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THE TAXONOMIC STATUS OF THE WYOMING TOAD, *BUFO BAXTERI* PORTER

HOBART M. SMITH¹, DAVID CHISZAR²,
JOSEPH T. COLLINS³, AND FRANK VAN BREUKELEN¹

¹ Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309-0334, USA; ² Department of Psychology, University of Colorado, Boulder, Colorado 80309-0345, USA; ³ The Center for North American Amphibians and Reptiles, 1502 Medinah Circle, Lawrence, Kansas 66047, USA

ABSTRACT: The population of toads in southeastern Wyoming named *Bufo hemiophrys baxteri* by Porter in 1968 is presumed to be extinct in nature, except perhaps for released, captive-bred specimens. It is sufficiently distinct in several respects, and sufficiently isolated geographically from its nearest relative, *B. h. hemiophrys*, that it should be regarded as a distinct species, forming a superspecies group with *B. hemiophrys*.

Although discovered by George Baxter in 1946 (Baxter and Meyer, 1982), existence of the Wyoming Toad was apparently first recorded by Stebbins (1954: 143, map p. 145), who learned about it from Baxter (Stebbins, personal communication) and listed it from Albany Co., southeastern Wyoming, under the name of *Bufo hemiophrys* Cope. The range of that species is otherwise limited to central western Canada and northern parts of the adjacent United States (Montana, North Dakota, Minnesota), southward in the Red River drainage to northeastern South Dakota. Thus a minimum of about 800 airline km separates the range of the Wyoming toad from that of its more northern closest relative (Figure 1).

The Wyoming population, abundant within 30 miles (48.3 km) of Laramie in the 1950's (Baxter and Meyer, 1982), is now thought to be extinct in nature (Baxter and Stone, 1985; Baxter, personal communication), none having been seen in the wild for some ten years, except for captive-bred releases. The species is federally classified as endangered and requires both federal and state permits for any activity involving it (Levell, 1997). However, specimens have been bred very successfully in several zoos and facilities of the Wyoming Game and Fish Department, with hopes of reestablishing the population in sanctuaries within the limits of its historical range.

Following his original report, Stebbins continued (1966) to refer the Wyoming population to *Bufo hemiophrys*, but added a more specific range: "along the Big and Little Laramie Rivers to about 15 miles north and 15 miles west of Laramie." Conant (1958, 1975) and Conant and Collins (1991) mapped, but did not name or discuss in detail this population in their guides to the eastern and central herpetofauna of North America, because this population fell outside the geographic range covered by them.

It remained for Porter (1968) to regard the Wyoming population as taxonomically distinct, naming it *Bufo hemiophrys baxteri* (holotype formerly KRP 5-164, now USNM 166434). That subspecies has been generally accepted since then (e.g., Baxter and Stone, 1980, 1985; Stebbins, 1985; Collins et al., 1978, 1982; Sanders, 1987;

Collins, 1990), was elevated to species rank by Packard (1971) and subsequently accepted at that rank without comment by Collins (1997), leaving *B. hemiophrys* without any subspecies. However, Cook (1983) regarded the Wyoming population as indistinguishable taxonomically from *B. hemiophrys*, although he interpreted that taxon as a subspecies of *B. americanus* (and Schmidt, 1953, placed it as a subspecies of *B. woodhousii*).

In response to numerous personal communications supportive of species rank for the Wyoming Toad, we re-examined its taxonomic status, concluding that both taxa are of species rank. To simplify communication, we reference *Bufo baxteri* and *B. hemiophrys* as distinct species throughout the remainder of this paper.

MATERIALS AND METHODS

Wild-caught specimens available for study included 25 males (no females) of *Bufo baxteri* from Albany Co., Wyoming: KU 79452, 8.5 mi S Bosler, 4 July 1963; KU 196252, Laramie, 14 June 1946; UCM 58931-6, near Laramie, 14 June 1946; UW H336 (7), same as preceding; UW H422 (10), same as preceding except no date.

