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Cover Page Footnote

Acknowledgements Monica Bugby, Don Morris, and Lauren Parry are thanked for their assistance in the field recovery of sediments from the Larramendy location. Don Morris is greatly appreciated for his decades of field work and discussions about NCI. We appreciate the tremendous help of Sandy L. Swift in wet sieving sediments, sorting matrix of microfaunal remains, and photography of specimens. Jack McGeehin, Jeff Pigati, and R. Randall Schumann (USGS) were extremely helpful in providing the chronology of the Larramendy deposits. We thank Superintendent Russel Galipeau, Laura Kirn, and other staff of Channel Islands National Park for facilitation of the collecting permit. Thanks is given to John Johnson and Santa Barbara Museum of Natural History administration for many aspects of the project. We thank the Larry D. Agenbroad Legacy Funds for Research at The Mammoth Site for funding this project. Helpful discussions and manuscript reviews were provided by Christopher N. Jass, Amy Henrici, and other anonymous reviewers.

Late Quaternary Chorus Frog (*Pseudacris*) from the Channel Islands, California

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Abstract.—Fossil and subfossil remains of the vertebrate faunas from the northern Channel Islands, southern California, have been studied for many decades. Continued interest has focused on skeletal remains of birds, rodents, and mammoths from archaeological and paleontological localities, but considerably less attention has been placed on the detailed description of the herpetofauna (salamanders, anurans [frogs and toads], lizards, and snakes) on the Channel Islands. We present descriptions of an ilium of an anuran from Santa Rosa Island (Larramendy North; radiocarbon dating at least 13,393 calibrated years ago) and two tibiofibulae San Miguel Island (Daisy Cave) dating from earliest and middle late Holocene layers. We identify the fossil ilium as *Pseudacris* sp. (chorus frog): 1) it is the lowest level that skeletal morphology permits us to attempt, 2) realizing that it appears morphologically closest to *P. regilla*, and 3) yet realizing that not all species of *Pseudacris* and *Hyla* have been directly compared or are understood. The extant amphibian fauna on these islands is depauperate. The remains presented here represent the first description of a fossil anuran from the northern Channel Islands. It is now understood that a chorus frog lived on glacial-age Santarosae Island, yet it is not understood when its distribution was reduced to just the present two largest islands, Santa Rosa and Santa Cruz.

Investigation of the Holocene and late Pleistocene terrestrial vertebrate faunas from the northern Channel Islands (NCI) off the coast of Santa Barbara California has received attention for many decades (see discussions in Damiani and Garcelon 2009) (Fig. 1). Of sustained interest has been the analysis of cultural artifacts along with skeletal remains of birds, rodents, and mammoths from archaeological and paleontological localities (e.g., Erlandson et al. 1996; Guthrie 1980, 1998, 2005; Johnson et al. 2002; Ainis and Vellanoweth 2012; Allen 2013; Muhs et al. 2015). What has received considerably less attention other than cursory listings is the detailed assessment of the herpetofauna (salamanders, anurans [frogs and toads], lizards, and snakes). The first and only insular Pleistocene-age salamander (*Batrachoseps*) from the Channel Islands was recovered in association with a late Pleistocene pygmy mammoth (*Mammuthus exilis*; 12,840 ± 140 yr B.P., CAMS-24429, AMS analysis; Agenbroad 1998, 2002; Mead et al. 2004). Here we report on the skeletal remains of the first fossil frog from localities on the NCI: one ilium from Laramendy North, Santa Rosa Island and two leg elements from Daisy Cave A, San Miguel Island.

