

Catalogue of American Amphibians and Reptiles.

Hall, J.A. 1998. *Scaphiopus intermontanus*.

Scaphiopus intermontanus Cope
Great Basin Spadefoot

Scaphiopus intermontanus Cope 1883:15, 18. Type localities, "within the limits of Salt Lake City, and ... from Pyramid Lake, Nevada," restricted to "Salt Lake City," Salt Lake County, Utah, USA by Schmidt (1953:59). Syntypes, Academy of Natural Sciences, Philadelphia (ANSP) 13787 (Utah, Salt Lake City) and 13788–89 (Nevada, Pyramid Lake) (not examined by author but confirmed to be adults; T. Daeschler, pers. comm.). Cope (1883) reported obtaining three or four specimens at Pyramid Lake, probably during July of 1882; however, only the two noted above have been found (Malnate 1971:351). Although Cope implied he was the collector at Salt Lake City, he was vague as to how he obtained the specimens from Pyramid Lake (Cope 1883).

Spea hammondii intermontana: Cope 1889:303. First use of this combination.

Spea intermontana: Cope 1896:1015. First use of this combination.

Scaphiopus hammondii intermontanus: Wright and Wright 1942:52. First use of this combination.

Spea hammondii intermontanus: Stejneger and Barbour 1943:39. Emendation of ending; however, the authors attributed the first use of this combination and spelling erroneously to Cope (1883).

Scaphorus hammondii intermontanus: Chenoweth 1950:532. Misspelling of *Scaphiopus*.

Spea intermontanus: Firschein 1950:77. Emendation of ending.

Scaphiopus hammondi intermontanus: Schmidt 1953:59. Emendation of ending.

Scaphiopus intermontana: Fitzner and Gray 1991:197. Emendation of ending.

• **Content.** No subspecies are recognized.

• **Definition.** Adult *Scaphiopus intermontanus* attain a total body length of between about 40–63 mm (see Descriptions; range calculated by compiling published data from references cited herein). Females tend on average to be slightly larger than males. The body is compact with relatively short hindlimbs. Hall et al. (1997) reported a ratio for adults of 1.15 for hindlimb length / snout-vent length. The snout is short, slightly turned up (pugnosed), and may be callused. Teeth are present on the upper jaw. The eyes have vertical, elliptically shaped pupils. The iris color is brassy with fine black reticulations. Poorly defined (rudimentary) parotoid and tibial glands and distinct tympana are present (Hall et al. 1997). A wedged-shaped (cuneiform), keratinized, black digging spade is present on the underside of the inner edge of each hind foot (may appear sickle-shaped during its early development; see Hall et al. 1997). Dorsally, the ground color may be gray, brown, or olive, and it is more or less mottled with darker color. Coloration generally matches the surroundings (Nussbaum et al. 1983). Ventrally, the skin is light gray, cream, or white. Skin tubercles may be present on the back, sides, and thighs; these can be red or orange and located within dark brown or black spots or blotches. A large dark blotch usually is present atop each eyelid; in some individuals these meet across the top of the head to form a V-shaped pattern. Usually present are a pair of light gray, irregularly outlined or



Figure 1. Recently transformed *Scaphiopus intermontanus* from Stevens County, Washington (photograph by William P. Leonard).



Figure 2. Adult *Scaphiopus intermontanus* from Grant County, Washington (photograph by William P. Leonard).

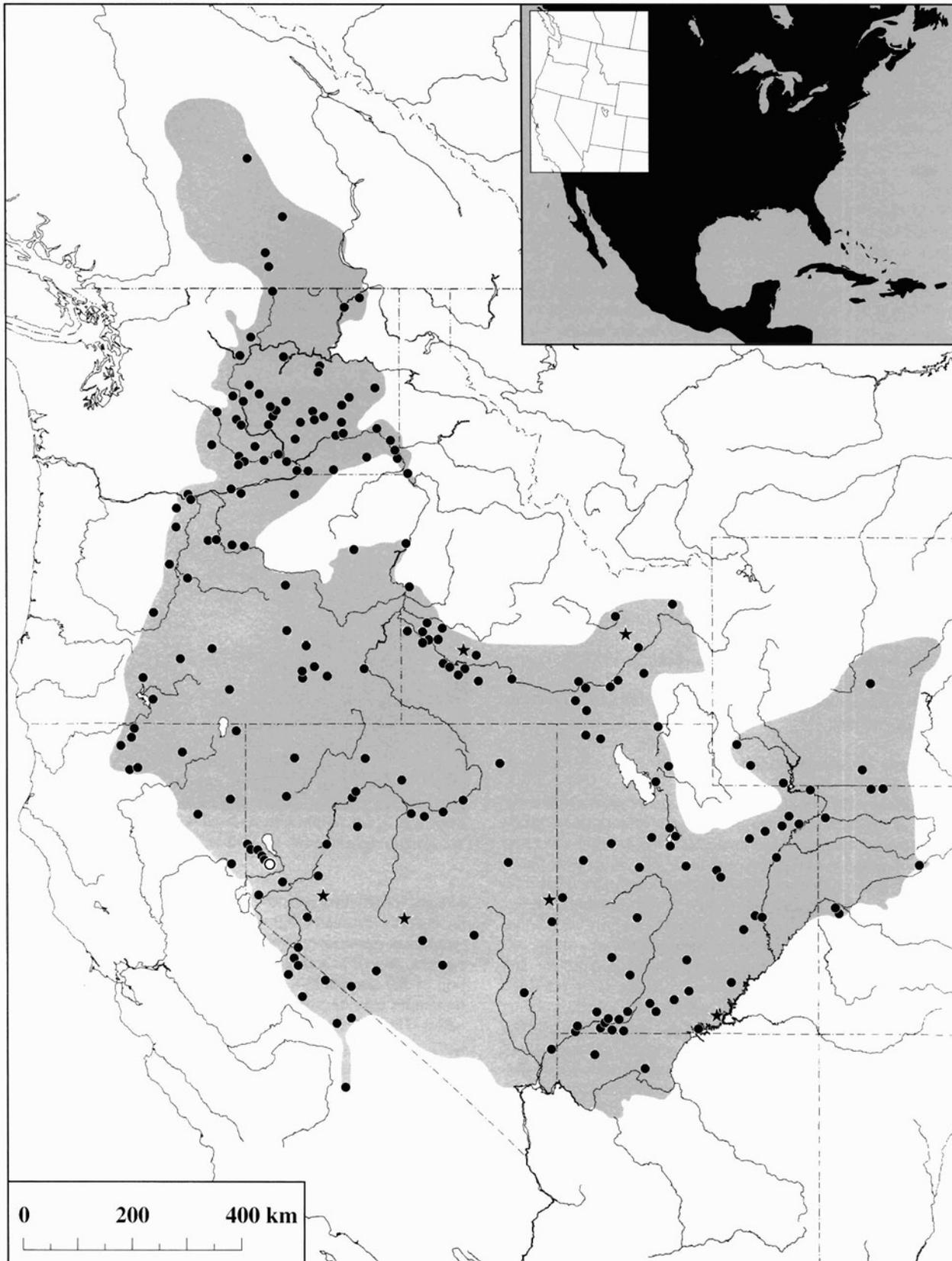
broken, longitudinal stripes that form an hourglass pattern on the dorsum. Similarly, light gray lines running from behind the tympanum posteriorly along the sides of the body also may be present, as well as a single light gray line on the posterior portion of the dorsum (i.e., over the urostyle). A frontoparietal fontanelle may be present, absent, or divided into two fontanelles (Hall 1993). An elevated ridge of bone runs longitudinally along the orbital margin of each frontoparietal bone. Also present is a humped-shaped glandular mass between the eyes. In contrast to females, males possess an internally divided vocal pouch (McAlister 1959), darker throat and chin, more extensive webbing on the hind feet (Chrapliwy 1956), keratinized excrescence on the medial surfaces of fingers one, two, and three (nuptial pads), and small conical (pointed projections) with keratinized apices scattered mostly across the dorsum (Hall et al. 1997). The nuptial pads, and perhaps the other character states except the vocal pouch, are only seasonally dimorphic.

At hatching larvae are 5–7 mm in total length. Before entering metamorphic climax they may attain lengths of up to 70

650.2

mm. Body shape is mostly globular to ovoid and is somewhat depressed. Coloration is dark gray, brown, or black. In dorsal view an area just anterior to the gut is relatively clear of pigmentation laterally and seems to separate a triangular-shaped

head from the abdomen. The abdomen has a golden iridescence, and gold or brassy flecks or patches are otherwise scattered about. The external nares are oriented anterolaterally with the opening rimmed dorsally and on the sides to form a short tube (Hall



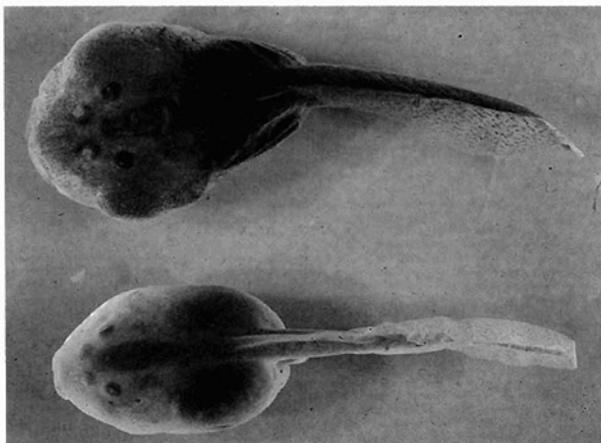


Figure 3. Dorsal views of predominately predaceous, carnivorous (top) and predominately herbivorous (bottom) larval morphological types of *Scaphiopus intermontanus*. The carnivorous morphological type is from Ada County, Idaho (photograph by John H. Larsen, Jr.).

1993). The eyes are positioned dorsally and close together, elevated slightly, and oriented anterolaterally (more laterally than the nares). A single spiracle is located low on the left side of the body (paragyrinid) with its aperture oriented mostly posteriorly and slightly dorsally. The vent tube opens posteromedially with a longitudinally oriented, slit-like aperture. The tail fins both form shallow arches. The dorsal fin stops at the body. At the site of maximum fin curvature and height, both dorsal and ventral fins are slightly greater in height than the tail musculature (Hall 1993). The tail tip has a slightly attenuated appearance. The brownish pigmentation of the tail musculature forms a chevron pattern (darker dorsally). The tail fins are pigmented in a brown reticulate pattern except for a clear area in the anterior of the ventral fin. The oral disc is protuberant and lacks emarginations. The distal portion of the oral disc forms a circular fold of tissue that surrounds the mouth opening: the anterior and posterior labia. The labial fold contains typically one to two rows of marginal papillae, except for an anterior gap where one of the labial tooth (denticle) rows resides. Typically, at full de-

velopment, four tooth rows are present on both the anterior and posterior labia (Hall 1993). The two rows on each labium closest to the mouth opening always have median gaps, the next row out usually, but not always, has a median gap, and the outermost row is always complete across the midline. The upper keratinized jaw forms a broad arch that extends laterally beyond the lateral limits of the lower jaw. The lower jaw forms a shallow to steep V. Both jaws are serrated. Variation in the jaw shape occurs — a median projection on the upper jaw and a notch and projections on the lower jaw may be present — and may be associated with carnivorous food habits. A keratinized knob of tissue is suspended from the roof of the buccal cavity. In one laboratory study, larvae entered metamorphic climax at a SVL of about 23 mm and completed climax at about 20 mm (Hall 1993).

• **Diagnosis.** *Scaphiopus intermontanus* adults can be distinguished externally from adult *S. holbrookii* (includes *hurterii*) by the absence of pectoral glands, smaller size (< 65 mm SVL), and a cuneiform-shaped digging spade. *Scaphiopus holbrookii* possesses pectoral glands, is larger in size (can be >80 mm SVL), and has a sickle-shaped digging spade. *Scaphiopus couchii* is similar in size to *S. holbrookii* and is the only *Scaphiopus* with a marbled coloration pattern. Internally, the presence of relatively large opercula, lack of dermal encrustation on the skull, lack of contact between the maxillae and squamosals, and completely divided vocal sac in males distinguish *S. intermontanus* from *S. couchii* and *S. holbrookii* (see Kluge 1966:19; the data for opercula are reversed in Table 5, but described correctly on page 10). Male *S. intermontanus* can be distinguished from all other *Scaphiopus* males by characteristics of its mating call (McAlister 1959, Northen 1970). Conflicts in the literature in regard to size differences between *S. intermontanus* and *S. bombifrons*, *S. hammondii*, and *S. multiplicatus*, possibly attributable to either geographic variation or misidentification of specimens, or both, preclude separation of these species on this basis. The presence of prominent ridges along the orbital margin of the frontoparietal bones, glandular material in the interorbital space, and a tendency towards closure of the frontoparietal fontanelle with bone in *S. intermontanus* distinguishes this species from *S. hammondii* and *S. multiplicatus*. Typically, *S. bombifrons* develops a rounded, bony "boss" atop each frontoparietal in contrast to the ridges of *S. intermontanus*, though

Map. Distribution of *Scaphiopus intermontanus*. The type localities are indicated by circles. Dots mark other localities. Fossil localities are indicated by stars. A question mark indicates an uncertain fossil site. The mapped location for the Pyramid Lake, Nevada syntype is arbitrary. The original citation for the specimens collected at Pyramid Lake (i.e., Cope 1883) provided no specific locality information other than that the locale was at a pond in proximity to the lake shoreline. All but one Arizona location (taken from the literature) are based on catalogued museum records. All fossil localities are taken from the literature. Museum records plotted on the map are from: AMNH, ANSP, BYU, CAS (includes CAS-SU), KU, MVZ, Oregon St. Univ., Roy. Brit. Columbia Mus., UCM, UMMZ, and USNM (all records obtained directly by the author); LACM, Univ. Puget Sound, and Washington St. Univ. (most records obtained via Kelly McAllister of the Washington Dept. Fish and Wildlife); and FMNH, Idaho St. Univ., Univ. of Idaho, Univ. of Louisville, and Univ. Texas at Arlington (records obtained via Charles Peterson of Idaho St. Univ.). Museum abbreviations are as found in Edwards (1975).

