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STATUS OF SPEA STAGNALIS COPE (1875), SPEA INTERMONTANUS COPE (1889), AND A SYSTEMATIC REVIEW OF SPEA HAMMONDI BAIRD (1839) (AMPHIBIA: ANURA)

Wilmer W. Tanner

ABSTRACT —In this report emphasis is placed on the dorsal skull characters of the genus Spea and the three species, bombifrons, hammondii, and intermontana. Spea hammondii is a polytypic species with at least three subspecies, hammondii, multiplicatus, and stagnalis, each of which is described and the distribution indicated. Drawings and photographs of skulls are provided for each species, with hammondii and intermontana receiving special consideration.

Few North American amphibians have had such a varied and uncertain systematic past as that of the spadefoot toad. Recent fossils have aided researchers in understanding the relationships between historic and modern species. These relationships strongly suggest that all spadefoot toads be retained in the family Pelobatidae. Cope (1875), based on material available to him, placed American species in the family Scaphiopodidae including two genera, Scaphiopus Holbrook (1836) and Spea Cope (1875).

The purpose of this study is a review of the species and/or subspecies of those taxa referable to the genus Spea; included are S. bombifrons Cope, S. intermontana Cope, and S. hammondii Baird. It is not the intent of this study to become involved in further justification of the family or a review of the generic taxa. This has been repeatedly discussed by numerous authors (Cope 1875, 1889, Tanner 1939, Zwiefel 1956, TiHen 1960, Holman 1963, Kluge 1966, Estes 1970, Brown 1976, Tanner 1989, and others).

The fossil record for the genus Spea, as reported by Holman (1963), TiHen (1960), Kluge (1966), Estes (1970), and others, indicates that Spea has been an identifiable group in the Great Plains of central North America since the Lower Miocene (S. neuter, Kluge 1966) and the Early Oligocene (Eopelobates grandis, Zwiefel 1956). If we accept the conclusions reached by Kluge (1966) that the dichotomy between Scaphiopus and Spea may have occurred as early as Late Miocene and has apparently continued to differentiate to the present, and since we can recognize each genus morphologically and can also delineate distinct differences in the life history of each, then it seems logical to recognize each generic group as distinct rather than to retain them in an inconsistent taxonomic relationship.

I consider the skull of Scaphiopus, with its dermal plates, to be primitive. This character is, I believe, more than a slight difference when compared with the skull of Spea. The loss of the dermal plates in Spea is considered a derived character. Obviously there are similarities that relate Scaphiopus and Spea, similarities that place them both in the North American branch of the family Pelobatidae. Based on the distinct differences in the skulls and other morphological, life history, and ecological differences discussed by Bragg (1944), Blair (1955, 1956), Zwiefel (1956), and Kluge (1966), I am persuaded to accept Spea as a genus rather than to continue dealing with a Scaphiopus-Spea complex (Tanner 1989).

The skull and external characteristics are well documented for bombifrons and intermontana. There is doubt as to whether hammondii has been adequately examined, particularly with regard to the skull characters and their relationships to the populations occurring in areas in southwestern United States and western and southern Mexico. Tanner (1989) demonstrated that the skull characters of Spea hammondii occur in a large series of populations, including those from southwestern United States and northwestern Mexico. By including those populations having a large frontoparietal fontanelle in one species...
(hammondii) and recognizing the external and ecological variables as subspecific characters, some systematic order can be realized.

*Spea hammondii* does not have the skull modification seen in *bombifrons* or *intermontana*. In all specimens examined the interorbitals are narrow without enlargements, and with a large interorbital fontanelle between them. Thus, in adults the area between the orbits is flat, or nearly so, and is covered by skin and layers of glandular and connective tissue that serve as a covering over the fontanelle and the cerebral hemispheres that lie below and are visible when the fontanelle is exposed. Two variations were noted. In a specimen from Sonora (UAZ 39069, Fig. 1), a small, circular, flattened bone is fitted into the enlarged posterior part of the fontanelle. It is attached to the interorbitals by fine strands of connective tissue. In specimens from California and Baja California the fontanelle is so positioned as to extend to or beyond the posterior edge of the orbits, a condition not often observed in other populations of *hammondii* nor in *bombifrons* or *intermontana* (Fig. 2).

