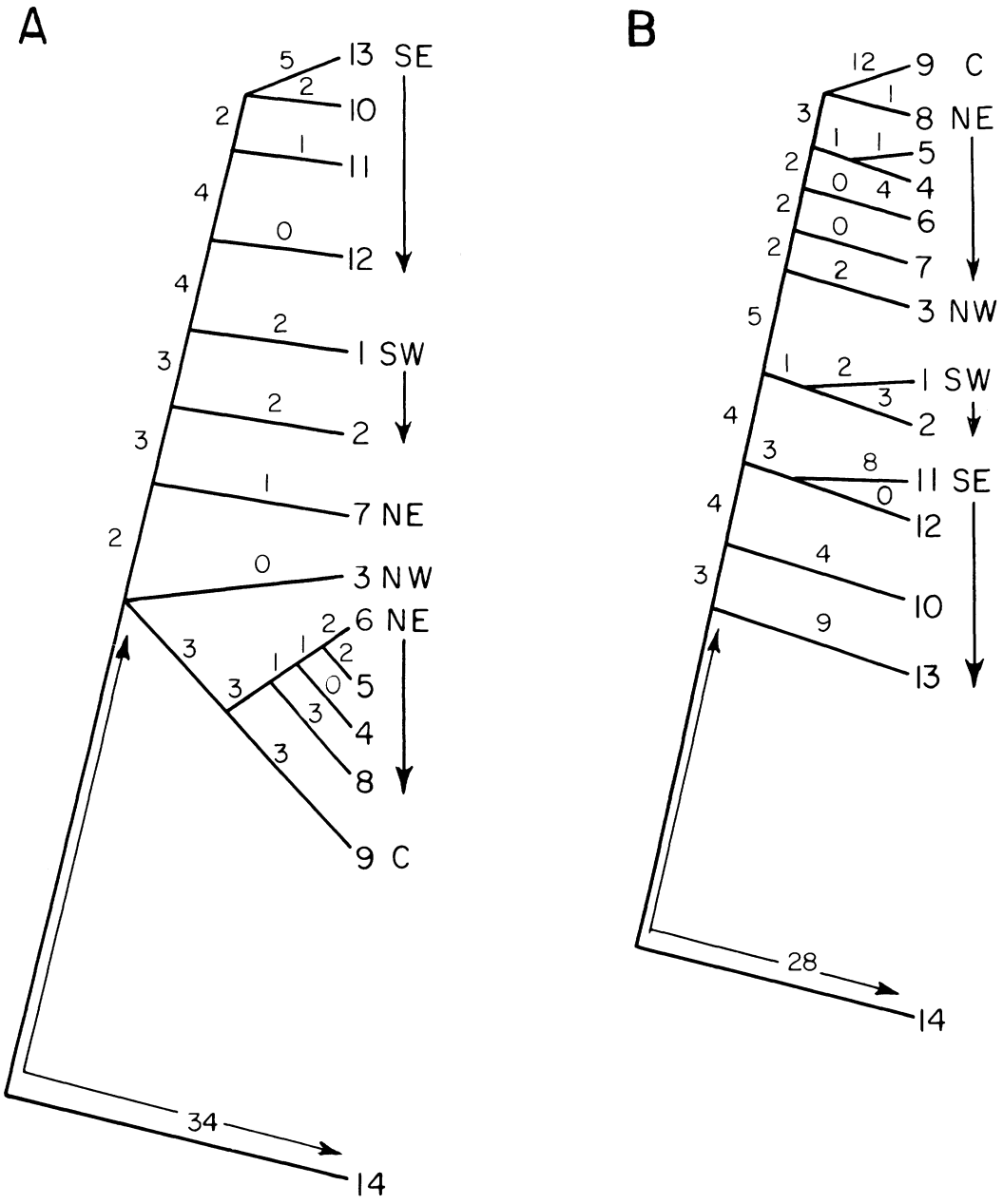


FIG. 4.—Maximum parsimony (Wagner) dendrograms for populations of *Batrachoseps campi* (localities 1–13) and *B. wrighti* (locality 14) based on (A) allele presence and absence, and (B) Rogers' genetic distance × 100. Designations beside locality numbers indicate the geographic position in the range of the species (northwest, northeast, central, southwest, or southeast).

