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# Vocal Sac Variation among Frogs of the Genus Rana from Western North America

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Vocal sac condition of 460 frogs was examined by dissection for five western North American *Rana (Rana boylii* group sensu Case, 1978): *R. aurora* (N = 280), R. boylii (N = 24), R. cascadae (N = 113), R. muscosa (N = 22) and R. pretiosa (N = 21). R. boylii consistently exhibits small, paired subgular sacs, whereas R. muscosa and R. pretiosa lack vocal sacs. R. cascadae typically lacks vocal sacs, whereas R. aurora may have no vocal sacs, a single asymmetric vocal sac, paired sac rudiments or paired vocal sacs. R. aurora exhibits a striking step-cline in vocal sac condition: northern populations lack vocal sacs, southern populations have small, paired subgular sacs and frogs with intermediate vocal sac conditions occur mostly in the 480 km between these northern and southern population assemblages. The two most common vocal sac variants within R. aurora (an absence of vocal sacs and paired subgular sacs) are congruent with available data that suggest trenchant morphological and behavioral differences between the two previously defined subspecies, R. a. aurora and R. a. draytonii. R. aurora, as currently defined, may actually be two species in secondary contact. Reduced vocal sac apparatus among members of the R. boylii group is correlated with their weak vocalizations.

VOCAL sac characteristics are important in anuran systematics because they can exhibit significant variation between related species (Boulenger, 1886; Tyler, 1971), but rarely vary intraspecifically (Liu, 1935). Although descriptions exist (Table 1), vocal sacs among *Rana* species endemic to western North America (*R. boylii* group sensu Case, 1978; *R. aurora, R. boylii, R. cascadae, R. muscosa* and *R. pretiosa*) have not been studied comprehensively. Boulenger

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Current taxon name	Author (A)	Named used by (A)	Vocal sac condition described by (A)
R. aurora aurora	Boulenger (1920)	R. aurora	absent
	Liu (1935)	R. aurora	absent
	Stebbins (1966)	R. aurora aurora	single or absent
R. aurora draytonii	Boulenger (1920)	R. draytonii	absent
	Liu (1935)	R. draytonii	paired subgular external
	Stebbins (1966)	R. aurora draytonii	single or absent
R. boylii	Boulenger (1920)	R. boylii	internal
	Liu (1935)	R. boylii boylii	paired subgular internal
	Zweifel (1955)	R. boylei	paired subgular internal
R. cascadae	Slater (in Wright and Wright, 1949)	R. cascadae	lacks external
R. muscosa	Liu (1935) Zweifel (1955)	R. boylii muscosa R. boylii sierrae R. muscosa	absent absent absent
R. pretiosa	Boulenger (1920)	R. pretiosa	absent
	Liu (1935)	R. pretiosa	paired lateral internal
	Svihla (1935)	R. pretiosa pretiosa	poorly developed

 TABLE 1. REPORTS OF VOCAL SAC CONDITION AMONG MEMBERS OF THE Rana boylii GROUP (SENSU CASE, 1978).

(1920) described R. aurora aurora, R. a. draytonii and R. pretiosa as lacking vocal sacs and R. boylii as possessing internal sacs. Later, Liu (1935) refined vocal sac nomenclature, describing R. boylii as having paired, subgular internal sacs with round sac openings and included R. muscosa among the forms lacking vocal sacs; Zweifel (1955) corroborated Liu's observations of vocal sac condition for these two taxa. However, Liu contradicted Boulenger (1920), describing R. a. draytonii as having paired, subgular external vocal sacs with round openings. Stebbins (1966) noted that R. aurora could have a single vocal sac. Liu (1935) also contradicted Boulenger in describing R. pretiosa as having paired, lateral internal vocal sacs with round openings and Svihla (1935) further obscured its description, indicating that R. pretiosa's vocal sacs were poorly developed. Slater (in Wright and Wright, 1949) noted that R. cascadae lacked external vocal sacs, whereas Case (1976) listed R. cascadae as lacking vocal sacs.

Apparent contradictions in the vocal sac condition of *R. aurora* and *R. pretiosa* and the indeterminate description of vocal sac condition provided for *R. cascadae* (Table 1) indicate that vocal sac conditions for several taxa within the *R. boylii* group are poorly known. We could not verify the vocal sac descriptions of previous authors except that of Zweifel (1955) because the repository collections or specimens examined were not listed. Significant behavioral, biochemical, chromosomal and morphological variation among populations of *R. aurora* (Hayes and Miyamoto, 1984; Green, 1985b) suggested that vocal sacs might provide additional data useful in understanding variation within that species. For these reasons, we examined vocal sac condition of frogs belonging to the *R. boylii* group.