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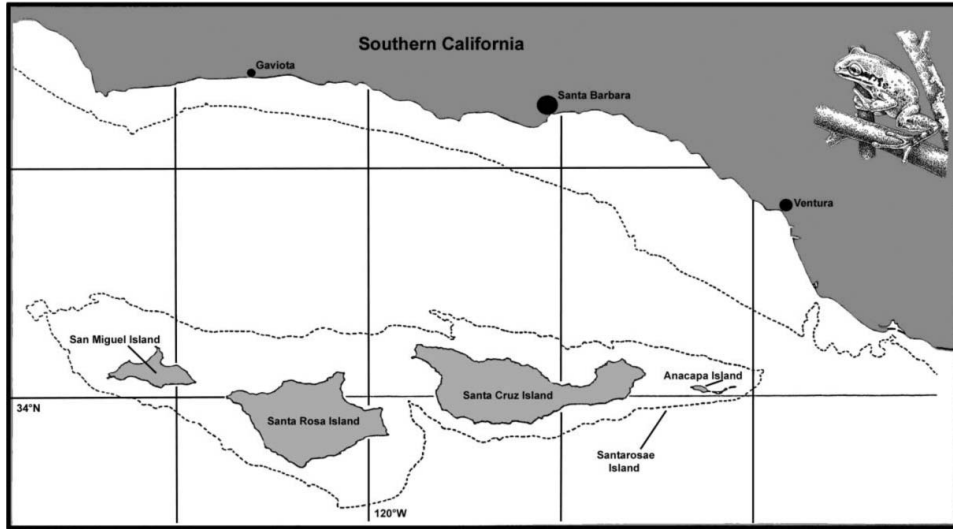


Fig. 1. Map of southern California showing the four islands that make the northern Channel Islands today and the outline of the Santarosae Island that existed with a lowering of sea levels during glacial stands of the Pleistocene. Dotted line denotes lower sea level shorelines. Today *Pseudacris regilla* (see text discussion) is found only on Santa Cruz and Santa Rosa islands, and along the coast of the mainland (see text). Fossil remains *Pseudacris* presented here are found on Santa Rosa and San Miguel islands. Line drawing adapted from Pacifichorticulture.org.

Materials and Methods

Of the multitude of archaeological and paleontological sites on the NCI that have produced microfaunal remains, few have produced remains of amphibians possibly due to collection bias [too large of sieve size used during excavations, e.g., 1.58 mm (1/16")]; although see Reddy and Erlandson 2012], or scope of research design not including potential of microfauna such as amphibians. Our sample from San Miguel Island represents sediments partly studied of its microfaunal remains previously sieved through 1.58 mm mesh screens. The specimen from Santa Rosa Island represents a sample recovered from sediments we collected, sieved through 0.5 mm (500 μ m) mesh, and sorted with the aid of a light microscope. All specimens were identified using the skeletal comparative collection at The Mammoth Site (Hot Springs, SD) and morphological characters provided in the literature (see discussions below). All specimens belong to the US National Park Service, Channel Islands National Park (CHIS), and are curated by the Santa Barbara Museum of Natural History (SBMNH).

Larramendy North, Santa Rosa Island.—The Larramendy Mammoth site is located in a canyon on the northwestern side of Santa Rosa Island. The general geology of the area is that of alternating alluvial packages of organic-rich clays, silts, sands, and gravels. A mammoth skull was recovered in 2016 from a gravel lens overlain by cross-bedded silty sands and trough cross-bedded sandy gravels. Samples of carbon were recovered from an organic-rich clay above the trough gravels and from a silty sand lens below the gravels, yet all stratigraphically above the mammoth skull. Two radiocarbon dates were obtained above the skull; mean probability ages of 13,106 (USGS 171250, conventional age 11,250 \pm 30 yr B.P.) and 13,393 (USGS 171252, conventional age 11,555 \pm 35 yr B.P.) calibrated years ago.

Eight meters north of the Larramendy skull is a 15 cm-thick sandy gravel lens (Larramendy North locality) that can be traced south to underlie the mammoth specimen. One anuran specimen (reported here) was recovered along with other amphibian and mammalian remains from within this lens. Because of the calibrated ^{14}C -dated alluvial relationship, the anuran remains are accepted to be at least 13,393 years old. Based on the relative lack of alluvial wear on the anuran, other micro-vertebrate, and mammoth remains, we presume that these specimens represent local canyon inhabitants that lived within the immediate environment.

Daisy Cave, San Miguel Island.—Daisy Cave (CA-SMI-261) and its adjoining rock-shelter, Cave A (CA-SMI-261A) are considered by archaeologists as a single fossil site, which is located on the northeastern coast of San Miguel Island (Fig. 1). The locality contains stratified artifact- and fossil-bearing deposits that have received numerous excavations (see overview in Erlandson et al. 1996). Renewed work in the cave in the mid-1980s and 1990s discovered stratified layers with hundreds of thousands of microvertebrate and avian remains (Guthrie 1980, 1998, 2005; Ainis and Vellanoweth 2012; Allen 2013). The chronology of the stratigraphy is well established for most of the cave with the lower levels (150–160 cm depth) reaching back to 18,670 calibrated years before present (cal yr B.P.; Beta-77070), which indicates that the locality was receiving skeletal remains before the use of the site by humans approximately 11,600 calibrated years ago (Erlandson et al. 1996).

