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Distribution, Variation, and Hybridization in a Relict Toad (*Bufo microscaphus*) in Southwestern Utah

By Albert P. Blair[1]

The common toad of southwestern Utah was described by Cope (1867) as *Bufo microscaphus*, but he subsequently (1889) relegated it to the synonymy of *B. columbiensis* (now *B. boreas*). In time the superficial resemblance of these weak-crested toads of southwestern Utah and adjacent Nevada and Arizona to *B. compactilis* led to the belief that they were *B. compactilis*. Linsdale (1940) referred them to this species, and, in view of apparent intergrades with *B. woodhousei*, called the two forms *B. c. compactilis* and *B. compactilis woodhousei*. Linsdale also referred the toad of southern coastal California to *B. compactilis californicus* on the basis of resemblance alone (disjunct range; no intermediates). Finally Shannon (1949) recognized that *B. compactilis* was not concerned in the problem and referred the two large toads of southwestern Utah to *B. w. woodhousei* and *B. woodhousei microscaphus*. Stebbins (1951), concurring generally with Shannon but considering the uncertain specimens as species hybrids rather than intergrades, called the common toad of southwestern Utah *B. m. microscaphus;* the coastal California toad he called *B. microscaphus californicus*. Schmidt (1953) followed Stebbins.

In view of the varied nomenclatural history of the common toad of southwestern Utah and the evolutionary problems suggested, it was decided to make a combined field-laboratory investigation. Accordingly the period May 19 to July 19, 1952, was devoted to field work. After

[1] Associate Professor of Zoology, the University of Tulsa, Oklahoma.

a brief collecting stop in west central Arizona and three days of study of *B. m. californicus* along the Mohave River, headquarters was established in St. George, Utah, and subsequent work was carried on from this base. This arrangement made possible simultaneous field work and experimental hybridizations. A brief trip to central Arizona was made early in July.

The area studied is a structurally complex region in which are exposed lava flows of very recent as well as older origin, Tertiary intrusives, pre-Cambrian metamorphics, and marine, lacustrine, and eolian sedimentaries (Cambrian-Eocene). Fenneman (1931) recognizes two physiographic provinces: the Basin and Range Province (Great Basin Section) and the Colorado Plateaus Province (High Plateaus of Utah Section and Grand Canyon Section). The Basin and Range Province (western part of the area under consideration) consists of isolated ranges, mostly dissected block mountains, separated by aggraded desert plains. The Colorado Plateaus Province consists of high block plateaus with dissected margins. Sandstones and limestones are prominent and colorful cliff makers. There has been some folding and much faulting, with the major faults, as the Hurricane, now expressed as prominent physiographic features. Virtually uneroded cinder cones and lava flows are conspicuous.

This is a region of low average annual rainfall (St. George, 8.73 inches; Enterprise, 16.67; Springdale, 14.51) fairly evenly scattered over the year (United States Government, 1946). June is the driest month, with May next. January, February, and March receive the greatest precipitation. Summer thunder showers in July, August, and September boost slightly the averages for these months. Flash floods of great violence sometimes occur; the flood of 1861–1862 is said to have swept the flood plain of the Virgin River virtually clean of vegetation.

Most of the area is drained by the Virgin River and its tributaries, with the chief source of water snow melt from the high plateaus to the northeast and spring water from the Navaho sandstone and other good aquifers. The Virgin River, with approximately a 200-mile course, is estimated to have had a virgin flow of 310,000 acre feet annually. Modern records are as follows: North Fork of the Virgin (Springdale, Utah), 78,000 acre feet; Virgin River (Virgin, Utah), 162,000 acre feet; Virgin River (Littlefield, Arizona), 204,000 acre feet; Santa Clara Creek (below Gunlock, Utah), 22,000 acre feet. At the present time water is diverted for the irrigation of approximately 36,000 acres annually (23,500 in Utah, 9800 in Nevada, 2800 in Arizona). Below LaVerkin, Utah, the Virgin receives mineral

spring contributions of carbonates, sulfates, and chlorides of calcium, magnesium, and sodium, and below Littlefield, Arizona, most of the low flow of the stream is made up of mineral waters from springs near Littlefield.

The altitudinal range of the area is from about 1200 feet in the Lake Mead area to approximately 11,000 feet on the high plateaus of the north. This altitudinal range encompasses a change from desert scrub through sagebrush to pinyon pine and juniper woodland, to Gambel's oak and western yellow pine, on up to blue spruce and Douglas fir, and finally to Engelmann spruce and subalpine fir. Three of the biotic provinces of Dice (1943) (Mohavian, Navahonian, Artemisian) and five of the life zones of Merriam (1898) (Lower Sonoran, Upper Sonoran, Transition, Canadian, Hudsonian) are included.

This study was made possible by a grant from the National Science Foundation. I am also indebted to Mr. Arthur S. Barclay who acted as field assistant; to my wife, Mrs. Winifred H. Blair, who aided in the field work and in care of the experimental hybrids; to Mr. Dean Stock of St. George, Utah, who assisted with much of the field work; and to Mr. Arthur F. Bruhn of Dixie College, St. George, who was of great assistance in many ways. The National Park Service made possible the collecting of specimens in Zion National Park, Grand Canyon National Park, and Pipe Springs National Monument. The Antuitrin S used in the experimental hybridizations was furnished by Parke, Davis and Company. For information concerning the extent of irrigation in southwestern Utah prior to the coming of the white man I am indebted to Messrs. Ramon D. Dangerfield, Robert C. Euler, Jesse D. Jennings, John C. McGregor, and Brad Stuart.

GENERAL OBSERVATIONS ON *BUFO MICROSCAPHUS*

With a single exception (Enterprise Reservoir in the Great Basin drainage) we found *B. microscaphus* restricted to Virgin River drainage in southwestern Utah (table 1; fig. 1). The distribution pattern is strikingly dendritic, and it is doubtful if the toads wander more than a few hundred yards from water, a fact not surprising in view of the forbidding desert landscape. This is apparently not true of *B. punctatus*, however, for during two months of intensive field work we saw not a single juvenile *B. punctatus*, although juveniles of *B. microscaphus* were common and those of *B. woodhousei* were occasionally seen. My impression is that the preferred habitat of *B. microscaphus* is the shore line of a rapid, rocky stream. The tributaries of the Virgin River are for the most part of this nature as is the Virgin

itself (the Paiute name for the river, "Pa-roos," means a dirty turbulent stream), except for the St. George basin and the lower reaches of the stream. The highest altitude at which we found *B. microscaphus* was 5800 feet at Enterprise Reservoir; no bufonid and only one anuran was found higher than this in the area studied.

Several species of anurans were found associated with *B. micro-*

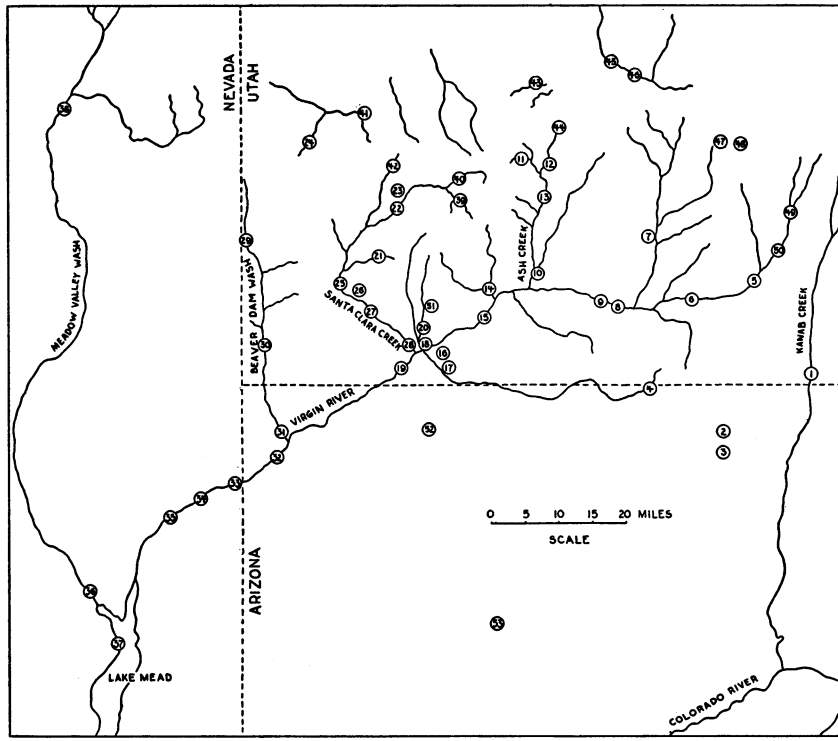

FIG. 1. Collecting localities. The numbers correspond to the numbers in table 1.

scaphus (table 2). Most ubiquitous was *Scaphiopus intermontanus* which ranges over the area studied and ascends to at least 8500 feet. Also wide ranging is *Hyla arenicolor* which we found up to 5000 feet. *Bufo punctatus* is widely distributed here, but we did not find it above approximately 4400 feet. *Bufo woodhousei* was found associated with *B. microscaphus* along the Virgin River from Harrisburg Junction, Utah, to Littlefield, Arizona. A very similar distribution holds for

TABLE 1

Bufo COLLECTION DATA

(Numbers correspond to numbers on figure 1; hybrids are putative hybrids between *Bufo microscaphus* and *B. woodhousei*.)

	Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade		Species
1	Kanab, Utah	Kanab Cr. pond area	6/9	5000	13°	8:00 P.M.	*woodhousei*
2	Moccasin, Ariz.	Irrigation pond	6/18[a]	5100		—	*woodhousei*
3	Pipe Spgs. Natl. Mon., Ariz.	Pond	6/18	5000		—	*woodhousei*
4	Short Creek, Ariz.	Irrigation ditch	6/19	5000	10°	7:00 A.M.	*microscaphus*
5	Mt. Carmel Jct., Utah	Virgin R., pond area	6/27	5200	20°	10:00 P.M.	*woodhousei*
6	Parunuweap Canyon above Shunesburg, Utah	Virgin R.	7/14[a]	4000–4500	14°	5:00 A.M.	*microscaphus*
					27°	3:00 P.M.	
					14–25°[b]	3:00 P.M.	
7	Zion Natl. Park, Utah	Birch Cr.	7/1[a]	4000	25°	3:00 P.M.	*microscaphus*
8	Rockville, Utah	Virgin R.	6/4	3700	15°	8:00 P.M.	*microscaphus*
	Rockville, Utah, 3½ W	Virgin R.	6/4[a]	3600	18°	6:00 P.M.	*microscaphus*
9	Grafton, Utah	Virgin R.	6/4	3700		—	*microscaphus*
10	LaVerkin, Utah, 1½ NNW	LaVerkin Cr.	7/10	3300	21°	10:00 P.M.	*microscaphus* *punctatus*
11	New Harmony, Utah	Town street	7/10	5250		—	*microscaphus*
12	New Harmony, Utah, 5 ESE	Taylor Cr.	7/10	5200	14°	9:00 P.M.	*microscaphus* *punctatus*
13	Pintura, Utah, 6 N	Ash Cr.	6/10	4850	17°	8:00 P.M.	*microscaphus*
14	Harrisburg Jct., Utah, 3½ NE	Quail Cr.	6/11	3100	18°	8:00 P.M.	*microscaphus* hybrids *punctatus*
15	Harrisburg Jct., Utah, 2 ENE	Virgin R.	6/4	2900		—	*microscaphus* *woodhousei*
	Harrisburg Jct., Utah, 2 ENE	Virgin R.	6/9	2900		—	*microscaphus* hybrids *woodhousei*