Museum locality data used in this account should be regarded as a secondary source of information, as the author did not confirm specimen identity. Based on other sources of information, published and otherwise, the author, however, in several cases did make changes to the interpretation of specimen identity recorded by some museums. Thus, some of the plotted locations may have been assigned by a museum to a different species within the genus *Scaphiopus*. Moreover, several museums had locality records for specimens identified as *S. intermontanus* that occurred outside of the distributional boundaries provided here. Again, based on other sources of information, these records were rejected and considered to represent other species of *Scaphiopus*. All errors of interpretation that may be present are solely the responsibility of the author. The distributional boundaries indicated here represent a hypothesis the accuracy of which is subject to field testing. In addition to museum records, sighting information and habitat association data were used to predict the range outline. No attempt has been made to predict areas of potentially unsuitable habitat that may occur within the boundaries. Because many museum records are >50 years old, *S. intermontanus* may not occur presently in all areas indicated by its historic distribution.

individuals of each species may approach the condition of the other (Northen 1970). Northen (1970) also found that some *S. bombifrons* individuals had similar amounts of glandular material overlying the boss area as can be found in *S. intermontanus* and that hybrids between *S. multiplicatus* and either *S. bombifrons* or *S. intermontanus* cannot be distinguished just on the basis of the condition of the frontoparietal bones. McAlister (1959) observed that compared with other *Scaphiopus*, *S. intermontanus* males had considerably more gular skin and subhyoid muscular modification potentially resulting in a comparatively greater amount of vocal pouch inflation in *S. intermontanus*.

Scaphiopus intermontanus larvae can be distinguished from larval *S. couchii* and *S. holbrookii* by the presence of the keratinized knob in the roof of the mouth, which these latter forms lack. *Scaphiopus intermontanus* larvae also are much larger in size for a given stage of development (Altig 1970, Altig and Johnston 1986). Compared with *S. bombifrons*, the body is more depressed, the dorsal fin does not rise as abruptly from the body, and the tail length / tail height ratio is greater: 2.0 or more in *S. intermontanus* (Hall 1993) and 1.9 or less in *S. bombifrons* (Altig 1970). Compared with *S. hammondi*, the tail height / tail musculature height ratio is greater: 3.0 or more in *S. intermontanus* (Hall 1993) and 2.9 or less in *S. hammondi* (Altig 1970: this authority did not recognize *S. multiplicatus* as a distinct species separate from *S. hammondi*; therefore, the reported criterion may apply to only one or the other species or to both).

• **Descriptions.** Adult *S. intermontanus* are described in Cope (1883, 1889), Snyder (1920), Tanner (1931), Logier (1932), Gordon (1939), Carl (1943), Chrapliwy (1956), Fichter and Linder (1964), Stebbins (1966, 1985), Blair et al. (1968), Cochran and Goin (1970), Behler and King (1979), Nussbaum et al. (1983), Green and Campbell (1984), Baxter and Stone (1985), MacMahon (1985), Macey and Papenfuss (1991a), Leonard et al. (1993), and Corkran and Thoms (1996). Quantitative data on adult size measures are provided in Cope (1889), Storer (1925; included among those for *S. hammondi*), Logier (1932), Tanner (1931, 1939), Chrapliwy (1956), Northen (1970), Nussbaum et al. (1983), and Hovingh et al. (1985). The collecting location of the specimens measured by Tanner (1931) is not specified; however, the context of the rest of the manuscript implies they are from Utah. Comparison of size data between citations is confounded by geographic variation in these measurements (Hovingh et al. 1985), inconsistent measurement techniques, and a failure to always separate the data according to sex. Linsdale (1940) provided semi-quantitative morphological data for adults and juveniles from a number of locations (mixed with data for other species of *Scaphiopus*). Ruthven and Gaige (1915) described the appearance of recently transformed and juvenile in-

dividuals. Tanner (1939) described the larvae, focusing mostly on the mouthparts, and provided some measurement data as well. Larvae also are described in Fichter and Linder (1964), Nussbaum et al. (1983), Green and Campbell (1984), Hall (1993), Leonard et al. (1993), and Corkran and Thoms (1996). Based on the locality information included, some of the descriptions of adults, juveniles, and larvae provided by Stebbins (1951) for *S. hammondi* apply to *S. intermontanus*. Wright and Wright (1942) and Wright and Wright (1949) described adults and larvae; however, they did so by directly quoting the descriptions provided by other authorities.

Besides the mating call audiospectrogram provided here, additional audiospectrograms can be found in Northen (1970) and Bogart (1971). Measurements of mating call variables are provided by Blair (1956), McAlister (1959), and Northen (1970). Blair (1956) and Northen (1970) also described geographic variation in the mating call, and Northen identified the quantitative effects of water temperature on call variables. Qualitative descriptions of the mating call are provided in Englehardt (1918), Snyder (1920), Wood (1935), Wright and Wright (1949), Stebbins (1951, 1966, 1972, 1985), Zweifel (1956), Fichter and Linder (1964), Cochran and Goin (1970), Smith (1978), Behler and King (1979), Froom (1982), Nussbaum et al. (1983), Green and Campbell (1984), MacMahon (1985), Leonard et al. (1993), and Corkran and Thoms (1996). Fouquette (1980) used individuals of *S. intermontanus* to determine a predictive relationship between environmental temperatures and body temperature that can be applied to anuran species, such as *S. intermontanus*, that call at night in water (but with about half the body surface exposed to air). A sound recording of *S. intermontanus* mating calls is commercially available (Davidson 1995).

• **Illustrations.** Black and white illustrations of adults are in Carl (1943), Stebbins (1951, 1954), Cook (1984), Green and Campbell (1984), and Zeiner et al. (1988). Color illustrations of adults were provided by Stebbins (1951, 1966, 1985) and Smith (1978). Black and white photographs of adults are in Grinnell and Storer (1924), Slevin (1928), Tanner (1931), Wright and Wright (1949), Chrapliwy (1956), Nussbaum et al. (1983), and Baxter and Stone (1985). Color photographs of adults were included in Behler and King (1979), Hammerson (1982a), MacMahon (1985), Macey and Papenfuss (1991a), Leonard et al. (1993), and Corkran and Thoms (1996).

Illustrations of the digging spade are provided in Cope (1889), Gordon (1939), Tanner (1939), Fichter and Linder (1964), Blair et al. (1968), Smith (1978), and Baxter and Stone (1985). Cope (1889) also provided additional illustrations of some aspects of adult external and oral morphology, and Baxter and Stone (1985)

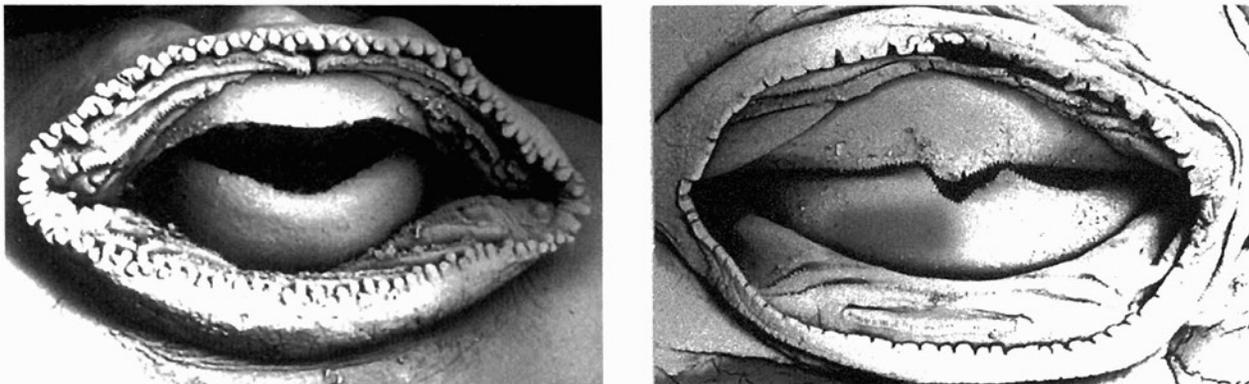


Figure 4. Views of oral discs of predominately herbivorous (left) and predominately predaceous, carnivorous (right) larval morphological types of *Scaphiopus intermontanus* that depict differences in jaw morphology. The carnivorous morphological type is from Ada County, Idaho (photograph by John H. Larsen, Jr.).

illustrated the area of the glandular boss between the eyes. Illustrations of adult *S. intermontanus* skulls are provided in Tanner (1939), Stebbins (1951), Zweifel (1956), Tanner (1989a, b), and Hall (1993). A black and white photograph of the digging spade is provided in Nussbaum et al. (1983). Black and white photographs of adult skulls are provided in Tanner (1939), Northen (1970; in my copy these photographs were of poor quality), and Tanner (1989b). McAlister (1959) provided a diagrammatic illustration of the larynx. Estes (1970) provided illustrations of two bones of the adult skull. Jurgens (1971) provided illustrations of whole-mounts and serial sections of the adult nasal region. Hall (1993) provided illustrations of skeletal ontogeny and scanning electron micrographs of individual adult skeletal features. Leonard et al. (1993) and Corkran and Thoms (1996) provided color photographs of the digging spade.

Stebbins (1951), Fichter and Linder (1964), and Hall (1993) provided illustrations of larval *S. intermontanus*. Stebbins's illustrations are labeled as *S. hammondii*; however, the locality information provided (i.e., near Vernal, Uintah County, Utah) places the reference specimen within the range of *S. intermontanus* and just outside the known range of what is now identified as *S. multiplicatus* (previously *S. hammondii*). These particular illustrations seem to have been used again in subsequent works by Stebbins (e.g., Stebbins 1985); however, they remained labeled as *S. hammondii*. Illustrations of larval mouthparts can be found in Stebbins (1951), Turner (1952), and Hall (1993). Arnold and Wassersug (1978) provided photographs of metamorphic and post-metamorphic aggregations. Illustrations of *S. intermontanus* developmental stage boundary characteristics, hindlimb ontogeny, and development of accessory structures of the eye can be found in Hall (1993) and Hall et al. (1997). These latter two citations also contain scanning electron micrographs of larvae at different stages of development with the emphasis on opercular and mouthpart development. Hall (1993) provided scanning electron micrographs of larval labial teeth (also see Altig and Pace 1974) and a larval neuromast organ, as well as an illustration of the larval lateral line system. Corkran and Thoms (1996) provided an illustration of an egg mass and color photographs of egg masses, different stage larvae, an otherwise transformed individual with a significant portion of its tail still remaining, and a juvenile.

• **Distribution.** *Scaphiopus intermontanus* ranges from south-central British Columbia, Canada south into the United States through most of eastern Washington and Oregon (except the northeast portion of Washington and the upper mesic slopes of the Blue Mountains region of both states), California east of the Sierra Nevada and north of San Bernardino County, and Nevada (except for the extreme southern tip) and east to southern Idaho (and a small portion farther north within Nez Perce County), Utah northwest of the Colorado River (but minus a northeast portion of the state), Arizona north of the Colorado River, northwestern Colorado, and southwestern Wyoming. Information on ecological amplitudes is provided in Pertinent Literature.

Locality records are presented in two ways. First, citations are identified that provide records from more than one state. Second, citations are identified that provide records or a description of distribution for an individual state or province.

Regional locality records, either as symbols on a map, written descriptions, or both, are provided in Cope (1883: Nevada and Utah, 1889: Idaho, Utah, and Washington; the Idaho record is identified as *S. bombifrons*), Slevin (1928: California, Idaho, Nevada, Oregon, Utah, and Washington; some of these records are confounded with the records for other species of *Scaphiopus*, but most apply to *S. intermontanus*), Storer (1925: California, Nevada, Oregon, and Washington; mixed with records of *S.*

hammondii), Wood (1935: Arizona and Utah), Tanner (1939: Arizona, Idaho, Nevada, Utah, and Washington), Blair (1955: Arizona, Nevada, and Utah), Chrapliwy (1956: Arizona, California, Idaho, Nevada, Oregon, Utah, and Wyoming), Northen (1970: Idaho, Oregon, Utah, Washington, and Wyoming), Nussbaum et al. (1983: British Columbia, Oregon, and Washington), Papenfuss (1986: California and Nevada), Tanner (1989b: Arizona, California, Idaho, and Utah), and Macey and Papenfuss (1991a: California and Nevada). Tanner (1989b) also

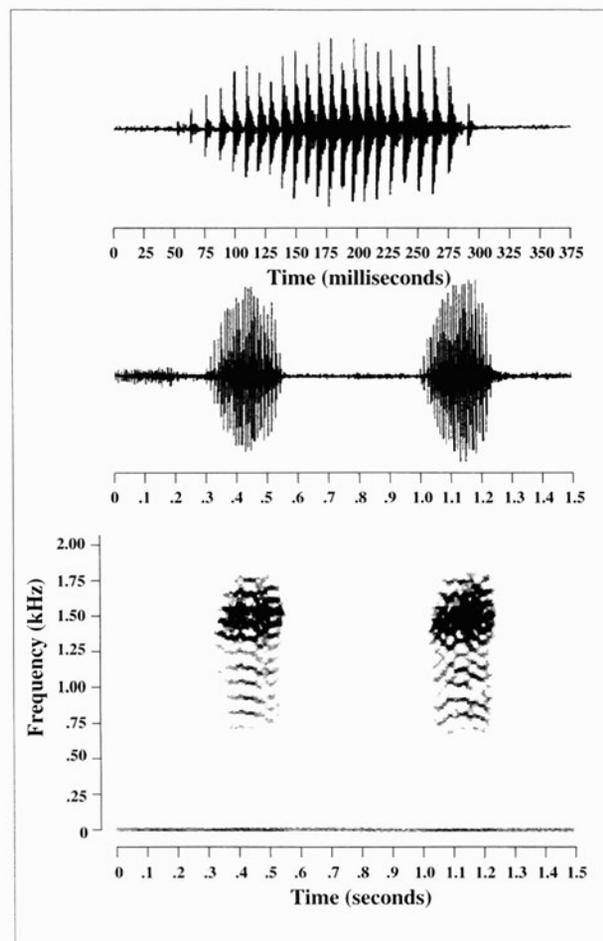


Figure 5. Audiospectrogram and oscillograms of the mating (advertisement) call of *Scaphiopus intermontanus*: Yakima County, Washington, 22 June 1995 at 2230, at an air temperature of 19°C and a water temperature of 21°C (recording by J.A. Hall). The individual called from near the shoreline with the lower portion of its body in the water and the rest exposed to air. The call was recorded in monophonic at a tape speed of 19 cm/sec with an Uher 4200 Report Stereo IC and Uher M517 remote control microphone. The call was analyzed with a Kay DSP Sona-Graph Model 5500. The audiospectrogram is based on a band width setting of 29 Hz. The expanded oscillogram (top) shows the fine temporal details of the call to the left. Dominant frequencies occur at about 1.4 and 1.5 kHz. Although the frequency traces shown here seem to be somewhat irregular, with no consistent up or down time-associated pattern, additional sound analysis at a band width of 15 Hz suggests that the frequency at the end of a call may be slightly lower than that at the beginning. Harmonics are spaced at about 0.1 kHz intervals. Faint harmonics (not captured during preparation of this figure) are present at 1.8 and 1.9 kHz with yet fainter harmonics present through 2.3 kHz. Call duration is about 0.25 sec with a pulse rate of about 90 pulses/sec (22–23 pulses per call).

included records from Linn County, Oregon; however, the location is questionable as this would be the only recorded occurrence of *S. intermontanus* from the west side of the Cascade Mountains. Hovingh et al. (1985: Arizona, Idaho, Nevada, Oregon, Utah, Washington, and Wyoming) also provided regional distribution information as part of an examination of geographic size variation in *S. intermontanus*; however, other than for Utah, the locality information is accurate only at the level of the state or a major geographic or political subdivision therein.