Also wild-caught were 62 *Bufo hemiophrys*: KU 98337-49, Roy State Lake Park, Marshall Co., South Dakota; KU 176031-2, Charleswood, Winnipeg, Manitoba, Canada; KU 196247-50, Clear Lake, Marshall Co., South Dakota; UCM 40945-53, 2.4 mi S Grand Forks, 1660 ft., Grand Forks Co., North Dakota; UCM 40954-8, 4.5 N Grand Forks; UCM 40961-3, 40965-76, 21.1 mi W, 0.5 mi S Grand Forks; UCM 40977, 40979-81, 13.7 mi N Arlington, Hamlin Co., North Dakota; UCM 40943-4, 2.5 mi E Carberry on old Hy 1, 1850 ft, Manitoba, Canada; UCM 42539-43, Strawberry Lake, 15 mi S Indian Head, Saskatchewan, Canada; UCM 42544-6, Basrut Cr., 3 mi W Carou on old Hy 1, Saskatchewan, Canada.

In addition, we examined 73 *Bufo baxteri* that died during the implementation of a captive breeding program, and which were necropsied and subsequently frozen by the Wyoming State Veterinary Commission. These specimens were later preserved in formalin and stored in alco-



Figure 1. Distribution of *Bufo hemiophrys* and *B. baxteri* (adapted from Conant and Collins, 1991: map 280).

hol, except for five that were skeletonized using dermestid beetles. Three skeletons of *B. hemiophrys* from North Dakota, one from Manitoba and one from Saskatchewan were prepared from the material listed above.

External features and body proportions were examined, mostly on wild-caught specimens, supplementing the information given for *Bufo hemiophrys* in Underhill (1961) and Cook (1983), for *B. baxteri* by Porter (1968), and for both taxa by Sanders (1987). Certain features were analyzed on the skeletons of each species, supplementing data in Sanders (1987). Measurements were made with dial calipers.

RESULTS

Numerous differences between *Bufo baxteri* and *B. hemiophrys* have been noted by Porter (1968), Sanders (1987) and ourselves (personal observations). We have found that by far the most reliable are those based on skull structure, the width of the vertebral line, and parotoid length. All others were statistically insignificant at the 0.005 level (Table 1), or too subjective to be quantified.

1. *Coronal crests.* In all five skulls of *Bufo hemiophrys*, coronal crests are sharply defined (Figure 2), passing medially from the interorbital crests and separating a broad, flat precoronal plane from a similar but short postcoronal plane. In all five *B. baxteri* skulls the coronal crests are absent (Figure 3), apparently as a result of the thickened rugosity and convergence of the interorbital crests in the coronal crest area.

2. *Interorbital crest structure.* As noted by Sanders (1987), the interorbital crests of *Bufo hemiophrys* are narrow, relatively sharp-edged, non-porous, widely separated and recurved. The latter feature presumably serves to anchor the soft tissue that forms the boss overlying the precoronal plane. On the contrary, the interorbital crests of *B. baxteri* are thickened and porous, relatively close to each other, and with irregular, fine sculpturing that makes them appear "deformed," as characterized by Sanders (1987: 21). Porter (1968) regarded a higher, "more prominent" boss as one of the diagnostic features of his new subspecies. That feature undoubtedly reflects the thicker bony foundation of the boss in *B. baxteri* than in *B. hemiophrys*.

3. *Interorbital crest shape.* In *Bufo hemiophrys* the interorbital crests are essentially parallel throughout most of their length, as far posterior as the level of the coronal crests, where they may converge slightly. Posterior to that level they flare laterally to join the postorbital crests, delimiting the anterolateral edge of the postcoronal plane. In *B. baxteri* the interorbital crests distinctly converge at and posterior to the level where the coronal crests would occur.

4. *Postcoronal plane.* This is a clearly defined area, sloped posteroventrally (as depicted in Sanders, 1987: figs. 1, 7), in *Bufo hemiophrys*. It is smooth and subtriangular, its apex directed posteriorly and ending at the foramen magnum. Its sides are delimited anteriorly by short parietal crests, weakly evident in two skulls. In *B. baxteri* the postcoronal plane is weakly evident, as the whole area tends to be sculptured, and no parietal crests are evident.

5. *Nasal bone structure.* In *Bufo hemiophrys* the nasal bones are smooth or (in one specimen) slightly rugose, although somewhat thickened. In *B. baxteri* they are strongly thickened, highly rugose and porous, with their rear edges distinctly higher than the precoronal plane on the paired frontoparietal bones.