### MATERIALS AND METHODS

Initially, we dissected at least 20 adult males selected from throughout the known geographic range of each of the five western ranid taxa. We examined additional specimens of R. aurora and R. cascadae because of the variation in vocal sac condition we encountered initially in these two taxa. We used published data on adult body sizes (SVL) as an initial guide for selecting males for dissection (R. aurora: Hayes and Miyamoto, 1984; R. boylii and R. muscosa: Zweifel, 1955; R. cascadae: Briggs and Storm, 1970; R. pretiosa: Morris and Tanner, 1969; Licht, 1975), but gonads were examined to determine unequivocally sex and maturity. Muscle nomenclature follows Tyler (1971). Specimens examined are listed in the appendix.

We reflected the skin of the throat to expose



Fig. 1. Diagrams showing superficial throat musculature and accessory structures of *Rana aurora* lacking vocal sacs with an undifferentiated interhyoideus muscle (left; USNM 39783—Mapleton, Douglas County, Oregon) and possessing paired, subgular sacs showing differentiation of the interhyoideus (right; MVZ 19060—1.6 km southeast Placerville, El Dorado County, California). Labeled muscles are the intermandibularis (a) and the interhyoideus (b). Stippled areas are aponeuroses.

the superficial musculature. The exposed intermandibularis and interhyoideus muscles were then reflected with a parasagittal incision to the right side of the median raphe, revealing any vocal sac on that side. The left side was examined by separating both muscles from their attachments and lifting them from the posterior edge of the interhyoideus. The floor of the mouth was examined for vocal sac openings, which, when present, were probed for their connection with the sacs.

Observations of vocalizing male R. a. draytonii were made during Feb. 1980 and Jan. 1981 at sites in San Luis Obispo and Santa Barbara Counties, California.

#### RESULTS

R. muscosa (N = 22) and R. pretiosa (N = 21) consistently lack vocal sacs and sac openings, as does R. cascadae, except for two individuals (MVZ 26765—Tumalo Creek, Deschutes County, Oregon; CAS 47716—Hoh River, near Fischers Ranch, Jefferson County, Washington) which have paired sac openings and sac rudiments. Examination of 93 additional individuals failed to reveal further variation within R. cascadae (N = 113). R. boylii (N = 24) consistently has small, paired subgular vocal sacs and openings. R. aurora either lacks vocal sacs entirely (48%; N = 135), or has small, paired, subgular vocal sacs and openings (42%; N = 117; Fig. 1); some R. aurora have a vocal sac apparatus that appears intermediate between the above conditions (10%; N = 28). Frogs from the southern part of the range (northern Baja California, Mexico, to the outlet of San Francisco Bay and inland to at least the American River drainage, California; N = 97) have the paired vocal sac condition, whereas frogs from north of the Klamath River system, Del Norte County, California, through British Columbia, Canada (N = 113), except for three individuals (AMNH 174—Seattle, Washington, and two from Coos County, Oregon [LACM 1660-Coos Head; CAS 29488—Myrtle Point] lack vocal sacs (Fig. 2). R. aurora from the intervening 480 km often exhibit vocal sac conditions intermediate between those found in northern and southern populations (Fig. 3). These intermediate individuals have either one asymmetric, rudimentary vocal sac and opening (either on the right or left side), or have two small sac rudiments with openings. Some R. boylii (N = 7) over 55 mm SVL and many R. aurora (N = 71) with paired subgular sacs have either loose, bag-like skin or indistinct folds of skin over the region of the vocal sac.