TABLE 1—*Continued*

	Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade	Species
						punctatus
	St. George, Utah	On highway	6/3	2900	—	*microscaphus*
16	St. George, Utah, 2 SE	Pool near Virgin R.	5/27	2700	—	*microscaphus* hybrids *woodhousei*
17	St. George, Utah, 4 SSE	Irrigation ditches	5/27	2800	—	*woodhousei* hybrids *punctatus*
	St. George, Utah	Concrete pool	5/28[a]	2950	—	*woodhousei*
18	St. George, Utah, 2S	Marsh	6/3	2700	—	*woodhousei*
	St. George, Utah, 1 S	Pond	5/26	2750	—	*woodhousei*
	St. George, Utah	On highway	7/9	2900	—	*microscaphus*
	St. George, Utah	Spring	6/30	3000	—	*woodhousei*
19	Bloomington, Utah	Irrigation ditch	6/15	2500	—	*microscaphus* *woodhousei* *punctatus*
	St. George, Utah, 2 SE	Marsh	6/7	2700	—	*woodhousei* hybrids
	St. George, Utah, 2 S	On road	6/3	2700	—	*microscaphus* hybrids
	St. George, Utah, 2 SE	Virgin R.	7/20	2700	—	*microscaphus*
	St. George, Utah, 2 S	Marsh	5/31	2700	—	*microscaphus* *woodhousei*
20	St. George, Utah	Watercress Spring	6/30	2900	21° 9:00 P.M.	*microscaphus* hybrids *woodhousei*
	St. George, Utah	Watercress Spring	7/9	2900	—	hybrids
	St. George, Utah	Watercress Spring	7/12	2900	—	*microscaphus*

TABLE 1—*Continued*

Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade	Species
					hybrids
					punctatus
St. George, Utah	Watercress Spring	7/20	2900	—	hybrids
					woodhousei
St. George, Utah, 2 S	Marsh	5/26	2700	—	*microscaphus*
					hybrids
					woodhousei
Bloomington, Utah	Virgin R. and marshes	6/13	2500	22°[c] 8:00 P.M.	*microscaphus*
				25°[d] 8:00 P.M.	hybrids
					woodhousei
					punctatus
St. George, Utah, 3 ESE	Virgin R. marsh and swamp	5/30	2700	21°[c] 8:00 P.M.	*microscaphus*
					hybrids
					woodhousei
					punctatus
21 Veyo, Utah, 6 SSW	Sand Cove Reservoir	5/28	4400	—	*microscaphus*
					hybrids
					punctatus
22 Central, Utah, 2 S	Baker Reservoir	7/9	4800	20° 10:00 P.M.	*microscaphus*
23 Central, Utah	Ditch	6/1	5000	—	*microscaphus*
Central, Utah	Irrigation ditch	7/9	5000	16° 9:30 P.M.	*microscaphus*
24 Enterprise, Utah, 10 SW	Enterprise Reservoir and Grassy Cr.	6/6	5800	18°[e] 8:00 P.M.	*microscaphus*
				15°[f] 8:00 P.M.	
25 Gunlock, Utah, 4 S	Santa Clara Cr.	6/28	3300	20° 8:00 P.M.	*microscaphus*
					punctatus
26 Santa Clara, Utah, 4 NW	Irrigation ditch and brook	6/5	3000	—	*microscaphus*
					punctatus
27 Santa Clara, Utah, 3 NW	Ivin's Reservoir	6/5	3000	—	*microscaphus*

TABLE 1—*Continued*

Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade		Species
						hybrids
						punctatus
28 St. George, Utah, 2 S	Santa Clara Cr.	5/26	2650	—		*microscaphus*
						hybrids
						punctatus
St. George, Utah, 2 S	Santa Clara Cr.	5/29	2650	23°	8:00 P.M.	*microscaphus*
						hybrids
						woodhousei
						punctatus
St. George, Utah, 2 S	Santa Clara Cr.	6/3	2650	—		*microscaphus*
						hybrids
						woodhousei
29 Motoqua, Utah	Beaver Dam Wash	7/11	3600	15°	8:00 P.M.	*microscaphus*
						punctatus
30 Arizona line, 8 N	Beaver Dam Wash	6/22	2800	18°	8:00 P.M.	*microscaphus*
						punctatus
31 Littlefield, Ariz.	Big Beaver Cr. (Beaver Dam Wash)	6/2	2100	—		*microscaphus*
						hybrids
						punctatus
32 Littlefield, Ariz., 4 SW	Virgin R.	6/25	1900	21°	10:00 P.M.	*microscaphus*
						hybrids
						woodhousei
						punctatus
33 Mesquite, Nevada	Temporary pond	6/2	1800	—		*woodhousei*
						hybrids
						cognatus
34 Bunkerville, Nev., 2½ SW	Virgin R.	6/25	1700	19°	8:00 P.M.	*woodhousei*
						hybrids

TABLE 1—*Continued*

	Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade		Species
							cognatus
	Mesquite, Nev.	Virgin R.	6/2	1800		—	*woodhousei*
35	Riverside, Nev.	Virgin R. and irrigation ditch	6/2	1650		—	*woodhousei* hybrids
36	Overton–Logandale road, Nev.	Irrigation ditches	5/24	1600		—	*woodhousei* hybrids
37	Overton Landing, Nev.	Lake Mead	5/24	—		—	*woodhousei*
	Overton, Nev.	On highway	6/2	1600		—	*woodhousei*
38	Caliente, Nev., 2 S	Meadow Valley Wash	6/16	4300	19°	8:00 P.M.	*microscaphus*
	Caliente, Nev., 2 S	Ryan State Park, spring and brook	6/16	4300	19°	8:00 P.M.	*microscaphus*
	Kirkland Jct., Ariz., 8 SE	On road along Hassayampa Cr.	7/6	3800	18°	8:00 P.M.	*microscaphus*
	Cottonwood, Ariz.	Verde R.	7/6	3300		—	*woodhousei*
	Cane Spgs., Ariz. (Hewitt Ranch)	Big Sandy R. at mouth of Trout Cr.	5/20	—		—	*microscaphus*
	Victorville, Cal.	Mohave R.	5/21	—		—	*californicus b. halophilus*
	Victorville, Cal.	Mohave R.	5/22	—		—	*californicus b. halophilus*
	Victorville, Cal.	Mohave R.	5/23	—	21.5°	8:30 P.M.	*californicus b. halophilus*
39	Pine Valley, Utah, 2 ESE	Pine Valley Reservoir	6/1	6500	8°	8:00 P.M.	—
	Pine Valley, Utah, 2 ESE	Pine Valley Reservoir	6/8[a]	6500		—	—
	Pine Valley, Utah, 2 ESE	Pine Valley Reservoir	6/23[a]	6500	8°[f]	6:00 P.M.	—
					16°[g]	6:00 P.M.	
	Pine Valley, Utah, 2 ESE	Pine Valley Reservoir	7/16[a]	6500	8°[f]	6:00 A.M.	—
					11°[e]	6:00 A.M.	

TABLE 1—*Continued*

Locality	Habitat	Month and Day, 1952	Altitude, in Feet	Water Temperature, in Degrees Centigrade	Species
40 Pine Valley, Utah, 2 NE	Reservoir	6/23	6900	10°[f] 8:00 P.M.	—
				16°[e] 8:00 P.M.	
41 Enterprise, Utah	Irrigation ditches	7/9	5300	21° 8:30 P.M.	—
42 Central, Utah, 4 NNW	Brook	7/16[a]	5800	15° 10:30 A.M.	—
Mt. Carmel Jct., Utah	Virgin R.	6/9	5000	14° 10:00 P.M.	—
Mt. Carmel Jct., Utah	Virgin R.	6/27	5000	15° 10:00 P.M.	—
43 Cedar City, Utah, 14 WSW	Brook	6/12	5800	16° 8:00 P.M.	—
Enterprise, Utah, 2 SE	Brook	7/9[a]	5800	19° 6:30 P.M.	—
44 Kanarraville, Utah	Irrigation ditches	7/10	5500	—	—
45 Cedar City, Utah	Coal Cr.	6/27[a]	5800	18° 2:00 P.M.	—
46 East of Cedar City, Utah	Coal Cr.	6/27[a]	6400	16° 2:30 P.M.	—
47 Long Valley Jct., Utah, 20 W	Navaho L.	6/27[a]	9100	14° 4:00 P.M.	—
48 Long Valley Jct., Utah, 17 W	Duck Creek L.	6/27[a]	8550	19°[g] 5:00 P.M.	—
49 Northeast of Glendale, Utah	Virgin R., pond area	6/27[a]	7100	17° 6:30 P.M.	—
50 Between Glendale and Orderville, Utah	Virgin R.	6/27	5500	15° 8:00 P.M.	—
51 St. George, Utah, 3 N	Temporary reservoir	7/3	3100	23° 8:30 P.M.	*punctatus*
52 St. George, Utah, 14 S (in Ariz.)	Concrete pool	6/24[a]	3500	25° 10:00 A.M.	*punctatus*
North Rim, Grand Canyon, Ariz.	Spring, brook, and pond	7/19[a]	7000	—	—
New Harmony, Utah	Pond	7/10[a]	5250	21° 8:00 P.M.	—
53 Mt. Trumbull, Ariz.	Ponds	6/21[a]	—	—	—

[a] Daytime collections.
[b] In springs.
[c] In river.
[d] In marsh.
[e] In reservoir.
[f] In creek
[g] In lake shallows.

TABLE 2

COLLECTION DATA, AMPHIBIAN SPECIES ASSOCIATED WITH *Bufo*

Locality	*Bufo* Species	Associated Amphibian Species
Kanab, Utah	*woodhousei*	—
Moccasin, Ariz.	*woodhousei*	*S. intermontanus* *A. tigrinum*
Pipe Spgs. Natl. Mon., Ariz.	*woodhousei*	*A. tigrinum*
Short Creek, Ariz.	*microscaphus*	*S. intermontanus* *H. arenicolor*
Mt. Carmel Jct., Utah	*woodhousei*	*S. intermontanus*
Parunuweap Canyon above Shunesburg, Utah	*microscaphus*	—
Zion Natl. Park, Utah	*microscaphus*	*R. pipiens* *H. arenicolor*
Rockville, Utah	*microscaphus*	—
Rockville, Utah, 3½ W	*microscaphus*	—
Grafton, Utah	*microscaphus*	*S. intermontanus*
LaVerkin, Utah, 1½ NNW	*microscaphus* *punctatus*	*R. pipiens*
New Harmony, Utah	*microscaphus*	—
New Harmony, Utah, 5 ESE	*microscaphus* *punctatus*	—
Pintura, Utah, 6 N	*microscaphus*	*H. arenicolor*
Harrisburg Jct., Utah, 3½ NE	*microscaphus* hybrids *punctatus*	*H. arenicolor*
Harrisburg Jct., Utah, 2 ENE	*microscaphus* *woodhousei*	*R. pipiens*
Harrisburg Jct., Utah, 2 ENE	*microscaphus* hybrids *woodhousei* *punctatus*	—
St. George, Utah	*microscaphus*	—
St. George, Utah, 2 SE	*microscaphus* hybrids *woodhousei*	—
St. George, Utah, 4 SSE	*woodhousei* hybrids *punctatus*	*S. intermontanus*
St. George, Utah	*woodhousei*	*H. arenicolor* *R. catesbeiana* *R. pipiens*
St. George, Utah, 2 S	*woodhousei*	—
St. George, Utah, 1 S	*woodhousei*	*S. intermontanus*
St. George, Utah	*microscaphus*	—
St. George, Utah	*woodhousei*	—