Citations that provide locality records or a description of distribution within individual states or British Columbia are as follows: Arizona, McKee and Bogert (1934), Durham (1956), and Lowe (1964); British Columbia, Cope (1893), Patch (1929), Logier (1932), Carl (1942, 1943), Mills (1948), Logier and Toner (1955, 1961), Froom (1982), Cook (1984), Green and Campbell (1984), and Harestad (1985b); California, Stejneger (1893), Grinnell and Camp (1917; some of the records are for *S. hammondii*), Grinnell and Storer (1924), Stebbins (1972), and Zeiner et al. (1988; including reports of *S. intermontanus* up to about 2700 m in the Bodie Hills, Mono County, California); and Colorado, Cary (1911), Maslin (1959), McCoy (1962a, b), Smith et al. (1965), and Hammerson (1982a, b, 1991). The identity of Cary's (1911) record (originally identified as a record for *S. hammondii*) was considered uncertain by McCoy (1962a), but later assumed to be *S. intermontanus* by Smith et al. (1965) on the basis of nearby records. The records for *S. intermontanus* in Maslin (1959) are identified as a record for *S. hammondii* (Garfield County) and a record for *Bufo woodhousii woodhousii* (see below). McCoy (1962b) reported that *S. intermontanus* occurred at intermediate altitudes and not on the valley floor of the Grand Valley of Colorado. Hammerson (1982a) reported *S. intermontanus* is present no higher than about 2150 m in Colorado. Records for additional states include: Idaho, Cope (1879), Van Denburgh and Slevin (1921b), Slater (1941), Tanner (1941), Evenden (1946), Linder and Sehman (1977), Sehman and Linder (1978), Reynolds et al. (1986), and Llewellyn (1997); Nevada, Taylor (1912), Ruthven and Gaige (1915), Snyder (1920), Van Denburgh and Slevin (1921a), Linsdale (1940), and La Rivers (1942). Linsdale (1940) reported occurrences from an altitudinal range of about 500–2300 m, with most localities between 1200–1850 m on the floors of major valleys. Records for Oregon are in Gordon (1939), Graf et al. (1939), and Nauman et al. (1996). Leonard et al. (1993) reported *S. intermontanus* can be found at elevations up to about 1500 m near Hart Mountain. For Utah, see Yarrow (1875, 1882), Van Denburgh and Slevin (1915), Englehardt (1918), Tanner (1927a, b, 1930, 1931), Cowles and Bogert (1936), Hardy (1938), Tanner (1940, 1958), Woodbury (1952), and Hovingh et al. (1985). Yarrow's (1875, 1882) Utah records were originally identified as either *Spea stagnalis*, *Scaphiopus varius varius*, or *S. couchii*. The Tanner (1927b, 1931) citations include a record from San Juan County probably referable today to *S. multiplicatus*. Blair (1955) reported occurrences from an altitudinal range of about 750–2600 m. For Washington, see Svihla and Svihla (1933), Slater (1955, 1964), Metter (1960), Fitzner and Gray (1991), Hallock (1995), and McAllister (1995). Two unpublished records have been recorded for Stevens County near the Columbia and Kettle Rivers, respectively (W.P. Leonard, pers. comm.) In Washington, *S. intermontanus* has been collected at elevations that range from about 200 m (Hall et al. 1997) to just over 1200 m (Metter 1960). For Wyoming, see Baxter (1947a, b) and Baxter and Stone (1985). Although the range of *S. intermontanus* crosses to the east side of the Continental Divide in central Wyoming, in Wyoming it is found mostly west of the Continental Divide and below about 1850 m (Baxter and Stone 1985).

Distribution maps that depict historic views of all or a major portion of the range of *S. intermontanus* are provided in Tanner

(1939), Wright and Wright (1949), Stebbins (1951, 1954, 1966, 1985), Turner (1952), Chrapliwy (1956), Zweifel (1956), Peabody and Savage (1958), Bragg (1965), Brown (1967, 1976), Northen (1970), Smith (1978), Behler and King (1979), and MacMahon (1985). The maps of Chrapliwy (1956) and Northen (1970) also include locality records. Citations that contain a word description of the range of *S. intermontanus*, but do not otherwise contain a distribution map, include Wright and Wright (1942), Stejneger and Barbour (1943), Schmidt (1953), Slater (1955), Bragg (1961, 1967), Blair et al. (1968), Cochran and Goin (1970), Pickwell (1972), Baxter and Stone (1985), Frost (1985), and Tanner (1989b).

Several published locality records associated with *S. intermontanus* and more recent interpretations of these records deserve comment. First, Hammerson (1982b) proposed corrections to two published records for western Colorado based on examination of the original specimens: one correction changed a record for *Bufo woodhousii woodhousii* in Moffat County (Maslin 1959) to *S. intermontanus* and a second changed a record for *S. intermontanus* in San Miguel County (Secoy and Brown 1968) to *S. multiplicatus*.

Second, uncertainty exists about *Scaphiopus* distribution in general in the four corners region of Arizona, Colorado, New Mexico, and Utah and specifically whether the range of *S. intermontanus* extends southeast of the Colorado River. Tanner (1939) included a specimen from San Juan County, Utah (southeast of the Colorado River) in his list of specimens studied for *S. intermontanus*. Lowe (1964) proposed that *S. intermontanus* can be found in the northern portions of Navajo and Apache Counties in Arizona, but provided no specific records; however, Chrapliwy (1956) reported examining a specimen of *S. intermontanus* originally collected in Navajo County and obtained from the private collection of F.A. Shannon. Gehlbach (1965) reported the occurrence of *S. intermontanus* from near El Morro National Monument in Valencia County, New Mexico. Two individuals were so identified based on skull characteristics. Based on Gehlbach's findings, Brown (1967, 1976) extended the range of *S. intermontanus* into northwestern New Mexico. McCoy (1962a) used skull characteristics to identify two specimens southeast of the Colorado River in Mesa County, Colorado as *S. intermontanus*. Some current museum records examined during preparation of this account contain locality records for *S. intermontanus* from San Juan County, Utah and Apache County, Arizona. Northen (1970) conducted an extensive search of the four corners region and found no evidence of *S. intermontanus* southeast of the Colorado River during the period of summer rains. Moreover, on two occasions when he failed to find *S. intermontanus* southeast of the river, Northen found the species actively breeding northwest of the river. Northen also examined the *S. intermontanus* specimen deposited by Gehlbach (1965) at Cornell University and concluded it was a female *S. bombifrons*. Northen did not cite Chrapliwy's (1956) thesis and, although he cited both Tanner (1939) and McCoy (1962a), he did not comment on their distribution records. Tanner (1989b) did note Tanner's (1939) San Juan record and based on his own examination of specimens on both sides of the Colorado River concluded *S. intermontanus* is likely not present southeast of the river in Utah. The most parsimonious conclusion that can be drawn from the preceding observations is that, pending other evidence to the contrary, *S. intermontanus* does not at present range southeast of the Colorado River in Arizona and Utah, does not occur in New Mexico, and is present in western Colorado mostly northwest of the river but also to a small geographic extent southeast of the river.

Third, specimens from southern Idaho have at times been assigned to *S. bombifrons* (Cope 1879, 1889; Slater 1941). Cope's original description is from his 1879 manuscript and is

based on larvae in the process of transformation. He gave no indication that specimens were collected. Cope did not describe *S. intermontanus* until later (Cope 1883). Tanner (1939) and Tanner (1941) identified the specimens from this area as *S. intermontanus*, which is the present interpretation. Unfortunately, the reports of Tanner (1939) and Tanner (1941) also created a fourth distribution problem. They suggested in part that the range of *S. hammondii* extended to northeastern Washington and from there through northern Idaho into western Montana. No *Scaphiopus* of any species is documented in northern Idaho, all Washington *Scaphiopus* are now considered *S. intermontanus*, and similarly all Montana *Scaphiopus* are referable to *S. bombifrons* (Stebbins 1985). Fifth, Peabody and Savage (1958) suggested that *S. intermontanus* was expanding its range into California's San Joaquin Valley via Walker Pass (also see Brown 1967). This has not been confirmed by collection records.

• **Fossil Record.** Fossil *S. intermontanus*, or material that is at least comparable to the recent form, has been recorded from three locales in Nevada and one in Utah (see reviews in Mead and Bell 1994, Holman 1995) and two locales in Idaho (see stars on map). Mead et al. (1982) identified *S. cf. intermontanus* limb bones in cave sediments from Smith Creek Cave in White Pine County near the Utah border; however, identity was determined without the aid of comparative material from recent *S. intermontanus*. The sediments were of late Wisconsinan age or older. Brattstrom (1976) had earlier recorded, in sediments of unknown age from the same cave, the presence of a parasphenoid he attributed to *S. cf. hammondii*. Because this location is outside the known range of other members of the genus and Brattstrom stated all identified species are found in the area of the cave today, the bone probably is actually referable to *S. intermontanus*. From sediments as old as 7100 yr (i.e., Holocene deposits) from the Gatecliff Rock Shelter in the Monitor Valley of central Nevada (Mead and Bell 1994), Mead et al. (1983) identified over 70 axial and appendicular skeletal bones and one maxilla of *S. cf. intermontanus*. At a second cave location in western Nevada, Hidden Cave near Fallon, Mead (1985) identified one *S. cf. intermontanus* bone in late Wisconsinan sediments (and nine other bones, all postcranial, in Holocene deposits). Mead and Bell (1994) reported the presence of *S. intermontanus* fossil material in late Wisconsinan deposits from Bechan Cave in southcentral Utah. Steadman et al. (1994) identified fossil *S. intermontanus* sphenethmoids and limb bones in late Wisconsinan and Holocene cave sediments from Rattlesnake Cave, Idaho National Engineering Laboratory, Bingham County, Idaho. These authorities also assigned some of the material found in the cave to *S. bombifrons*. Their findings imply the two species co-occurred at this location prior to about 3000 yr ago. Murray (1992) assigned a fossil cervical vertebra found in late Holocene cave sediments from Dinosaur Cave, Elmore County, Idaho to *S. cf. intermontanus*. Finally, Van Devender et al. (1991) hypothesized that some of the anuran material collected from late Wisconsinan sediments at Daggett, San Bernardino County, California could be assigned to *S. intermontanus* (see question mark on map). The location is outside the current known range of all *Scaphiopus* species, but could have been occupied during a glacial period when conditions were more mesic.

• **Pertinent Literature.** Few comprehensive works address in any detail the biology of *S. intermontanus*. Two dissertations have been dedicated to the biology of *S. intermontanus*: Northen (1970) and Hall (1993). Northen's contribution has remained unpublished, whereas that of Hall's has been published in part as Hall et al. (1995, 1997). Blair (1956), Hovingh et al. (1985), and Brown (1989) are three other substantive publications that concentrate solely on the biology of *S. intermontanus*. A publi-

cation such as Bragg (1965), though useful as a comprehensive work on *Scaphiopus* biology in general, provides little information specific to *S. intermontanus*. The preceding citations and others are annotated below by grouping citations according to a particular aspect of the biology of *S. intermontanus*.

Habitat Associations.—As part of a larger study of terrestrial vertebrate habitat associations in southeastern Washington, Dice (1916) identified *S. intermontanus* as a species characteristic of the Columbia Basin sagebrush (*Artemisia tridentata*) fauna. Within this vegetation type, Dice identified *S. intermontanus* as having a major association with sagebrush habitat (i.e., habitat within which it occurs most abundantly) and a minor association with water-margin habitat. Bernard and Brown (1977) described *S. intermontanus* as an inhabitant of sagebrush flats, plains grassland, and pinyon-juniper woodland; however, in Arizona and Utah, habitat occupancy also extended upward in elevation into the spruce-fir forest. Zweifel (1956) and Stebbins (1985) provided similar descriptions minus the plains grassland; Stebbins included semi-desert shrublands as an occupied habitat. Bernard and Brown (1977) also identified the distribution of *S. intermontanus* as it related to physiographic regions (also see Corkran and Thoms 1996) and Küchler's (1975) potential natural vegetation associations for the western United States. The preceding citations identified *S. intermontanus* habitat associations as they relate generally to the Great Basin and Columbia Basin; Stewart (1994) described similar associations as they related to the occurrence of *S. intermontanus* at the fringes of the Mojave Desert. Macey and Papenfuss (1991b) described habitat associations of this species in the White-Inyo mountains region of California and Nevada. Some authors have described *S. intermontanus* habitat associations by use of the life zone concept (Grinnell and Storer 1924, Tanner 1931, Slater 1955). Zweifel (1956) suggested that rather than a direct adaptation to particular vegetation types, *S. intermontanus* responds in the same way as vegetation to similar climate and soil conditions.

