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Conserved Ontogeny of Color Pattern Leads to the Misdiagnosis of Scincid Lizards of the *Plestiodon skiltonianus* Species Complex

Skinks of the *Plestiodon skiltonianus* species complex, which includes the Western Skink (*P. skiltonianus*), the San Lucan Skink (*P. lagunensis*), and Gilbert's Skink (*P. gilberti*), can be very difficult to distinguish unless geographic information accompanies the specimen. This is due to similarity in the ontogeny of color pattern among the different recognized taxa, regional polymorphism in scale and color pattern characters, and a lack of fixed character differences that reliably distinguish each species across the range of the complex (Rodgers and Fitch 1947; Taylor 1935). Some authors have suggested that *P. skiltonianus* and *P. gilberti* be treated as conspecific (e.g., Camp 1916; Cope 1900; Grinnell and Camp 1917; Van Denburgh 1896), and certain statements in the literature (e.g., "…young [*P. g. gilberti*] specimens are marked just like the young and most adults of *skiltonianus*" [Smith 1946, p. 385]) have only added to the confusion. Phylogenetic analyses have also done little to resolve these taxonomic issues, as separate *P. gilberti* lineages have evolved multiple times within a paraphyletic *P. skiltonianus* (Brandley et al. 2012; Richmond and Reeder 2002), and species delimitation varies widely depending on the concept of species (Richmond and Jockusch 2007; Richmond et al. 2011). For the remainder of the paper, we place the name "*gilberti*" in quotation marks to reflect the nonmonophyly of these lineages except where *P. gilberti* is specifically referred to in earlier studies.

The main characters used to distinguish members of the *P. skiltonianus* complex in the field include body size, dorsal color pattern, tail color (pink vs. blue), and to a lesser degree limb length, supralabial count, nuchal scale count, and a few others related to scalation (Grismer 1996; Rodgers 1944; Rodgers and Fitch 1947). Size (SVL) can be effective for differentiating adult individuals in most areas, but is of little use for young specimens. Color pattern is useful to a degree, but dorsal stripes are retained longer into adulthood in certain *"gilberti"* populations than in others, especially in females, and in some areas the stripes are often never completely lost. Aberrantly large *P. skiltonianus* also have very degraded, or in some cases, no stripes at all (JQR, pers. obs.). Juvenile tail color is useful in regions where pink-tailed *"gilberti"* approach or are syntopic with *P. skiltonianus*; however, *"gilberti"* populations in the northern and central Sierra Nevada, as well as in scattered populations in the east Mojave Desert and the Panamint Mountains, are blue-tailed. Allopatry and different juvenile tail colors distinguish juvenile *P. lagunensis* in southern Baja California from *P. skiltonianus* in northern Baja California, but the adult phenotypes of the two species are similar enough that some authors have regarded them as conspecific (Linsdale 1932; Schmidt 1922; Stejneger and Barbour 1933; Tanner 1988).

One of the most widely used characters for distinguishing juveniles of *P. skiltonianus* and "*gilberti*," aside from tail color when the differences are obvious, is the distance that the dark lateral stripes extend onto the tail (Fig. 1). In various field guides and species descriptions, it is commonly stated that this stripe extends much further in *P. skiltonianus* (ca. 1/3 to 1/2 way down the tail) than it does in "*gilberti*"; in the latter, this stripe purportedly ends at the base of the tail just posterior to the hind limbs (Behler and King 1979; Jones and Lovich 2009; Lemm 2006;

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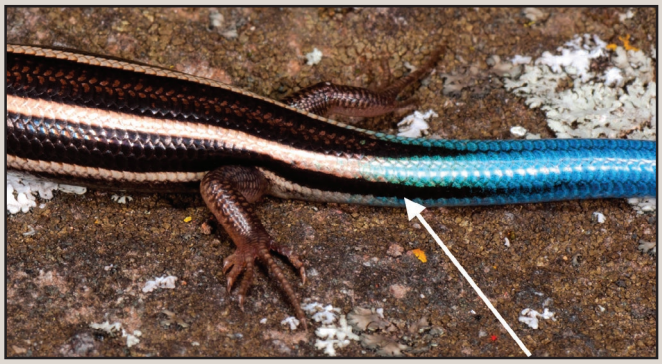

FIG. 1. Example of the lateral tail stripe character in a juvenile *Plestiodon skiltonianus* from Tehama County, California (ca. 520 m elev.).