TABLE 2—*Continued*

Locality	*Bufo* Species	Associated Amphibian Species
Bloomington, Utah	*microscaphus* *woodhousei* *punctatus*	*S. intermontanus*
St. George, Utah, 2 SE	*woodhousei* hybrids	—
St. George, Utah, 2 S	*microscaphus* hybrids	—
St. George, Utah, 2 SE	*microscaphus*	—
St. George, Utah, 2 S	*microscaphus* *woodhousei*	*R. pipiens*
St. George, Utah	*microscaphus* hybrids *woodhousei*	*S. intermontanus* *R. catesbeiana*
St. George, Utah	hybrids	—
St. George, Utah	*microscaphus* hybrids *punctatus*	—
St. George, Utah	hybrids *woodhousei*	—
St. George, Utah, 2 S	*microscaphus* hybrids *woodhousei*	*R. pipiens*
Bloomington, Utah	*microscaphus* hybrids *woodhousei* *punctatus*	*S. intermontanus*
St. George, Utah, 3 ESE	*microscaphus* hybrids *woodhousei* *punctatus*	*S. intermontanus* *R. pipiens*
Veyo, Utah, 6 SSW	*microscaphus* hybrids *punctatus*	*S. intermontanus* *H. arenicolor*
Central, Utah, 2 S	*microscaphus*	—
Central, Utah	*microscaphus*	*S. intermontanus*
Central, Utah	*microscaphus*	—
Enterprise, Utah, 10 SW	*microscaphus*	*S. intermontanus*
Gunlock, Utah, 4 S	*microscaphus* *punctatus*	*S. intermontanus* *H. arenicolor*
Santa Clara, Utah, 4 NW	*microscaphus* *punctatus*	*H. arenicolor*
Santa Clara, Utah, 3 NW	*microscaphus* hybrids *punctatus*	*H. arenicolor*

TABLE 2—*Continued*

Locality	*Bufo* Species	Associated Amphibian Species
St. George, Utah, 2 S	*microscaphus*	*R. pipiens*
	hybrids	
	punctatus	
St. George, Utah, 2 S	*microscaphus*	*S. intermontanus*
	hybrids	*R. pipiens*
	woodhousei	
	punctatus	
St. George, Utah, 2 S	*microscaphus*	—
	hybrids	
	woodhousei	
Motoqua, Utah	*microscaphus*	—
	punctatus	
Arizona line, 8 N	*microscaphus*	—
	punctatus	
Littlefield, Ariz.	*microscaphus*	—
	hybrids	
	punctatus	
Littlefield, Ariz., 4 SW	*microscaphus*	—
	hybrids	
	woodhousei	
	punctatus	
Mesquite, Nev.	*woodhousei*	—
	hybrids	
	cognatus	
Bunkerville, Nev., 2½ SW	*woodhousei*	—
	hybrids	
	cognatus	
Mesquite, Nev.	*woodhousei*	—
Riverside, Nev.	*woodhousei*	—
	hybrids	
Overton-Logandale road, Nev.	*woodhousei*	*R. catesbeiana*
	hybrids	*H. regilla*
Overton Landing, Nev.	*woodhousei*	*R. catesbeiana*
Overton, Nev.	*woodhousei*	*R. catesbeiana*
Caliente, Nev., 2 S	*microscaphus*	*S. intermontanus*
		R. pipiens
		R. catesbeiana
Caliente, Nev., 2 S	*microscaphus*	—
Kirkland Jct., Ariz., 8 SE	*microscaphus*	—
Cottonwood, Ariz.	*woodhousei*	—
Cane Spgs., Ariz. (Hewitt Ranch)	*microscaphus*	*R. pipiens*
Victorville, Cal.	*californicus*	*H. regilla*
	b. halophilus	*R. catesbeiana*
Victorville, Cal.	*californicus*	*H. regilla*
	b. halophilus	*R. catesbeiana*

TABLE 2—*Continued*

Locality	*Bufo* Species	Associated Amphibian Species
Victorville, Cal.	*californicus*	*H. regilla*
	b. halophilus	*R. catesbeiana*
Pine Valley, Utah, 2 ESE	—	—
Pine Valley, Utah, 2 ESE	—	Unidentified tadpoles
Pine Valley, Utah, 2 ESE	—	—
Pine Valley, Utah, 2 ESE	—	—
Pine Valley, Utah, 2 NE	—	*S. intermontanus*
Enterprise, Utah	—	—
Central, Utah, 4 NNW	—	—
Mt. Carmel Jct., Utah	—	—
Mt. Carmel Jct., Utah	—	*S. intermontanus*
Cedar City, Utah, 14 WSW	—	—
Enterprise, Utah, 2 SE	—	*S. intermontanus*
Kanarraville, Utah	—	—
Cedar City, Utah	—	—
East of Cedar City, Utah	—	—
Long Valley Jct., Utah, 20 W	—	—
Long Valley Jct., Utah, 17 W	—	*S. intermontanus*
Northeast of Glendale, Utah	—	—
Between Glendale and Orderville, Utah	—	—
St. George, Utah, 3 N	*punctatus*	*S. intermontanus*
		H. arenicolor
St. George, Utah, 14 S (in Arizona)	*punctatus*	—
North Rim, Grand Canyon, Ariz.	—	*S. intermontanus*
New Harmony, Utah	—	*S. intermontanus*
Mt. Trumbull, Ariz.	—	*S. intermontanus*

Rana pipiens, which is not too common in the area, but the leopard frog ranges farther up the river than *B. woodhousei*. The introduced bullfrog was found at St. George, at Caliente, Nevada, and in the Overton-Logandale region of Nevada; in the area occupied by *B. microscaphus*, my observation is that the bullfrog has not been very successful in becoming established. *Hyla regilla* and *Bufo cognatus* were found calling in choruses with *B. woodhousei* in the lower Virgin drainage but were nowhere found associated with *B. microscaphus*.

Aquatic reptilian predators are apparently lacking in the Virgin River drainage where *B. microscaphus* is found. *Thamnophis elegans vagrans* was very common at Pine Valley, Utah, above the altitudinal limit of *B. microscaphus*. The soft-shelled turtle, *Amyda ferox emoryi*,

is in the Colorado River drainage but has not ascended the Virgin River to the range of *B. microscaphus*.

The breeding season of *B. microscaphus* is not correlated with rainfall. June, the month of lowest rainfall, marks the height of the breeding season in southwestern Utah (we found mature tadpoles in late May in central Arizona). On one occasion when a late afternoon shower was followed by a drizzle of rain in the night, there seemed to be no significant effect on breeding activity of toads or other anurans.

Bufo microscaphus does not form large localized calling aggregations, as *B. woodhousei* and *B. punctatus* may do, but individuals are strung out along the shore. Artificial reservoirs, the banks of which are often rocky, are very frequently utilized, but the Virgin River flood plain sloughs and marshes which *B. woodhousei* finds suitable are sparingly or not at all used. The call, a trill, ranges from a high pitch (very similar to that of *B. americanus*) to one much lower and huskier.

That the males of *B. microscaphus* show no more discrimination in clasping than bufonid males in general seems indicated by cross-matings observed during the two months of field work. A male *B. microscaphus* was observed clasping a female *B. punctatus* and another was seen clasping a female *Scaphiopus intermontanus*. The reciprocal crosses of both of these combinations were also observed.

The eggs of *B. microscaphus* are laid in long strings in normal bufonid fashion. Actual counts of five clutches of laboratory-laid eggs gave the following numbers: 4279, 4216, 3872, 3712, 3153. Tadpoles develop to a very large size (for bufonids) and attain adult markings some time before metamorphosis. Metamorphosing tadpoles were observed in July.

VARIATION IN *BUFO MICROSCAPHUS*

In the following comparisons *B. microscaphus* were used only from localities where no *B. woodhousei* were found, and *B. woodhousei* from localities where no *B. microscaphus* were found. For statistical comparison the difference between two means was divided by the standard error of the difference between the means, with a resultant value of 3.0 or greater being taken as significant.

Body Length

There is considerable inherent sampling danger in comparing populations as to body length; nevertheless it is probably worth while to examine this feature. The distance from tip of snout to anal opening was measured with vernier calipers, with the specimen extended on

TABLE 3

BODY LENGTH (IN MILLIMETERS) OF *Bufo microscaphus* MALES

(No toads were used from localities where both *B. microscaphus* and *B. woodhousei* were found.)

	N	Mean	Standard Deviation
Birch Creek	61	56.94 ± 0.32	2.49 ± 0.22
Ash Creek	31	57.57 ± 0.80	4.47 ± 0.57
Quail Creek	123	54.45 ± 0.30	3.36 ± 0.21
Grafton	118	52.77 ± 0.29	3.15 ± 0.20
Sand Cove Reservoir	95	56.25 ± 0.42	4.14 ± 0.30
Ivin's Reservoir	59	59.67 ± 0.52	4.02 ± 0.37
Enterprise Reservoir	61	61.47 ± 0.50	3.90 ± 0.35
Motoqua	27	61.89 ± 0.54	2.82 ± 0.38
Beaver Dam Wash, 8 N	24	60.75 ± 0.69	3.39 ± 0.49
Big Beaver Creek	45	57.39 ± 0.66	4.41 ± 0.46
Meadow Valley Wash	67	57.75 ± 0.43	3.51 ± 0.30

a flat surface. The largest male *B. microscaphus* from the southwestern Utah and adjacent Arizona and Nevada area measured 69.6 mm. and came from Ivin's Reservoir (one from Hassayampa Creek in central Arizona measured 71.1 mm.). This compares with 86.7 mm. for a male *B. woodhousei* from Mt. Carmel Junction, Utah. The smallest *B. microscaphus* showing male secondary sex characteristics was a 46.1-mm. individual from Baker Reservoir; this compares with a 50.1-mm. *B. woodhousei* from Mesquite, Nevada. The largest female *B. microscaphus* observed (Ivin's Reservoir) measured 83.4 mm., comparing with 83.5 mm. for a *B. woodhousei* female from Kanab Creek (a female from the Verde River in central Arizona measured 91.2 mm.).

In a comparison of body lengths of male *B. microscaphus* populations (tables 3 and 4), it is observed that the three populations with greatest body length (Enterprise Reservoir, Motoqua, Beaver Dam Wash, 8 N) are reasonably contiguous geographically; the same can be said for the two populations with smallest body size. Of 55 comparisons of population with population, 36 show significant differences.

In a comparison of *B. woodhousei* populations with those of *B. microscaphus* (table 6), Kanab Creek males differ from all male *B. microscaphus* populations. However, the Moccasin male toads do not differ significantly from those of Motoqua, Enterprise Reservoir, and Beaver Dam Wash, 8 N male *B. microscaphus*, nor do male

TABLE 4

COMPARISON ($d/\sigma d$) OF BODY LENGTHS OF MALE *Bufo microscaphus*

	Birch Creek	Ash Creek	Quail Creek	Grafton	Sand Cove Reservoir	Ivin's Reservoir	Enterprise Reservoir	Motoqua	Beaver Dam Wash, 8 N	Big Beaver Creek	Meadow Valley Wash
Birch Creek		0.7	5.7	9.6	1.3	4.4	7.6	7.5	5.0	0.6	1.5
Ash Creek	0.7		3.6	5.6	1.4	2.2	4.1	4.4	3.0	0.1	0.1
Quail Creek	5.7	3.6		4.0	3.4	8.6	12.0	12.0	8.3	4.0	6.2
Grafton	9.6	5.6	4.0		6.8	11.0	15.0	14.8	10.6	6.4	9.6
Sand Cove Reservoir	1.3	1.4	3.4	6.8		5.1	7.9	8.2	5.5	1.4	2.4
Ivin's Reservoir	4.4	2.2	8.6	11.0	5.1		2.4	2.9	1.2	2.7	2.8
Enterprise Reservoir	7.6	4.1	12.0	15.0	7.9	2.4		0.5	0.8	4.9	5.6
Motoqua	7.5	4.4	12.0	14.8	8.2	2.9	0.5		1.3	5.2	6.0
Beaver Dam Wash, 8 N	5.0	3.0	8.3	10.6	5.5	1.2	0.8	1.3		3.5	3.6
Big Beaver Creek	0.6	0.1	4.0	6.4	1.4	2.7	4.9	5.2	3.5		0.4
Meadow Valley Wash	1.5	0.1	6.2	9.6	2.4	2.8	5.6	6.0	3.6	0.4	

TABLE 5

BODY LENGTH (IN MILLIMETERS) OF MALE *Bufo woodhousei*

(No toads were used from localities where both *B. microscaphus* and *B. woodhousei* were found.)

