

THE TAXONOMIC STATUS OF *BOLITOGLOSSA RESPLENDENS* (AMPHIBIA: CAUDATA)

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ABSTRACT: Electrophoretic analysis of Chiapan populations of *Bolitoglossa resplendens* reveals great similarity to Guatemalan populations of the morphologically similar *B. lincolni*. Study of additional specimens from populations of salamanders in the Cuilco Mountains of Guatemala reveals greater genetic variability than detected previously. Accordingly, *B. resplendens* is considered to be a junior synonym of *B. lincolni*.

Key words: Taxonomy; Allozymes; *Bolitoglossa resplendens*; *Bolitoglossa lincolni*; *Bolitoglossa franklini*

THE *Bolitoglossa franklini* group includes four species of plethodontid salamanders that occur in isolated areas of humid, montane forest in Guatemala and adjacent Chiapas, Mexico (Wake and Lynch, 1976, 1982). In a recent revision of the group (Wake and Lynch, 1982), we described *B. meliana*, a distinctive all-black species that occurs in the geologically ancient mountains of central Guatemala, and we synonymized two previously recognized species (*B. brevipes* and *B. nigroflavescens*) under *B. franklini*. As presently understood, *B. franklini* consists of a series of populations of moderately large, black salamanders that are marked with irregular patches of silvery, brassy, or green-white iridophores. The species occurs discontinuously in cloud forests from the eastern Sierra Madre of Chiapas to the middle portion of the Pacific escarpment of southern Guatemala. The remaining two species in the *franklini* group (*B. lincolni* and *B. resplendens*) are strikingly patterned red and black salamanders that closely resemble one another but differ in color from all other known *Bolitoglossa*.

The species-level taxonomy of neotropical plethodontids is frequently somewhat arbitrary, because many of these salamanders occur as montane isolates separated by unsuitable lowland habitat. Closely related forms are almost always allopatric, and each isolate tends to exhibit a distinctive combination of genetic and morpho-

logical traits, a reflection of longstanding isolation (Wake and Lynch, 1982). Thus, Stuart (1943) described *B. lincolni* from the isolated Sierra de los Cuchumatanes of northwestern Guatemala, and McCoy and Walker (1966) described the very similar *B. resplendens* as a distinct species that is endemic to the Meseta Central of Chiapas, Mexico. During the early 1970's, we discovered two new populations of red and black *Bolitoglossa* that were morphologically similar to what may be termed the *lincolni-resplendens* complex. One of the new populations inhabits the isolated Montañas de Cuilco of western Guatemala; the other occurs in a limited area along the Pacific escarpment of Guatemala, in the vicinity of San Marcos. At the time of our 1976 monograph, no specimens of *B. lincolni* had been collected since the time of Stuart's (1943) original description, and we tentatively assigned both new populations to the better-known *B. resplendens* (Wake and Lynch, 1976). Subsequently, Paul Elias succeeded in obtaining a fresh series of *B. lincolni* from the Cuchumatanes, and based on his morphometric comparison of specimens from all four of the red and black populations, he recommended that *B. resplendens* be reduced to a junior synonym of *B. lincolni* (Elias, 1984). An electrophoretic survey of the *franklini* group (Wake and Lynch, 1982) revealed a moderately high degree of genetic similarity among all of the species except *B. meliana*,

TABLE 1.—Allozyme frequencies at 15 loci in four populations previously referred to *B. lincolni* and *B. resplendens*, and one population of *B. franklini nigroflavescens*. Samples 2 and 3 are from Cuilco populations previously referred to *B. resplendens*. The most slowly migrating band is designated "a." Abbreviations are those used by Wake and Lynch (1982).