Fossil frog remains reported here were recovered from two test pits (TP-1, TP-2) excavated in 1986 (field notes Don Morris; NPS archive) in the middle and inner chambers of Cave A (CA-SMI-261A), areas that have received less chronological assessment. The location of TP-1 is on the stratigraphic profile of the middle chamber of Cave A (Erlandson et al. 1996, Fig. 4). The fossil sample from TP-1 was recovered from excavation layer 3B (field notes Don Morris, 1986; NPS archive), however it is not clear how this layer designation relates to the chronological strata (I–XV) established in Erlandson et al. (1996, Fig. 4). The depth of field notes layer 3B appears to be equivalent to the depth of chronological stratum XII (a distance of about 3 m apart). Radiocarbon data “suggests that the base of the [cultural] midden inside Cave A may have been deposited as much as 10,060 yr ago” (Erlandson et al. 1996: 366). A radiocarbon date from Stratum XIV is approximately 18,600 (Beta-77070) but could be recording an “old wood” issue (Erlandson et al. (1996: 369). The anuran bone from this test pit is conservatively assumed to be at least 10,060 years old based on the above discussion (earliest Holocene).

The fossil from TP-2 level 1, from the back portion in Cave A cannot be dated accurately based on stratigraphy. Based on field notes (Don Morris, 1986; NPS archive), the stratigraphy in this area of Cave A does not appear to be mixed. Level 1 sediments represent the top 5 cm of deposit and have not been radiocarbon dated. Based on discussion and data presented in Erlandson et al. (1996, Table 1), the fossil frog from this area dates less than about 3,000 years old (middle late Holocene).

Excavated sediments from both test pits were, for the most part, screened through a 3.16 mm (1/8”) mesh in the field and then processed through 1.58 mm (1/16”) mesh in the lab before microfossils were removed. Screened vertebrate remains displayed a mixture of white, brown, and dark-brown colored skeletal remains in all excavated strata. Due to the lack of digestive etching or mastication breakage, all microvertebrate remains are attributed to the stomach pellets produced by the barn owl (*Tyto alba*; Guthrie 2005). Other bird species, such as the burrowing owl (*Athene cunicularia*; e.g., Trulio and Higgins 2012; Wingert 2012), recovered in the cave and elsewhere on the island also produce stomach

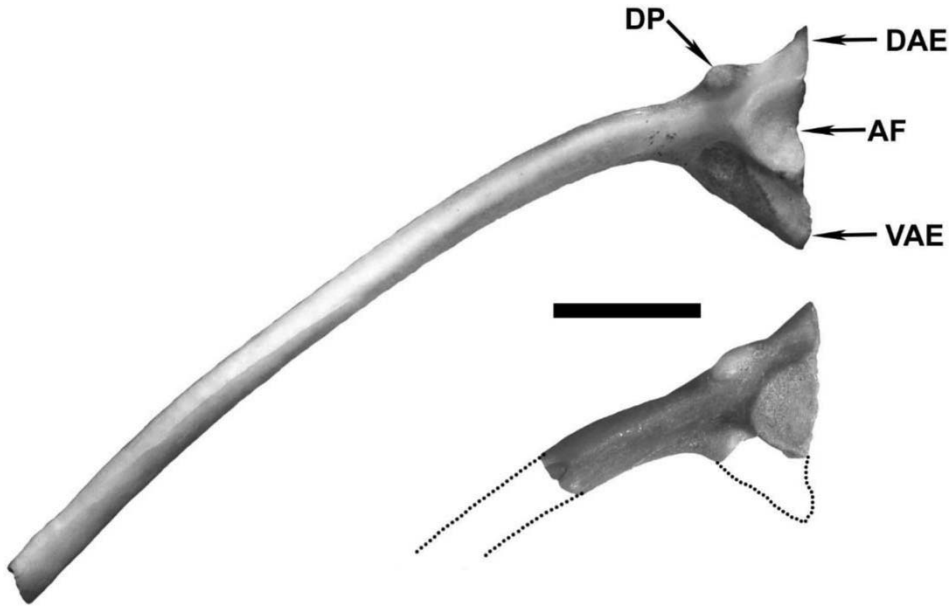


Fig. 2. Left ilia of extant *Pseudacris regilla* (top; svl = 40 mm) and fossil *Pseudacris* sp. from Santa Rosa Island, Northern Channel Islands, CA, bottom (CHIS 46774). Abbreviations: AF, acetabular fossa; DAE, dorsal acetabular expansion; DP, dorsal prominence (tubercle); VAE, ventral acetabular expansion. Scale bar equals 2 mm.