	N	Mean	Standard Deviation
Mesquite	101	60.84 ± 0.25	2.52 ± 0.17
Moccasin	34	62.37 ± 0.53	3.09 ± 0.37
Kanab Creek	40	64.35 ± 0.61	3.90 ± 0.43
Bunkerville	39	55.23 ± 0.42	2.61 ± 0.30

TABLE 6

COMPARISON ($d/\sigma d$) OF BODY LENGTHS OF MALE *Bufo microscaphus* AND MALE *Bufo woodhousei*

	Kanab Creek	Moccasin	Mesquite	Bunkerville
Motoqua	3.0	0.6	1.7	9.7
Enterprise Reservoir	3.6	1.2	1.1	9.5
Beaver Dam Wash, 8 N	3.9	1.8	0.1	6.8
Ivin's Reservoir	5.8	3.6	2.0	6.6
Meadow Valley Wash	8.8	6.7	6.2	4.1
Ash Creek	6.7	5.0	3.9	2.5
Big Beaver Creek	7.7	5.8	4.8	2.7
Birch Creek	10.7	8.7	9.6	3.2
Sand Cove Reservoir	10.9	9.0	9.3	1.7
Quail Creek	14.5	13.0	16.3	1.5
Grafton	17.1	15.8	21.0	4.8

TABLE 7

HIND LEG LENGTH/BODY LENGTH

(No toads were used from localities where both *B. microscaphus* and *B. woodhousei* were found.)

	N	Mean	Standard Deviation
Male *B. microscaphus*	802	1.351 ± 0.002	0.057 ± 0.001
Female *B. microscaphus*	300	1.315 ± 0.003	0.060 ± 0.002
Male *B. woodhousei*	242	1.334 ± 0.003	0.049 ± 0.002
Female *B. woodhousei*	98	1.320 ± 0.005	0.049 ± 0.003

TABLE 8

VARIATION IN HIND LEG LENGTH/BODY LENGTH, MALES

	N	Mean	Standard Deviation
Birch Creek	61	1.405 ± 0.007	0.057 ± 0.005
Ash Creek	31	1.414 ± 0.010	0.055 ± 0.007
Quail Creek	123	1.381 ± 0.005	0.051 ± 0.003
Grafton	118	1.403 ± 0.004	0.049 ± 0.003
Parunuweap Canyon	23	1.383 ± 0.010	0.048 ± 0.007
Harrisburg Junction	56	1.393 ± 0.008	0.054 ± 0.005
Rockville	9	1.422 ± 0.022	0.065 ± 0.013
St. George	239	1.355 ± 0.003	0.053 ± 0.002
St. George *B. microscaphus*	48	1.399 ± 0.006	0.044 ± 0.005
St. George hybrids	34	1.358 ± 0.010	0.062 ± 0.007
St. George *B. woodhousei*	157	1.341 ± 0.004	0.045 ± 0.003
Baker Reservoir	27	1.401 ± 0.007	0.038 ± 0.005
Santa Clara Creek	143	1.394 ± 0.004	0.052 ± 0.003
Santa Clara Creek *B. microscaphus*	130	1.397 ± 0.003	0.033 ± 0.002
Santa Clara Creek *B. woodhousei*	9	1.364 ± 0.010	0.031 ± 0.007
Ivin's Reservoir	59	1.378 ± 0.006	0.049 ± 0.004
Gunlock	41	1.381 ± 0.007	0.045 ± 0.005
Sand Cove Reservoir	95	1.427 ± 0.006	0.064 ± 0.005
Enterprise Reservoir	61	1.386 ± 0.006	0.048 ± 0.004
Big Beaver Creek (Littlefield)	45	1.387 ± 0.008	0.056 ± 0.006
Beaver Dam Wash, 8 N	24	1.348 ± 0.009	0.044 ± 0.006
Beaver Dam Wash (Motoqua)	27	1.316 ± 0.009	0.047 ± 0.006
Virgin River (Littlefield)	25	1.373 ± 0.008	0.041 ± 0.006
Virgin River (Littlefield) *B. microscaphus*	6	1.388 ± 0.014	0.036 ± 0.010
Virgin River (Littlefield) hybrids	11	1.362 ± 0.012	0.041 ± 0.008
Virgin River (Littlefield) *B. woodhousei*	8	1.375 ± 0.014	0.040 ± 0.010
Mesquite	101	1.317 ± 0.004	0.038 ± 0.003
Virgin River (Bunkerville)	39	1.325 ± 0.007	0.043 ± 0.005
Virgin River (Riverside)	8	1.325 ± 0.020	0.056 ± 0.014
Muddy River	13	1.326 ± 0.014	0.051 ± 0.010
Meadow Valley Wash	67	1.381 ± 0.006	0.050 ± 0.004
Moccasin	34	1.362 ± 0.009	0.054 ± 0.006
Kanab Creek	40	1.365 ± 0.007	0.042 ± 0.005
Pipe Springs National Monument	7	1.349 ± 0.022	0.058 ± 0.016
Mohave River	27	1.362 ± 0.011	0.057 ± 0.008
Hassayampa Creek	9	1.355 ± 0.015	0.046 ± 0.011

Mesquite toads differ from those of Motoqua, Beaver Dam Wash, 8 N, Enterprise Reservoir, or Ivin's Reservoir. Finally, Bunkerville male *B. woodhousei* are smaller than male *B. microscaphus* of nine of the 11 populations considered; they do not differ significantly from

TABLE 9

VARIATION IN HIND LEG LENGTH/BODY LENGTH, FEMALES

	N	Mean	Standard Deviation
Birch Creek	12	1.335 ± 0.014	0.048 ± 0.010
Ash Creek	25	1.328 ± 0.010	0.050 ± 0.007
Quail Creek	13	1.318 ± 0.014	0.051 ± 0.010
Taylor Creek	8	1.285 ± 0.013	0.039 ± 0.010
Parunuweap Canyon	5	1.395 ± 0.023	0.051 ± 0.016
Harrisburg Junction	38	1.332 ± 0.007	0.046 ± 0.005
Rockville	6	1.328 ± 0.018	0.044 ± 0.013
St. George	78	1.298 ± 0.006	0.050 ± 0.004
St. George *B. microscaphus*	25	1.313 ± 0.011	0.055 ± 0.007
St. George hybrids	36	1.280 ± 0.007	0.044 ± 0.005
St. George *B. woodhousei*	17	1.313 ± 0.010	0.042 ± 0.007
Baker Reservoir	16	1.315 ± 0.011	0.045 ± 0.008
Santa Clara Creek	28	1.318 ± 0.010	0.053 ± 0.007
Santa Clara Creek *B. microscaphus*	25	1.315 ± 0.010	0.053 ± 0.007
Ivin's Reservoir	30	1.300 ± 0.010	0.058 ± 0.007
Gunlock	24	1.323 ± 0.012	0.059 ± 0.008
Sand Cove Reservoir	24	1.360 ± 0.010	0.048 ± 0.007
Enterprise Reservoir	40	1.304 ± 0.007	0.043 ± 0.005
Big Beaver Creek (Littlefield)	19	1.317 ± 0.014	0.062 ± 0.010
Beaver Dam Wash, 8 N	11	1.268 ± 0.009	0.029 ± 0.006
Beaver Dam Wash (Motoqua)	15	1.222 ± 0.019	0.074 ± 0.013
Virgin River (Littlefield)	12	1.335 ± 0.011	0.038 ± 0.008
Virgin River (Bunkerville)	43	1.318 ± 0.007	0.048 ± 0.005
Virgin River (Riverside)	30	1.292 ± 0.005	0.030 ± 0.003
Meadow Valley Wash	30	1.339 ± 0.008	0.042 ± 0.005
Kanab Creek	8	1.365 ± 0.024	0.068 ± 0.017
Pipe Springs National Monument	9	1.364 ± 0.010	0.031 ± 0.007
Mohave River	11	1.337 ± 0.018	0.060 ± 0.013
Hassayampa Creek	6	1.282 ± 0.011	0.027 ± 0.008

Ash Creek, Quail Creek, Big Beaver Creek, or Sand Cove Reservoir male *B. microscaphus*.

HIND LEG LENGTH/BODY LENGTH

Hind leg length was determined by extending the hind leg at right angle to the axis of the body and measuring from the center of the anal opening to the tip of the longest toe.

When male *B. microscaphus* were lumped together, a hind leg/body length ratio of 1.351 was determined (table 7). This differs significantly

TABLE 10

VARIATION IN HIND LEG LENGTH/BODY LENGTH, JUVENILES

	N	Mean	Standard Deviation
Birch Creek	68	1.328 ± 0.005	0.043 ± 0.004
Ash Creek	32	1.294 ± 0.011	0.062 ± 0.008
Grafton	9	1.297 ± 0.025	0.076 ± 0.018
Taylor Creek	23	1.299 ± 0.009	0.045 ± 0.006
Harrisburg Junction	29	1.330 ± 0.008	0.041 ± 0.005
Rockville	29	1.298 ± 0.009	0.047 ± 0.006
St. George	7	1.292 ± 0.025	0.066 ± 0.017
Baker Reservoir	25	1.304 ± 0.007	0.038 ± 0.005
Santa Clara Creek	18	1.315 ± 0.010	0.042 ± 0.007
Santa Clara Creek *B. microscaphus*	15	1.312 ± 0.012	0.044 ± 0.008
Ivin's Reservoir	8	1.290 ± 0.010	0.028 ± 0.007
Gunlock	38	1.351 ± 0.013	0.082 ± 0.009
Sand Cove Reservoir	12	1.365 ± 0.013	0.047 ± 0.009
Enterprise Reservoir	6	1.242 ± 0.026	0.063 ± 0.018
Big Beaver Creek (Littlefield)	8	1.345 ± 0.036	0.101 ± 0.025
Virgin River (Bunkerville)	13	1.269 ± 0.019	0.068 ± 0.013
Virgin River (Riverside)	7	1.292 ± 0.021	0.056 ± 0.015
Meadow Valley Wash	23	1.282 ± 0.006	0.030 ± 0.004
Moccasin	12	1.332 ± 0.011	0.038 ± 0.007
Creek, Santa Clara, 4 NW	11	1.271 ± 0.008	0.027 ± 0.006

from the similar ratio of 1.315 for females ($d/\sigma d$ = 10.0). When 14 individual populations are considered, all show males and females differing significantly (table 12). However, lumped collections of *B. woodhousei* show no significant difference between males and females ($d/\sigma d$ = 2.4), and this is also true of each collection taken individually. When individual populations of *B. microscaphus* are considered, 10 of 11 populations show juveniles and females failing to differ significantly.

Lumped collections show male *B. microscaphus* differing significantly from male *B. woodhousei* ($d/\sigma d$ = 4.7).