Activity Periods.—Linsdale (1938) and Metter (1960) observed juvenile toadlets foraging during daylight hours; however, Linsdale reported that most individuals used any available crevice or depression to burrow out of site by early morning. Svihla (1953) also reported that *S. intermontanus* burrows into sand or hides under rocks during the day. *Scaphiopus intermontanus* emerges to forage on rainy nights and also may forage on rainless nights when the humidity is high enough to cause dew (Nussbaum et al. 1983, Preston and Hatch 1986). Fichter and Linder (1964) and Green and Campbell (1984) provided general descriptions of the activity periods of adults. Linsdale (1940) reported extreme sighting dates of 28 March and 2 October for adults in Clark County, Nevada.

Food and Feeding Behavior.—Adult *S. intermontanus* may eat ants, beetles, grasshoppers, crickets, and flies (Nussbaum et al. 1983). Based on five adult specimens from Utah, Tanner (1931) provided the only published stomach contents analysis. These data were later summarized by Whitaker et al. (1977). Larvae are capable of eating both plant and animal food (Nussbaum et al. 1983, Green and Campbell 1984, Hall et al. 1995). Linsdale (1938) observed larvae feeding at the surface film of water and on the carcasses of conspecifics. Wood (1935) observed larvae seemingly feeding on vegetable matter either contained within or growing on cattle dung. Cope (1889) reported individuals in the midst of metamorphosis — still with complete tails and small gape, but capable of hopping — feeding on grasshoppers. Although Cope identified these individuals as *S. bombifrons*, based on current locality information they probably were *S. intermontanus*. Trowbridge (1942) repeated the sightings of the last three authors.

Predation.—Wright and Wright (1949) reported *S. intermontanus* remains in the dung of coyotes (*Canis latrans*). Both

Gleason and Craig (1979) and Green et al. (1993) reported predation on *S. intermontanus* adults by burrowing owls (*Athene cucularia*), though Green et al. concluded the toads were killed but not eaten by the owls. Green and Campbell (1984) stated the skin secretions of adults are potent and bad tasting, which supports Nussbaum et al. (1983) suggestion the secretions probably repulse predators. Harestad (1985a) observed American crows (*Corvus brachyrhynchos*) preying on *S. intermontanus* larvae, and Wood (1935) found larvae in the stomachs of garter snakes (*Thamnophis elegans vagrans*).

Longevity.—No published information is available for longevity in *S. intermontanus* either under natural conditions or in captivity. I personally have kept a mature male (i.e., at least two or three years old when captured) for four years in captivity. Without referring to specific observations, Northen (1970) stated that adult *Scaphiopus* may live to be 8–10 years of age.

Reproductive Behavior.—Linsdale (1938) was the first to describe that breeding activity in *S. intermontanus* can occur independent of rainfall. Subsequent investigators either confirmed independently this observation with additional data (Stebbins 1951, Zweifel 1956, Northen 1970, Blair 1976, Hovingh et al. 1985) or repeated the observations of others (Bragg 1945, 1961, 1965; Brown 1976). Zweifel (1956) postulated that *S. intermontanus* may be adaptively shifting its breeding behavior to one more suited to a region where summer rains are most uncertain. Hovingh et al. (1985) suggested that rainfall may trigger emergence from hibernation; however, breeding is delayed because individuals must first travel to scarce water resources (in some cases over 15 km). Contrary to *Scaphiopus* species in the southwest United States that breed in response to summer rains, Van Devender et al. (1991) suggested that, within the Great Basin, *S. intermontanus* must breed in response to a winter-spring rainfall climate.

Scaphiopus intermontanus breeds in a variety of temporary and permanent waters that include rain pools, roadside and irrigation ditches, flooded fields, intermittent and permanent desert springs, the edges and pools of intermittent and permanent streams, and pond and reservoir edges (Englehardt 1918, Logier 1932, Wood 1935, Hardy 1938, Linsdale 1938, Wright and Wright 1949, Woodbury 1952, Blair 1955, Fichter and Linder 1964, Northen 1970, Nussbaum et al. 1983). Hovingh et al. (1985) characterized *S. intermontanus* breeding habitat in the Bonneville Basin of Utah. Breeding sites were in temporary or permanent springs and human-made reservoirs, were generally at elevations less than 1600 m, possessed a water chemistry of pH 7.2–10.4 and total dissolved solids 170–4800 mg/L, and generally lacked aquatic vegetation.

Bragg (1945) inferred from statements made by Tanner (1939) that *S. intermontanus* may be indiscriminate as to the depth of water in which it will breed; however, male *S. intermontanus* do not swim nor generally float in open water while calling (Northen 1970). Instead, they call near shore with the body partially submerged in water (Fouquette 1980), either while partially floating and holding on to objects or while sitting in shallow water (Stebbins 1951, Northen 1970). Northen (1970) observed geographic variation in calling behavior. Additionally, males may call during daylight hours (Linsdale 1938, Northen 1970) and they may call and breed without the formation of large breeding choruses (Stebbins 1951, Blair 1956; but also see Green and Campbell 1984). Males develop keratinized nuptial excrescence on the inner sides of the first three fingers during the breeding season (Nussbaum et al. 1983). Amplexus is inguinal (Carl 1942, Nussbaum et al. 1983, Green and Campbell 1984). These latter traits are possibly the basis for Tanner's (1939) report that males are difficult to dislodge once clasped to a female during amplexus. Northen (1970) provided evidence that female *S. intermontanus* respond preferentially to

the mating call of their own species versus the mating call of *S. multiplicatus*. Breeding may take place anywhere from April through July depending on local conditions (Wright and Wright 1949).

Eggs are deposited in small packets of about 10–40 eggs that are attached to either submerged vegetation, floating sticks, upper surfaces of small rocks, or on a muddy bottom (Englehardt 1918, Snyder 1920, Fichter and Linder 1964, Nussbaum et al. 1983, Stebbins 1985, Leonard et al. 1993). Egg masses have been described as short strings (Englehardt 1918), not as strings but as a flat sheet one layer deep (Snyder 1920), and as grape-to-plum-sized clusters (Corkran and Thoms 1996). Livezey and Wright (1947) did not include *S. intermontanus* in their key to anuran eggs of the United States; however, they did repeat the observations of Snyder (1920). Booth (1942) described the eggs as containing two jelly envelopes and appearing greenish olive. The number of eggs deposited in a packet and the type and availability of substratum deposited on probably determine the shape of the egg mass. Females deposit multiple clusters as total egg complement may equal 300–500 (Fichter and Linder 1964, Nussbaum et al. 1983, Stebbins 1985) or even approach 800 eggs (Leonard et al. 1993). Females also may deposit clusters communally (Snyder 1920).

Development.—Neither detailed individual egg morphology nor embryonic development has been described in *S. intermontanus*. Logier (1932), Durham (1956), Harestad (1985a) and Hovingh et al. (1985) provided field observations on measures of larval growth and size at metamorphosis in *S. intermontanus*. Durham (1956) also correlated some of his measurements with descriptions of morphological changes. Observations reported by Wood (1935) imply that larvae in the field may be capable of emerging from the water within about two weeks after egg fertilization. Brown (1989) monitored the development and growth of laboratory-raised larvae. He provided growth data and correlated changes in morphology with periods of development. Hall (1993) and Hall et al. (1997) provided a detailed description of ontogeny in *S. intermontanus* from the just-hatched larva through the adult using individuals raised under controlled laboratory conditions. At 25°C, hatching occurred within two days, metamorphic climax began after about 19 additional days, and climax lasted at least 12 more days. Temporal differentiation of external characters was used to construct a boundary-delineated staging table for the species. Growth data and data on the effects of rearing temperature and geographic origin on larval, labial tooth-row formula variation also were provided. Some aspects of *S. intermontanus* ontogeny were found to be unique, at least when compared with published accounts for other anurans (e.g., opercular development). Changes in rearing conditions affected the rate and relative timing of certain developmental events in *S. intermontanus*. Hall (1993) also described the accompanying ontogenetic changes in skeletal development in *S. intermontanus*.

Intraspecific larval growth inhibition via an alga cell may occur in *S. intermontanus* (Rose and Rose 1961). Kluge and Farris (1969) described vertebral development and also suggested the absence of ribs may result from a developmental rib-diapophysis fusion. Individuals are thought to reach sexual maturity in two to three years (Nussbaum et al. 1983, Green and Campbell 1984). Several observations have been made in regard to *S. intermontanus* metamorphs leaving the water, and in some instances beginning to feed, while still retaining a significant portion of their tail (Cope 1889, Ruthven and Gage 1915, Logier 1932, Wood 1935, Nussbaum et al. 1983, Hall 1993, Hall et al. 1997).

Larval Social Behavior.—Bragg (1946, 1950) described what he referred to as incipient or incidental cannibalism in *S. intermontanus* larvae. Durham (1956), however, was unequivocal

about the occurrence of cannibalism. Arnold and Wassersug (1978) documented aggregational behavior in *S. intermontanus* larvae, metamorphosing individuals, and post-metamorphs and speculated on its significance. Hall et al. (1995) investigated discrimination behavior by larval *S. intermontanus* in laboratory choice tests using kin- and diet-based cues. An association preference for kin was not detected; however, larvae did demonstrate an ability to discriminate certain diet-based cues.

Physiology.—In a series of studies, Thorson and Svihla (1943) and Thorson (1955, 1956) investigated water economy and tolerance to water loss (i.e., dehydration) and their relationship to degree of terrestriality in a number of anurans. Adaptation to terrestriality by *S. intermontanus* was not achieved by changes in skin permeability, but rather by an increased tolerance to dehydration compared with other species; individuals could survive up to about a 48% loss of body weight in water loss and a 61% loss of total body water. The results of these studies have been referenced and discussed extensively in the literature, but consistently identified as characteristic of *S. hammondi*, by a number of authorities: McClanahan (1967), Mayhew (1968), Claussen (1969), Porter (1972), Goin et al. (1978), and Shoemaker et al. (1992). Hillman and Sommerfeldt (1981) also reported comparative dehydration tolerance results for *S. intermontanus* based on data from Hillman (1980); however, a check of this latter reference indicates the results are assignable to *S. couchii* and not to *S. intermontanus*. Hillman and Sommerfeldt (1981) did use *S. intermontanus* individuals in a comparative study of systemic blood flow distribution during dehydration, hypovolemia, and salt load. Blood flow increased proportionately to the head during both dehydration and hypovolemia; however, the magnitude of the redistribution did not correlate with a species' tolerance to dehydration.

Linsdale (1938) reported an ability of adult *S. intermontanus* to change their ground color. Jasinski and Gorbman (1967) described the relationship of hypothalamic neurosecretion to different environmental conditions in specimens that included *S. intermontanus* individuals. Clark et al. (1969) tested individuals of *S. intermontanus* for the presence of blood parasites with negative results. Jaeger and Hailman (1973) and Hailman and Jaeger (1974) surveyed adult anuran phototactic responses to white light intensity and spectrally dominant stimuli, respectively. They found *S. intermontanus* to be monotonically photopositive for the range of intensities presented and to demonstrate a blue-mode response in spectral dominance preference tests. As part of comparative survey of oil droplets in the eyes of adult anuran amphibians, Hailman (1976) found that *S. intermontanus* lacked retinal oil droplets but possessed yellow epithelial oil droplets. Oil droplets may function in chemical storage and may have taxonomic significance, but their presence does not correlate with a particular phototactic behavior. Dimmitt and Ruibal (1980) provided empirical data for adult *S. intermontanus* on gross assimilation efficiency, voluntary food intake rate, and gross conversion efficiency. The results, when compared with those for *S. couchii* and *S. multiplicatus* and viewed in the context of other ecological data, prompted these authorities to speculate that, because it inhabits supposedly less arid regions, *S. intermontanus* has a longer activity period and hence less of a need to store energy quickly. Hillman (1982) found a linear correlation between exercise heart rate and maximal oxygen consumption rate in *S. intermontanus*, which was consistent with the hypothesis that blood oxygen transport is the limiting process for maximal oxygen consumption rates in anuran amphibians. Morey and Janes (1994) reported otherwise unpublished data that over a wide range of body sizes, *S. intermontanus* metamorphs lose far more than 50% of their total dry mass and stored body fat to complete metamorphosis.

Morphology.—Kluge (1966) described selective features of

the adult skeleton of *S. intermontanus*. Estes (1970) described the morphology of a few of the individual bones of the adult skull. Jurgens (1971) described the morphology of the adult nasal region. Rocek (1981) described the condition of the adult nasal bones based on a figure in Zweifel (1956). As part of a study on the phylogeny of primitive frogs (archaeobatrachians), Cannatella (1985) coded the condition of 181 different morphological characters in *S. intermontanus*. Van Devender et al. (1991) described characteristics of the radioulna and a presacral vertebra. Hall (1993) provided comprehensive descriptions of both the larval and adult skeletal morphology. Steadman et al. (1994) described features of the sphenethmoid and ilium. Hall (1993) and Hall et al. (1997) described features of the external morphology and skin histology of metamorphosing and adult individuals. Some variations in the morphology of the adult axial skeleton are described by Ritland (1955), Kluge (1966), and Hall (1993). Various authorities have commented on the morphology of the frontoparietal bones, in particular their dorsal elevation (i.e., boss) and the presence, absence, or geographic variation of an associated frontoparietal fontanelle, either by referring to original observations (Cope 1889, Tanner 1939, Zweifel 1956, Kluge 1966, Northen 1970, Tanner 1989b, Hall 1993), referring to the observations of others (Tanner 1989a), or without referring to any data (Firschein 1950).