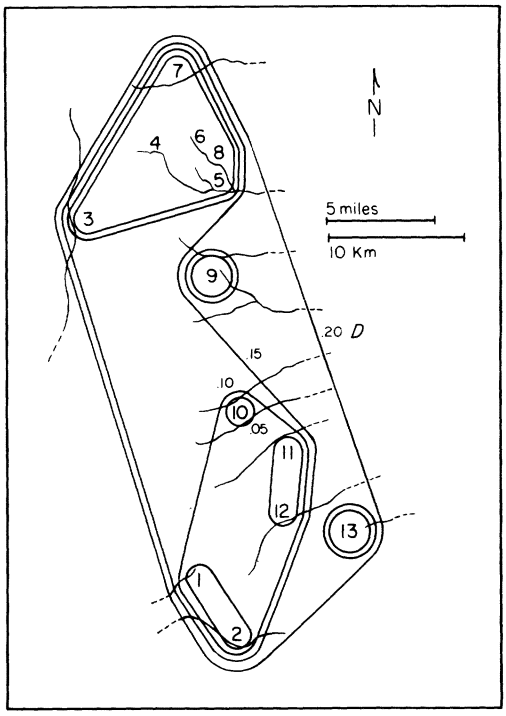


FIG. 5.—Geographic distribution of Nei's genetic distance in *Batrachoseps campi*. Contour interval is $D = 0.05$. Numbered localities are the same as in Fig. 2.

rial pocket gopher *Thomomys bottae*, and Wright (1978) calculated .435 for the house mouse *Mus musculus*; these are both exceptionally high values for mammals (see survey in Wright, 1978). $\bar{F}_{ST}$ observed in *B. campi* is higher than that recorded for *Aneides flavipunctatus*, another genetically variable western plethodontid (.28; Larson, 1980). These studies involve much larger geographic areas than that occupied by *B. campi*. To give some idea of the importance of geographic scale to this measure, the mean value of the relatively widespread *Plethodon websteri* in eastern United States is .742 (Highton, 1979; Larson and Highton, 1978), whereas Hedgecock (1978) reported values of .062 in a microgeographic analysis of *Taricha rivularis* in two different drainage systems (values for 8 loci and 6 populations in the same local drainage system were .024 and .029 for two sets of samples). Considering the relatively small geographic range of *B. campi*, the populations show a high degree of genetic subdivision.

Geographic differentiation in *B. campi* is also evident on a multilocus basis. The pairwise matrix of genetic distance (D, Table 2) was clustered according to the UPGMA algorithm (Sneath and Sokal, 1973) and the resulting clustering levels of D are indicated as contours on a map of sample localities (Fig. 5). The six northern populations are well separated from the others, and together form a relatively tight group. Among the southern populations, Hunter Canyon (13) is distinct. Some differentiation occurs between the western (1, 2) and eastern (10, 11, 12) populations in the south. The apparent distinctiveness of the Willow Springs population (9) may be an artifact of the use of only a single specimen. A similar pattern, obtained by clustering the pairwise matrix of D_R according to the Wagner tree algorithm for distance matrices, is evident in Fig. 4b. Again, the six northern populations are distinct from the southern populations, and Hunter Canyon is relatively isolated.