In a comparison of male *B. microscaphus* of 17 localities, of 137 comparisons 42 show significant differences (table 13). The shortest hind legs (relatively) are found in the Motoqua and Beaver Dam Wash, 8 N populations (which are contiguous), while the longest hind legs are in the Sand Cove Reservoir population; the Sand Cove Reservoir population differs significantly from 12 of the 16 populations

TABLE 11

VARIATION IN HIND LEG LENGTH/BODY LENGTH, FEMALES AND JUVENILES

	N	Mean	Standard Deviation
Birch Creek	80	1.329 ± 0.005	0.043 ± 0.003
Ash Creek	57	1.309 ± 0.008	0.063 ± 0.006
Quail Creek	14	1.318 ± 0.013	0.049 ± 0.009
Grafton	12	1.315 ± 0.021	0.073 ± 0.015
Taylor Creek	31	1.289 ± 0.009	0.053 ± 0.007
Harrisburg Junction	67	1.328 ± 0.005	0.045 ± 0.004
Rockville	35	1.302 ± 0.008	0.047 ± 0.006
St. George	85	1.298 ± 0.006	0.052 ± 0.004
St. George *B. microscaphus*	29	1.312 ± 0.011	0.057 ± 0.007
St. George *B. woodhousei*	19	1.313 ± 0.009	0.040 ± 0.006
Baker Reservoir	41	1.308 ± 0.006	0.041 ± 0.005
Santa Clara Creek	46	1.317 ± 0.007	0.049 ± 0.005
Santa Clara Creek *B. microscaphus*	40	1.315 ± 0.008	0.050 ± 0.005
Ivin's Reservoir	38	1.298 ± 0.009	0.053 ± 0.006
Gunlock	62	1.340 ± 0.010	0.075 ± 0.007
Sand Cove Reservoir	36	1.362 ± 0.008	0.048 ± 0.006
Enterprise Reservoir	46	1.296 ± 0.011	0.077 ± 0.008
Big Beaver Creek (Littlefield)	27	1.325 ± 0.015	0.077 ± 0.010
Beaver Dam Wash, 8 N	12	1.272 ± 0.009	0.030 ± 0.006
Virgin River (Littlefield) hybrids	6	1.348 ± 0.017	0.043 ± 0.012
Virgin River (Bunkerville)	56	1.309 ± 0.007	0.049 ± 0.005
Virgin River (Riverside)	37	1.292 ± 0.006	0.037 ± 0.004
Meadow Valley Wash	53	1.312 ± 0.006	0.049 ± 0.005
Moccasin	17	1.336 ± 0.009	0.037 ± 0.006
Kanab Creek	9	1.359 ± 0.022	0.066 ± 0.016
Creek, Santa Clara, 4 NW	14	1.275 ± 0.008	0.030 ± 0.006
Pipe Springs National Monument	11	1.369 ± 0.011	0.035 ± 0.007
Mohave River	12	1.338 ± 0.017	0.058 ± 0.012

with which it was compared, and the Motoqua and Beaver Dam Wash, 8 N populations differ significantly from 14 and 11, respectively, of the 16 populations with which each was compared.

In a comparison of male *B. microscaphus* with male *B. woodhousei* (table 13), significant differences were found in about half of the comparisons (63 of 119).

PAROTOID GLAND LENGTH/PAROTOID GLAND WIDTH

No significant difference between males and females was found when 15 populations of *B. microscaphus* were considered individually

TABLE 12

COMPARISON ($d/\sigma d$) OF SEXES FOR HIND LEG LENGTH/BODY LENGTH

	Males-Females and Juveniles	Females-Juveniles	Males-Females
B. m. microscaphus			
Birch Creek	8.8	0.4	4.4
Ash Creek	8.1	2.2	6.0
Quail Creek	4.5	–	4.2
Grafton	4.1	–	–
Taylor Creek	–	0.8	–
Parunuweap Canyon	0.4	–	–
Harrisburg Junction	6.7	0.1	5.7
Rockville	5.1	–	–
Baker Reservoir	10.0	0.8	6.6
Ivin's Reservoir	7.3	0.7	6.7
Gunlock	3.3	1.5	4.1
Sand Cove Reservoir	6.5	0.3	5.7
Enterprise Reservoir	7.1	2.3	8.9
Big Beaver Creek	3.6	0.7	4.3
Beaver Dam Wash, 8 N	5.9	–	6.2
Beaver Dam Wash (Motoqua)	4.4	–	4.4
Meadow Valley Wash	8.1	5.7	4.2
Hassayampa Creek	–	–	3.9
B. woodhousei			
Virgin River (Bunkerville)	1.6	2.4	0.7
Virgin River (Riverside)	1.5	0.0	1.6
Moccasin	2.0	–	–
Kanab Creek	0.2	–	0.0
Pipe Springs	0.8	–	0.6
B. m. californicus			
Mohave River	1.1	–	1.1

(table 14). Comparison of males and juveniles of 10 populations showed a significant difference only for Birch Creek. Comparison of females and juveniles of 10 populations showed no significant differences. Accordingly, males, females, and juveniles were lumped for each locality.

The shortest parotoid glands (relatively) were found in the Enterprise Reservoir, Rockville, and Meadow Valley Wash populations (table 15), which are not contiguous. The longest parotoid glands were found in the Hassayampa Creek, Quail Creek, and Gunlock populations, which are not contiguous.

Of 190 comparisons of population with population, 53 show sig-

TABLE

COMPARISONS ($d/\sigma d$) OF

Parotoid Gland Length/Parotoid Gland Width
Males, Females, and Juveniles

Hind Leg Length/Body Length Males	Birch Creek	Ash Creek	Quail Creek	Grafton	Taylor Creek	Parunuweap Canyon	Harrisburg Junction	Rockville	St. George	St. George (B. microscaphus)	St. George (hybrids)	St. George (B. woodhousei)	Baker Reservoir	Santa Clara Creek	Santa Clara Creek (B. microscaphus)	Santa Clara Creek (hybrids)
Birch Creek		2.0	2.5	0.5	0.2	1.6	1.7	3.8	13.1	0.5	4.6	20.3	1.8	0.0	1.2	1.2
Ash Creek	0.7		3.9	1.6	1.3	2.9	0.7	1.3	12.9	1.2	5.3	18.1	0.5	2.0	1.1	1.9
Quail Creek	2.7	2.9		2.9	1.9	0.1	4.2	5.8	10.5	2.5	2.9	17.5	4.1	2.5	3.8	0.4
Grafton	0.2	1.0	3.4		0.1	1.9	1.1	2.5	13.2	0.1	4.9	20.1	1.2	0.5	0.6	1.3
Taylor Creek	-	-	-	-		1.5	0.9	2.5	9.4	0.2	3.9	14.4	0.9	0.2	0.5	1.2
Parunuweap Canyon	1.8	2.1	0.1	1.8	-		2.8	4.3	7.9	1.8	2.5	13.0	2.8	1.6	2.4	0.5
Harrisburg Junction	1.1	1.6	1.2	1.1	-	0.7		2.4	14.5	0.7	5.7	21.7	0.2	1.7	0.5	1.7
Rockville	0.7	0.3	1.8	0.8	-	1.6	1.2		14.8	2.5	6.9	21.0	2.1	3.8	2.8	2.4
St. George	6.4	5.6	4.4	9.6	-	2.6	4.4	3.0		11.0	4.5	6.4	13.9	13.0	14.6	3.0
St. George (B. microscaphus)	0.6	1.2	2.3	0.5	-	1.3	0.6	1.0	6.5		4.5	16.7	0.8	0.6	0.3	1.4
St. George (hybrids)	3.8	3.2	2.0	4.1	-	2.0	2.7	2.7	0.2	3.5		9.5	5.7	4.6	5.5	0.8
St. George (B. woodhousei)	7.9	6.7	6.2	10.9	-	3.8	5.8	3.6	2.8	8.0	1.5		20.7	19.8	22.0	5.3
Baker Reservoir	0.4	1.0	2.3	0.2	-	1.4	0.7	0.9	6.0	0.2	3.5	7.4		1.8	0.6	1.7
Santa Clara Creek	1.3	1.8	2.0	1.5	-	1.0	0.1	1.2	7.8	0.6	3.3	9.3	0.8		1.2	1.2
Santa Clara Creek (B. microscaphus)	1.0	1.6	2.7	1.2	-	1.3	0.4	1.1	9.9	0.2	3.7	11.2	0.5	0.6		1.5
Santa Clara Creek (hybrids)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Santa Clara Creek (B. woodhousei)	3.3	3.5	1.5	3.6	-	1.3	2.2	2.3	2.9	2.9	0.4	2.1	3.0	2.7	3.1	-
Ivin's Reservoir	2.9	3.0	0.3	3.4	-	0.4	1.5	1.9	3.4	2.4	1.7	5.1	2.4	2.2	2.8	-
Gunlock	2.4	2.7	0.0	2.7	-	0.1	1.1	1.7	3.4	1.9	1.8	4.9	2.0	1.6	2.1	-
Sand Cove Reservoir	2.3	1.1	5.8	3.3	-	3.7	3.4	0.2	10.7	3.2	5.9	11.9	2.8	4.5	4.4	-
Enterprise Reservoir	2.0	2.4	0.6	2.3	-	0.2	0.7	1.5	4.7	1.5	2.4	6.2	1.6	1.1	1.6	-
Big Beaver Creek (Littlefield)	1.6	2.1	0.6	1.7	-	0.3	0.5	1.4	3.7	1.2	2.2	5.1	1.3	0.7	1.0	-
Beaver Dam Wash, 8 N	5.0	4.9	3.2	5.5	-	2.6	3.7	3.1	0.7	4.7	0.7	0.7	4.6	4.6	5.1	-
Beaver Dam Wash (Motoqua)	7.8	7.2	6.3	8.8	-	4.9	6.3	4.4	4.1	7.6	3.1	2.5	7.4	7.9	8.5	-
Virgin R. (Littlefield)	3.0	3.2	0.8	3.3	-	0.7	1.7	2.0	2.1	2.6	1.1	3.5	2.6	2.3	2.4	-
Virgin R. (Littlefield) B. microscaphus	1.0	1.5	0.4	1.0	-	0.2	0.3	1.3	2.3	0.7	1.7	3.2	0.8	0.4	0.6	-
Virgin R. (Littlefield) hybrids	3.0	3.3	1.4	3.2	-	1.3	2.1	2.3	0.5	2.7	0.2	1.6	2.8	2.5	2.8	-
Virgin R. (Littlefield) B. woodhousei	1.9	2.2	0.4	1.9	-	0.4	1.1	1.7	1.3	1.5	0.9	2.3	1.6	1.3	1.5	-
Mesquite	10.9	9.0	9.9	15.2	-	6.1	8.4	4.6	7.6	11.3	3.8	4.2	10.4	13.6	16.0	-
Virgin River (Bunkerville)	8.0	7.2	6.5	9.6	-	4.7	6.3	4.2	3.9	8.0	2.7	1.9	7.6	8.5	9.4	-
Virgin River (Riverside)	3.7	3.9	2.7	3.8	-	2.5	3.1	3.2	1.4	3.5	1.4	0.7	3.5	3.3	3.5	-
Muddy River	5.0	5.1	3.6	5.2	-	3.3	4.1	3.6	2.0	4.7	1.8	0.9	4.8	4.6	4.9	-
Meadow Valley Wash	2.6	2.8	0.0	3.0	-	0.1	1.2	1.7	3.8	2.1	1.9	5.5	2.1	1.8	2.3	-
Moccasin	3.7	3.8	1.8	4.1	-	1.5	2.5	2.5	0.7	3.4	0.2	2.1	3.4	3.2	3.6	-
Kanab Creek	4.0	4.0	1.8	4.7	-	1.4	2.6	2.4	1.3	3.6	0.5	2.9	3.6	3.5	4.2	-
Creek, Santa Clara, 4 NW	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pipe Springs	2.4	2.6	1.4	2.4	-	1.4	1.8	2.3	0.2	2.1	0.3	0.3	2.2	2.0	2.1	-
Mohave River	3.2	3.4	1.5	3.5	-	1.4	2.2	2.4	0.6	2.9	0.2	1.7	2.9	2.7	3.0	-
Hassayampa Creek	3.0	3.2	1.6	3.0	-	1.5	2.2	2.5	0.0	2.7	0.1	0.9	2.7	2.5	2.7	-