The frontoparietal characteristics also have been used in a comparative sense, and often with differing results, to interpret the phyletic position of *S. intermontanus* in relation to other species within the subgenus *Spea* (Tanner 1939, Chrapliwy 1956, Zweifel 1956, Kluge 1966, Northen 1970). Bragg (1945) modified Tanner's (1939) interpretation based on his own assessment of the contribution of larval morphology toward discerning relationships within *Spea*; however, he was not yet aware that morphological variability among *Spea* larvae confounded accurate species identification (see below). Estes (1970) also provided a phylogeny, but did not indicate its basis.

McAlister (1959) described the vocal structures in male *S. intermontanus*. As part of a larger comparative study, Dunlap (1960) described the myology of the pelvic area and hindlimb in three specimens he identified as *S. hammondi* (Dunlap followed the check list of Schmidt [1953] who did not recognize *S. intermontanus* as a full species); however, at least one of these specimens was collected in Ritzville, Washington (D.G. Dunlap, pers. comm.). This would make this particular specimen *S. intermontanus*. Probably the other *Scaphiopus* specimens also were collected in Washington, and are *S. intermontanus*, as Dunlap conducted his work in Pullman, Washington, and used local specimens when available (Dunlap 1960).

Wood (1935) described albino *S. intermontanus* larvae he encountered in the wild. As part of a taxonomic key, Altig (1970) provided some information on larval morphology; however, the description included *S. hammondi* as well. Altig and Pace (1974) provided measurement data for larval labial teeth. Altig and Johnston (1986) characterized a number of larval morphological (and a single ecological) traits. Hall (1993) described the ecomorphology of late-stage larvae including mouthpart components. Morphological variability, especially as it relates to larval structures associated with feeding, has been documented in *S. intermontanus* (Tanner 1939, Turner 1952, Acker and Larsen 1979) and its occurrence cited by Orton (1954), Pfennig (1990, 1992), Pfennig et al. (1993), and Blaustein and Walls (1995). The underlying developmental mechanisms that lead to these divergent morphologies remain to be determined.

Genetics.—Sage et al. (1982) found no difference in the albumins of *S. intermontanus* from Mono County, California and *S. hammondi* from the border of Alameda and San Joaquin Counties, California. Wiens and Titus (1991) provided allozyme data on 21 electrophoretic loci in *S. intermontanus*. Based on

these allozyme data and a single morphological character, Wiens and Titus placed *S. intermontanus* as the sister taxon of *S. bombifrons* and as a more derived taxon than both *S. multiplicatus* and *S. hammondii*; however, their results also raised the possibility that *S. intermontanus* is itself a paraphyletic taxon (see Comment). An individual *S. intermontanus* from Mesa County, Colorado shared more alleles with *S. bombifrons* than it did with three individuals of *S. intermontanus* from Deschutes County, Oregon. Wiens and Titus (1991) also confirmed that *S. intermontanus* contains a duplication of the S-Icdh-A locus, which had been previously detected in other species of the subgenus *Spea* (Sattler and Mecham 1979) and which Wiens and Titus considered to be a synapomorphy of *Spea* (but see Simovich and Sassaman 1986, for a criticism of the gene duplication hypothesis). Chromosome morphology and number have not been determined directly for *S. intermontanus*; however, hybridization studies reported by Brown (1967, 1976), in which interspecific crosses between *S. intermontanus* and either *S. bombifrons*, *S. hammondii*, or *S. multiplicatus* all demonstrate a high degree of genetic compatibility, suggest that *S. intermontanus* contains a similar complement of chromosomes to what has been identified in these species: 26 diploid chromosomes (Wasserman 1970). Hybrids between *S. intermontanus* and *S. multiplicatus* are found in nature in eastern Utah where the species are sympatric; however, Northen (1970) detected no morphological evidence of introgression in *S. intermontanus*.

Biogeography.—Peabody and Savage (1958) identified *S. intermontanus* as an element of the Madro-Tertiary fauna that dispersed northward from Mexican centers of origin. Although *S. intermontanus* dispersed to occupy principally the Great Basin, these authors thought *S. intermontanus* was expanding its range into California's San Joaquin Valley via Walker Pass. They provided no evidence for this conjecture and current collection records do not support their hypothesis. Based on fossil evidence, *S. intermontanus* was present during the Pleistocene in the more southern parts of the Great Basin. Although Nussbaum et al. (1983) hypothesized that desert species, such as *S. intermontanus*, did not (re)invade their present range within the Pacific Northwest until after the Pleistocene, fossil finds by Steadman et al. (1994) support the interpretation that at least *S. intermontanus* may have been present in the Pacific Northwest toward the end of the Pleistocene (see Fossil Record). It also may have been present in Mojave Desert refugia during the late Pleistocene (Hovingh et al. 1985). Its presence today in a portion of the Mojave Desert — in the southern Owens Valley of California — is due to the surface water connectivity between the northern (Great Basin) and southern portions of the valley (Macey 1986). Major rivers have been proposed to either have posed a barrier to its dispersal (i.e., Colorado River: Tanner 1989b), at most a partial barrier to its dispersal (i.e., Colorado River: Northen 1970), or no barrier at all (i.e., Columbia River: Storm 1966).

Conservation Status.—A number of earlier reports commented that *S. intermontanus* was widely distributed or, in appropriate habitat, relatively common (e.g., Grinnell and Storer 1924, Wood 1935, Blair 1955, Endemic Species Committees 1982); however, some recent citations have reported population declines or indicated *S. intermontanus* is of local conservation concern (Orchard 1992, Corkran and Thoms 1996, Collins 1996, Drost and Fellers 1996). Drost and Fellers (1996) visited the same sites surveyed by Grinnell and Storer (1924) and did not detect the presence of *S. intermontanus*. Habitat loss as a consequence of land conversion and hydroelectric projects probably have impacted populations at least locally (Orchard 1992, Leonard et al. 1993); however, irrigation for agriculture (Nussbaum et al. 1983) and the development of water resources for range management purposes (Hovingh et al. 1985) have at

the same time created new habitat for *S. intermontanus*. At least as of 1980, *S. intermontanus* was not identified as a species of conservation concern by United States government resource agencies (Bury et al. 1980).

• **Nomenclature History.** Some of the nomenclatural changes indicated in the synonymy deserve comment. Initially, those associated with the species status of *S. intermontanus* will be addressed. The taxon as first described by Cope (1883) was accorded full species rank in the genus *Scaphiopus*. Garman (1884) apparently followed Cope — though his citation of an authority for this seems to be in error — and included *S. intermontanus* in his checklist of North American reptiles and amphibians. Cope (1889), however, later reduced *S. intermontanus* to a subspecies under *Spea hammondii*. Cope (1867) had earlier erected the genus *Spea* as a sister taxon to *Scaphiopus*. Cope (1896) later used the combination *Spea intermontana*; however, whether he really intended a taxonomic change was unclear. Whereas in his 1889 manuscript Cope identified three subspecies of *hammondii*, he identified only *Spea hammondii bombifrons* as a subspecies in the 1896 manuscript; however, he made no specific comments about the taxonomic changes. Subsequent taxonomic treatments either placed *S. intermontanus* into synonymy with *S. hammondii* (Stejneger and Barbour 1917, 1923, 1933, 1939; Storer 1925; Slevin 1928, 1934; Wright and Wright 1933; Linsdale 1940; Logier and Toner 1942), again accorded the taxon full species rank either within the genus *Scaphiopus* (Tanner 1939; Stejneger and Barbour 1943; Bragg 1944, 1945; Blair 1956; Zweifel 1956; McAlister 1959; Gorham 1963; Wasserman 1964; Kluge 1966; Stebbins 1966, 1985; Blair et al. 1968; Cochran and Goin 1970; Estes 1970; Northen 1970; Pickwell 1972; Dowling 1975; Collins et al. 1978, 1982; Behler and King 1979; Harding 1983; MacMahon 1985) or within the genus *Spea* (Firschein 1950, Chrapliwy 1956, Smith et al. 1965, Smith 1978, Nussbaum et al. 1983), or accepted Cope's (1889) subspecific designation, but not his erection of a new genus (Wright and Wright 1942; Stebbins 1951, 1954; Wright and Wright 1949; Schmidt 1953; Bragg 1965). Apparently, Dickerson (1906) was the only authority who both accepted Cope's (1889) subspecific designation and his recognition of the genus *Spea*, yet this acknowledgment existed only as a footnote. Others even suggested the possibility, but did not formally propose, that *S. intermontanus* may be either conspecific with (Gehlbach 1965) or may be a subspecies of *S. bombifrons* (Shannon 1953, Zweifel 1956). The preceding indicates there has been little consensus over the years concerning *Scaphiopus* taxonomy; however, subsequent to Bragg's (1965) manuscript, and bolstered by Northen's (1970) unpublished yet still supporting evidence, *S. intermontanus* has been regarded as a distinct species. When the first comprehensive checklist this century of the amphibian species of the world was published (Frost 1985), *intermontanus* was identified as a species within the genus *Scaphiopus* (subgenus *Spea*). Taxonomic classification of *intermontanus* seemed to have stabilized; however, subsequent to the publishing of the checklist some authorities have proposed to again elevate *Spea* to generic rank (see Comment).

Second, are those nomenclature changes that seem to have been made in error and did not represent formal proposals to emend epithet spellings. The Stejneger and Barbour (1943), Chenoweth (1950), Firschein (1950), and Fitzner and Gray (1991) citations seem to fit into this category.

• **Remarks.** Several bibliographic references (Banta 1965, Altig and Christensen 1976), Campbell et al. 1982) are available that identify, and in some cases annotate, sources of information applicable to *S. intermontanus* and *Scaphiopus* biology in general. Most, but not all, of the applicable references are identi-

fied in this account; however, Campbell et al. (1982) includes several references to Pacific Northwest species checklists and keys — some unpublished — that are not included here.

• **Etymology.** The generic name *Scaphiopus* is derived from two Greek root words that have been transcribed into Latin. *Scaphi(o)* is derived from the word *skapheion*, “shovel, spade” and *pus* is derived from the word *pous*, “foot” (Century 1913). *Scaphi* is the transcribed stem portion of *skapheion* and “o” is a connective vowel for joining stems. *Scaphiopus* can be literally translated as “spadefoot.” The specific name *intermontanus* is of Latin origin: *inter*, “between, among” and *montanus*, “of mountains” (Brown 1956). The subspecific name *Spea* also is of Greek origin. It is derived from the word *speos*, “cave” (Century 1913) plus the feminine Latin ending “a.”

• **Comment.** To maintain consistency, nomenclatural and species status for amphibian taxa other than *S. intermontanus* that have been referred to in this account are as in Frost (1985). Thus, spellings and species status in the text may not reflect how a particular taxon was originally identified.

Scaphiopus intermontanus is arguably the least studied species among the North American spadefoots; however, the comparatively fewer citations that seem to address it is in part a consequence of its taxonomic history. For most of the time since Cope (1883) first described the species, it either has not been accepted universally as a distinct species or its subspecific status has been underemphasized or misidentified. For example, a significant portion of the literature that purports to address *S. hammondi* actually addresses, based on currently accepted species status and distribution, *S. intermontanus*. In preparing this account, every effort was made to use locality information to decide whether a finding in the literature related to *S. intermontanus* or to another species of *Scaphiopus*. Only when necessary for clarity have some of these misidentifications been specifically identified in the text. A few citations remain ambiguous as to which taxa they addressed, either because locality information was not provided or the current systematics of *Scaphiopus* was not acknowledged. In some cases, a citation was included if indirect evidence could be used to make a reasonable determination that the citation probably applied to *S. intermontanus*.

The authority used here to properly place the taxon described is Frost (1985). Although some recent citations (e.g., Collins 1990) resurrected Cope’s (1867) use of the genus *Spea* and reestablished the use of the synonym *Spea intermontana* (but see Banks et al. 1987, for a contrary opinion), the proposed change is rejected here. Since the publication of Frost (1985), three lines of evidence have been proposed as justification for elevation of *Spea* to generic rank. First, Tanner (1989a, b) argued that *Spea* should be recognized as a full genus based primarily on skull characteristics that distinguished *Spea* complex species from other species of *Scaphiopus*. The skull features Tanner used, however, were those that previous authorities, such as Kluge (1966) and Zweifel (1956), had considered when relegating *Spea* to subgeneric status (though Kluge acknowledged this was arbitrary on his part). Thus, Tanner did not provide any new data to justify a taxonomic change. Second, as part of a phylogenetic analysis, Cannatella (1985) identified a number of morphological synapomorphies that separately supported the monophyly of *Spea* and the monophyly of the remainder of the species of *Scaphiopus* separate from *Spea*. Cannatella never did publish these findings — though his results were summarized by Wiens and Titus (1991) — and though he did express an opinion that on the basis of the morphological differences *Spea* should be elevated to generic rank, he did so with no strong conviction. Third, Wiens and Titus (1991) identified a number

of potential allozymic synapomorphies that also united *Spea*, but they cautioned that their results should be considered equivocal because insufficient outgroups were used. They implied a preference for recognizing *Spea* as a genus; however, their opening paragraph also implies some equivocation on this position. Collins (1990) did not provide a published reference to justify his use of *Spea intermontana*. Duellman (1993) represented an interim updating of Frost (1985). In Table 1 of his manuscript, Duellman seemingly modified Frost by recognizing *Spea* as a genus consisting of four species (with *Scaphiopus* correspondingly reduced to consisting of only two species). Although Duellman (1993), in his introduction, indicated that changes from Frost (1985) would be based on published information and would be appropriately indicated, this was not the case for *Scaphiopus* and *Spea*. Under the subfamily Pelobatinae and genus *Scaphiopus* all that was added was a comment that discussed the recognition of the subgenera *Scaphiopus* and *Spea* (Duellman 1993: 215). No information was provided that indicated recognition of *Spea* as a genus or its basis.