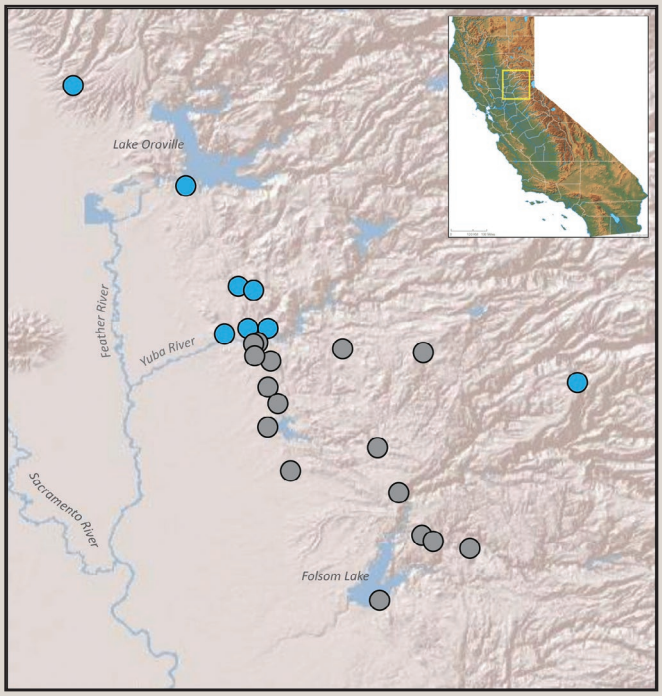

FIG. 2. Map of the Yuba River study region indicating DNA sampling locations for *P. skiltonianus* (blue dots) and *P. "gilberti"* (gray dots). The outlier *P. skiltonianus* locality south of the Yuba River represents a high elevation population at Red Point, Placer Co. (~1430 m), first published in Rodgers and Fitch (1947) and revisited during this study. Several additional high elevation populations from this region referred to as either *P. skiltonianus* or *P. "gilberti"* in museum collections have not yet been sequenced and require taxonomic attention.

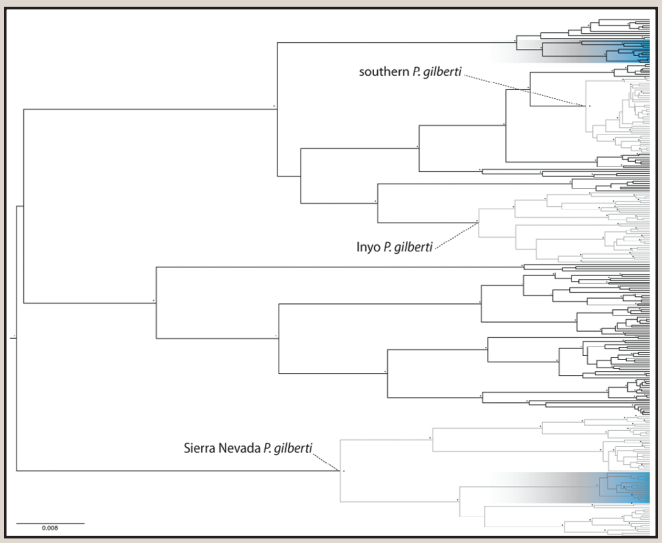

FIG. 3. Maximum clade credibility tree for ND4 mitochondrial haplotypes within the *P. skiltonianus* group; the tree was estimated using a model partitioned Bayesian analysis in BEAST v1.7 (Drummond et al. 2012; 20×10^6 iterations with a 10% burn-in). Gray branches denote separate "*gilberti*" lineages; black branches denote *P. skiltonianus*/*P. lagunensis*. Bullets indicate posterior probabilities ≥ 0.95. Shaded blue-gray boxes highlight haplotypes recovered on the north (*P. skiltonianus*) and south sides (Sierra Nevada "*gilberti*") of the Yuba River, California.

Macey and Papenfuss 1991; Rodgers and Fitch 1947; Smith 1946; Smith and Brodie 1982; Stebbins 2003; Stebbins and McGinnis 2012; Storer et al. 2004; Tanner 1957, 1988). However, like the other characters used to differentiate *P. skiltonianus* and "*gilberti*," we have detected notable variation in the extension of the lateral tail stripe in populations of both species, and below we present data that describe how the character fails to differentiate the two in certain parts of the range.