3

OAD POPULATIONS

Santa Clara Creek (B. woodhousei)	Ivin's Reservoir	Gunlock	Sand Cove Reservoir	Enterprise Reservoir	Big Beaver Creek (Littlefield)	Beaver Dam Wash, 8 N	Beaver Dam Wash (Motoqua)	Virgin R. (Littlefield)	Virgin R. (Littlefield) B. microscaphus	Virgin R. (Littlefield) hybrids	Virgin R. (Littlefield) B. woodhousei	Mesquite	Virgin River (Bunkerville)	Virgin River (Riverside)	Muddy River	Meadow Valley Wash	Moccasin	Kanab Creek	Creek, Santa Clara, 4 NW	Pipe Springs	Mohave River	Hassayampa Creek	Hewitt Ranch
.3	2.6	2.0	2.3	5.4	0.9	0.4	0.1	6.8	1.3	8.4	7.2	16.3	11.4	10.4	7.1	3.9	15.2	18.0	0.7	10.8	0.2	4.1	0.5
.9	0.0	3.5	0.2	2.2	0.9	1.8	1.8	7.4	1.9	8.9	7.7	15.4	11.1	10.5	7.7	0.9	14.9	17.5	0.7	11.2	1.3	5.0	0.9
.6	5.5	0.5	4.8	8.0	2.9	1.1	1.8	5.5	0.6	6.8	6.3	14.0	9.0	8.5	6.1	6.3	13.4	16.2	2.3	9.6	2.0	2.7	2.0
.5	2.0	2.4	1.7	4.7	0.5	0.8	0.5	5.5	1.4	8.6	7.3	16.4	11.5	10.5	7.2	3.2	15.3	18.1	0.3	11.0	0.1	4.3	0.1
.2	1.5	1.5	1.3	3.4	0.5	0.5	0.2	6.1	1.3	7.1	6.8	12.4	8.4	8.4	6.6	2.3	12.4	14.9	0.4	9.7	0.0	3.6	0.2
.5	3.4	0.2	3.2	5.3	2.1	0.8	1.3	5.0	0.7	5.9	6.0	10.8	6.9	7.1	5.8	4.2	11.2	13.8	1.8	8.7	1.5	2.4	1.6
.8	0.9	3.6	0.6	3.8	0.3	1.5	1.4	7.6	1.7	9.4	7.7	17.7	12.7	11.5	7.7	2.2	16.3	19.0	0.3	11.5	0.9	5.0	0.4
.5	1.5	5.4	1.8	0.9	2.2	3.0	3.2	8.5	2.4	10.3	8.4	17.7	13.3	12.2	8.4	0.5	16.7	19.3	1.9	12.3	2.6	6.1	1.9
.3	15.3	10.9	15.1	17.5	11.5	8.4	10.6	0.2	2.3	0.2	2.4	4.5	0.7	0.5	1.7	16.4	5.4	8.5	9.4	4.1	9.8	3.6	8.8
.4	1.4	2.1	1.2	3.6	0.3	0.8	0.5	6.6	1.4	7.9	7.1	14.2	9.8	9.5	7.0	2.4	11.0	16.4	0.2	10.4	0.2	4.1	0.0
.3	6.3	3.3	6.1	8.1	4.6	3.2	4.1	2.9	0.4	3.3	4.5	7.8	3.8	4.3	4.1	7.1	8.3	11.0	4.2	6.7	4.0	0.2	3.9
.8	22.5	17.9	22.3	24.5	17.6	13.2	16.6	3.9	4.3	4.8	0,1	1.2	6.8	4.5	1.1	23.6	0.4	3.8	14.2	0.6	15.2	7.7	13.3
.8	0.7	3.6	0.4	3.4	0.4	1.6	1.5	7.5	1.7	9.3	7.7	17.0	12.3	11.2	7.7	1.8	16.0	18.7	0.4	11.5	1.0	5.0	0.5
.3	2.6	2.0	2.3	5.4	0.9	0.4	0.1	6.8	1.3	8.4	7.2	16.3	11.4	10.3	7.0	3.9	15.2	18.0	0.7	10.8	0.2	4.1	0.5
.7	1.5	3.2	1.2	4.4	0.0	1.2	1.0	7.4	1.6	9.2	7.6	17.6	12.6	11.3	7.5	2.8	16.2	19.0	0.0	11.4	0.6	4.8	0.1
.4	1.9	0.6	1.9	2.8	1.5	0.9	1.1	2.5	0.2	2.7	3.9	4.7	2.7	3.1	3.5	2.3	5.3	6.8	1.4	5.0	1.2	0.9	1.3
	5.0	3.8	5.0	5.8	4.6	3.9	4.2	0.4	2.0	0.4	1.3	1.3	0.6	0.1	0.7	5.4	1.9	3.4	4.4	1.9	4.3	2.1	4.3
.1		4.5	0.3	2.9	1.0	2.1	2.1	8.0	1.8	10.0	8.0	18.3	13.5	12.1	8.0	1.2	16.9	19.6	0.8	11.9	1.5	5.5	1.0
.3	0.3		4.3	7.2	2.5	0.8	1.4	5.7	0.8	7.1	6.5	14.1	9.4	8.9	6.3	5.8	13.7	16.6	1.9	9.8	1.6	3.0	1.7
.3	5.7	4.9		3.2	0.8	1.9	1.9	7.9	1.9	9.8	7.9	18.1	13.3	11.9	7.9	1.5	16.7	19.4	0.7	11.8	1.3	5.3	0.8
.0	0.9	0.5	4.8		3.4	3.9	4.4	9.3	2.7	11.6	8.9	20.2	15.6	13.8	9.0	1.6	18.5	21.1	2.6	13.2	3.6	7.0	2.7
.7	0.9	0.5	4.0	0.1		1.1	0.9	6.9	1.6	8.3	7.3	14.8	10.4	9.9	7.2	2.1	14.3	17.0	0.0	10.7	0.5	4.4	0.1
.1	2.7	2.8	7.3	3.5	3.2		0.3	5.5	1.0	6.4	6.4	11.4	7.5	7.6	6.2	2.9	14.5	14.0	0.9	9.2	0.5	3.1	0.7
.5	5.7	5.7	10.2	6.4	5.8	2.5		6.3	1.2	7.6	6.9	13.9	9.4	9.1	6.7	3.2	13.5	13.5	0.7	10.1	0.3	3.7	0.5
.7	0.5	0.7	5.4	1.3	1.2	2.0	4.7		2.0	0.0	2.2	0.8	0.2	0.5	1.6	8.6	3.9	6.2	6.3	3.4	6.2	2.4	6.0
.3	0.6	0.4	2.5	0.1	0.0	2.4	4.3	0.9		2.1	3.4	3.9	2.0	2.5	3.0	2.3	4.4	5.8	1.5	4.2	1.3	0.5	1.4
.1	1.1	1.3	4.8	1.7	1.7	0.9	3.0	0.7	1.4		2.3	3.6	0.2	0.6	1.7	10.7	4.5	7.3	7.3	3.8	7.4	2.8	6.9
.6	0.1	0.3	3.4	0.7	0.7	1.6	3.5	0.1	0.6	0.7		0.3	2.6	2.0	0.6	8.4	0.4	2.1	7.0	0.5	6.9	4.1	6.8
.3	8.4	7.9	15.2	9.5	7.8	3.1	0.1	6.2	4.8	3.5	3.9		4.6	3.1	0.5	19.4	1.4	4.6	12.3	1.3	13.0	6.5	11.7
.1	5.7	5.6	11.0	6.6	5.8	2.0	0.7	4.5	4.0	2.6	3.1	0.9		1.1	2.0	14.5	5.8	8.9	8.5	4.5	8.9	3.0	8.0
.7	2.5	2.6	4.8	2.9	2.8	1.0	0.4	2.2	2.5	1.5	2.0	0.3	0.0		1.3	12.9	4.2	6.9	8.5	3.4	8.7	3.6	8.1
.2	3.4	3.5	6.6	3.9	3.7	1.3	0.6	2.9	3.1	1.9	2.4	0.6	0.0	0.0		8.4	1.3	3.3	6.8	1.4	6.7	3.7	6.6
.4	0.3	0.0	5.4	0.5	0.6	3.0	6.0	0.8	0.4	1.4	0.3	8.8	6.0	2.6	3.6		17.7	20.4	1.6	12.5	2.4	6.2	1.7
.1	1.4	1.6	6.0	2.2	2.0	1.0	3.6	0.9	1.5	0.0	0.7	4.5	3.2	1.6	2.1	1.7		2.9	12.4	0.2	12.9	7.1	11.8
.0	1.4	1.6	6.6	2.2	2.0	1.4	4.2	0.7	1.4	0.2	0.6	5.9	4.0	1.8	2.4	1.7	0.2		14.9	2.1	15.4	9.5	14.2
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		9.9	0.4	3.9	0.1
.6	1.2	1.3	3.4	1.6	1.6	0.0	1.3	1.0	1.4	0.5	0.9	1.4	1.0	0.8	0.8	1.4	0.5	0.6	-		9.9	6.0	9.5
.1	1.2	1.4	5.1	1.9	1.1	0.9	3.2	0.8	1.4	0.0	0.7	3.8	2.8	1.6	2.0	1.5	0.0	0.2	-	0.5		3.7	0.2
.5	1.4	1.5	4.4	1.9	1.8	0.4	2.2	1.0	1.6	0.3	0.9	2.4	1.8	1.2	1.4	1.6	0.4	0.6	-	0.2	0.3		3.7

TABLE 14

COMPARISON ($d/\sigma d$) OF SEXES FOR PAROTOID GLAND LENGTH/PAROTOID GLAND WIDTH

	Males-Females	Males-Juveniles	Females-Juveniles
B. m. microscaphus			
Birch Creek	0.4	3.1	2.0
Ash Creek	0.1	0.9	1.0
Quail Creek	0.9	–	–
Taylor Creek	0.3	–	–
Harrisburg Junction	1.5	2.2	0.8
Baker Reservoir	1.7	2.2	0.5
Ivin's Reservoir	0.3	1.0	1.1
Gunlock	1.0	2.8	1.4
Sand Cove Reservoir	1.5	1.1	2.0
Enterprise Reservoir	0.3	0.1	0.3
Big Beaver Creek	0.2	0.8	0.5
Beaver Dam Wash, 8 N	1.1	–	–
Beaver Dam Wash (Motoqua)	0.7	–	–
Meadow Valley Wash	0.2	2.9	2.2
Hassayampa Creek	0.2	–	–
B. woodhousei			
Virgin River (Bunkerville)	0.5	1.7	1.2
Virgin River (Riverside)	0.7	0.2	1.3
Moccasin	1.1	–	–
Kanab Creek	0.7	–	–
Pipe Springs	0.5	–	–
B. m. californicus			
Mohave River	0.7	–	–

nificant differences (table 13). Hassayampa Creek toads differ significantly from 17 of the 19 populations with which they were compared. Other populations showing most divergence are Enterprise (differs from 13 of 19), Gunlock (differs from nine of 19), Quail Creek (differs from eight of 19), and Meadow Valley Wash (differs from seven of 19).

Comparison of 20 populations of *B. microscaphus* with seven populations of *B. woodhousei* shows a significant difference in every comparison (table 13).