Although having a taxonomic classification accurately reflect the evolutionary relationships of organisms is important, one can argue that maintaining a stable taxonomy is just as important. This account provides examples of the confusion created in the literature by changes in taxonomy. I consider higher taxonomic changes that do not reflect a change in relationships as ill-advised. Although the choice of using the taxonomic checklist of Frost (1985) is itself arbitrary, a starting point is necessary. Frost (1985) at least represented an assessment of the findings of the published literature through June 1984 and also served to stabilize *Scaphiopus* taxonomy. I reject the elevation of *Spea* to generic rank on the grounds that insufficient justification has been provided to consider such a change. I offer several lines of reasoning. First, as already discussed in part in Hall et al. (1997), recent morphological analyses (i.e., Cannatella 1985; Tanner 1989a, b) did not affect the previously recognized phylogenetic relationships of the species in the genus *Scaphiopus*. As pointed out by Kluge (1966), higher taxonomic categories are arbitrary — whether based on morphology or adaptive features (Inger 1958) — and to continue to argue about whether *Scaphiopus* and *Spea* should be accorded generic or subgeneric rank is without merit. Second, Cannatella (1985), Tanner (1989a, b), and Wiens and Titus (1991) did not seem to consider Sage et al.’s (1982) caution based on albumin data that the subgenus *Scaphiopus* may be a paraphyletic taxon, nor did they recognize observations by Chrapliwy (1956), Kluge (1966), and Estes’s (1970) that *S. couchii* may have morphological affinities (uncoded by Cannatella 1985) that align it with the *Spea* group (some of Cannatella’s synapomorphies for *Spea* also can be questioned). Thus, recognition of even the current subgenera within *Scaphiopus* may be untenable. Third, any formal proposal to change *Scaphiopus* taxonomy as a result of a revised interpretation of phyletic relationships also should address the effect on included fossil or otherwise related taxa (e.g., see Estes 1970:323). In regard to fossil *Scaphiopus*, both Chrapliwy (1956) and Zweifel (1956) hesitated to assign several fossil species to either species group within *Scaphiopus*. Tihen (1960) referred a number of these fossil species to *Spea* on the basis of the degree of post-sacral webbing. Although Kluge (1966) adopted Tihen’s taxonomy without comment, he also indicated that his review of variation in the degree of post-sacral webbing in *Scaphiopus* did not enable him to characterize the *Scaphiopus* or *Spea* groups of species. Fourth, two of the primary sources of evidence used for recognizing *Spea* as a genus are either unpublished (i.e., Cannatella 1985) or lack sufficient outgroups for making the appropriate phyletic inference (i.e., Wiens and Titus 1991).

As described in the Pertinent Literature, the findings of Wiens

and Titus (1991) raise the concern that *S. intermontanus* may be paraphyletic. An individual of *S. intermontanus* from Colorado seemed to be more closely related to *S. bombifrons* than it was to a population of *S. intermontanus* from Oregon. Sample sizes were small and only two distant populations of *S. intermontanus* were sampled. Although Northen (1970) found that *S. intermontanus* and *S. bombifrons* seem to be allopatric, based on an analysis of mating calls he hypothesized that the species may have had some past contact. Thus, an alternative explanation to Wiens and Titus's (1991) findings could be that some amount of past introgression has occurred between the two species (at least in Colorado). Obviously, more work is needed on quantifying geographic variation to determine whether the Colorado individual is an outlier or indicative of a more complex taxonomic picture in *S. intermontanus* than currently recognized.

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Literature Cited

- Acker, R.L. and J.H. Larsen, Jr. 1979. A functional analysis of morphological variation in larval *Scaphiopus intermontanus* [abstract]. *Amer. Zool.* 19:1012.
- Altig, R. 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26:180–207.
- and M.T. Christensen. 1976. A bibliography of tadpole biology. *Smithsonian Herpetol. Info. Serv.* (31):i + 33 p.
- and G.F. Johnston. 1986. Major characteristics of free-living anuran tadpoles. *Smithsonian Herpetol. Info. Serv.* (67):i + 75 p.
- and W.L. Pace. 1974. Scanning electron photomicrographs of tadpole labial teeth. *J. Herpetol.* 8:247–251.
- Arnold, S.J. and R.J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology* 59:1014–1022.
- Banks, R.C., R.W. McDiarmid, and A.L. Gardner (eds.). 1987. Checklist of Vertebrates of the United States, the U.S. Territories, and Canada. U.S. Dept. Int., Fish Wildl. Serv. Res. Publ. 166, Washington, D.C.
- Banta, B.H. 1965. An annotated chronological bibliography of the herpetology of the state of Nevada. *Wasmann J. Biol.* 23:1–224.
- Baxter, G.T. 1947a. The amphibians and reptiles of Wyoming. *Wyoming Wild Life* 11(8):30–34.
- . 1947b. The amphibians and reptiles of Wyoming — II. *Wyoming Wild Life* 11(10):29–31.
- and M. D. Stone. 1985. *Amphibians and Reptiles of Wyoming*. 2nd ed. Wyoming Game and Fish Dept., Cheyenne.
- Behler, J.L. and F.W. King. 1979. *The Audubon Society Field Guide to North American Reptiles and Amphibians*. Alfred A. Knopf, New York.
- Bernard, S.R. and K.F. Brown. 1977. *Distribution of Mammals, Reptiles, and Amphibians by BLM Physiographic Regions and A.W. Kuehler's Associations for the Eleven Western States*. U.S. Dept. Int., Bur. Land Man. Tech. Note 301, Denver, Colorado.
- Blair, A.P. 1955. Distribution, variation, and hybridization in a relict toad (*Bufo microscaphus*) in southwestern Utah. *Amer. Mus. Nov.* (1722):1–38.
- Blair, W.F. 1956. Mating call and possible stage of speciation of the Great Basin spadefoot. *Texas J. Sci.* 8:236–238.
- . 1976. 8. Adaptation of anurans to equivalent desert scrub of North and South America, p.197–222. *In* D.W. Goodall (ed.), *Evolution of Desert Biota*. Univ. Texas Press, Austin.
- , A.P. Blair, P. Brodkorb, F.R. Cagle, and G.A. Moore. 1968. *Vertebrates of the United States*. 2nd ed. McGraw-Hill, New York.
- Blaustein, A.R. and S.C. Walls. 1995. Chapter 4. Aggregation and kin recognition, p. 568–602. *In* H. Heatwole and B. Sullivan (eds.), *Amphibian Biology, Volume 2: Social Behavior*. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.
- Bogart, J.P. 1971. Afinidades entre los géneros de anuros en las familias Pelobatidae y Ceratophrynidae como se muestra por análisis cromosómico. *Acta Zool. Lilloana* 28:19–29.
- Booth, E.S. 1942. Field Key to the Amphibians and Reptiles of the Northwest. Unpubl. Report, copyrighted by the author.
- Bragg, A.N. 1944. The spadefoot toads in Oklahoma with a summary of our knowledge of the group. *Amer. Nat.* 78:517–533.
- . 1945. The spadefoot toads in Oklahoma with a summary of our knowledge of the group. II. *Amer. Nat.* 79:52–72.
- . 1946. Aggregation with cannibalism in tadpoles of *Scaphiopus bombifrons* with some general remarks on the probable evolutionary significance of such phenomena. *Herpetologica* 3:89–97.
- . 1950. Observations on *Scaphiopus*, 1949 (Salientia: Scaphiopodidae). *Wasmann J. Biol.* 8:221–228.
- . 1961. A theory of the origin of spadefooted toads deduced principally by a study of their habits. *Anim. Behav.* 9:178–186.
- . 1965. *Gnomes of the Night: The Spadefoot Toads*. Univ. Pennsylvania Press, Philadelphia.
- . 1967. Recent studies on the spadefoot toads. *Bios* 38:75–84.
- Brattstrom, B.H. 1976. A Pleistocene herpetofauna from Smith Creek Cave, Nevada. *Bull. So. California Acad. Sci.* 75:283–284.
- Brown, H.A. 1967. Embryonic temperature adaptations and genetic compatibility in two allopatric populations of the spadefoot toad, *Scaphiopus hammondi*. *Evolution* 21:742–761.
- . 1976. The status of California and Arizona populations of the western spadefoot toads (Genus *Scaphiopus*). *Nat. Hist. Mus. Los Angeles Co. Contr. Sci.* (286):1–15.
- . 1989. Tadpole development and growth of the Great Basin spadefoot toad, *Scaphiopus intermontanus*, from central Washington. *Can. Fld.-Nat.* 103:531–534.
- Brown, R.W. 1956. *Composition of Scientific Words*. Rev. ed. Priv. publ.
- Bury, R.B., C.K. Dodd, Jr., and G.M. Fellers. 1980. *Conservation of the Amphibia of the United States: A Review*. U.S. Dept. Int., Fish Wildl. Serv. Res. Publ. 134, Washington, D.C.
- Campbell, R.W., M.G. Shepard, B.M. Van Der Raay, and P.T. Gregory. 1982. *A Bibliography of Pacific Northwest Her-*

- petology. Brit. Columbia Prov. Mus., Heritage Rec. No. 14, Victoria.
- Cannatella, D.C. 1985. A Phylogeny of Primitive Frogs (archaeobatrachians). Ph.D. Diss. Univ. Kansas, Lawrence.
- Cary, M. 1911. A biological survey of Colorado. N. Amer. Fauna (33):1-259.
- Carl, G.C. 1942. The western spadefoot toad in British Columbia. *Copeia* 1942:129.
- . 1943. The Amphibians of British Columbia. Brit. Columbia Prov. Mus., Hndbk. No. 2, Victoria.
- Century. 1913. The Century Dictionary and Cyclopedia. The Century Co., New York.
- Chenoweth, W.L. 1950. Records of amphibians and reptiles from New Mexico, Utah, and Arizona. *Trans. Kansas Acad. Sci.* 53:532-534.
- Chrapliwy, P.S. 1956. Taxonomy and Distribution of the Spadefoot Toads of North America (Salientia: Pelobatidae). M.S. Thesis. Univ. Kansas, Lawrence.
- Clark, G.W., J. Bradford, and R. Nussbaum. 1969. Blood parasites of some Pacific Northwest amphibians. *Bull. Wildl. Dis. Assoc.* 5:117-118.
- Claussen, D.L. 1969. Studies on water loss and rehydration in anurans. *Physiol. Zoöl.* 42:1-14.
- Cochran, D.M. and C.J. Goin. 1970. The New Field Book of Reptiles and Amphibians. G.P. Putnam's Sons, New York.
- Collins, J.P. 1996. A status survey of three species of endangered / sensitive amphibians in Arizona. Unpubl. final rept. submitted to the Arizona Game and Fish Dept.
- Collins, J.T. (ed.). 1990. Standard Common and Current Scientific Names for North American Amphibians and Reptiles. 3rd ed. SSAR Herpetol. Circ. No. 19.
- , 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. 2nd ed. SSAR Herpetol. Circ. No. 12.
- , J.E. Huheey, J.L. Knight, and H.M. Smith. 1978. Standard Common and Current Scientific Names for North American Amphibians and Reptiles. Misc. Publ. SSAR Herpetol. Circ. No. 7.
- Cook, F.R. 1984. Introduction to Canadian Amphibians and Reptiles. *Natl. Mus. Nat. Sci.: Natl. Mus. Canada*, Ottawa.
- Cope, E.D. 1867. On the structure and distribution of genera of the arciferous Anura. *J. Acad. Nat. Sci. Phila.*, ser. 2, 6:67-112 + 1 pl.
- . 1879. A contribution to the zoölogy of Montana. *Amer. Nat.* 13:432-441.
- . 1883. Notes on the geographical distribution of Batrachia and Reptilia in western North America. *Proc. Acad. Nat. Sci. Philadelphia* 35:10-35.
- . 1889. The Batrachia of North America. *Bull. U.S. Natl. Mus.* (34):525 p. + 86 pls.
- . 1893. A contribution to the herpetology of British Columbia. *Proc. Acad. Nat. Sci. Phila.* 45:181-184.
- . 1896. The geographical distribution of Batrachia and Reptilia in North America. *Amer. Nat.* 30:886-902, 1003-1026.
- Corkran, C.C. and C. Thoms. 1996. Amphibians of Oregon, Washington and British Columbia. Lone Pine, Edmonton, Alberta.
- Cowles, R.B. and C.M. Bogert. 1936. The herpetology of the Boulder Dam region (Nev., Ariz., Utah). *Herpetologica* 1:33-42.
- Davidson, C. 1995. Frog and Toad Calls of the Pacific Coast: Vanishing Voices. Library of Natural Sounds, Cornell Lab. Ornithol., Ithaca, New York.
- Dice, L.R. 1916. Distribution of the land vertebrates of south-eastern Washington. *Univ. California Publ. Zool.* 16:293-348 + 3 pls.
- Dickerson, M.C. 1906. The Frog Book: North American Toads and Frogs with a Study of the Habits and Life Histories of Those of the Northeastern States. Doubleday, Page, and Co., New York (printed in 1907).
- Dimmitt, M.A. and R. Ruibal. 1980. Exploitation of food resources by spadefoot toads (*Scaphiopus*). *Copeia* 1980:854-862.
- Dowling, H.G. 1975. A classification and checklist of the species of amphibians and reptiles found in the United States and Canada, p. 175-189. *In* H.G. Dowling (ed.), 1974 Yearbook of Herpetology, Vol. 1. HISS Publ. Herpetol. No. 8, New York.
- Drost, C.A. and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. *Conserv. Biol.* 10:414-425.
- Duellman, W.E. 1993. Amphibian Species of the World: Additions and Corrections. *Spec. Publ. Univ. Kansas Mus. Nat. Hist.* (21):iii + 372 p.
- Dunlap, D.G. 1960. The comparative myology of the pelvic appendage in the Salientia. *J. Morphol.* 106:1-76.
- Durham, F.E. 1956. Amphibians and reptiles of the North Rim, Grand Canyon, Arizona. *Herpetologica* 12:220-224.
- Edwards, S.R. (ed.). 1975. Collections of Preserved Amphibians and Reptiles in the United States. Misc. Publ. SSAR Herpetol. Circular No. 3.
- Endemic Species Committees. 1982. Endemic Amphibians and Reptiles of the Colorado River System: A Status Report. Colorado River Wildlife Council.
- Englehardt, G.P. 1918. Batrachians from southwestern Utah. *Copeia* (60):77-80.
- Estes, R. 1970. New fossil pelobatid frogs and a review of the genus *Eopelobates*. *Bull. Mus. Comp. Zool. Harv.* 139:293-339.
- Evenden, F.G., Jr. 1946. Notes on the herpetology of Elmore County, Idaho. *Copeia* 1946:256-257.
- Fichter, E. and A.D. Linder. 1964. The Amphibians of Idaho. *Spec. Publ. Idaho St. Univ. Mus.*, Pocatello.
- Firschein, I.L. 1950. A new record of *Spea bombifrons* from northern Mexico and remarks on the status of the *hammondi* group of spadefoot anurans. *Herpetologica* 6:75-77.
- Fitzner, R.E. and R.H. Gray. 1991. The status, distribution and ecology of wildlife on the U.S. DOE Hanford Site: a historical overview of research activities. *Environ. Monit. Assess.* 18:173-202.
- Fouquette, M.J., Jr. 1980. Effect of environmental temperatures on body temperature of aquatic-calling anurans. *J. Herpetol.* 14:347-352.
- Froom, B. 1982. Amphibians of Canada. McClelland and Stewart, Toronto.
- Frost, D.R. (ed.). 1985. Amphibian Species of the World: A Taxonomic and Geographical Reference. Allen Press and Assoc. Syst. Collections, Lawrence, Kansas.
- Garman, S.W. 1884. The North American reptiles and batrachians. A list of the species occurring north of the Isthmus of Tehuantepec, with references. *Bull. Essex Inst.* 16:3-46.
- Gehlbach, F.R. 1965. Herpetology of the Zuni Mountains region, northwestern New Mexico. *Proc. U.S. Natl. Mus.* 116:243-332 + 4 pls.
- Gleason, R.L. and T.H. Craig. 1979. Food habits of burrowing owls in southeastern Idaho. *Great Basin Nat.* 39:274-276.
- Goin, C.J., O.B. Goin, and G.R. Zug. 1978. Introduction to Herpetology. 3rd ed. W.H. Freeman, San Francisco.
- Gordon, K. 1939. The Amphibia and Reptilia of Oregon. *Oregon St. Monogr. Stud. Zool.* (1):1-82.
- Gorham, S.W. 1963. The comparative number of species of amphibians in Canada and other countries. III. Summary