Vocal sacs in *R. aurora* (when present), *R. boylii* and the two aberrant *R. cascadae* are similarly positioned. In *R. boylii* and southern populations of *R. aurora*, vocal sacs of preserved frogs are small, extending posteriorly beyond the interhyoideus and anteriorly to beneath the posterior edge of the intermandibularis. Even in frogs with the most expanded vocal sacs, these rarely extend medially beyond the lateral borders of the underlying geniohyoideus. In individuals having distinct vocal sacs, the interhyoideus muscle overlying the sacs is differentiated so that fibers are incorporated into the vocal sac wall (Fig. 1), a condition ap-



Fig. 2. Geographic distribution of vocal sac variants among northern (left map) and southern (right map) populations of *Rana aurora*. The symbols indicate the vocal sac condition; the intermediate category includes all variants excepting the paired and absent conditions. See text for details of the descriptions of various vocal sac conditions. Symbol size denotes the numbers of individuals examined: small circle = 1 individual, intermediate circles = 2 individuals, large circles = 3 or more individuals. Scale is identical on both maps.

parent even in frogs preserved without distended sacs. In frogs preserved with distended vocal sacs, the anterior and posterior fibers of the interhyoideus pass dorsally to the sacs before their mandibular insertion, which makes the vocal sacs appear as though they protrude through that muscle. However, in no case did we observe posterolateral or supramandibular extensions of the interhyoideus, conditions associated with laterally inflating vocal sacs (Liu, 1935; Tyler, 1971; Drewes, 1984). Among frogs having rudimentary vocal sacs (some R. aurora and two R. cascadae), we found little differentiation of the interhyoideus and the rudimentary sacs did not extend beyond the muscle's posterior border.

In all species with vocal sacs present, their openings are small, round and inconspicuous, but may appear slit-like because they are often hidden by tissue folds in the floor of the mouth. The openings are located lateral to the posterior margin of the tongue, penetrating the floor of the mouth just lateral to the anterior cornua of the hyoid. The borders of vocal sac openings are often thickened and the openings constricted, suggesting a sphincter. We heard *R. a. draytonii* vocalize in the field 86 different times. On 31 of these occasions, we observed vocalizing males (Hayes and Miyamoto, 1984); vocalization was always performed in air, floating on the water. All vocalizations were weak, audible at up to 10 m in the absence of other noise and barely audible if one were immediately adjacent to vocalizing frogs when co-occurring *Hyla regilla* were calling.

## DISCUSSION

We discuss the taxa whose vocal sac condition did not vary significantly and compare these data to discrepancies in the literature; we then address the problem of vocal sac variation within *R. aurora*. A clarification of vocal sac terminology is warranted because we have avoided the conventional terms used to describe the condition of the skin overlying the vocal sacs. External sacs have visibly modified overlying skin, whereas internal sacs lack such modification (Liu, 1935). Though he continued to use these terms, Liu considered them misleading because in both conditions, the vocal sacs are internal. Liu defined *R. boylii* as having internal sacs, whereas we found that differentiation of the vocal sac skin in *R. boylii* is variable, as it is in individuals of *R. aurora* possessing distinct vocal sacs. Skin differentiation, presumably a function of age, was more evident in larger frogs, but may vary seasonally according to reproductive condition (Inger, 1956). This may explain the variation in skin condition we observed among larger frogs. Thus, because a single condition of the skin overlying the vocal sacs is not a definitive character, we simply noted external skin variation within each taxon and whether or not sacs were present.

The *R. boylii* and *R. muscosa* we examined fit previous descriptions of these species having paired subgular vocal sacs and no vocal sacs, respectively and we found no obvious intraspecific variation. Except for two individuals that had rudimentary paired, subgular vocal sacs and openings, individuals of *R. cascadae* also lacked vocal sacs. Case (1978) found unexplained electrophoretic variation within *R. cascadae*, but the disjunct geographic location of our two aberrant individuals and the lack of any obvious correlation with electrophoretic or other data suggest that they are anomalous.

Consistent with Boulenger (1920), all R. pretiosa we examined lacked vocal sacs or vocal sac openings. Liu's (1935) contradictory report of paired lateral vocal sacs in R. pretiosa is puzzling and remains unverifiable because he presented no list of specimens examined. The situation was complicated further by Svihla (1935), who stated that vocal sacs in R. pretiosa were poorly developed. Liu's "R. pretiosa" may have been a member of the R. pipiens species complex (which have paired, lateral vocal sacs), because some members of this complex look similar to R. pretiosa. Svihla's questionable analysis was not based on dissections; his description of loud vocalization by R. pretiosa contradicts other observations (Turner, 1958; Licht, 1969b; Morris and Tanner, 1969).