pellets and could be contributors, as well, to the bone deposits. A number of species of owls (Tytonidae, Strigidae) frequent the NCI today and likely did in the past (Collins and Jones 2015). Field studies indicate that there is only one instance of an owl pellet on one of the islands that contained an obvious transport from the continental coast (*Thomomys bottae*; PWC field notes). Studies of the food habit of eagles and barn owls from the islands have not shown that anurans or salamanders form a part of their diet today, but reptiles are occasionally recorded (Rudolph 1970; Fellers and Drost 1991; Collins et al. 2005; Erlandson et al. 2007; Collins and Latta 2009; Newsome et al. 2010, 2015). Worldwide anurans are rare in the diet of *Tyto* today (Jaksić et al. 1982).

Results and Discussion

Fossil remains.—Ilium.—A single left ilium (CHIS 46774; Fig. 2) was recovered from Larramendy North. The specimen is fragmented, being 4.8 mm in length with 50% of the ilial shaft preserved (measurements follow those in Bever 2005). No dorsal ilial crest is present. A fragment of the ventral acetabular expansion exists, indicating that the specimen originally had at least a minimal flange. The dorsal acetabular expansion is complete and pointed yet not overly prominent and is 0.8 mm in height. The acetabular fossa is 10.0 mm long and 15.0 mm in height. The tubercle on the dorsal prominence is pronounced, tall, positioned posterior to the anterior edge of the acetabular fossa, with a round, blunt apex oriented both anteriorly and laterally.

Comparison of CHIS 46774 with extant taxa includes species from around North America and not limited to just California species or with fossil species presumed to be or reported to be from the Pleistocene of the western region. The ilium is often considered

to be one of the best skeletal elements upon which to base fossil anuran identifications. Unfortunately, the morphological traits on the bone show a wide range of variation, both inter-specifically and ontogenetically. Bever (2005) did a detailed analysis of ilial characters on *Bufo* (now considered to include multiple genera). His results indicate that no distinctive morphologies in the ilium of extant *Bufo* species are known that permit a complete unambiguous species-level diagnosis. However, there are morphologies on the ilium from select anuran families that do permit some generic-level identifications and will be used here.

Although size alone is a poor character to use to make an identification, it does permit some comparative aspects that when grouped with osteological characters does allow for a certain degree of classification. Without the presence of a dorsal ilial crest on the ilium, CHIS 46774 does not belong to any member within the true frogs, Ranidae. Size ranges (using snout-vent length; svl) within extant scaphiopodids (spadefoot toad, Scaphiopodidae) *Scaphiopus* (*Sc. couchi* svl = 22–78 mm, n = 14; *Sc. holbrookii* svl = 37–61 mm, n = 8; *Sc. hurterii* svl = 50 mm) and *Spea* (*Sp. intermontana* svl = 35–53 mm, n = 6; *Sp. bombifrons* svl = 43–55 mm, n = 6; *Sp. hammondii* svl = 24–~60 mm; n = 5; *Sp. multiplicata* svl = 48–50 mm, n = 3) all have a low-rise to non-existent (juveniles) dorsal protuberance unlike what is observed on CHIS 46774.

Bufoidea is a large and complex family of true toads. All North American members used to be considered within a single genus, *Bufo*; now these have been segregated into separate genera. *Anaxyrus cognatus* (Great Plains toad svl = 61 mm) has a distinctly tall, steep-sided dorsal protuberance. The small *Anaxyrus debilis* (green toad svl = 33) has a distinct, low-rising dorsal protuberance, along with a short, lobbed ventral acetabular expansion, and a short dorsal acetabular expansion, all different than observed on CHIS 46774. *Anaxyrus microscaphus* (Arizona toad svl = 33 mm) along with *Incilius mazatlanensis* (Sinaloa toad svl = 75 mm) and the large *I. alvarius* (Colorado River toad svl = ~110 mm) have a prominent, steep-sided dorsal protuberance unlike CHIS 46774. Other large and small North American bufoeids follow suit with those described above indicating to us that CHIS 46774 is not from Bufoidea.