The preceding five cranial features are evident externally to a certain extent, but the overlying skin and boss obscure details. Particularly useful externally is the interorbital crest shape. In *Bufo hemiophrys* the posterior ends of the crests almost invariably diverge at least slightly where they join the postorbital crests (usually not evident externally). In *B. baxteri* the interorbital crests almost invariably converge toward the posterior end, or at least remain parallel, with no more than slight evidence of divergence. Unfortunately, the coronal crests are not



Figure 2. Dorsal view of skulls of *Bufo hemiophrys*. Right, UCM 40974, 21.1 mi W, 0.5 mi S Grand Forks, 1660 ft, Grand Forks Co., North Dakota, length 14.9 mm. Left, UCM 40945, 2.4 mi S Grand Forks, 1660 ft, Grand Forks Co., North Dakota, length 15.5 mm.

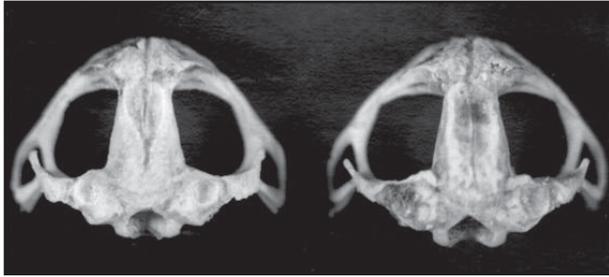


Figure 3. Dorsal view of skulls of *Bufo baxteri* (captive bred). H. M. Smith temporary nos. 6766 (right, length 13.8 mm), 36281 (left, length 12.9 mm).

distinguishable in non-skeletal specimens.

6. *Boss structure.* The preceding five modifications of the median cranial skeleton presumably anchor the soft-tissued boss so characteristic of this group. The boss is narrower (Sanders, 1987: 21) and higher (Porter, 1968: 588, 592) in *Bufo baxteri* than in most *B. hemiophrys* (Sanders, 1987: 21). In *B. hemiophrys* the recurved inner surface of the interorbital crests and the coronal crests may help to hold the boss tissue in place, whereas in *B. baxteri* the expanded, sculptured and porous surfaces of the crests and the nasals presumably serve the same purpose in a different way, thereby eliminating the coronal crests.

7. *Vertebral light line.* Porter (1968) was the only previous worker to have observed that the vertebral light line is narrower in *Bufo baxteri* than in *B. hemiophrys*. It is a useful key character, 97% of the latter having the line over 1.5 mm in width at about the level of the second pair of paravertebral dark spots, only 3% of *B. baxteri* (Table 1). Porter's figures are comparable: 2.2-3.8 mm, $M=2.8$, $n=34$ for *B. hemiophrys*, 0.9-2.6 mm, $M=1.8$, $n=34$ for *B. baxteri*.

8. *Parotoid glands.* The parotoid glands of *Bufo baxteri* are usually more distinct, more elevated, smoother, and more frequently separated from the postorbital crests than in *B. hemiophrys*. In the latter, the parotoids are

often difficult to distinguish in their entirety, being lower and of much the same texture and color as the surrounding skin.

In addition, the parotoids are significantly shorter in wild-caught *Bufo baxteri* than in *B. hemiophrys* (Table 1). The mean interparotoid distance was not significant at the 0.005 level. However, parotoid length plus minimum interparotoid distance was significant at the 0.005 level (Table 1). Parotoid width is the same in both species (Table 1).

9. *Size.* *Bufo baxteri* is significantly smaller than *B. hemiophrys* (Table 1). In our sample of 23 wild-caught specimens of *B. baxteri*, 59.5 mm SVL was the maximum length observed (and the maximum recorded for the species), only three measuring 56 mm or more. In *B. hemiophrys*, 69 mm SVL was the maximum measurement in our sample of 38, and 29 of those exceeded 55 mm. None of Porter's (1968) 34 *B. baxteri* exceeded 58 mm SVL, whereas over half of his 34 *B. hemiophrys* did, reaching 67.5 mm SVL. *B. hemiophrys*, actually reaches a much greater length than was attained by our samples or Porter's: 85 mm SVL in males, 91 mm in females (Cook, 1964: 266). However, Cook (1983: 27) recorded great local variation of sample means, from 45.8 mm in Manitoba to 70.8 mm in Alberta. He further noted that "The largest *B. a.[mericanus] hemiophrys* sample means (61.2 mm and larger) are in the prairie region of southern Alberta and Saskatchewan. There is no clear-cut geographic or vegetation region arrangement of the other groups, though there is a tendency for the sample means to be smaller in the east and larger in the west." That generalization suggests that *B. baxteri* may have been derived from eastern rather than western populations, although ventral pigmentation suggests the converse.