Of the species we examined, only *R. aurora* exhibits significant variation in vocal sac condition. We observed all the vocal sac conditions (absent, single and paired) noted by previous investigators of *R. aurora*; we found that the distribution of vocal sac variants exhibits a clear geographic pattern: northern and southern populations each approach uniformity in vocal sac condition over a latitudinal range of nearly 1000 km (Fig. 2) and the intervening 480 km has a complex distribution of vocal sac variants (Fig. 3). Frogs from the southern part of the



Fig. 3. Geographic distribution of vocal sac variation within northern California populations of *Rana aurora*. Denotation of symbols and symbol sizes are as in Fig. 2.

range have the paired condition originally described by Liu (1935), whereas northern frogs have the condition indicated by Boulenger (1920), no vocal sacs. *R. aurora* from the intervening 480 km include individuals with the single (though asymmetric) vocal sac as noted by Stebbins (1966). That certain Washington frogs were considered by Boulenger (1920) to be *R. a. draytonii* may explain the contradictory report of this taxon lacking vocal sacs (Table 1). Furthermore, *R. aurora* from Nevada, descendants of transplanted California frogs (Linsdale, 1940) identified biochemically as *R. a. draytonii* (Green, 1985a), have paired vocal sacs.

Outside the zone of vocal sac variation, the vocal sac condition of northern and southern populations is congruent with the markedly different male vocalization behaviors and egg deposition patterns known for some of these same populations (Hayes and Miyamoto, 1984). The presence of vocal sacs corresponds with aerial vocalization in southern populations, whereas in northern populations, the absence of vocal sacs corresponds with underwater vocalization. Vocal sacs are well known to amplify calls made in air (Bogert, 1960), but may not be an advantage to vocalization underwater (Wells, 1977).

The zone of variation in vocal sac condition coincides with northern California river systems that parallel the coast for most of their length (Fig. 3), so river corridors may have allowed population interchange along a north-south axis. The close relationship between populations of the fishes, Catostomus occidentalis and Lavina symmetricus, occupying the Russian, Eel and Mad rivers and populations occupying the Sacramento-San Joaquin river system, has been reason to postulate their entry into the former three river systems from the Sacramento-San Joaquin through the Clear Lake basin (Moyle, 1976). The Russian, Eel and Mad river systems also may have served as a route of exchange between populations of R. aurora occupying a north coastal position (lacking vocal sacs) and those occurring in the Sacramento-San Joaquin river system (possessing paired vocal sacs). The distribution of frogs suggesting this pattern differs from that of the aforementioned fishes by including the Klamath-Trinity river system (Fig. 2).

Human-aided movement of frogs may have complicated the pattern of vocal sac variation within R. aurora. Extensively exploited commercially in California prior to 1900 (Jennings and Hayes, 1985), R. aurora collected from remote sites were transported to "frog farms," really just depots where frogs were held temporarily in ponds prior to their export to major trade centers such as San Francisco (Lockington, 1879; Collins, 1892; Storer, 1933). By 1899, commercial froggers in California had increased their range to include Humboldt County (Jennings and Hayes, 1985). Humboldt County frogs transported by land to San Francisco had to be moved across nearly the entire breadth of the zone of vocal sac variation and mixing with the intervening populations may have occurred.

The broad zone of heterogeneity in vocal sac condition within *R. aurora* makes difficult any explanation of the origin of the geographic pattern. Zone size alone precludes its being attributed simply to anomalous variation. However, congruence between vocal sac conditions of northern and southern population assemblages and other characteristics distinctive to these populations provides an hypothesis of its origin: two well-differentiated, historical entities, approximately corresponding to the subspecies R. a. aurora and R. a. draytonii defined by Camp (1917), are now subsumed under the name R. aurora. If this hypothesis is correct, the zone of variation may represent a region of secondary contact perhaps altered by human agency. We suggest this hypothesis for two reasons. First, available data suggest discordant variation within individuals. Discordant recombination of parental character states in hybrid individuals has been suggested as perhaps the only unambiguous phenotypic evidence for the hybrid origin of samples in which the putative parental taxa are rare (Sweet, 1984). The R. aurora we examined from the Klamath-Trinity river system have an adult body size (SVL = 42.5-67.0 mm; N = 27) that does not differ significantly from that of northern frogs, but is significantly smaller than that of larger southern frogs (Mann-Whitney U; P < 0.025 for both; Hayes and Miyamoto, 1984). Yet, 10 of these individuals have paired vocal sac rudiments, one has a single, asymmetric vocal sac on the right side and the remainder have paired, subgular sacs similar to those we observed in southern populations. Although the small size of other samples taken from the zone of vocal sac variation does not justify detailed discussion, many suggest discordant recombination between the vocal sac and body size character states indicative of the putative northern and southern parental taxa. Second, the asymmetric, single vocal sac condition, albeit rare in our examinations (N = 3), is unreported as a vocal sac condition defining any species within the genus Rana. Among the over 100 Rana species for which vocal sac condition is known (Liu, 1935; Zweifel, 1955), all have paired openings and of the species having a single sac, it is symmetric or median. This suggests that the alternative invoking the presence of a third taxon with the asymmetric, single vocal sac condition is unlikely. Such an alternative also leaves unresolved the status of the remaining individuals with symmetric "intermediate" vocal sac conditions.