- of species of anurans. *Can. Fld.-Nat.* 77:13–48.
- Graf, W., S.G. Jewett, Jr., and K.L. Gordon. 1939. Records of amphibians and reptiles from Oregon. *Copeia* 1939:101–104.
- Green, D.M. and R.W. Campbell. 1984. The Amphibians of British Columbia. *Brit. Columbia Prov. Mus., Hndbk. No. 45*, Victoria.
- Green, G.A., R.E. Fitzner, R.G. Anthony, and L.E. Rogers. 1993. Comparative diets of burrowing owls in Oregon and Washington. *Northwest Sci.* 67:88–93.
- Grinnell, J. and C.L. Camp. 1917. A distributional list of the amphibians and reptiles of California. *Univ. California Publ. Zool.* 17:127–208.
- Grinnell, J. and T.I. Storer. 1924. *Animal Life in the Yosemite: An Account of the Mammals, Birds, Reptiles, and Amphibians in a Cross-section of the Sierra Nevada*. Univ. California Press, Berkeley.
- Hailman, J.P. 1976. Oil droplets in the eyes of adult anuran amphibians: a comparative survey. *J. Morphol.* 148:453–468.
- and R.G. Jaeger. 1974. Phototactic responses to spectrally dominant stimuli and use of colour vision by adult anuran amphibians: a comparative survey. *Anim. Behav.* 22:757–795.
- Hall, J.A. 1993. Post-embryonic Ontogeny and Larval Behavior of the Spadefoot Toad, *Scaphiopus intermontanus* (Anura: Pelobatidae). Ph.D. Diss. Washington State Univ., Pullman.
- , J.H. Larsen, Jr., and R.E. Fitzner. 1997. Postembryonic ontogeny and larval behavior of the spadefoot toad, *Scaphiopus intermontanus* (Anura: Pelobatidae): external morphology. *Herpetol. Monogr.* 11:124–178.
- , J.H. Larsen, Jr., D.E. Miller, and R.E. Fitzner. 1995. Discrimination of kin- and diet-based cues by larval spadefoot toads, *Scaphiopus intermontanus* (Anura: Pelobatidae), under laboratory conditions. *J. Herpetol.* 29:233–243.
- Hallock, L.A. 1995. Inventory of amphibians and reptiles at the Hanford Site. Unpubl. rept., The Nature Conservancy, Seattle, Washington.
- Hammerson, G.A. 1982a. Amphibians and Reptiles in Colorado. Colorado Div. Wildlife, Denver.
- 1982b. Amphibian and reptile distribution in Colorado: corrections of erroneous records. *Herpetol. Rev.* 13:53–54.
- 1991. Geographic distribution: *Spea intermontana* (Great Basin spadefoot). *Herpetol. Rev.* 22:64.
- Harding, K.A. 1983. *Catalogue of New World Amphibians*. Pergamon Press, Elmsford, New York.
- Hardy, R. 1938. An annotated list of reptiles and amphibians of Carbon County, Utah. *Utah Acad. Sci., Arts Lett.* 15:99–102.
- Harestad, A.S. 1985a. Life history notes: *Scaphiopus intermontanus* (Great Basin spadefoot toad). Mortality. *Herpetol. Rev.* 16:24.
- 1985b. Geographic distribution: *Scaphiopus intermontanus* (Great Basin spadefoot). *Herpetol. Rev.* 16:31.
- Hillman, S.S. 1980. Physiological correlates of differential dehydration tolerance in anuran amphibians. *Copeia* 1980:125–129.
- 1982. Effects of DL-propranolol on exercise heart rate and maximal rates of oxygen consumption in *Scaphiopus intermontanus*. *Experientia* 38:940–941.
- and R.W. Sommerfeldt. 1981. Microsphere studies of amphibian systematic blood flow redistribution during dehydration, hypovolemia, and salt load. *J. Exp. Zool.* 218:305–308.
- Holman, J.A. 1995. *Pleistocene Amphibians and Reptiles in North America*. Oxford Univ. Press, New York.
- Hovingh, P., B. Benton, and D. Bornholdt. 1985. Aquatic parameters and life history observations of the Great Basin spadefoot toad in Utah. *Great Basin Nat.* 45:22–30.
- Inger, R.F. 1958. Comments on the definition of genera. *Evolution* 12:370–384.
- Jaeger, R.G. and J.P. Hailman. 1973. Effects of intensity on the phototactic responses of adult anuran amphibians: a comparative survey. *Z. Tierpsychol.* 33:352–407.
- Jasinski, A. and A. Gorbman. 1967. Hypothalamic neurosecretion in the spadefoot toad, *Scaphiopus hammondi*, under different environmental conditions. *Copeia* 1967:271–279.
- Jurgens, J.D. 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. *Ann. Univ. Stellenbosch* 46 ser. A(2):1–146.
- Kluge, A.G. 1966. A new pelobatine frog from the Lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. *Nat. Hist. Mus. Los Angeles Co. Contr. Sci.* (113):1–26.
- and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18:1–32.
- Küchler, A.W. 1975. Potential natural vegetation of the conterminous United States. Map (scale 1:3,168,000). Amer. Geogr. Soc., New York.
- La Rivers, I. 1942. Some new amphibian and reptile records for Nevada. *J. Entomol. Zool.* 34:53–68.
- Leonard, W.P., H.A. Brown, L.L.C. Jones, K.R. McAllister, and R.M. Storm. 1993. *Amphibians of Washington and Oregon*. Seattle Audubon Soc., Seattle, Washington.
- Linder, A.D. and R.W. Sehman. 1977. Herpetofauna of the Idaho National Engineering Laboratory Site. *J. Idaho Acad. Sci.* 13:43–46.
- Linsdale, J.M. 1938. Environmental responses of vertebrates in the Great Basin. *Amer. Midl. Nat.* 19:1–206.
- 1940. Amphibians and reptiles in Nevada. *Proc. Amer. Acad. Arts Sci.* 73:197–257.
- Livezey, R.L. and A.H. Wright. 1947. A synoptic key to the sa-lientian eggs of the United States. *Amer. Midl. Nat.* 37:179–222.
- Llewellyn, R.L. 1997. Geographic distribution: *Spea intermontana* (Great Basin spadefoot). *Herpetol. Rev.* 28:94.
- Logier, E.B.S. 1932. Some account of the amphibians and reptiles of British Columbia. *Trans. Roy. Can. Inst.* 18 part 2:311–336.
- and G.C. Toner. 1942. Amphibians and reptiles of Canada. *Can. Fld. Nat.* 56:15–16.
- 1955. Check-list of the Amphibians and Reptiles of Canada and Alaska. *Contr. Roy. Ontario Mus. Zool. Palaeontol.* No. 41, Toronto.
- 1961. Check List of the Amphibians and Reptiles of Canada and Alaska: A Revision of Contribution. No. 41. *Contr. Roy. Ontario Mus.* No. 53, Toronto.
- Lowe, C.H. 1964. Part 3 Amphibians and reptiles of Arizona, p. 153–174. *In* C.H. Lowe (ed.), *The Vertebrates of Arizona*. Univ. Arizona Press, Tucson.
- Macey, J.R. 1986. The biogeography of a herpetofaunal transition between the Great Basin and Mojave Deserts, p. 119–128. *In* C.A. Hall, Jr. and D.J. Young (eds.), *Natural History of the White-Inyo Range, Eastern California and Western Nevada and High Altitude Physiology*. White Mountain Res. Stat. Symp. Aug. 23–25, 1985. Vol. 1. Univ. California Regents.
- and T.J. Papenfuss. 1991a. 9 Amphibians, p. 277–290 + 10 pls. *In* C.A. Hall (ed.), *Natural History of the White-Inyo Range: Eastern California*. California Nat. Hist. Guides 55. Univ. California Press, Berkeley.
- and T.J. Papenfuss. 1991b. 10 Reptiles, p. 291–360 + 44 pls. *In* C.A. Hall (ed.), *Natural History of the White-Inyo Range: Eastern California*. California Nat. Hist. Guides 55. Univ. California Press, Berkeley.
- MacMahon, J. 1985. *The Audubon Society Nature Guides: Deserts*. Alfred A. Knopf, New York.
- Malnate, E.V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Phila-