Genic structuring between geographic localities is also suggested by the significant correlation between D_R and geographic distance between sample localities ($r = .597$; $P < .001$). This may be visualized by comparison of the branching diagrams constructed from D_R and from geographic distance according to the method of Fitch and Margoliash (1967). There is no effective way to compare phenograms based on these two different kinds of distance matrices, but as can be seen from inspection of Fig. 6 the general pattern is similar. In particular, the northeastern populations (4–8) stand out as a unit, as do the southeastern populations (10–12). Northern and southern units are apparent, ignoring our central population (9) that is known from one individual. Geographic distance may be misleading in an area of such extreme topographic relief, however, and the effec-

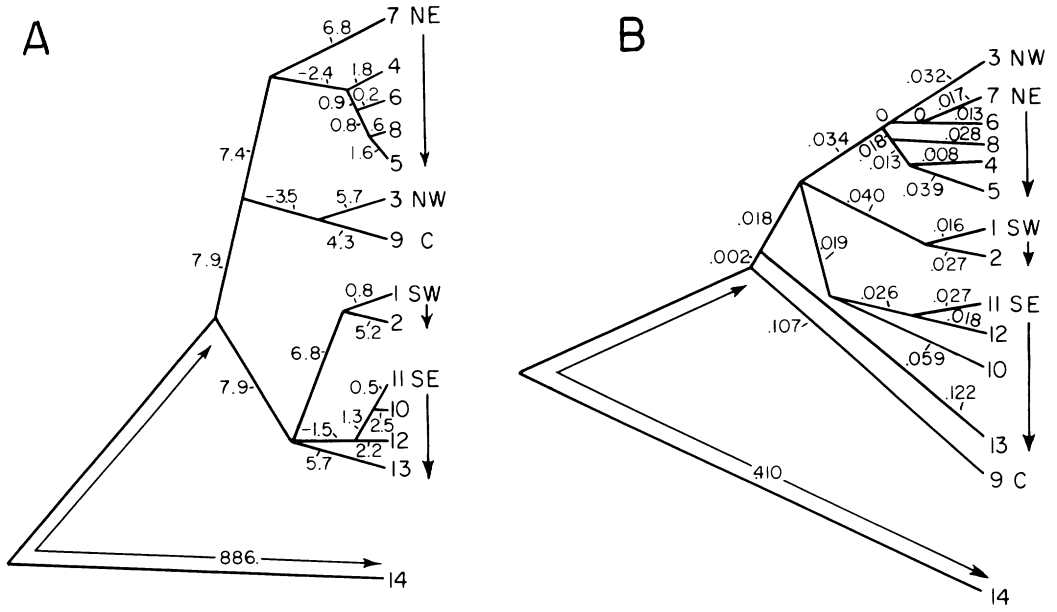


FIG. 6.—Dendrograms of populations of *Batrachoseps campi* (1–13) and *B. wrighti* (14) constructed by method of Fitch and Margoliash. (A) Geographic distance (km) between localities, 15.7% standard deviation; (B) Rogers' genetic distance, 16.1% standard deviation. Locality designations are the same as in Fig. 2.

tive distance between populations separated by high ridges (as, for example, in the case of populations 1 and 2 compared with population 13) might be greatly underestimated.

Mean heterozygosity for the seven populations represented by nine or more specimens is .06 (range = .04–.08). These values are lower than the averages for amphibians summarized in Nei (1975) and Nevo (1978), but they are comparable to heterozygosity values observed among many other taxa of *Batrachoseps*. Only 2 of 9 taxa studied by Yanev (1978) had mean values greater than the mean observed in *B. campi* while 7 taxa had the same or slightly lower means than *B. campi*. The mean heterozygosity in *B. campi* is lower than reported values from studies of some plethodontid salamanders (for example, .103 for 22 populations of *Aneides flavipunctatus*; see Larson, 1980), but higher than others (.048, .041, .034, for 3, 18, and 8 populations of the three species of the *Plethodon welleri* group, respectively; Larson and Highton, 1978).

Batrachoseps campi shows great genic differentiation over a small geographic area. This implies that the seemingly restricted habitat available to these salamanders is functionally discontinuous. We postulate that a combination of small population size, with accompanying genetic drift and restricted gene flow, are the factors primarily responsible for the observed level of differentiation in the species. The high level of genetic differentiation between these populations suggests that they have been isolated from each other for a long time (Nei, 1971; Sarich, 1977).