Vocal sac data suggest a close relationship among members of the *R. boylii* group (sensu Case, 1978). Members of the group have limited development of the vocal sac apparatus; four taxa (*R. a. aurora, R. cascadae, R. muscosa* and *R. pretiosa*) lack vocal sacs and the remaining two (*R. a. draytonii* and *R. boylii*) have small, paired subgular sacs. Except for the dubious report by Svihla (1935), all species also have weak vocalizations (*R. aurora*: Storer, 1925; Stebbins, 1966; Licht, 1969b; our data; R. boylii: Storer [MS] in Stebbins, 1951; R. cascadae: Wright and Wright, 1949; Stebbins, 1966; R. muscosa: Storer [MS] in Stebbins, 1951; R. Zweifel, pers. com.; R. pretiosa: Turner, 1958; Morris and Tanner, 1969; Licht, 1969b), a pattern emphasized by some authors who indicate that vocalizations are nearly inaudible in mixed choruses with the much smaller-sized, but loudvoiced hylids (Turner, 1958; Morris and Tanner, 1969; Licht, 1969b; our data). Wells (1977) commented that a few ranids lacking vocal sac apparatus had reduced vocalization strength, but he did not discuss phylogenetic implications. Sonograms of vocalizations currently exist for only two of the six taxa (R. a. aurora and R. pretiosa: Licht, 1969a, b), but a complete data set might prove instructive in testing the contested monophyly of the group (Case, 1978; Farris et al., 1979, 1982).

## Appendix 1

Material examined.—Sample sizes follow the species name. Localities are listed alphabetically by country, state and county, respectively. Some collections had several specimens catalogued under the same museum number; the number of specimens is listed in parentheses following the museum number. For some of the latter, the University of Michigan material had the collector's number available to differentiate individuals; these are indicated as RAN (=Ronald A. Nussbaum collection numbers). Collection standard symbolic codes follow Leviton et al. (1985) except for California State University, Chico (CSUC). The UMF numbering system is hyphenated and does not indicate specimen series.

Rana aurora (280).—MEXICO: BAJA CALIF-ORNIA: La Grulla—MVZ 9838, CAS 57239-40, 57251-2, 57254-5, 57270, 57272, 57274, 57276-8, 57280, 57282-3, 57286, 57291, 57293, San Jose, 750 m-MVZ 9663, Valladores, 810 m-MVZ 9830, 9833. USA: CAL-IFORNIA: Alameda; no specifics—CAS-SU 8564, Edith Street near Moraga Rd., Oakland-MVZ 12625, Lake Chabot-USNM 52895, Temescal—CAS 13260, pond near Thornhill—MVZ 7151, Butte; 1.6 km toward Oroville from Feather Falls—CSUC 1101-3, Del Norte; 3.2 km N Klamath-CAS-SU 5888, 9.6 km N Klamath—LACM 91003, 91011-2, near Klamath-MVZ 29954, El Dorado; 1.6 km southeast Placerville-MVZ 19060, Humboldt; Arcata-