CHIS 46774 is similar to a number of smaller, more delicate anurans within the families Hylidae, Microhylidae, Eleutherodactylidae, and Craugastoridae; comparisons are made with members of these clades. *Pseudacris regilla* (Hylidae) ilia used in this study are from specimens that have a svl ranging from 32–44 mm (n = 6); also used were *P. triseriata* with svl ranging from 21–29 mm (n = 16), and *P. cadaverina* with svl of 45 mm. The ilium of *Gastrophryne* (narrow-mouth toad; Microhylidae, svl = 20–40 mm), *Eleutherodactylus* (chirping frog; previously in part within *Syrrophus*, Eleutherodactylidae, svl = 16–38 mm), and *Ascaphus* (tailed frog; lives today in the wet environments of the northwest of the USA; *Ascaphus*, svl = 25–51 mm) are minute, distinctly smaller than that of *Pseudacris* and the fossil. The ilium of *Ascaphus* has a large acetabulum in comparison to the acetabular expansions, and the dorsal prominence and tubercle are nearly absent (see Ritland 1955; Gardner et al. 2010), unlike the fossil presented here. The ilium of the minute *Acris* (cricket frog, Hylidae, svl = 16–32 mm; eastern USA) has a miniscule dorsal crest on the ilial shaft unlike what is observed on the fossil and *Pseudacris* (Chantell 1968a). *Craugastor* (barking frog; southern Arizona and east; Craugastoridae; previously in part *Eleutherodactylus*) is a larger frog (svl = 51–95 mm) and has distinctly small acetabular expansions and dorsal prominence as compared those found on *Pseudacris* spp. The ilium of *Smilisca* (lowland burrowing treefrog of southwestern Arizona today; another hylid once referred to as *Pternohyala*; svl = 38–63 mm) is about the size of that of many *Hyla* and has a pronounced

dorsal tubercle on a less pronounced dorsal prominence. The tubercle is knob-like, linear in shape ($n = 2$ in comparisons), and almost touches the acetabulum, features which are unlike those found on smaller *Pseudacris regilla* and the fossil.

Holman (2003) aptly points out that the ability to identify all species within North American Hylidae using isolated skeletal elements is surely not possible. We agree; however, there are characters on select elements, such as the ilium, that do permit a more refined level of identification than just the genus. A number of characters of the ilium have been used to identify species of both *Pseudacris* and its sister-taxon, *Hyla* (Lynch 1965, 1966; Chantell 1968b; Holman 2003). The ilium of the eastern-southeastern USA *H. cinerea* (Green treefrog) has been well-studied with regards to ontogenetic changes (Lynch 1965). The dorsal prominence enlarges through life but the tubercle, which also enlarges, never develops into a pronounced knob (Lynch 1965: Fig. 4) as observed on *Pseudacris regilla* and the fossil. *Hyla arenicolor* (Canyon treefrog) is a larger frog than *P. regilla* and it never produces the large dorsal prominence with distinctive knob tubercle of the chorus frog and fossil. A large, knob-like dorsal tubercle on *P. regilla* and the fossil are near identical; somewhat similar, yet less pronounced tubercles are found on the extinct, late Pleistocene *H. baderi* (Lynch 1965; Florida) and the extinct, late Miocene *P. nordensis* (Chantell 1964; Nebraska). Chantell (1970) found that the dorsal acetabular expansion is distinctly 'longer' on *H. arenicolor* and *P. cadaverina* (reported then as *Hyla californiae*) as compared to *P. regilla* and as seen on the fossil. In our study here using a single comparative specimen we concur with this finding.

Given the above discussion, we identify the fossil ilium as *Pseudacris* sp.: 1) it is the lowest level that skeletal morphology permits us to attempt, 2) realizing that it appears morphologically closest to *P. regilla*, and 3) yet realizing that not all species of *Pseudacris* and *Hyla* have been directly compared or are understood.