Genetic divergence.—The magnitude of intraspecific differentiation is indicated by the summary distance measures D and D_R which are presented in Table 2. The range of D within *B. campi* is .01–.23 (mean = .12 ± .06 SD). The range of D_R is .03–.25 (mean = .14 ± .06 SD). These rather great differences for nearby

TABLE 2.—Nei's genetic distance (above diagonal) and Rogers' genetic distance (below diagonal) between populations of *Batrachoseps campi* (1–13) and *B. wrighti* (14).

Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14
French Spring	1	.011	.071	.095	.105	.088	.069	.104	.207	.116	.087	.057	.165	.751
Long John Canyon	2 .043		.101	.132	.143	.124	.105	.150	.250	.152	.135	.096	.168	.795
Barrel Springs	3 .100	.106		.043	.064	.029	.020	.045	.127	.105	.115	.092	.199	.655
Upper Lead Canyon	4 .142	.157	.085		.010	.007	.020	.033	.129	.135	.141	.144	.233	.690
Lower Lead Canyon	5 .156	.176	.108	.047		.022	.040	.030	.138	.132	.133	.145	.222	.687
Upper Addie Canyon	6 .128	.137	.061	.037	.063		.006	.036	.146	.125	.144	.136	.228	.664
Waucoba Canyon	7 .102	.108	.041	.058	.091	.029		.046	.159	.118	.138	.115	.222	.665
Lower Addie Canyon	8 .145	.162	.080	.054	.074	.056	.067		.103	.145	.092	.094	.203	.670
Willow Creek Canyon	9 .218	.227	.136	.161	.178	.162	.162	.128		.213	.168	.178	.201	.721
McElvoy Canyon	10 .149	.160	.130	.165	.170	.151	.142	.168	.221		.078	.093	.133	.679
Keynot Canyon	11 .137	.152	.144	.167	.164	.161	.166	.115	.188	.102		.015	.169	.715
Cove Spring	12 .095	.110	.116	.184	.192	.167	.138	.133	.189	.113	.045		.163	.721
Hunter Canyon	13 .204	.185	.214	.250	.244	.243	.233	.221	.218	.161	.196	.197		.732
Hidden Lake, Oregon	14 .537	.552	.485	.512	.507	.494	.492	.497	.518	.500	.517	.520	.522	

populations occupying a small geographic range reflect the high degree of subdivision already documented (compare these values with the much less differentiated *Plethodon cinereus* on the Del-Mar-Va Peninsula [Highton, 1977], and *Taricha rivularis* in northern California [Hedgecock, 1978]).

The most divergent population is Hunter Creek (13), which has a D of about .2 or greater relative to all northern populations. The six northern populations are only slightly differentiated from each other (populations 3–8 have values of D ranging from .01–.06). The two southwestern populations (1, 2) are also only slightly differentiated (D = .01).

Initial electrophoretic comparisons of one population of *B. campi* to other species of *Batrachoseps* by Yanev (1978) revealed that only one species, *B. wrighti*, has a genetic distance (D) to *B. campi* of less than 1.0, while D between *B. campi* and *B. stebbinsi* is 1.4 and distances between *B. campi* and all remaining species in the genus are greater than 1.5 (*B. aridus* was not available for study). Genetic distances of *B. wrighti* to other *Batrachoseps* exceed 1.0. We accordingly concentrated our attention on the relationship of *B. wrighti* to *B. campi*, utilizing all known populations of *B. campi* in our comparisons. D between the various populations of *B. campi* and *B. wrighti* ranges from .65–.75 (mean = .71 ± .04 SD). Thus, electrophoretic criteria suggest that while *B. campi* is more similar to *B. wrighti* than to any other species in the genus, the distance between these species is relatively large (cf. Highton and Larson, 1979). *Batrachoseps campi* is not simply a slightly differentiated isolate of a widespread species that is distributed elsewhere in more mesic environments. No close relationship is postulated of *B. campi* to any other described species of *Batrachoseps*.

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