During recent survey work on *Plestiodon* populations in the western foothills of the northern Sierra Nevada in Yuba County, California, we discovered what appeared to be juvenile *P. skiltonianus* just south of the Yuba River in an area that is reported to be exclusive to "*gilberti*," based on the bright blue tail color and the continuation of the dark lateral stripe well past the hindlimbs (Rodgers and Fitch 1947). A longstanding notion exists that *P. skiltonianus* is essentially restricted to the north side of the river, which runs perpendicular to the Sierra Nevada, and that the range of "*gilberti*" extends north to the Yuba River from the south but does not cross it (Rodgers 1944; Rodgers and Fitch 1947; Stebbins 2003; Fig. 2). Only four isolated *P. skiltonianus* populations have been formally documented from the immediate south side of the Yuba River (Rodgers and Fitch 1947; specimens MVZ 190472,190479; this study), occurring mainly in the conifer zone at approximately 900–1450 m, whereas "*gilberti*" occurs at lower elevation in blue oak woodland and grassland only on the south side of the river. This purported distribution is perplexing, as there are no salient habitat differences on either side of Yuba River, and none of the other major river drainages south of Yuba County have presented barriers that limit the distribution of "*gilberti*" along the western slope of the Sierra Nevada (although they may have intermittently in the past). Thus, we were not surprised to find *P. skiltonianus* south of the Yuba River. Because both species were expected to have blue-tailed juveniles and scale counts were ambiguous, our identification of juvenile specimens relied mainly on the degree to which the dark, lateral stripe extended onto the tail.

To confirm our identifications, we extracted DNA from small tail clips (~ 10.0 mm) preserved in 95% ethanol from 28 individuals and sequenced 16 for their ND4 mitochondrial haplotypes (~1500 bp: Dryad repository: doi:10.5061/dryad.2873b). We then compared these sequences to a large ND4 dataset representing the entire range of the *P. skiltonianus* complex (Fig. 3). *Plestiodon skiltonianus* and "*gilberti*" in Yuba County (the latter regarded as *P. g. placerensis*; de Quieroz and Reeder 2012) have high mitochondrial sequence divergence and are easily distinguishable based on their haplotypes (Richmond and Jockusch 2007; Richmond and Reeder 2002). Surprisingly, we found that all skinks sampled on the south side of the Yuba River below 1430 m had

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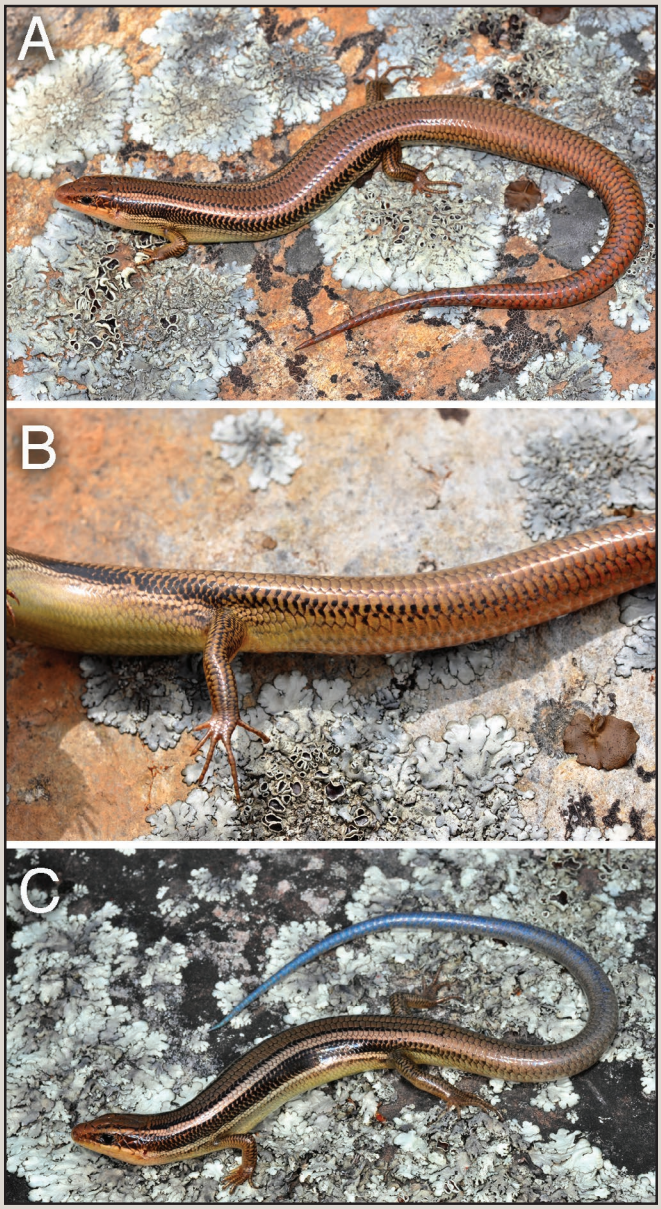

FIG. 4. A) Adult female "*gilberti*" found just south of the Yuba River, California (ca. 100 m elev.). B) Closer, lateral view of the tail (female A), illustrating retention of the lateral stripe and its extension past the hind limb. C) Young adult female "*gilberti*" from this same locality showing the light dorsolateral striping and the dark, lateral tail striping extending well past the hindlimbs, similar to *P. skiltonianus*.