Tibiofibula.—Two tibiofibulae were recovered from Daisy Cave (SMI-261A): Test 1, Level 3B (CHIS 46773), Test 2, Level 1 (CHIS 46772). Tibiofibula CHIS 46772 is nearly complete with a length of 13.0 mm and a mid-diaphysis diameter of 0.9 mm. CHIS 46773 is nearly complete with only the proximal end absent above the crista cruris; length is 15.0 mm with a mid-diaphysis diameter of 0.8 mm. Both tibiofibulae are slightly more robust (especially at the distal end) than those observed for extant *Pseudacris regilla* (svl = 40 mm; length 16.2–19.0 mm; diameter 0.8 mm; $n = 2$). Overall the tibiofibulae of anurans have a generalized morphology with differences observed within some families at the generic level. Tibiofibulae within the Hylidae are typically long and slender. The NCI fossils presented here are within the morphological shape and size observed for the larger forms of *Pseudacris* (e.g., *P. regilla*) and *Hyla* (e.g., *H. arenicolor*, *H. chrysoscelis*) and unlike the smaller and more delicate, or distinctly long-and-slender tibiofibulae observed on, e.g., *P. triseriata*, *Acris* spp., *H. cinerea*, *H. squirella*, *H. femoralis*, to name a few. Due to the non-distinctiveness in morphology and the uncertainties mentioned above, the identification of the two tibiofibulae is cf. *Pseudacris*. A detailed study of the morphological variation among tibiofibulae should be attempted to better resolve the identification issues but is beyond the scope here.

Extant chorus frog and other Californian anurans.—Recent molecular analysis of treefrog phylogenetics produced a non-ranked clade (Arboranae) consisting of three families, including the chorus frogs in Hylidae (Duellman et al. 2016). Hylidae, as described by these authors, contains seven subfamilies with upwards of 670+ species. Results from molecular assessments vary within the family, with contrasting uses and combinations of genera and species (see discussions and details within Recuero et al. 2006; Wiens et al. 2010; Du-

ellman et al. 2016). Of importance here are the chorus frogs within the family Hylidae, a clade distributed nearly worldwide. Most are small, long-legged frogs, often with adhesive toe pads used in climbing. Eggs are deposited in water or on vegetation adjacent to water, thereby supporting their aquatic larvae, an important consideration when discussing insular sustainability.

Here we follow Stebbins and McGinnis (2012) and recognize the taxa *Pseudacris regilla* (Pacific chorus frog; sometimes referred to as *P. hypochondriaca*, Baja chorus frog, Green et al. 2013) and *P. cadaverina* (California chorus frog) as the only hylid frogs in California today. In this taxonomic scenario only *P. regilla* is thought to be indigenous on the NCI. Green et al. (2013) have *P. regilla* in the extreme north, coastal portion of California with *P. sierra* (Sierra treefrog) occurring over much of the state and *P. hypochondriaca* only in the more southern western part of the state and out on the Channel Islands. *Pseudacris regilla* (following Stebbins and McGinnis 2012) is a small frog (svl = 19–50 mm) that occurs today throughout California and north except in desert regions without perennial streams or oases. This species will coexist with *P. cadaverina* along coastal southern California. Living in a wide variety of environments, a habitat generalist, *P. regilla* can be found in the slightly brackish marshes at sea level. *Pseudacris cadaverina* is slightly larger than *P. regilla* (svl = 32–57 mm) and lives today in the Transverse and Peninsular ranges of southern California south into Baja California, Mexico, and is more closely bound to areas of freshwater than is *P. regilla* (Stebbins and McGinnis 2012).

Other hylids such as *P. triseriata* (Western chorus frog), *Hyla arenicolor* (Canyon treefrog), and *H. eximia* (Mountain treefrog) occur well to the east of western California, in Arizona, Idaho, Sonora (Mexico), and Utah. Other anurans living today in California include the spadefoot toads (*Spea*, *Scaphiopus*; Scaphiopodidae), tailed frog (*Ascaphus*; Ascaphidae), true toads (*Anaxyrus*, *Bufo*, *Incilius*; Bufonidae), and true frogs (*Lithobates*, *Rana*; Ranidae) (Stebbins 2003; Green et al. 2013).