MVZ 2358, Big Lagoon-MVZ 51398, 1.6 km E Carlotta-MVZ 38809, 6.4 km W Elk Grove—MVZ 42488, 8.0 km N Orick—CAS 80185-91, 80194-207, 6.4 km N Orick-MVZ 44497, Redwood Park, 5.6 km southeast Scotia—MVZ 62400, 62402, Lake; Cole Creek, 5.6 km north-northwest Hobergs-MVZ 72251, Los Angeles; Mint Canyon-USNM 53262, Placerita Canyon-SDSNH 19538, 19540-1, 19543-5, San Gabriel Canyon-LACM 26584-5, UMF 53-413 (3), 5-13 km northeast Sunland, Trancas Canyon-LACM 13464, 13487, Marin: Dillon Beach, Pacific Marine Station-MVZ 59330, Inverness-CAS 63733, 6.4 km W Inverness-MVZ 5087, Sausalito-CAS 13259, Tomales, 0.8 km northwest Marshall-MVZ 40547, Mendocino; N fork Big River, 17.7-22.5 km E Mendocino-MVZ 178537-8, 178541, Mendocino City-MVZ 5095, Mill Creek, 5.6 km N Ft. Bragg-MVZ 40973-5, Monterey; Carmel-CAS 13838, Monterey-USNM 3369, 18954, Napa; Calistoga-USNM 52883, 22.4 km W Monticello Dam-MVZ 77984, 3.2 m southwest Napa—MVZ 4395, Orange; Harding Canyon-LACM 91067, 106023, 1.6 km northwest Tucker Bird Sanctuary-LACM 91056, Placer: Michigan Bluff-MVZ 6111, San Benito; Bear Gulch Creek, Pinnacles National Monument-CAS-SU 16976, Bear Gulch Reservoir, Pinnacles National Monument-UMMZ 119018, 16 km east-southeast Gonzales-CAS-SU 10661, San Bernardino; Mojave River near Deep Creek—UMMZ 89783 (2), Deep Creek near mouth Mojave River-UMMZ 116649, Mojave River at Victorville-SDSNH 7005, 7009, 7013, 7021-3, 7025, 7027, 7030, San Diego; 9.7 km east-southeast Banner, Sentenac Canyon—LACM 91105, MVZ 27185, 31613-4, Campo-CAS 40387, Jamul Creek, El Nido P.O.-USNM 22081, 16 km W the Narrows-MVZ 61069, Mouth of Peterson Canyon-CAS 50846, 50848, Sentenac Canyon—SDSNH 31307-10, 39390, 7.6 km N Warner Springs-LACM 91099, San Francisco; San Francisco-USNM 35518, San Luis Obispo; 4.0 km S San Luis Obispo—CAS 57631, San Mateo; Alpine Rd.—CAS-SU 13071, Mills Lake near Millbrae—CAS-SU 8262, 0.4 km S Stone Circle—CAS-SU 8256, Stone Circle-CAS-SU 13394, 13397, Santa Barbara; Canada de la Gaviota-LACM 135329, 135336, 135342, Base of Mono Dam-UMMZ 89787, Santa Clara; no specifics-UMF 79-9, Lagunita—CAS-SU 4781, S shore Lagunita—CAS-SU 20178, Santa Cruz; near junction of Spring Valley and San Andreas Rds.-MVZ 105222, Corralitos Mountains-MVZ 16120, 4.8 km N Corralitos-UMMZ 66657, Scotts Valley near Granite Creek Rd.