Under the presumably better conditions of captivity, however, *Bufo baxteri* has the potential of reaching considerably greater size than would be likely under natural conditions. Of the 73 captive-bred specimens at hand, 21 are at least 56 mm in SVL measurement, and the largest measures 70.5 mm SVL. In nature, it is unlikely that such a size would be attained.

Table 1. Comparison of selected mensural characters in *Bufo hemiophrys* and *B. baxteri*.

character	<i>B. hemiophrys</i>				<i>B. baxteri</i>				t	df	Sig. at $p < .005$
	n	μ	range	SEM	n	μ	range	SEM			
Vertebral line width (VLW)	37	2.6	1.3-4.2	0.11	63	0.8	0.1-1.7	0.04	17.58	98	yes
Parotoid length (PL)	38	10.4	8.0-13.5	0.25	23	9.1	8.0-11.5	0.19	3.60	59	yes
Interparotoid distance (IPD)	38	9.7	7.0-14.5	0.23	23	8.6	7.0-10.5	0.19	3.18	59	no
Parotoid width (PW)	38	5.7	3.5-7.0	0.15	23	5.6	4.5-6.5	0.12	0.32	59	no
PL + IPD	38	20.1	15.0-24.5	0.39	23	17.7	15.0-20.5	0.28	4.21	59	yes
Body length	38	57.9	42.0-69.0	0.98	23	52.7	47.0-59.5	0.76	3.75	59	yes
Skull width (SW)	5	17.5	16.6-18.5	0.37	5	17.6	15.4-18.9	0.59	0.14	8	no
Skull length (SL)	5	14.5	13.6-15.5	0.37	5	13.4	12.9-13.8	0.16	2.83	8	no
SL/SW	5	0.83	0.79-0.89	0.02	5	0.76	0.71-0.83	0.02	2.60	8	no
TF/SL	5	1.34	1.30-1.38	0.02	5	1.25	1.18-1.37	0.04	2.33	8	no
F/SL	5	1.39	1.37-1.40	0.01	5	1.35	1.16-1.58	0.07	0.58	8	no
HL/SL	5	2.73	2.68-2.78	0.02	5	2.60	2.34-2.95	0.10	1.24	8	no
RU/SL	4	0.75	0.60-0.87	0.06	5	0.76	0.63-0.86	0.04	0.19	7	no
H/SL	5	1.11	1.07-1.15	0.01	5	1.11	0.96-1.22	0.05	0.04	8	no
FL/SL	4	1.85	1.67-1.98	0.07	5	1.87	1.59-2.08	0.08	0.18	7	no

Characters: F, femur length; FL, humerus plus radioulna lengths; H, humerus length; HL, femur plus tibiofibula length; RU, radioulna length, TF, tibiofibula length. All measurements given in mm. Because of the large number of statistical comparisons, alpha was set at 0.005 to reduce the chance of a type I error.



Figure 4. Ventral views of *Bufo hemiophrys* (left, UCM 42545, Basrut Creek, 3 mi W Carou, old Hy 1, Saskatchewan, Canada, 55.5 mm SVL) and *B. baxteri* (right, captive bred, HMS temp. no. 36284, 51.5 mm SVL).

10. *Ventral pattern* (Figure 4). Pigmentation is usually heavy on the venter of *Bufo baxteri* (as dark as or darker than score 6 of Cook, 1983: 7, figure 5, especially in captive-bred specimens, although Cook [personal communication] rated all eight specimens he examined in which the character-state was determinable as 5) and often extends onto the limbs, especially in captive-bred specimens. The venter of our samples of *B. hemiophrys* is usually less heavily pigmented than in *B. baxteri*. According to Cook (1983), the venter of *B. hemiophrys* may be immaculate; pigment reduction is greatest in the eastern part of the range of the species, least toward the west.

11. *Dorsal pattern* (Figure 5). Commonly *Bufo hemiophrys* exhibits three pairs of small paravertebral spots on the dorsum, whereas they are not (or weakly) evident in *B. baxteri*, especially in captive-bred specimens, which tend to be nearly all black dorsally.