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FIG. 5. A) Juvenile *Plestiodon skiltonianus* from just north of the Yuba River, California (ca. 265 m elev.); B) Juvenile "*gilberti*" from just south of Yuba River (ca. 100 m elev.); C) Juvenile "*gilberti*" from Tuolumne County, California (ca. 785 m elev.) showing lateral tail stripe stopping closer to the hind limbs, but still extending notably past them.

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Sierran "*gilberti*" haplotypes, and all those sampled on the north side of the river regardless of elevation had pure *P. skiltonianus* haplotypes, consistent with the supposition of Rodgers (1944) and Rodgers and Fitch (1947). We also noted that while adult male "*gilberti*" in this area completely lose the striped color pattern, as is generally the case for "*gilberti*," adult females retain dark lateral stripes on the flanks and well onto the tail, immediately below the area where the light dorsolateral stripe runs along the body axis in juveniles (Fig. 4; also noted in Rodgers 1944). This same pattern has been noted in other parts of the species' distribution (e.g., creeks along the eastern slopes of California's inner Coast Ranges; JQR, pers. obs.), where lateral stripes extend well beyond the hindlimbs even in some of the largest adult females. Thus, a character that is typically lost early in ontogeny in some parts of the "*gilberti*" range, or is absent altogether, is retained in adult females in other areas, particularly the northern Sierra Nevada.

In his description of *P. g. placerensis*, Rodgers (1944) did not address the lateral tail stripe character, and later accounts identifying this and other *P. gilberti* subspecies provide information about tail color (pink or blue), supralabial count, but little else (e.g., Jones and Lovich 2009; Stebbins 2003). Rodgers and Fitch (1947) provided qualitative descriptions of the ontogeny of *P. skiltonianus* and the different forms of "*gilberti*," illustrating varying degrees in the loss of the dorsolateral stripes and the bright tail color. However, variation in the extension of the dark, lateral tail stripe for "*gilberti*" was not discussed. Consistent with the descriptions of Rodgers and Fitch (1947), we have found that hatchling, juvenile, and younger adult female "*gilberti*" (Fig. 4c)

in Yuba County appear to be *P. skiltonianus* upon initial inspection; in both forms, the tail color is bright blue and the lateral tail stripe extends well beyond the hind limbs (although the stripe may continue further on the tail in *P. skiltonianus* north of the Yuba River than it does in "*gilberti*" south of the Yuba River [Fig. 5a, b]). The similarity in this character between species fades further south in the Sierra Nevada foothills (Fig. 5c), where the dark lateral stripe ends closer to the base of the tail in young "*gilberti*."

Because of the variability of this character across the range of the species complex, we consider it unreliable for distinguishing *P. skiltonianus* and "*gilberti*" over large portions of the range of the *P. skiltonianus* complex. Despite years of field collecting and DNA sequence data from hundreds of individuals (including sequences obtained from museum specimens that were incorrectly identified as *P. skiltonianus*), we have yet to recover a *P. skiltonianus* specimen from locations south of the Yuba River, with the exception of a single site at approximately 1430 m and 14 km SSE of the Yuba River, until Tulare County in the southern Sierra Nevada. We suspect that a number of museum specimens collected from this same region at lower elevation are incorrectly identified as *P. skiltonianus* and instead belong to the Sierran "*gilberti*" lineage as identified in Richmond and Reeder (2002). In fact, bright blue juvenile tail color and the continuation of the dark, lateral stripe past the hindlimbs are the two characters that appear largely responsible for these misidentifications.

Perhaps the most interesting finding of our survey work is that *P. skiltonianus* and "*gilberti*" are most similar in the ontogeny of color pattern where their distributions meet but do not overlap at the Yuba River. Yet in southern California where the two species are syntopic, for example, they are easily distinguished by juvenile and adult color pattern (*P. skiltonianus* juveniles have blue tails and light dorsal stripes throughout adulthood whereas juvenile "*gilberti*" have pink tails and no stripes as adults), and adult body size. In fact, adult body size is more divergent in southern California than anywhere else in the range of the species complex, and is a predominant factor contributing to their reproductive isolation (Richmond and Jockusch 2007; Richmond et al. 2011). This suggests that sympatry in southern California may have influenced phenotypic divergence of the two forms, whereas allopatry in the northern Sierra Nevada may have contributed to retention of the ancestral juvenile color pattern.

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