In spite of these modifications, *hammondii* has retained a simplified skull that implies a primitive condition with few derived characters. If *hammondii* represents the primitive species in the genus *Spea*, it becomes more difficult to assign a population or subspecies as the rootstock of the species and of the genus.

Skull characters (i.e., the relationships of the frontoparietal fontanelle, its size and position) do not vary greatly within the wide range sampled (western Texas west to southern California and south in the adjoining Mexican states of Chihuahua, Sonora, and Baja California). Single skulls from populations in Nuevo León, Morelos, and Oaxaca also appear to be part of the *hammondii* assemblage. On the bases of variations in the frontoparietal area of the skull, three species of the genus *Spea* are recognized: *hammondii*, for its narrow, unmodified interorbitals that are separated by a large interorbital fontanelle (Fig. 3); *bombifrons*, for its enlarged boss on the anterior of each interorbital, a reduced interorbital fontanelle posterior to the enlarged bosses, and a groovelike channel between the bosses extending as a depression between the nasals (Fig. 4); *intermontana*, for a general enlargement of the interorbitals without a boss, with the interorbitals arched medially, and with thin bone extending mesially to reduce or eliminate the fontanelle (Fig. 5). In both *bombifrons* and *intermontana* the interorbital fontanelle is reduced in size anteriorly, leaving a smaller fontanelle.

There is also an additional feature that is characteristic of the species of the genus *Spea*, in that the spade is wedge-shaped. This is in contrast to members of the genus *Scaphiopus* in which the spade is sickle-shaped. The basic ground color for the genus *Spea* is a dark gray with a tinge of dark greenish yellow (for color patterns and comparisons see Stebbins 1955, plate 10). In some specimens there may be light stripes or spots on the dorsum, but the pattern is not a reticulation as is observed in most specimens of *Scaphiopus couchii*. There

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*Fig. 1. Spea hammondii stagnalis* Cope (or an undescribed subsp.): a, 3 mi (hwy rd) N Fronteras, Sonora, Mexico, UAZ 39069 (photo of dorsal view of skull); b, interorbitals and fontanelle complex enlarged to show separate thin bone in posterior part of fontanelle.

*Fig. 2. Spea hammondii hammondii* Baird: a, San Diego, San Diego Co., BYU 2141 (dorsal view of skull); b, enlargement of interorbitals, adjoining bones, and their position to each other and the orbit. Note that the interorbitals are flat, without bosses of bony protuberances extending into the fontanelle.
is an indication that S. couchii, whose distribution overlaps the distribution of bombifrons and hammondii, is larger in the adult S-V length. This has been my observation from specimens of both genera collected in Chihuahua, Mexico. Certainly, in our field surveys, we have had no difficulty differentiating Spea specimens from Scaphiopus couchii, based solely on size and color pattern.

It may not be possible to differentiate all specimens of Spea to their proper taxon by external examination. This is particularly the case in some subspecies of hammondii. Perhaps, for this reason, Cope (1875) used skull characters in separating the species in the genus Spea. The species S. bombifrons will be dealt with briefly as it is taxonomically well established and its distribution indicated by Conant (1975) and Stebbins (1985). Most of this study will deal with the species hammondii and intermontana. Within these species an attempt is undertaken to compare skull characters, particularly from the dorsal aspect, to visualize variation in the populations that occur in numerous valleys throughout much of western United States and Mexico.