12. *Spiculation*. The specimens of *Bufo hemiophrys* have a horny spicule at the tip of most warts, whereas few or no spicules are present on the warts in *B. baxteri*. They are even present on warts on the parotoid glands in some of the former species, thus contributing to the difficulty in delimiting the parotoids.

13. *Outer metatarsal tubercle*. The large, free-edged metatarsal tubercle of *Bufo hemiophrys* is usually blackened, presumably by retention of corneous epithelium, whereas the tubercle is usually pale in *B. baxteri*. Both species exhibit intermediate conditions in a small percentage of specimens.

14. *Mating calls*. Porter (1968: 585, 593) reported that the frequency of mating calls is lower (1450-1700 cps) in *Bufo baxteri* than in *B. hemiophrys* (1600-1900 cps); the pulse rate is slower (37-47 Hz vs 34-58 [27-103 in Cook, 1983: 46]); and the duration longer (4-12 sec vs 4-9 sec [2.1-5.7 sec in Cook, 1983: 46]).

15. *Tympanum*. As noted by Sanders (1987: 18), the tympanum tends to be indistinct or poorly delimited in *Bufo hemiophrys*; it is more distinctly delimited in *B. baxteri*.

16. *Head proportions*. Porter (1968: 588, 593) noted that the head is narrower in *Bufo baxteri* than in *B. hemiophrys*. Measurements of our sample of nonskeletonized

specimens did not substantiate that observation (Table 1).

17. *Limb proportions*. Porter (1968: 588, 593) reported that the limbs of *Bufo baxteri* were shorter than those of *B. hemiophrys*, if the shorter tibiofibula and radioulna to SVL length ratios that he provided are reliable criteria. We found measurements of these parameters on preserved specimens to be unreliable. Measurements of those elements and of the femur and humerus in proportion to skull length in skeletonized specimens produced some means that were less in *B. baxteri*, but none of these differences were significant at the 0.005 level (Table 1).

DISCUSSION

Our limited sample of *Bufo hemiophrys* does not illustrate the complete variation in the characters examined over the entire range of this widely-distributed species (Figure 1). The studies by Underhill (1961), Cook (1983) and Sanders (1987) document extensive variation in the characters they analyzed, and it can be assumed that similar variation occurs in the characters we have utilized. The vertebral line and skull features are probably less variable than any of the others, and perhaps are reasonably constant in each species. It may well be that most of the distinctive attributes of *B. baxteri* occur in some individuals of *B. hemiophrys*, but there is no evidence of this, and it is unlikely that any considerable proportion of them occur in any population other than *B. baxteri*.

Based on our analysis, *Bufo hemiophrys* and *B. baxteri* are consistently different morphologically and are widely separated geographically. In our opinion, those apparent facts justify assignment of species rank to both taxa, as first proposed by Packard (1971). It should be noted that Packard did not use the combination *B. baxteri*, which first appeared in print in Collins (1997).

Although the shared morphological features of these two species strongly suggest common origin, at least one other possibility exists. To be sure, origin from *Bufo woodhousii*, as Schmidt (1953) suggested by making *B. hemiophrys* a subspecies of *B. woodhousii*, is unlikely. Cook's (1983) conclusion of conspecificity of *B. americanus* and *B. hemiophrys* suggests that *B. baxteri* might well have originated independently from *B. americanus*, paralleling *B. hemiophrys* but not derived from it. The

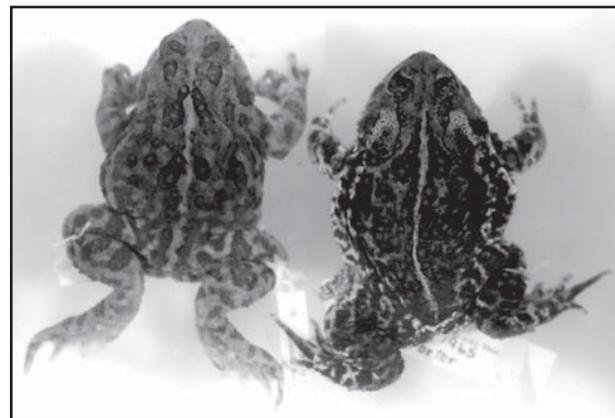


Figure 5. Dorsal views of *Bufo hemiophrys* (left, UCM 40956, 4.5 mi N Grand Forks, 1660 ft, Hy 81, Grand Forks Co., North Dakota, 56.5 mm SVL) and *B. baxteri* (right, captive bred, HMS temp. no. 6765, 61 mm SVL)