Locus	Sample*				
	1	2	3	4	5
Mpi	a (0.21) b (0.79)	b	b	b	a (0.05) b (0.95)
Gpd	a	a	a	a	a
Me	a	a	a	a	a (0.55) b (0.45)
Pgd	b	c	b	b	a (0.35) b (0.40) c (0.25)
Icd-1	a	a	a	a	a
Icd-2	b (0.93) c (0.07)	c	a (0.67) b (0.33)	c	b
Mdh-1	b	a	a	b	b
Mdh-2	a (0.71) d (0.29)	a	a (0.17) b (0.83)	a	a (0.90) c (0.10)
Gpi	b	b (0.50) c (0.50)	b (0.50) c (0.50)	b (0.93) c (0.07)	a (0.10) b (0.80) c (0.10)
Ldh-1	b (0.71) c (0.29)	b (0.50) c (0.50)	b (0.83) c (0.17)	c	a (0.20) c (0.80)
Ldh-2	a	a (0.57) b (0.43)	a	a	a
Got-1	b	b	b (0.83) c (0.17)	b (0.64) d? (0.36)	a (0.05) b (0.90) d? (0.05)
Got-2	b	b	a (0.33) b (0.67)	b	b
Sod	a	a	a	a	a
Pept	a	a	a	a	a

* 1 = *B. lincolni*, Uspantán, El Quiché, Guatemala (n = 7); 2 = *B. resplendens*, Montañas de Cuilco, 10 km W and 8.5 km S of La Democracia (by air), Huehuetenango, Guatemala (n = 7); 3 = Montañas de Cuilco, Planes de Peña Blanca, 1.5 km NE Peña Blanca, Huehuetenango, Guatemala (n = 3); 4 = *B. resplendens*, Meseta Central de Chiapas, Chiapas, Mexico (n = 7; for Got-1, n = 6); 5 = *B. franklini nigroflavescens*, S Motozintla, Chiapas, Mexico (n = 10).

and led us to advocate the suppression of *B. nigroflavescens* and *B. brevipes*. At that time, we noted the marked morphological similarity between *B. resplendens* and *B. lincolni*, but we deferred any formal taxonomic action because of the absence of tissue samples from the topotypic population of *B. resplendens* in the Meseta Central of Chiapas. An additional complication in interpreting the genetic relatedness of *franklini*-group populations stems from the fact that hybridization is known to occur between *B. franklini* and putative *B. resplendens* along a narrow, secondary contact zone near San Marcos, Guatemala

(Wake et al., 1980). Such hybridization, if in fact it occurs (or occurred in the past) elsewhere within the range of the *franklini*-group, may explain the anomalously high genetic similarities that we documented between some populations of *B. franklini* and *B. lincolni* or *B. resplendens* (Wake and Lynch, 1982).

After several futile attempts to obtain topotypic *B. resplendens* from the Chiapan highlands, J.F.L. and Theodore J. Papenfuss succeeded in collecting the species from two closely spaced localities in the Meseta Central, 6.4–8.4 km north of Chamula along the road to Pantelho. The sal-

amanders, which co-occurred with *B. hartwegi*, were dug out of dirt banks at elevations of 2200–2310 m in areas of heavily disturbed oak and oak–pine forest. The native vegetation at the two collecting sites closely resembled the habitat of *B. resplendens* near San Marcos, Guatemala (Wake and Lynch, 1976). Through the efforts of Paul Elias, we also have obtained additional specimens of *B. resplendens* from the Cuilco mountains. Although the new Cuilco specimens are from a different population than that studied by Wake and Lynch (1982), the two populations are within a few kilometers of each other. In an attempt to finally resolve the question of the validity of *B. resplendens*, we used starch gel electrophoresis to compare allozyme frequencies in the four known isolates of the *resplendens-lincolni* complex. We included an additional sample of *B. franklini nigroflavescens* in our survey for comparative purposes. Our methods were the same as those described in Wake and Lynch (1982). However, because our tissue samples were very small in quantity, we were severely limited in the number of comparison gels that could be run. Thus, only 15 proteins could be scored reliably in the present study (as opposed to 17 in our previous study). The proteins are listed, and our results summarized, in Table 1.