The species Spea bombifrons, with an enlarged boss at the anterior of the interorbitals, is uniquely different from all others in the genus (Fig. 4). Our collecting records indicate that it prefers a grassland habitat in contrast to hammondii and intermontana, both having been found in a variety of habitats. Although its geographical range is primarily in the grasslands of the Great Plains, it is now found in suitable habitats in eastern Arizona, most of New Mexico, and in the San Juan River basin of southern Colorado and southeastern Utah.
Specimens examined throughout this wide area show a very similar series of skull characters. This is in contrast to my findings in hammondii.
The wide-ranging Spea hammondii has modifications not only in the skull characters (Fig. 3) but also in its external anatomy and life history. A brief discussion of the above characters will aid in understanding the systematics of S. hammondii. 

Skulls examined from specimens representing populations of hammondii in Mexico (Nuevo León to Baja California and south to Oaxaca) and southwestern United States (Texas west to California) all have a large interorbital fontanelle, with the interorbitals narrow, relatively flattened dorsally, and without modifications (Fig. 3). Size and position in relation to the orbits vary. In the California and Baja California populations the fontanelle may extend beyond the posterior margins of the orbits. In other populations (Arizona and New Mexico, for example) the fontanelle is shorter, usually not extending beyond the posterior margins of the orbits. Although the size of the fontanelle varies with the size of specimens, its position in relation to the orbits usually does not.

The development of a flattened disc of bone in the posterior of the fontanelle in one specimen from a population in Sonora (UAZ 39069) may indicate a strengthening of the dorsal skull area as has occurred in both bombifrons and intermontana. This may also be a further indication that hammondii is the primitive group in the genus Spea.

The species Spea hammondii has extensive population segments, many of them isolated geographically as well as ecologically. Under these conditions it is not surprising that subspecies can be recognized. It has not been possible to examine the numerous Mexican populations in the eastern states (Nuevo León) and populations south of Durango, and to this extent this report is incomplete. This report is a preliminary study involving limited data from widely dispersed populations. A far more detailed study, including added field data and considerably more morphological and ecological data, would be necessary to fully understand the genus Spea. A comparison of the external anatomy of specimens from the mountains of western Chihuahua with those in south central Mexico suggests that additional subspecies may exist in Mexico. However, materials available have provided data that suggest the following subspecies of the species S. hammondii be recognized.

Spea hammondii hammondii Baird
Hammond’s spadefoot

Diagnosis.—Interorbitals narrow, widely separated by an enlarged fontanelle; fontanelle usually extending beyond the posterior margin of orbits (Fig. 2); dorsal tubercles small, not numerous on back; large, S-V 55–65 mm; adapted to a late-winter or early-spring (March) breeding season to correspond with the rainy season.

Distribution.—In the central valleys of California and south into northern Baja California. This subspecies does not extend into the deserts of southeastern California and is separated from the subspecies in Arizona by extensive deserts.

Spea hammondii stagnalis Cope
Desert spadefoot

Diagnosis.—Interorbitals narrow, fontanelle to but usually not beyond the posterior margin of the orbits (Fig. 3); dorsal tubercles usually small and widely separated; smaller, S-V 50–55 mm; color with light spots or irregular dorsolateral stripes; adapted to breeding when late-spring or summer rains occur, varying with the occurrence of rainstorms in various areas from May to September.

Distribution.—In central and southern Arizona south of the Mogollon Rim; south into central Sonora; east into New Mexico, and north to include the San Juan River basin of New Mexico, southwestern Colorado, extreme southeastern Utah, and a corner of northeastern Arizona; east into western Texas and presently including isolated populations in Nuevo León, Mexico; south from New Mexico into Chihuahua and Durango, Mexico. In the Mexican states of Chihuahua and Durango populations occur in valleys along the eastern edge of the Sierra Madre, with a distribution in a relatively narrow belt between the mountains to the west and the eastern deserts.

Spea hammondii multiplicata Cope
Mexican mountain spadefoot

Diagnosis.—Interorbitals narrow, fontanelle large, usually not reaching posterior margins of orbits (Figs. 3d–g) (the skull structures for most populations south of Durango were not examined); dorsal tubercles greatly enlarged and numerous on dorsum of body;
color usually a uniform dark greenish brown; smaller, S-V 50–55 mm; adapted to breeding during the late-spring and summer rains (this varies from south to north and with elevation).