DORSAL STRIPE

In this, as in the following three characters, toads were inspected and placed in one of three categories. Such a procedure, in which a not entirely discontinuous variation is placed on a discontinuous

TABLE 15

VARIATION IN PAROTOID GLAND LENGTH/PAROTOID GLAND WIDTH

	N	Mean	Standard Deviation
Birch Creek	141	1.648 ± 0.014	0.171 ± 0.011
Ash Creek	88	1.596 ± 0.022	0.206 ± 0.016
Quail Creek	136	1.701 ± 0.015	0.171 ± 0.010
Grafton	130	1.638 ± 0.015	0.173 ± 0.011
Taylor Creek	32	1.642 ± 0.027	0.155 ± 0.019
Parunuweap Canyon	28	1.697 ± 0.026	0.123 ± 0.018
Harrisburg Junction	123	1.615 ± 0.014	0.161 ± 0.010
Rockville	43	1.559 ± 0.019	0.124 ± 0.013
St. George	323	1.947 ± 0.018	0.322 ± 0.013
St. George *B. microscaphus*	77	1.634 ± 0.022	0.191 ± 0.015
St. George hybrids	70	1.795 ± 0.028	0.238 ± 0.020
St. George *B. woodhousei*	176	2.111 ± 0.018	0.242 ± 0.013
Baker Reservoir	68	1.611 ± 0.016	0.135 ± 0.012
Santa Clara Creek	190	1.649 ± 0.014	0.191 ± 0.010
Santa Clara Creek *B. microscaphus*	170	1.625 ± 0.013	0.166 ± 0.009
Santa Clara Creek hybrids	10	1.735 ± 0.068	0.217 ± 0.048
Santa Clara Creek *B. woodhousei*	10	1.975 ± 0.073	0.233 ± 0.052
Ivin's Reservoir	97	1.596 ± 0.014	0.139 ± 0.010
Gunlock	102	1.690 ± 0.015	0.156 ± 0.011
Sand Cove Reservoir	132	1.602 ± 0.014	0.165 ± 0.010
Enterprise Reservoir	107	1.537 ± 0.015	0.157 ± 0.011
Big Beaver Creek (Littlefield)	72	1.624 ± 0.021	0.175 ± 0.015
Beaver Dam Wash, 8 N	36	1.664 ± 0.028	0.171 ± 0.020
Beaver Dam Wash (Motoqua)	42	1.652 ± 0.021	0.133 ± 0.015
Virgin River (Littlefield)	37	1.937 ± 0.042	0.241 ± 0.028
Virgin R. (Littlefield) *B. microscaphus*	9	1.756 ± 0.079	0.238 ± 0.056
Virgin R. (Littlefield) hybrids	17	1.937 ± 0.031	0.130 ± 0.022
Virgin R. (Littlefield) *B. woodhousei*	11	2.100 ± 0.061	0.202 ± 0.043
Mesquite	102	2.076 ± 0.022	0.217 ± 0.015
Virgin River (Bunkerville)	97	1.927 ± 0.020	0.194 ± 0.014
Virgin River (Riverside)	45	1.965 ± 0.027	0.180 ± 0.019
Muddy River	17	2.045 ± 0.054	0.218 ± 0.038
Meadow Valley Wash	125	1.571 ± 0.014	0.161 ± 0.010
Moccasin	52	2.127 ± 0.028	0.199 ± 0.020
Kanab Creek	49	2.247 ± 0.030	0.211 ± 0.021
Creek, Santa Clara, 4 NW	15	1.625 ± 0.029	0.111 ± 0.020
Pipe Springs National Monument	18	2.139 ± 0.043	0.181 ± 0.030
Mohave River	39	1.642 ± 0.025	0.158 ± 0.018
Hassayampa Creek	15	1.805 ± 0.035	0.135 ± 0.025
Hewitt Ranch	7	1.631 ± 0.031	0.083 ± 0.022

TABLE 16

VARIATION IN FOUR QUALITATIVE CHARACTERS

	Dorsal Stripe			Cranial Crests			Thigh Markings			Pectoral Markings		
	Absent	Faint	Good	Faint	Good	Plateau	Unicolor	Intermediate	Mottled	Immaculate	One Spot	Spotted
Birch Creek	130	11	0	141	0	0	138	3	0	113	28	0
Ash Creek	86	2	0	88	0	0	85	3	0	81	7	0
Quail Creek	104	31	1	136	0	0	127	9	0	135	1	0
Grafton	129	1	0	130	0	0	129	1	0	128	2	0
Taylor Creek	30	2	0	32	0	0	32	0	0	32	0	0
Parunuweap Canyon	28	0	0	28	0	0	28	0	0	27	0	1
Harrisburg Junction	116	6	1	121	1	1	121	2	0	119	3	1
Rockville	41	2	0	42	0	1	42	1	0	41	2	0
St. George	91	122	111	90	37	197	76	52	196	129	31	164
St. George *B. microscaphus*	65	13	0	73	5	0	68	8	2	62	14	2
St. George hybrids	23	41	7	15	21	35	7	23	41	26	13	32
St. George *B. woodhousei*	3	68	104	2	11	162	1	21	153	41	4	130
Baker Reservoir	60	8	0	68	0	0	68	0	0	57	11	0
Santa Clara Creek	159	24	6	169	13	7	153	32	4	160	27	2
Santa Clara Creek *B. microscaphus*	156	13	0	163	6	0	147	21	1	148	20	1
Santa Clara Creek hybrids	2	8	0	6	4	0	6	3	1	3	6	1
Santa Clara Creek *B. woodhousei*	1	3	6	0	3	7	0	8	2	9	1	0
Ivin's Reservoir	90	7	0	96	1	0	83	14	0	94	3	0
Gunlock	97	5	0	102	0	0	101	1	0	83	19	0
Sand Cove Reservoir	104	28	0	132	0	0	120	12	0	105	26	1
Enterprise Reservoir	71	36	0	107	0	0	93	14	0	74	32	1
Big Beaver Creek	66	6	0	72	0	0	71	0	1	71	1	0

TABLE 16—*Continued*

	Dorsal Stripe			Cranial Crest			Thigh Markings			Pectoral Markings		
	Absent	Faint	Good	Faint	Good	Pla-teau	Uni-color	Inter-mediate	Mot-tled	Immac-ulate	One Spot	Spot-ted
Beaver Dam Wash, 8 N	36	0	0	36	0	0	35	1	0	35	1	0
Beaver Dam Wash (Motoqua)	35	7	0	42	0	0	39	2	1	40	2	0
Virgin River (Littlefield)	10	21	5	12	9	15	21	10	5	8	8	20
Virgin River (Littlefield) *B. microscaphus*	8	1	0	7	2	0	8	1	0	6	3	0
Virgin River (Littlefield) hybrids	2	13	1	5	6	5	8	5	3	2	5	9
Virgin River (Littlefield) *B. woodhousei*	0	7	4	0	1	10	5	4	2	0	0	11
Mesquite	0	39	63	0	3	99	6	51	44	89	2	11
Virgin River (Bunkerville)	1	58	36	1	26	68	12	65	18	34	42	19
Virgin River (Riverside)	0	13	32	1	3	41	0	0	45	9	16	20
Muddy River	4	9	4	0	7	10	1	11	5	9	5	3
Meadow Valley Wash	75	50	0	122	3	0	120	5	0	114	11	0
Moccasin	0	3	49	0	1	51	0	0	52	23	14	15
Kanab Creek	1	31	17	0	6	43	0	0	49	13	3	33
Creek, Santa Clara, 4 NW	13	2	0	15	0	0	14	1	0	11	4	0
Pipe Springs National Monument	0	2	16	0	2	16	0	1	17	2	2	14
Hassayampa Creek	15	0	0	15	0	0	11	4	0	4	10	1
Hewitt Ranch	7	0	0	7	0	0	2	5	0	4	3	0
Mohave River	39	0	0	39	0	0	16	23	0	38	1	0

scale, leaves much to be desired but is believed to have some merit in reflecting the reality of species variation.

Most *B. microscaphus* lack, or at best have but a faint, dorsal stripe (table 16). Four populations had no individual with dorsal stripe (Parunuweap Canyon, Beaver Dam Wash, 8 N, Hassayampa Creek, and Hewitt Ranch). Other populations showed varying percentages of striped toads, the extreme being Meadow Valley Wash with 40 per cent of weakly striped toads. Only two toads were classified as having a good dorsal stripe (one each from Quail Creek and Harrisburg Junction).

By contrast, in *B. woodhousei* the majority of individuals exhibited a good dorsal stripe, some had a weak dorsal stripe, and a very few lacked a stripe.

Cranial Crests

Toads were classified as having faint (or no) cranial crests, good cranial crests, or cranial crests filled in to form a plateau. Of 20 populations of *B. microscaphus*, 16 had only toads with faint cranial crests (table 16). On the other hand, the *B. woodhousei* populations showed a majority of toads with a plateau and a smaller fraction with good cranial crests.

Thigh Markings

The concealed surface of the thigh was classified as unicolor (usually dark), intermediate, or mottled. Some variation was found in *B. microscaphus* with respect to thigh markings, for example, all 68 toads of the Baker Reservoir collection had unicolor thighs, while 14 of 97 Ivin's Reservoir toads had thighs classified as intermediate (table 16). Populations of *B. woodhousei* were more variable. For example, Mesquite had six unicolor, 51 intermediate, and 44 mottled as compared with Bunkerville's 12 unicolor, 65 intermediate, and 18 mottled, and Riverside's all (45) mottled.

Pectoral Markings

As concerns pectoral markings, toads were classified as having the venter immaculate, with a pectoral spot, or with pectoral spots. *Bufo microscaphus* rarely show pectoral spotting; populations ranged from 100 per cent with immaculate venters to 80 per cent with immaculate venters (20 per cent with pectoral spot). Populations of *B. woodhousei* were more variable (table 16). For example, Mesquite toads were classified as 89 immaculate, two with pectoral spot, and 11 with

TABLE 17

COMPOSITION OF TOAD COLLECTIONS FROM LOCALITIES WHERE BOTH *Bufo microscaphus* AND *Bufo woodhousei* WERE FOUND

	B. microscaphus	Hybrids	*B. woodhousei*
Virgin River (Littlefield)	9	17	11
Virgin River (Harrisburg Junction)	120	2	1
Santa Clara Creek near mouth	170	10	9
Watercress Springs	10	35	2
St. George area (minus Watercress Springs)	67	35	173

pectoral spotting, while Kanab Creek toads were classified as 13 immaculate, three with pectoral spot, and 33 with pectoral spotting.

DORSAL COLOR AND MARKINGS

No quantitative determinations were attempted, but it was noticed that *B. microscaphus* is extremely variable as to dorsal color and markings. Many individuals are reddish brown (the Navaho sandstone is frequently reddish). Very pale individuals with distinct dark dorsal spots occur (probably with a frequency of considerably less than one in 100) and are virtually indistinguishable at casual glance from *B. m. californicus*. Some individuals have the glossy skin which is to be seen in *B. boreas* and *B. canorus*, while others lack this sheen. The extent of dorsal spotting is variable.

NATURAL HYBRIDIZATION

No toad was found which would appear to be a hybrid between *B. microscaphus* and *B. punctatus*. At Sand Cove Reservoir on May 28 a

TABLE 18

VARIATION IN HIND LEG LENGTH/BODY LENGTH OF ST. GEORGE MALE TOADS

	N	Mean	Standard Deviation
Watercress Springs hybrids	6	1.335 ± 0.015	0.038 ± 0.011
St. George hybrids (minus Watercress Springs)	28	1.363 ± 0.012	0.066 ± 0.009
St. George *B. microscaphus*, June 13	23	1.407 ± 0.008	0.040 ± 0.006
St. George *B. woodhousei*, May 30	82	1.335 ± 0.005	0.043 ± 0.003

TABLE 19

COMPARISON ($d/\sigma d$) OF HIND LEG LENGTH/BODY LENGTH IN ST. GEORGE MALE TOADS

Watercress Springs hybrids—St. George hybrids (minus Watercress Springs)	1.4
Watercress Springs hybrids—St. George *B. microscaphus*, June 13	4.2
Watercress Springs hybrids—St. George *B. woodhousei*, May 30	0.0
St. George hybrids (minus Watercress Springs)—St. George *B. microscaphus*, June 13	3.0
St. George hybrids (minus Watercress Springs)—St. George *B. woodhousei*, May 30	2.1
St. George *B. microscaphus*, June 13—St. George *B. woodhousei*, May 30	7.6

male *B. punctatus* was found clasping a female *B. microscaphus* and a male *B. microscaphus* was found clasping a female *B. punctatus*.