- delphia (ANSP). Proc. Acad. Nat. Sci. Phila. 123:345–375.
- Maslin, T.P. 1959. An annotated check list of the amphibians and reptiles of Colorado. Univ. Colorado Stud., Ser. Biol. (6): vi + 98 p.
- Mayhew, W.W. 1968. Biology of desert amphibians and reptiles, p. 195–356. In G.W. Brown, Jr. (ed.), Desert Biology: Special Topics on the Physical and Biological Aspects of Arid Regions. Vol. 1. Academic Press, New York.
- McAlister, W.H. 1959. The vocal structures and method of call production in the genus *Scaphiopus* Holbrook. Texas J. Sci. 11:60–77.
- McAllister, K.R. 1995. Distribution of amphibians and reptiles in Washington State. Northw. Fauna 3:81–112.
- McClanahan, L., Jr. 1967. Adaptations of the spadefoot toad, *Scaphiopus couchii*, to desert environments. Comp. Biochem. Physiol. 20:73–99.
- McCoy, C.J., Jr. 1962a. Noteworthy amphibians and reptiles from Colorado. Herpetologica 18:60–62.
- . 1962b. Herpetofaunal dispersal in the Grand Valley of Colorado [abstract]. J. Colorado-Wyoming Acad. Sci. 5:41.
- McKee, E.D. and C.M. Bogert. 1934. The amphibians and reptiles of Grand Canyon National Park. Copeia 1934:178–180.
- Mead, J.I. 1985. Chapter 11. Paleontology of Hidden Cave: amphibians and reptiles, p. 162–170. In D.H. Thomas (ed.), The Archaeology of Hidden Cave, Nevada. Anthropol. Pap. Amer. Mus. Nat. Hist. 61, part 1.
- and C.J. Bell. 1994. Late Pleistocene and Holocene herpetofaunas of the Great Basin and Colorado Plateau, p. 255–275. In K.T. Harper, L.L. St. Clair, K.H. Thorne, and W.M. Hess (eds.), Natural History of the Colorado Plateau and Great Basin. Univ. Colorado Press, Niwot, Colorado.
- , D.K. Grayson, and R.W. Casteel. 1983. The paleontology of Gatecliff Shelter: fish, amphibians, and birds, p. 129–135. In D.H. Thomas (ed.), The Archaeology of Monitor Valley. 2
- Gatecliff Shelter. Anthropol. Pap. Amer. Mus. Nat. Hist. 59, part 1.
- , R.S. Thompson, and T.R. Van Devender. 1982. Late Wisconsinan and Holocene faunas from Smith Creek Canyon, Snake Range, Nevada. Trans. San Diego Soc. Nat. Hist. 20:1–26.
- Metter, D.E. 1960. The Distribution of Amphibians in Eastern Washington. M.S. Thesis. Washington State Univ., Pullman.
- Mills, R.C. 1948. A check list of the reptiles and amphibians of Canada. Herpetologica 4(2nd suppl.):1–15.
- Morey, S.R. and D.N. Janes. 1994. Variation in larval habitat duration influences metamorphosis in *Scaphiopus couchii*, p. 159–165. In P.R. Brown and J.W. Wright (eds.), Herpetology of the North American Deserts: Proceedings of a Symposium. Southw. Herpetol. Soc. Spec. Publ. 5.
- Murray, L.K. 1992. Faunal Description and Taphonomy of Dinosaur Cave in the Western Snake River Plain of Idaho. M.S. Thesis, Northern Arizona Univ., Flagstaff.
- Nauman, R.S., T. Lossen, and K. Pfeifer. 1996. Geographic distribution: *Spea intermontana* (Great Basin spadefoot). Herpetol. Rev. 27:210.
- Northern, P.T. 1970. The Geographic and Taxonomic Relationships of the Great Basin spadefoot toad, *Scaphiopus intermontanus*, to other members of the subgenus. Ph.D. Diss. Univ. Wisconsin, Madison.
- Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. Univ. Press Idaho, Moscow.
- Orchard, S.A. 1992. Amphibian population declines in British Columbia, p. 10–13. In C.A. Bishop and K.E. Petit (eds.), Declines in Canadian Amphibian Populations: Designating a National Monitoring Strategy. Occ. Pap. No. 76. Can. Wildl. Serv., Ottawa.
- Orton, G.L. 1954. Dimorphism in larval mouthparts in spadefoot toads of the *Scaphiopus hammondi* group. Copeia 1954:97–100.
- Papenfuss, T.J. 1986. Amphibian and reptile diversity along elevational transects in the White-Inyo Range, p. 129–136. In C.A. Hall, Jr. and D.J. Young (eds.), Natural History of the White-Inyo Range, Eastern California and Western Nevada and High Altitude Physiology. White Mountain Res. Stat. Symp. Aug. 23–25, 1985. Vol. 1. Univ. California Regents.
- Patch, C.L. 1929. Some amphibians of western North America. Can. Fld.-Nat. 43:137–138.
- Peabody, F.E. and J.M. Savage. 1958. Evolution of a coast range corridor in California and its effect on the origin and dispersal of living amphibians and reptiles, p. 159–186. In C.L. Hubbs (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Publ. 51, Washington, D.C.
- Pfennig, D. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. Oecologia 85:101–107.
- Pfennig, D.W. 1992. Proximate and functional causes of polyphenism in an anuran tadpole. Funct. Ecol. 6:167–174.
- , H.K. Reeve, and P.W. Sherman. 1993. Kin recognition and cannibalism in spadefoot tadpoles. Anim. Behav. 46:87–94.
- Pickwell, G. 1972. Amphibians and Reptiles of the Pacific States. Dover Publ., New York (unabridged replication of the original work published in 1947 by Stanford Univ. Press).
- Porter, K.R. 1972. Herpetology. W.B. Saunders, Philadelphia.
- Preston, W.B. and D.R.M. Hatch. 1986. The plains spadefoot, *Scaphiopus bombifrons*, in Manitoba. Can. Fld.-Nat. 100:123–125.
- Reynolds, T.D., J.W. Connelly, D.K. Halford, and W.J. Arthur. 1986. Vertebrate fauna of the Idaho National Environmental Research Park. Great Basin Nat. 46:513–527.
- Ritland, R.M. 1955. Studies on the post-cranial morphology of *Ascaphus truei*. I. Skeleton and spinal nerves. J. Morphol. 97:119–177.
- Rocek, Z. 1981. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. Acta Univ. Carol. Biol. 1980:1–164.
- Rose, S.M. and F.C. Rose. 1961. Growth-controlling exudates of tadpoles, p. 207–218. In F.L. Milthorpe (ed.), Mechanisms in Biological Competition. Symp. Soc. Exp. Biol. No. 15.
- Ruthven, A.G. and H.T. Gaige. 1915. The reptiles and amphibians collected in northeastern Nevada by the Walker-Newcomb expedition of the University of Michigan. Occ. Pap. Mus. Zool. Univ. Michigan 8:1–33 + 5 pls.
- Sage, R.D., E.M. Prager, and D.B. Wake. 1982. A Cretaceous divergence time between pelobatid frogs (*Pelobates* and *Scaphiopus*): immunological studies of serum albumin. J. Zool. Lond. 198:481–494.
- Sattler, P.W. and J.S. Mecham. 1979. Gene duplication at an isocitrate dehydrogenase locus in *Scaphiopus*. J. Hered. 70: 352–353.
- Schmidt, K.P. 1953. A Check List of North American Amphibians and Reptiles. 6th ed. ASIH, Univ. Chicago Press, Chicago.
- Secoy, D.M. and W.M. Brown. 1968. New county records in the herpetofauna of Colorado. Southw. Nat. 13:105–106.
- Sehman, R.W. and A.D. Linder. 1978. Amphibian and Reptilian Fauna of the Idaho National Engineering Laboratory Site. IDO-12086. U.S. Department of Energy. Nat. Tech. Info. Serv., Springfield, Virginia.
- Shannon, F.A. 1953. *Scaphiopus bombifrons*, a state record for Arizona. Herpetologica 9:127–128.
- Shoemaker, V.H., S.S. Hillman, S.D. Hillyard, D.C. Jackson, L.L. McClanahan, P.C. Withers, and M.L. Wygoda. 1992. 6. Exchange of water, ions, and respiratory gases in terrestrial

- amphibians, p. 125–150. In M.E. Feder and W.W. Burggren (eds.), *Environmental Physiology of the Amphibians*. Univ. Chicago Press, Chicago.
- Simovich, M.A. and C.A. Sassaman. 1986. Four independent electrophoretic markers in spadefoot toads. *J. Hered.* 77:410–414.
- Slater, J.R. 1941. The distribution of amphibians and reptiles in Idaho. *Occ. Pap. Dept. Biol. Coll. Puget Sound* (14):78–109.
- . 1955. Distribution of Washington amphibians. *Occ. Pap. Dept. Biol. Coll. Puget Sound* (16):122–154.
- . 1964. County records of amphibians for Washington. *Occ. Pap. Dept. Biol. Univ. Puget Sound* (26):237–242.
- Slevin, J.R. 1928. The amphibians of western North America. *Occ. Pap. California Acad. Sci.* (16):152 p + 23 pls.
- . 1934. *A Handbook of Reptiles and Amphibians of the Pacific States: Including Certain Eastern Species*. Spec. Publ. California Acad. Sci., San Francisco.
- Smith, H.M. 1978. *A Guide to Field Identification: Amphibians of North America*. Golden Press, New York.
- , T.P. Maslin, and R.L. Brown. 1965. Summary of the distribution of the herpetofauna of Colorado. *Univ. Colorado Stud., Ser. Biol.* (15):i + 52 p.
- Snyder, J.O. 1920. *Scaphiopus* in northern Nevada. *Copeia* (86): 83–84.
- Steadman, D.W., J.I. Mead, R.C. Bright, and C. Force. 1994. Late Quaternary Plants and Animals from Rattlesnake Cave, Snake River Plain, Idaho. Foundation-001. *Env. Sci. Res. Found., Idaho Falls, Idaho*.
- Stebbins, R.C. 1951. *Amphibians of Western North America*. Univ. California Press, Berkeley.
- . 1954. *Amphibians and Reptiles of Western North America*. McGraw-Hill, New York.
- . 1966. *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin, Boston.
- . 1972. *Amphibians and Reptiles of California*. Univ. California Press, Berkeley.
- . 1985. *A Field Guide to Western Reptiles and Amphibians*. 2nd ed. Houghton Mifflin, Boston.
- Stejneger, L. 1893. Annotated list of the reptiles and batrachians collected by the Death Valley Expedition in 1891, with descriptions of new species. *N. Amer. Fauna* (7):159–228.
- and T. Barbour. 1917. *A Check List of North American Amphibians and Reptiles*. Harvard Univ. Press, Cambridge, Massachusetts.
- . 1923. *A Check List of North American Amphibians and Reptiles*. 2nd ed. Harvard Univ. Press, Cambridge, Massachusetts.
- . 1933. *A Check List of North American Amphibians and Reptiles*. 3rd ed. Harvard Univ. Press, Cambridge, Massachusetts.
- . 1939. *A Check List of North American Amphibians and Reptiles*. 4th ed. Harvard Univ. Press, Cambridge, Massachusetts.
- . 1943. *A Check List of North American Amphibians and Reptiles*. 5th ed. *Bull. Mus Comp. Zool. Harv.* 93(1):xix + 260 p.
- Stewart, G.R. 1994. An overview of the Mohave Desert and its herpetofauna, p. 54–69. In P.R. Brown and J.W. Wright (eds.), *Herpetology of the North American Deserts: Proceedings of a Symposium*. Southw. Herpetol. Soc. Spec. Publ. 5.
- Storer, T.I. 1925. A synopsis of the Amphibia of California. *Univ. California Publ. Zool.* 27:342 p. + 18 pls.
- Storm, R.M. 1966. Amphibians and reptiles. *Northw. Sci.* 40: 138–141.
- Svihla, A. 1953. Diurnal retreats of the spadefoot toad *Scaphiopus hammondi*. *Copeia* 1953:186.
- and R.D. Svihla. 1933. Amphibians and reptiles of Whitman County, Washington. *Copeia* 1933:125–128.
- Tanner, V.M. 1927a. Distributional list of the amphibians and reptiles of Utah. *Copeia* (163):54–58.
- . 1927b. An ecological study of Utah Amphibia [abstract]. *Proc. Utah Acad. Sci.* 4:6–7.
- . 1930. The amphibians and reptiles of Bryce Canyon National Park, Utah. *Copeia* 1930:41–43.
- . 1931. A synoptical study of Utah Amphibia. *Proc. Utah Acad. Sci.* 8:159–198.
- . 1939. A study of the genus *Scaphiopus*, the spadefoot toads. *Great Basin Nat.* 1:3–20 + 3 pls.
- Tanner, W.W. 1940. Notes on the herpetological specimens added to the Brigham Young University vertebrate collection during 1939. *Great Basin Nat.* 1:138–146.
- . 1941. The reptiles and amphibians of Idaho No. I. *Great Basin Nat.* 2:87–97.
- . 1958. Herpetology of Glen Canyon of the Upper Colorado River Basin. *Herpetologica* 14:193–195.
- . 1989a. Amphibians of western Chihuahua. *Great Basin Nat.* 49:38–70.
- . 1989b. Status of *Spea stagnalis* Cope (1875), *Spea intermontanus* Cope (1889), and a systematic review of *Spea hammondi* Baird (1839) (Amphibia: Anura). *Great Basin. Nat.* 49:503–510.
- Taylor, W.P. 1912. Field notes on amphibians, reptiles, and birds of northern Humboldt County, Nevada. *Univ. California Publ. Zool.* 7:319–436 + 6 pls.
- Thorson, T.B. 1955. The relationship of water economy to terrestrialism in amphibians. *Ecology* 36:100–116.
- . 1956. Adjustment of water loss in response to desiccation in amphibians. *Copeia* 1956:230–237.
- and A. Svihla. 1943. Correlation of the habitats of amphibians with their ability to survive the loss of body water. *Ecology* 24:374–381.
- Tihen, J.A. 1960. On *Neoscaphiopus* and other Pliocene pelobatid frogs. *Copeia* 1960:89–94.
- Trowbridge, M.S. 1942. Studies on the normal development of *Scaphiopus bombifrons* Cope. II. The later embryonic and larval periods. *Trans. Amer. Microsc. Soc.* 61:66–83.
- Turner, F.B. 1952. The mouth parts of tadpoles of the spadefoot toad, *Scaphiopus hammondi*. *Copeia* 1952:172–175.
- Van Denburgh, J. and J.R. Slevin. 1915. A list of the amphibians and reptiles of Utah, with notes on the species in the collection of the Academy. *Proc. California Acad. Sci., ser. 4, 5:* 99–110 + 3 pls.
- . 1921a. A list of the amphibians and reptiles of Nevada, with notes on the species in the collection of the Academy. *Proc. California Acad. Sci., ser. 4, 11:*27–38.
- . 1921b. List of the amphibians and reptiles of Idaho, with notes on the species in the collection of the Academy. *Proc. California Acad. Sci., ser. 4, 11:*39–47.
- Van Devender, T.R., J.I. Mead, and A.M. Rea. 1991. Late Quaternary plants and vertebrates from Picacho Peak, Arizona. *Southw. Nat.* 36:302–314.
- Wasserman, A.O. 1964. Recent and summarized interspecific hybridizations within the Pelobatidae. *Texas J. Sci.* 16:334–341.
- . 1970. Chromosomal studies of the Pelobatidae (Salientia) and some instances of ploidy. *Southw. Nat.* 15:239–248.
- Whitaker, J.O., Jr., D. Rubin, and J.R. Munsee. 1977. Observations on food habits of four species of spadefoot toads, genus *Scaphiopus*. *Herpetologica* 33:468–475.
- Wiens, J.J. and T.A. Titus. 1991. A phylogenetic analysis of *Spea* (Anura: Pelobatidae). *Herpetologica* 47:21–28.
- Wood, W.F. 1935. Encounters with the western spadefoot, *Scaphiopus hammondi*, with a note on a few albino larvae. *Copeia* 1935:100–102.

- Woodbury, A.M. 1952. Amphibians and reptiles of the Great Salt Lake Valley. *Herpetologica* 8:42-50.
- Wright, A.A. and A.H. Wright. 1933. Handbook of Frogs and Toads. The Frogs and Toads of the United States and Canada. Comstock, Ithaca, New York.
- and —. 1942. Handbook of Frogs and Toads. The Frogs and Toads of the United States and Canada. 2nd ed. Comstock, Ithaca, New York.
- Wright, A. H. and A. A. Wright. 1949. Handbook of Frogs and Toads of the United States and Canada. 3rd ed. Comstock, Ithaca, New York.
- Yarrow, H.C. 1875. Report upon the collection of batrachians and reptiles made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1872, 1873, and 1874. Report upon the geographical and geological explorations and surveys west of the 100th meridian (Wheeler Survey). Vol. 5, Zool., Ch. 4:509-584 + 10 pls.
- . 1882. Check list of North American Reptilia and Batrachia, with catalogue of specimens in U. S. National Museum. Bull. U.S. Natl. Mus. (24):vi + 249 p.
- Zeiner, D.C., W.F. Laudenslayer, Jr., and K.E. Mayer. 1988. California's Wildlife, Volume I: Amphibians and Reptiles. State of California, Dept. Fish and Game, Sacramento.
- Zweifel, R.G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. *Amer. Mus. Nov.* (1762):1-45.
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