**Distribution.**—Occurs in the high mountains and plateaus of western Chihuahua and Durango. Populations south of these states appear to be a part of this subspecies. The range may, as noted by Smith and Taylor (1948), extend into central and southeastern Mexico.

*Spea intermontana* Cope
Great Basin spadefoot

**Diagnosis.**—Interorbitals enlarged, arched medially, and convex between orbits; interorbital fontanelle greatly reduced by mesial extensions of the interorbitals. In some individuals only a small remnant of the fontanelle remains, and it is always the posterior part. No enlarged boss is present. There is a convex enlargement of the interorbitals near the orbits that produces rainbowlike arches between the orbits (Fig. 5). Between the interorbitals is a concavity with variable-sized fontanelles (this depends on the individual and population) that is filled with glandular and connective tissue. In adults this may appear as a boss between the orbits, but it is an entirely different structure from that of *bombifrons*. Larger, S-V 55–60 mm; color pattern similar to that of *bombifrons* and *hammondii*. Greenish or dark gray and with dorsolateral light spots or irregularly shaped stripes. Breeding seasons occur during the summer when rains are adequate.

**Distribution.**—West of the Colorado River in Utah and northern Arizona, and in the river valleys of the high plateaus that drain east into the Colorado River and west into the Great Basin. Primarily in the cold desert valleys of the Great Basin of western Utah, central and northern Nevada, southern Idaho, and Oregon, and in the Columbia River basin of western Idaho, southeastern Oregon, eastern Washington, and southeastern British Columbia.

**Remarks.**—The Colorado River appears to divide the ranges of *S. intermontana* from *S. hammondii* in Utah and northern Arizona. Tanner (1939) included San Juan County, Utah, in the range of *intermontana*. Specimens examined east of the river in southeastern Utah (Montezuma Creek, SE of Blanding, Utah) are *hammondii* and have the same skull characters as those examined from San Juan County in northwestern New Mexico. Indications are that the Colorado River and perhaps the desert areas along both sides have served as barriers to these species.

Populations west of the river from Kane County north to Uintah County show varying degrees in the development of the interorbitals. In all specimens examined there are two features that characterize these populations, and the species *intermontana*. First, the interorbitals are arches dorsally, producing a convex structure when viewed laterally. The interorbitals are without a distinct boss. Second, there are varying degrees of bone and associated connective tissues extending into the interorbital fontanelle. In all specimens examined the reduction in the size of the fontanelle is more apparent anteriorly, with the posterior part being reduced slowly and the last area to be closed. The series of figures show the skull structures from north to south in the environs of basins draining east into the Colorado River and west into the Great Basin (Fig. 5); although the basic skull characters are present, there is a north-to-southcline in which a progression of fontanelle closure is obvious.

Those specimens examined, from the Great Basin areas west of the Colorado River and from Idaho, all have the arched interorbitals and either a thickening of the interorbitals or thin extensions of bone into the fontanelle. In either case the size of the fontanelle is reduced and the dorsal aspect of the skull more massive when compared with the same structures in *hammondii*.