current consensus that *B. hemiophrys* is a species distinct from *B. americanus* does not alter the possibility of direct origin of *B. baxteri* from *B. americanus*. The phylogeny of *B. baxteri* is thus uncertain at the present time, although it is likely to be one of the two possibilities here indicated. Either phylogenetic concept is consonant with specific rank of *B. baxteri*.

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LITERATURE CITED

- BAXTER, G. T. AND J. S. MEYER.
1982. The status and decline of the Wyoming toad, *Bufo hemiophrys baxteri*. J. Colo.-Wyo. Acad. Sci. 14: 33.
----- AND M. D. STONE.
1980. Amphibians and reptiles of Wyoming. Cheyenne, Wyoming, Wyoming Game and Fish Dept. 135 pp.
1985. Amphibians and reptiles of Wyoming. Second edition. Cheyenne, Wyoming, Wyoming Game and Fish Dept. 137 pp.
- COLLINS, J. T.
1990. Standard common and current scientific names for North American amphibians and reptiles. Third edition. Soc. Study Amph. Rept., Herp. Circ., (19): i-iii, 1-41.
1997. Standard common and current scientific names for North American amphibians and reptiles. Fourth edition. Soc. Study Amph. Rept., Herp. Circ., (25): i-iii, 1-40.
- , R. CONANT, J. E. HUHEEY, J. L. KNIGHT, E. M. RUNDQUIST AND H. M. SMITH.
1982. Standard common and current scientific names for North American amphibians and reptiles. Second edition. Soc. Study Amph. Rept., Herp. Circ., (12): i-iv, 1-28.
-----, J. E. HUHEEY, J. L. KNIGHT AND H. M. SMITH.
1978. Standard common and current scientific names for North American amphibians and reptiles. Soc. Study Amph. Rept., Herp. Circ., (7): i-iv, 1-36.
- CONANT, R.
1958. Peterson field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian. Boston, Houghton Mifflin. xviii +366 pp.
1975. Peterson field guide to reptiles and amphibians of eastern and central North America. Second edition. Boston, Houghton Mifflin. xviii +429 pp.
----- AND J. T. COLLINS.
1991. Peterson field guide to reptiles and amphibians. Eastern and central North America. Boston, Houghton Mifflin. xx +450 pp.
- COOK, F. R.
1964. The rusty colour phase of the Canadian toad, *Bufo hemiophrys*. Canadian Field-Naturalist 78: 263-267.
1983. An analysis of toads of the *Bufo americanus* group in a contact zone in central northern North America. Nat. Mus. Nat. Sci. [Canada], Publ. Nat. Sci., (3): i-viii, 1-89.
- LEVELL, J. P.
1997. A field guide to reptiles and the law. Second Edition. Excelsior, Minnesota, Serpent's Tale. viii +9-240 pp.
- PACKARD, G. C.
1971. Inconsistency in application of the biological species concept to disjunct populations of anurans in southeastern Wyoming and north-central Colorado. J. Herpetol. 5: 191-193.
- PORTER, K. R.
1968. Evolutionary status of a relict population of *Bufo hemiophrys* Cope. Evolution 22: 583-594.
- SANDERS, O.
1987. Evolutionary hybridization and speciation in North American indigenous toads. Waco, Texas, Baylor Univ. ix +110 pp.
- SCHMIDT, K. P.
1953. A check list of North American amphibians and reptiles. Chicago, Univ. Chicago. viii +280 pp.
- STEBBINS, R. C.
1954. Amphibians and reptiles of western North America. New York, McGraw-Hill. xxiv +537 pp.
1966. Peterson field guide to western reptiles and amphibians. Boston, Houghton Mifflin. xvi +279 pp.
1985. Peterson field guide to western reptiles and amphibians. Second edition. Boston, Houghton Mifflin. xvi +336 pp.
- UNDERHILL, J. C.
1961. Intraspecific variation in the Dakota toad, *Bufo hemiophrys*, from northeastern South Dakota. Herpetologica 17: 220-227.

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