The story is otherwise with regard to *B. microscaphus* and *B. woodhousei*. The two species were found associated in relatively few localities, all along or very close to the Virgin River, but at all such localities some apparent hybrids were found (table 17). The number of specimens for these localities is too small for reliable statistical analysis in most instances. The population at Watercress Springs, a very restricted spring-brook-marsh area at the northwest edge of St. George, is of particular interest, because here 35 of the 47 toads collected were classified as hybrids. Of the 35 putative hybrids, seven show a cranial plateau (characteristic of *B. woodhousei*) combined with no dorsal stripe (characteristic of *B. microscaphus*), and nine show mottled thigh (characteristic of *B. woodhousei*) combined with no dorsal stripe. Tables 19, 21, and 23 give hind leg/body and parotoid length/parotoid width ratio comparisons for these toads

TABLE 20

VARIATION IN HIND LEG LENGTH/BODY LENGTH OF ST. GEORGE FEMALE TOADS

	N	Mean	Standard Deviation
Watercress Springs hybrids	29	1.271 ± 0.008	0.042 ± 0.005
Watercress Springs *B. microscaphus*	6	1.255 ± 0.008	0.020 ± 0.006
St. George hybrids (minus Watercress Springs)	7	1.321 ± 0.010	0.026 ± 0.007
St. George *B. microscaphus*, June 13	11	1.351 ± 0.013	0.043 ± 0.009
St. George *B. woodhousei* (minus Watercress Springs)	15	1.315 ± 0.011	0.044 ± 0.008

TABLE 21

COMPARISON ($d/\sigma d$) OF HIND LEG LENGTH/BODY LENGTH IN ST. GEORGE FEMALE TOADS

Watercress Springs hybrids—Watercress Springs *B. microscaphus*	1.4
Watercress Springs hybrids—St. George hybrids (minus Watercress Springs)	3.9
Watercress Springs hybrids—St. George *B. microscaphus*, June 13	5.2
Watercress Springs hybrids—St. George *B. woodhousei* (minus Watercress Springs)	3.2
Watercress Springs *B. microscaphus*—St. George hybrids (minus Watercress Springs)	5.1
Watercress Springs *B. microscaphus*—St. George *B. microscaphus*, June 13	6.2

and others of the St. George area. Table 24 compares Watercress Springs hybrids, St. George hybrids, St. George *B. microscaphus*, and St. George *B. woodhousei* (a value of 0 is assigned to no dorsal stripe, faint cranial crest, and unicolor thigh; a value of 1 is given to faint dorsal stripe, good cranial crest, and intermediate thigh markings; a value of 2 is given to good dorsal stripe, plateau, and mottled thigh: the numbers assigned to each specimen are added, giving an extreme of 0 for *B. microscaphus* and 6 for *B. woodhousei*). Macroscopic examination of gonads of 15 Watercress Springs hybrids showed organs of normal size.

In four localities where no *B. woodhousei* were found, a few toads were classified as hybrids (Sand Cove Reservoir, 12 of 132; Ivin's Reservoir, two of 97; Big Beaver Creek, one of 72; Quail Creek, six of 137). Likewise, in four localities where no *B. microscaphus* were found, some toads were classified as hybrids (Overton-Logandale

TABLE 22

VARIATION (PAROTOID GLAND LENGTH/PAROTOID GLAND WIDTH) IN ST. GEORGE MALE AND FEMALE TOADS

	N	Mean	Standard Deviation
Watercress Springs *B. microscaphus*	9	1.489 ± 0.042	0.126 ± 0.030
Watercress Springs hybrids	35	1.699 ± 0.031	0.182 ± 0.022
St. George hybrids (minus Watercress Springs)	35	1.891 ± 0.042	0.248 ± 0.030
St. George *B. woodhousei*, May 30	87	2.145 ± 0.025	0.233 ± 0.018
St. George *B. microscaphus*, June 13	34	1.666 ± 0.033	0.192 ± 0.023

TABLE 23

COMPARISON ($d/\sigma d$) OF PAROTOID GLAND LENGTH/PAROTOID GLAND WIDTH IN ST. GEORGE MALE AND FEMALE TOADS

Watercress Springs hybrids—St. George hybrids (minus Watercress Springs)	3.2
Watercress Springs hybrids—St. George *B. woodhousei*, May 30	11.2
Watercress Springs hybrids—St. George *B. microscaphus*, June 13	0.7
Watercress Springs hybrids—Watercress Springs *B. microscaphus*	4.0
Watercress Springs *B. microscaphus*—St. George *B. microscaphus*, June 13	3.3

area of Nevada, six of 17; Riverside, Nevada, one of 45; Bunkerville, Nevada, 2½ SW, six of 95; Mesquite, Nevada, one of 102).

EXPERIMENTAL HYBRIDIZATIONS

Crosses involving eight combinations of *B. m. microscaphus* with other species or subspecies were carried out (table 25). Most hybridizations were made by stripping eggs of females which had been stimulated with fresh amphibian pituitary or Antuitrin S into a sperm suspension; a few were made with male clasping female. Tadpoles were reared in shallow white enamel pans, 10 to 15 tadpoles per pan, with water changed every day. *Chara*, *Myriophyllum*, and filamentous algae were added to each pan. Boiled lettuce was the staple diet item, supplemented with chopped earthworms and phyllopods and uncooked beef, pork, and lamb (the tadpoles seemed particularly fond of lamb). One batch of tadpoles was lost to bacterial contamination when uneaten food was not removed. Another batch was lost for unknown reason; they became emaciated and died over a considerable period

TABLE 24

VARIATION IN ST. GEORGE TOADS

(A value of 0 is assigned to no dorsal stripe, faint cranial crest, and unicolor thigh; a value of 1 is assigned to faint dorsal stripe, good cranial crest, and intermediate thigh markings; a value of 2 is assigned to good dorsal stripe, cranial plateau, and mottled thigh. The three numbers assigned to each specimen are added, giving a total ranging from 0 to 6.)

	0	1	2	3	4	5	6
Watercress Springs hybrids	1	4	1	3	11	12	3
St. George area hybrids (minus Watercress Springs)	0	5	7	7	10	2	1
St. George area *B. microscaphus* (minus Watercress Springs)	54	5	5	1	1	1	0
St. George area *B. woodhousei* (minus Watercress Springs)	0	0	1	4	18	58	88

TABLE 25

EXPERIMENTAL HYBRIDIZATIONS

1. *B. m. microscaphus* (Veyo, Utah, 6 SSW) × *B. m. californicus* (Victorville, California). Some larvae abnormal and some apparently normal; metamorphosis
2. *B. m. californicus* (Victorville, California) × *B. m. microscaphus* (St. George, Utah). Metamorphosis
3. *B. m. microscaphus* (St. George, Utah) × *B. woodhousei* (St. George, Utah). Metamorphosis
   B. m. microscaphus (Pintura, Utah, 6 N) × *B. woodhousei* (Kanab, Utah)
4. *B. woodhousei* (St. George, Utah) × *B. m. microscaphus* (St. George, Utah). Metamorphosis
5. *B. m. microscaphus* (Veyo, Utah, 6 SSW) × *B. punctatus* (St. George, Utah). Some larvae abnormal and some apparently normal; metamorphosis
6. *B. punctatus* (St. George, Utah) × *B. m. microscaphus* (St. George, Utah). Difficulty in gastrulation; one abnormal larva formed; no metamorphosis
7. *B. m. microscaphus* (Veyo, Utah, 6 SSW) × *B. compactilis* (Luling, Texas). Some larvae abnormal and some apparently normal; metamorphosis
8. *B. m. microscaphus* (Veyo, Utah, 6 SSW) × *B. boreas halophilus* (Victorville, California). Some larvae abnormal and some apparently normal; metamorphosis

of time, while another pan of the identical cross went through quite uneventfully. Metamorphosis took place at 25 days to six weeks. At metamorphosis the young toads were preserved.

DISCUSSION

Bufo m. microscaphus has enjoyed a varied nomenclatural history, having been associated with *B. boreas*, *B. woodhousei*, *B. compactilis*, and *B. microscaphus californicus*. It is certainly very similar structurally to *B. m. californicus*. I am unable to add materially to any understanding of the relationship of *B. m. microscaphus* and *B. m. californicus* other than to point out that the cross of female *B. m. microscaphus* with male *B. m. californicus* showed reduced viability of zygotes while the reverse cross did not. It is also to be noted that a small per cent of the southwestern Utah *B. m. microscaphus* have a color pattern similar to the *B. m. californicus* of the Mohave River.

Bufo microscaphus appears to have little in common with *B. compactilis*. With *B. woodhousei* it appears to have the relationship of two allopatric species meeting in a narrow zone of secondary intergradation. I am not so sure that *B. microscaphus* has no relationship with *B. boreas*, in fact, I would be tempted, from superficial observation, to believe that there has been some introgression of *B. boreas* genes into the population sometime in the past, even though there is no present contact.

Bufo microscaphus is amazingly reminiscent of *B. americanus*, and I am inclined to hypothesize that it represents an isolated remnant of an *americanus*-like stock which was widespread over the plains and westward during a more mesic period. With the drying up of the west it vanished except in that part of Utah and Arizona where perennial springs and snow melt produced moisture adequate for its survival. Even here it was forced into a strictly dendritic distribution pattern and its breeding season modified to come at the time of maximum runoff from melting snow. With a dendritic distribution pattern the development of a high degree of local differentiation is a logical consequence.

The isolating mechanisms separating *B. microscaphus* and *B. punctatus* would not appear to be sufficiently formidable to account for the complete lack of genic exchange between the two species. The two species breed at the same time, in the same bodies of water to a very considerable extent, they have very similar calls, the males of one species at least occasionally clasp females of the other species, and they are capable of producing viable offspring if the mating involves female of *B. microscaphus* and male of *B. punctatus* (it is to be noted, also, when the relative sizes of the two species are considered, that this is a more likely clasping combination than female *B. punctatus* and male *B. microscaphus*). Yet, for unknown reasons, hybrids are completely lacking.

On the other hand, the extrinsic isolating mechanisms separating *B. microscaphus* and *B. woodhousei* appear to be more formidable, yet hybrids are found wherever the two species occur together. While the two species breed at the same time, to a very considerable extent they utilize different breeding sites, the calls are quite different, and the breeding aggregations differ in their spatial relations (linear in *B. microscaphus*, areal in *B. woodhousei*).

Bufo microscaphus and *B. woodhousei* are by and large allopatric species, meeting in southwestern Utah only along the narrow flood plain of the Virgin River. The explanation for such a distribution may well lie in the fact that only along the flood plain are found suitable breeding sites for both species. *Bufo woodhousei* prefers ponds, sloughs, or marshes, while *B. microscaphus* seems to prefer running brooks and streams. Along the Virgin both types of waters (lotic and lentic) are abundant, but along the tributaries lentic water is virtually absent. Whether or not such habitat preferences can adequately explain the failure of *B. woodhousei* to ascend the tributaries is not clear. *Bufo woodhousei* is notorious for its ability to occupy diverse habitats from sea level to at least 8500 feet, and it is

possible that competition (for food, for living space, for breeding sites) with *B. microscaphus* enters into the picture. Possibly *B. woodhousei* might ascend the tributaries, despite the lack of preferred breeding waters, but for the fact that the territory is already occupied by a large population of *B. microscaphus* in their optimum habitat. Should *B. woodhousei* be able to reach the impoundments on the tributaries (Ivin's Reservoir, Sand Cove Reservoir, Enterprise Reservoir, etc.) it seems quite reasonable to suppose that they might compete on even terms or perhaps even supplant *B. microscaphus*.

An alternative, although not completely exclusive, explanation of the distribution of the two toad species under discussion would envisage *B. woodhousei* as a very late arrival in the Virgin River drainage, one which has not ascended the tributaries simply because it has not had time to do so. If so, the invasion probably came from upstream as well as downstream (the toads of the Kanab Creek-Pipe Springs area differ rather markedly from those of the lower Virgin River). The practice of irrigation (the white man has irrigated land here for the last one hundred years, and the Paiute, pre-Paiute, Developmental Pueblo, and Modified Basketmaker cultures for thousands of years) has greatly increased the number of suitable breeding sites for *B. woodhousei*. Yet one would, with such an explanation, where it is a matter of a time element, expect some variation in the extent to which *B. woodhousei* has migrated up the tributaries. The fact is that it simply has not migrated up the rapid rocky tributaries at all.

Perhaps the nearest approximation to the truth would be that *B. woodhousei* is limited by habitat preference and competition to the narrow flood plain of the Virgin River, and that it is a relatively recent arrival in the Virgin River drainage, and hence there has been little introgression of *B. woodhousei* genes into the gene pool of the *B. microscaphus* populations of the tributaries.

The data on experimental hybridization augment previous data indicating a high degree of crossability for bufonid species of the United States.

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