**Material Examined**

*Spea bombifrons.*—Arizona: Cochise Co., Chiricahua Mt, BYU 8932; Lupton, BYU 8829; Apache Co., Navajoland, Many Farms, LACM 127299. Kansas: Douglas Co., 2 mi NE Lawrence, KU 153450; Meade Co., Rexroad Ranch, KU 22145, 22170; Morton Co., Rolla, KU 7180; Rush Co., Nekoma, KU 35030. New Mexico: San Juan Co., 2 mi NW Blanco, UNM 2843–51; Valencia Co., UNM 37883, 37893. Chihuahua: Colonia Dublán, BYU 415; outskirts Cd. Chihuahua, BYU 10440–44; 13 mi E Rancho Flores Magon, BYU 13962–66.
Spea hammondii hammondii.—CALIFORNIA: San Joaquin Co., Corral Hollow Rd, UC 68255, 176016; Corral Hollow Rd (Hwy J–2) 5 mi W to 5 mi E Alameda–San Joaquin Co. line, UC 145191–92; Corral Hollow, 30 mi E San Joaquin Co. line, UC 145187; Corral Hollow Rd, KU 176016; Corral Hollow nr Livermore, BYU 37055; Madera Co., San Joaquin Range Expt. Station, UC 77404; San Joaquin Range, nr O’Neals, UC 64186, 77041–42; San Diego Co., San Diego, BYU 2141; Baja California Norte, El Rosario, BYU 34551; Punta Bunda, BYU 2761.

Spea hammondii multiplicata.—CHIHUAHUA: Chihuhiuchupa, BYU 14388–402, 14404–13, 15391–409; 11.1 mi NW Ypemopa, UAZ 34818; 2 mi S Creel on rd to La Buja, BYU 15598, 17081; Cerocohuhi, BYU 15502–03. MORELLO: 3 km W Cuauixico, KU 84590. NUEVO LEÓN: 33 km S San Roberto, KU 117350. OAXACA: 6 km SE Oaxaca, KU 117345; Mexico, San Juan Teotihuacan (the Citadel), BYU 13195–96.

Spea hammondii stagnalis.—NEw MEXico: Eocene Plateau, northwest, USNM 8653, 25335 (cotypes); McKinley Co., 7 mi N 3.5 mi E Crownpoint, UNM 3236, 24141; Rio Arriba Co., 42 mi N Espanola (US Hwy 84), UNM 24401; 0.5 mi S Cuba (NW Hwy 197), UNM 24360; Sandoval Co., 7.2 mi NW Blanco, UNM 2843–47, 2849, 2850–51; San Juan Co., 17.6 mi N San Juan, McKinley Co. line, UNM 18957–62, 24132–40, 24150, 24155–56, 24160–61; 0.5 mi W Kirtland, UNM 47613–14. San Juan Co., 3 mi S Espanola, UNM 24371, UNM 38062–63 (no locality), 30 mi W Los Lunas, Hwy 6, UNM 15992, 25 mi W Los Lunas, UNM 15989, near Grants, KU 7183; Valencia Co., 1 mi E Rio Grande Gorge Bridge, UNM 13576–77; Taos Co., near Inscription Rock, KU 7177. ARIZONA: Apache Co., Navajoland, Many Farms, LACM 127298; Cochise Co., Chiricahua Mt, BYU 8839, 8939. TEXAS: Brewster Co., BYU 2767, KU 10276, Benton, BYU 2149, 2764. UTAH: San Juan Co., Montezuma Creek, BYU 18460–61. CHIHUAHUA: 12 mi SE Babicara, BYU 14453–67, 15571–80; 10 mi W San Francisco del Oro, BYU 15677; Colonia Dublan, BYU 415; 0.3–18.3 mi SE Madera, UAZ 34649–51, 34656–61, 34663–64, 34666–68, 35040; Ypemopa, UAZ 34652–55, 34804–13; 3.8 mi SE Ypemopa, UAZ 34814; 6.2–6.6 mi NW Ypemopa, UAZ 34815–17, 35401; 2 mi S Santa Clara, MVZ 70622–45; 1 mi S 0.5 mi E Santa Clara, MVZ 72790; 5 mi N Cerro Campana, MVZ 72791; Ojo de Laguna, MVZ 72792; Arroyo Mesteno (Sierra del Nido), MVZ 72877–89. DURANGO: 18.8 mi N Cd. Durango, BYU 15513–27, 15835–37; 10 mi NE Cd. Durango, BYU 10436–39. SONORA: 3 mi (hwy rd) N Fronteras, UAZ 39069; 0.6 mi (Mex. Rd 2) E jet Janos-Cavarea and Agua Prieta Rds, UAZ 39065; 34.1 mi S Nogales, BYU 23990.