-MVZ 68037, Shasta; Clear Creek, S Redding—UMMZ 71495, Tuolumne; Mather—AMNH 104141, 104143-5, 3.8 km northwest Sonora—MVZ 134088, Ventura; 7.2 km N Piru—UMMZ 89781. NEVADA: Nye; Duckwater—MVZ 186380-3, UMMZ 84829 (2), Smoky Valley, 200 m east-southeast Millett-MVZ 37078, Millett-MVZ 12788. **OREGON:** Clatsop; Cannon Beach—CAS 63831, Old Fort Clatsop—MVZ 34208, 34219, 34225, northwest side Saddle Mountain-UMMZ 133695, Saddle Mountain State Park—OSUC 4189, 0.4 km W Saddle Mountain State Park-OSUC 4151, Coos; Coos Head—LACM 1660, Johnson Creek, 6.4 km southeast Bandon-UMMZ 133433 (3: RAN 7078, 7081-2), Myrtle Point-CAS 29470, 29472, 29475, 29488-9, Curry; 1 km north-northeast Langlois-MVZ 56210-1, 3.2 km N Ophir-MVZ 56140, Pistol River—OSUC 606, 17.7 km above mouth of Rogue River-MVZ 17171, 18590, 8 km above Gold Beach, Rogue River—MVZ 14970, Douglas; Tahkenitch Camp, 9.6 km N Gardiner-MVZ 64547-8, 2.4-4.0 km E Elkton-MVZ 38960, Lane; 1.6 km N Blue River High School-UMMZ 133098, Mapleton-USNM 39783, McKenzie Bridge-USNM 54110, Lincoln; Newport-UMMZ 64932 (2), Yaquina-USNM 45449, Linn; Peoria Rd., 3.2 km W Corvallis-UMMZ 134182, Multnomah; Columbia River near Oneonta Gorge-UMMZ 133400, Oneonta Gorge-UMMZ 133392, Polk; Black Rock, 6.4 km W Falls City—UMMZ 133058, 0.4 km N Pedee-UMMZ 133451 (2: RAN 2303, 2305), 3.2 km northwest Pedee—UMMZ 133402 (3: RAN 8946, 8948-9), Tillamook; Rockaway—LACM 26589. WASHINGTON: County unstated; Olympic Peninsula and several km S Tacoma—CAS-SU 8641, Puget Sound—USNM 9420, Clallam; Elk Lake—CAS 66354, 66356-7, Lake Crescent-CAS 30422, 30424-7, 30430, 30432, Mora-USNM 64397-8, Neah Bay-USNM 46066, 3.2 km E Sequim-MVZ 70466, Clark; Vancouver-USNM 61498-9, Cowlitz; Maratta Creek— UMMZ 133405, Grays Harbor; Aberdeen-USNM 45799, Grenville—USNM 46063, Melbourne—CAS 24107, Quinault—CAS 29990, 3.2 km S Westport, Twin Harbors Park—MVZ 146032-4, Jefferson; Hoh River-UMMZ 132951, Hoh River, 12.8 km E US Hwy 101-UMMZ 132952 (2: RAN 1508, 1510), Hoh Road, 3.7 km E Hwy 101-USNM 209473, 29 km E US Hwy 101-MVZ 146327, Hoh Road, 5.6 km W Olympic National Forest-USNM 209474, King; E Bellevue, 21 m—MVZ 38639, Seattle—AMNH 164, 166-7, 174, 178, Kitsap; Bremerton—USNM 64107-8, Klickitat; Bingen-MVZ 61773-4, Lewis; 12.8 km W Chehalis—USNM 61493, Toledo—USNM 46069, Mason; McTaggart Creek—AMNH 20719, CAS 55349, Pacific; Ilwaco-USNM 61484, Shoalwater Bay-USNM 3345, South Bend-CAS 29904, 29907-8, Trapp Creek-CAS 29927, Pierce; Mt. Rainier-LACM 76544, San Juan; San Juan Island-UMMZ 97212, Snohomish; S fork Stillaguamish River near Verlot-UMMZ 132954, Skagit; Chuckanut, 8.0 km S Bellingham-CAS-SU 3732-3, Wahkiakum; Cathlamet-USNM 61490-1, Gray's River-LACM 26588, 8 km N Skamokawa-UMMZ 133697. CANADA: BRITISH COLUMBIA: Beaver Lake, Vancouver-UBC 466-8, 472-6, 1047, Nanaimo, Newcastle Island-MVZ 12401, 12403, 16 km N Kamloops-CAS-SU 10902.