Conclusions

The four islands of the NCI, southern California, have received many decades of work relating to natural and human history. Paleontological and zooarchaeological analyses have focused on the skeletal remains of the pygmy mammoth, birds, and micro-mammals (see previous references) in addition to paleobotanical studies including those related to fire history (Chaney and Mason 1930; Anderson et al. 2008; Kennett et al. 2008; Anderson et al. 2010; Hardiman et al. 2016;). These analyses have produced a detailed story about climatic, cultural, and environmental changes through the late Pleistocene and Holocene. Amphibians and reptiles in the fossil and subfossil record have barely received any attention due to their scant remains recognized in, or recovered from, the sedimentary record. Reptile remains (snakes and lizards) recovered from owl roost localities have received cursory presentations in a few studies centered on other taxa or cultural remains (e.g., Guthrie 1993; Allen 2013). Remains of the first fossil slender salamander (*Batrachoseps*) from NCI were recovered in 1997–1998 adjacent to a mammoth skeleton being excavated from late Pleistocene sediments on Santa Rosa Island (Mead et al. 2004); the retrieval methodology was to use 700 μm or smaller meshes to wet sieve for microfauna. This same procedure is being used now to locate additional remains from predominantly geological and paleontological localities and is producing new information about the insular herpetofauna.

Chorus frog.—The extant amphibian fauna on the NCI is depauperate (Schoenherr et al. 1999). The salamander, *Batrachoseps pacificus* is endemic on all four islands while

B. nigriventris is known only from Santa Cruz Island, but also from the adjacent coastal California (Stebbins and McGinnis 2012). Known also from the adjacent coastal California, *Pseudacris regilla* inhabits only Santa Cruz and Santa Rosa islands today. *Rana draytonii* (red-legged frog) was introduced to Santa Cruz Island in the early 1900s by ranch hands working on the island (Jennings 1988) and disappeared sometime soon after being collected in May 1919 (Sweet and Leviton 1983). The detailed analysis of sedimentary deposits from the islands is helping to assess the insular history of the amphibian fauna of the NCI.

Presented here are the fossil skeletal remains of 1) *Pseudacris* sp. from alluvial sediments with a radiocarbon date of approximately 13,393 cal yr B.P. from Santa Rosa Island and 2) cf. *Pseudacris* from Daisy Cave (CA-SMI-261A) from possibly earliest and middle late Holocene levels on San Miguel Island. At 13,000 years ago, the four islands of NCI were still connected due to lower sea levels creating the single island, Santarosae (see discussion in Reeder-Myers et al. 2015). The implication of the existence of this single-island scenario and the recovery of *Pseudacris* on San Miguel Island is that the chorus frog likely occurred over the entire Santarosae landmass, given the presence of more extensive freshwater habitat available for frogs. With rising sea levels, Santarosae began to separate into the individual islands by about 11,000 yr B.P. with Santa Cruz separating from Santa Rosa and San Miguel between about 9,900 and 9,400 yr B.P., and Santa Rosa separating from San Miguel between 9,400 and 9,100 yr B.P. (Reeder-Myers et al. 2015). One would expect the *Pseudacris* population on San Miguel Island to disappear as sea levels rose and the island shrunk in size becoming isolated from Santa Rosa Island. However, the species likely persisted on the two largest islands (Santa Rosa and Santa Cruz) due to the greater availability of suitable freshwater breeding habitat and to the larger overall size of each island and *Pseudacris* population. A question arises as to when the suitable habitat for *Pseudacris* did disappear from San Miguel Island. The specimens from Daisy Cave provide little to answer this other than to indicate that the chorus frog did once inhabit San Miguel Island where it does not today.

How and when *Pseudacris* first inhabited Santarosae (or its individual islands) is not understood. Given the geology of the islands and continent, we assume that the chorus frog colonized the insular habitat via rafting vegetation from coastal California (e.g., ‘overwater waif distribution’ in Savage 1967). The fossil remains of *Pseudacris* are not suitable for species identification in our view (following Bell et al. 2010). One parsimonious conclusion, however, given the current geographic distribution of the taxon, is that the insular fossils represent *P. regilla*. The previous discussion indicates that the ilium is most similar in morphological features to *P. regilla*, and does provide a reason as to why the fossil likely does not represent *P. cadaverina*, another chorus frog living along the adjacent southern California coast. But until more fossil remains of the frog are recovered and those remains are deemed useful for species-level identification, we err on the conservative side in case there was actually a different species of chorus frog on Santarosae during the Pleistocene which became extinct and has since been replaced by the extant form.