Spea intermontana.—ARIZONA: Coconino Co., Pleasant Valley, Kaibab Forest, BYU 45. CALIFORNIA: Mono Co., Hot Creek, S Mono Lake, BYU 21975–82, on Hwy 165 0–10 mi E jet with Hwy 295, UC 145204. IDAHO: Ada Co., Kuna Cave, BYU 44; Butte Co., A.E.C. Test Site, Arco, BYU 30221–25, 30338, 30341, 30651–76; Canyon Co., 45 mi S Nampa on Hwy 45, BYU, 40684–89; Fremont Co., Eggin, BYU 8177. OREGON: Linn Co., Sweet Home, BYU 31440–44 + 18 untagged specimens. UTAH: Beaver Co., Beaver, BYU 12764–65; Wah Wah Mts, Pine Grove Canyon Reservoir, BYU 36924–27; Box Elder Co., Rossette, BYU 13037; Carbon Co., Helper, BYU 2055, 2058–63, 2070, 2073–74, 2800; Price, BYU 2169 + 30 tadpoles; Daggett Co., Bridgeport, BYU 14171–72, 14181; 2 mi S Linwood, BYU 14180. Duchesne Co., Duchesne, BYU 8085–87. Emery Co., Green River, BYU 47; 18 mi SW Green River, BYU 47, 787. Garfield Co., jet Boulder Creek–Escalante River, BYU 2017, 2022, 2263, 2772; 10 mi S Coyote Gulch, BYU 16679; 10 mi S Escalante, BYU 49, 50, 785; Henrieville, BYU 12921; 15 mi NW Hite, Hag Springs, BYU 16647, 22105; Pasey Lake, BYU 52; Steam Creek below road at Lakes, BYU 1936, 1958, 1968, 1970–71, 1973, 1975, 1977–79, 2768. Juab Co., 5 mi W Cherry Creek, BYU 9074–76 + 5 untagged specimens; Cherry Creek, BYU 9071; Ekker Ranch, W. Jericho, BYU 9422, 9431–36; Jericho Pond, BYU 9424, 9428–30, tadpoles no. 38382 with 33 specimens + 2 young toads; Playa Lake, 9 mi E Callao, BYU 14803–07, 14809. Kane Co., Crossing of the Fathers, BYU 14724, 14958, 16716; Grosvenor Arch, BYU 41085–87; Navajo Wells, 14 mi W Kanab, BYU 23608–13 + 53 untagged specimens; Orderville, BYU 477, 1638, 1950, 2165; Paria River, BYU 12501; Willow Spring Tank, BYU 51, 55, 786, 788–89, 798–800, 8714. Millard Co., Flowell,
BYU 23483–84, 10 mi S Gandy, BYU 46, 783–84; Salt Lake Co., Draper, BYU 23332–33. Sunpete Co., Indianola, BYU 2977. Tooele Co., Dog Area, Dugway Proving Grounds, BYU 14790–91, Government Creek, Dugway Proving Grounds, BYU 14789; Dugway Proving Grounds, 14801–10. Uintah Co., mouth of Brush creek, BYU 545. Utah Co., Cedar Valley sand dunes, 1 mi S Fairfield, BYU 2864; Orem, 400 S and U.P. Railroad, BYU 8340, 8342, 8344; Palmyra, BYU 23583, Provo (river bottoms), BYU 14801–02, Salem Pond, BYU 32074; Spanish Fork, BYU 23480. Wayne Co., Torrey, BYU 16557. Washington Co., Berry Springs, 3 mi W Hurricane, BYU 3720–21, 3732, 3736–38; Ivans Bench, BYU 9843. Ivans Reservoir, BYU 23505–49; Rockville, BYU 11315; St. George, BYU 2775, 5657; Terry’s Ranch, BYU 12818; Zions Natl. Park, BYU 43, 780, 2773.

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