The Chiapan sample (near-topotypic *B. resplendens*) is closely similar in allozymes present to the Cuchumatan sample (near-topotypic *B. lincolni*) and also to the Cuilco population previously referred to *B. resplendens*. The larger sample size now available from the Cuilco region has revealed the presence of several previously undetected alleles, with the result that the similarity between this and the remaining red-and-black populations is higher than was evident in our 1982 study. Finally, all four populations of the *resplendens-lincolni* complex show close genetic affinities with *B. franklini*.

These new findings lead us to concur with Elias (1984) in recommending that *B. resplendens* be reduced to a junior synonym of *B. lincolni*. We know of no ob-

jective genetic or morphological basis for subspecific designation of any of the four known isolates of *B. lincolni*. In view of the close genetic relationship between the latter species and *B. franklini* (Table 1), a case could be made for synonymizing these two taxa. However, *B. franklini* differs from *B. lincolni* in color pattern (see above and Wake et al., 1980), limb proportions (*B. franklini* has longer limbs), and ecology (*B. franklini* is restricted to cloud forest, where it typically inhabits arboreal bromeliads; *B. lincolni* usually occurs at higher elevations in somewhat drier oak or oak–pine forest, and is more terrestrial). Hybridization between the two taxa is confined to a very narrow (about 100 m) band of disturbed habitat at the cloud forest-drier forest ecotone, in an area that we interpret as a secondary contact zone (Wake et al., 1980; Wake and Lynch, 1982). Limited genetic exchange between “good” biological species is widespread among plethodontid salamanders and other organisms (for a review, see Larson, 1984), and the existence of a narrow zone of hybridization does not, in our view, constitute critical evidence against the status of *B. franklini* and *B. lincolni* as valid species. The Nei genetic distance separating populations of *B. franklini* and *B. lincolni* from immediately above and below the San Marcos hybrid zone is 0.45 (Wake et al., 1980), a value that is similar to Nei distances between such well-established North American species pairs as *Plethodon glutinosus* and *P. yonahlossee*, *P. cinereus* and *P. richmondi*, or *Desmognathus fuscus* and *D. ochrophaeus* (see summary in Larson, 1984).

In summary, the *Bolitoglossa franklini* group, as presently understood, contains just three species: *B. franklini* (Schmidt, 1936), *B. lincolni* (Stuart, 1943), and *B. meliana* (Wake and Lynch, 1982).

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REDISCOVERY AND TAXONOMIC IDENTITY OF *OREODEIRA GRACILIPES* GIRARD, 1857 (LACERTILIA: AGAMIDAE)

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ABSTRACT: *Oreodeira gracilipes* Girard, 1857, a monotypic genus known from a single subadult female specimen supposedly collected in New South Wales, Australia by the U.S. Exploring Expedition, is a junior synonym of *Agama agama africana*, a subspecies based on the holotype of *Tropidolepis africanus* Hallowell, 1844, and was probably collected in Liberia, Africa. A stepwise discriminant function analysis of 19 mensurable and meristic characters classifies the holotype with specimens from Liberia, rather than with Ghana or Nigeria.

Key words: *Oreodeira gracilipes*; *Agama agama africana*; *Tropidolepis africanus*; Agamidae; Africa; Australia; Liberia

A SINGLE subadult female lizard, supposedly collected by the U.S. Exploring Expedition in New South Wales, Australia, was described by Charles Girard (1857) as a new genus and species, *Oreodeira gracilipes*. The following year (1858:419-422), he described the specimen in greater detail and placed it with the group Phrynocephali (southwestern and central Asian genus *Phrynocephalus*) of the subfamily Acrodontes of the Iguanidae: i.e., the Agamidae as recognized today.

Boulenger (1885:412-413) quoted Gi-

rard's entire original description, but he commented that until a male specimen had been obtained, taxonomic assignment within the Agamidae could not be made.

No published mention was made of this specimen until recently, when Wermuth (1967) listed it as a questionable genus and species but stated that it probably belonged to the genus *Amphibolurus* from Australia. Cogger et al. (1983) apparently confused their notes with another species, because they listed it as *Strobilurus torquatus* Wiegmann, 1834 (Iguanidae). They