Channel Islands.—The maritime Mediterranean climate of moist winters and warm, dry summers of the NCI is largely controlled by the oceanic currents that sweep by southern California. Based on the bathymetry, this scenario was likely similar during the late Pleistocene glacial regime. San Miguel, Santa Rosa, and the western end of Santa Cruz islands are almost constantly bathed by strong northwesterly winds, which then create greater precipitation on the western and northern sides of the highlands of each island (or most of Santarosae in the late Pleistocene) (Junak et al. 1995; Schoenherr et al. 1999). Each island

today has its own peculiarities in geology, island size, mountain elevations, temperature, and precipitation. Santa Cruz Island is the largest of the islands, has two distinct mountain ridges with a Central Valley in the middle, has two distinct geological histories, has abundant groundwater with numerous springs and seeps, and is likely the most studied of the islands' natural history. Today the local vegetation on the islands is dominated by grassland and shrubland species along with patchy woodlands and chaparrals (see overview in Junak et al. 1995 and Schoenherr et al. 1999). Clearly the presence of humans on the islands, especially since the ranching enterprises of the 19th century, has drastically altered the pre-human environments. Details about the vegetation history of the NCI is still in its infancy of being understood.

Placing the fossil chorus frog into a reconstructed habitat is not straightforward due to the complexities of the plant fossil data. On Santa Cruz Island, Chaney and Mason (1930) recovered macrobotanical remains in Cañada de los Sauces that record the existence of a late Pleistocene coniferous plant community including *Pseudotsuga* (Douglas fir), *Cupressus* (cypress), and *Pinus* (pine) radiocarbon dating $16,600 \pm 270$ cal yr B.P. (Anderson et al. 2008). A coastal salt marsh (Abalone Rocks Marsh; Cole and Liu 1994) and a small ephemeral wetland (Soledad Pond, island central) on Santa Rosa Island were studied and provide community reconstructions. At 11,900 cal. yr B.P. Santa Rosa Island had a variety of communities including pine forests, coastal sage scrub, and grasslands in the central portion of the island; coastal records indicate at least some coniferous forest occurrence. The transition from the late Pleistocene to Holocene was a period of major environmental change (see overview in Anderson et al. 2010). The record from the central-island pond suggests increasingly drier conditions during the early Holocene; the pond had dried more than once during this time (approximately 9,150 to 6,800 cal yr B.P.). Arlington Canyon on the island records a pine woodland during the late Pleistocene (Kennett et al. 2008). Plant records from Daisy Cave, San Miguel Island provide a similar late Pleistocene plant community reconstruction (see overview in Erlandson et al. 1996; Anderson et al. 2010).

The reconstructed late Pleistocene flora for Santarosae during the late glacial climate includes forest and woodland habitats with a diverse understory, as is characteristic of modern northwest coastal California. All of the above implies that habitat reconstruction of the late Pleistocene through Holocene plant community structure was somewhat complex and may have changed quickly at the end of the last glacial maximum. As the plant communities transformed their mosaic structures and responded to both climate and sea level changes, so too would the herpetofaunal species, especially the moisture-dependent amphibians. With the above frog fossils now known from Santa Rosa Island (Larramendy North) and San Miguel Island (Daisy Cave), it is understood that the chorus frog, *Pseudacris* sp., lived on glacial-age Santarosae Island, but it is not understood when its distribution was reduced to just the two largest islands, Santa Rosa and Santa Cruz.

If the fossils do represent *Pseudacris regilla*, and the late Pleistocene species had the same "habitat generalist" requirements and ability to live in "slightly brackish cattail marshes at sea level" as the living form (Stebbins and McGinnis 2012:181), then the climate changes at the end of the Pleistocene with transformations in the vegetation mosaic may not have had much direct impact on the frog. As long as some sort of vegetation occurred along brackish marshes, ponds, and streams, along with the sustainability of the seeps and springs, the frog should have evaded any major population crisis. However, the rise in sea level beginning around 11,000 years ago may have caused the critical reduction in distribution. At some point, *Pseudacris* found Anacapa and San Miguel, the smallest islands, uninhabitable. Whether this is due to lack of ponding water, seeps, and springs, or habitat destruction

due to fires is not understood at this time. The possibility of changes in distribution and density of the frog could have occurred during the known dry period 9,159–6,800 cal yr B.P., as recorded at Soledad Pond, Santa Rosa, which recorded distinct dry-pond episodes (Anderson et al. 2010). Future paleontological research on the NCI should examine both rock shelter deposits (raptor roosts) and open-air alluvial (geological) localities on all four islands with the methodology to wet sieve screen washing all sediments through 0.5 mm (500 μm) screens, sort retained matrix with the aid of a microscope, and develop an accurate site-specific chronology.

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