Rana boylii (24).—USA: CALIFORNIA: Butte; Cherokee Creek—CAS 2583-5, 2587-8, Humboldt; Bull Creek—LACM 13620-2, Klamath—LACM 1661, Redwood Creek— MVZ 38765, 38769, 2.8 km W Willow Creek near Boise Public Camp—MVZ 41245, Los Angeles; Cattle Canyon—LACM 91524, Elizabeth Lake Canyon—LACM 13765, E fork San Gabriel River—LACM 13723, 13744, Mendocino; Willits—CAS 28718, 28726, 28740, Siskiyou; Elliot Creek—LACM 26610-1, Ventura; Sespe Creek—LACM 13697, 13702. OREGON: Douglas; Cow Creek at Hwy 99—MVZ 18602.

Rana cascadae (113).—USA: CALIFORNIA: Butte; Coon Hollow-MVZ 57340-1, Plumas; Butt Creek—MVZ 69501, 69504, 69506, Domingo Creek-LACM 76641-2, Willow Lake and Creek—LACM 76617, 76626, Warner Creek, near Chester-CAS-SU 2083, Shasta; Emerald Lake—MVZ 136125, Dersch Meadows—MVZ 136138, 32 km northwest Fall River Mills-MVZ 56845, Manzanita Lake-MVZ 10142, 41238, 57707-8, 57087, Moosehead Creek-MVZ 70512, King's Creek Meadow-MVZ 148944, Siskiyou; Antelope Creek-MVZ 17940, Bartle-MVZ 60496, USNM 110133, Colby Meadows-MVZ 74316, Dale Creek-MVZ 17942, Tehama; Elam Creek—CAS-SU 11062, Lassen Road, 32. km W Black Butte-MVZ 10005, Trinity; 0.2 km northwest Upper Canyon Creek—MVZ 94817, Gumboot Lake— CAS 13303, Tamarack Lake—MVZ 161143-4, 161146, Union Creek-MVZ 136144, 136146, Ward Lake-MVZ 97951. OREGON: Deschutes; Tumalo Creek, 17.7 km W Bend-MVZ 26730, 26755, 26758, Tumalo Creek, 24.1 km W Bend-MVZ 26760, 26765, 26774, Douglas; Crater Lake, government headquarters-CAS-SU 9941-2, 9945, Diamond Lake-CAS 85045, Kelsay River, 1250 m-MVZ 70356, pond S Diamond Lake-CAS-SU 9944, West Lava Camp-LACM 13428-9, Jackson; Rustler Peak area-MVZ 146047, Klamath; Munsar Creek, 1.6 km S Crater Lake P.O.-MVZ 57711, Munson Meadow-MVZ 50263, 6.4 km N, 3.2 km E Fort Klamath—MVZ 67543, Lane; 1.6 km E Scott Lake-MVZ 79190. WASHINGTON: Clallam; Cat Creek headwaters-USNM 64363, 64366-74, Canyon Creek, 4.8 km S Soleduck River—USNM 64389, Lake Crescent—CAS 30425, 30436-9, 30441, 30443, Elk Lake-CAS 66340, 66342-3, 66346-9, 66351, Jefferson; Dosewallips River headwaters—USNM 64391-2, Hoh River, near Fischer's Ranch—CAS 47710-1, 47714-6, Quinault River, head N Fork-USNM 64347, 64349-50, 64352, 64355, 64357, 64359, 64361–2, Lewis; Paradise Valley—LACM 91529-30, 91533, Soda Springs-MVZ 92833, 92836, Mason; Mt. Steel, Lake Cushman-UMMZ 64861, 64864-5, Antler Creek, Lake Cushman-UMMZ 64859, Lake Cushman-UMMZ 48529, Pierce; Mt. Rainier-MVZ 190821-2, Mowich Lake-CAS-SU 5897-8, Skamania; Spirit Lake—MVZ 111056, Yakima; 4.8 km E Chinook Pass—CAS-SU 7415-6.

Rana muscosa (22).—USA: CALIFORNIA: Los Angeles; E fork San Gabriel River—LACM 26654, 26658, N fork San Gabriel River— LACM 13736, W fork San Gabriel River—CAS 27389, 27391, 27396, 27403, LACM 26643, Waterman Guard Station—LACM 13749, Madera; Ediza Lake—LACM 1970-1, 1973, Rosalie Lake—LACM 1962, Mariposa; Vogelsang Lake—CAS 55385, 55408, Placer; Five Lakes, near Squaw Valley—MVZ 71850, 71852, Riverside; Andreas Canyon—LACM 106057, Skunk Cabbage Meadow, 5.6 km northeast Idyllwild—LACM 91276, Tahquitz Canyon— LACM 91279, Tuolumne; vicinity of Tuolumne Pass—CAS 55498, 55505.

Rana pretiosa (21).—CANADA: BRITISH COLUMBIA: Hazelton—CAS 8465, Stikine River at Doch-da-on Creek-CAS 7322. USA: ALASKA: Southeastern (District); Sergief Island, mouth of Stikine River-MVZ 7336. IDAHO: Blaine; Alturas Lake-LACM 91057, 91511. MONTANA: Ravall; 19.3 km northwest Darby-LACM 91518. NEVADA: Elko; 17.7 km southeast Tuscarora LACM 8510, Nye; Clear Creek, Toivabe Mtns.—MVZ 186464. OREGON: Crook; 9.7 km E, 4.8 km S Wildcat Mtn.-MVZ 26805-6. UTAH: Salt Lake; 9.7 km south-southeast Salt Lake—MVZ 53663. WASHINGTON: County unstated; Puget Sound-USNM 131512, Kittitas; Robinson Canyon—LACM 51355, Lewis; near Ohanapecosh, Mt. Rainier Natl. Park-MVZ 187332, Okanogan; Black Pine Lake—LACM 51354, Snohomish; 1.6 km N Lake Washington—MVZ 16762, Walla Walla; Walla Walla— MVZ 37146, no specifics-LACM 28806, 28809, 28814. Wyoming: Park; Yellowstone Park, Lake cabin area-MVZ 72002.

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