Herpetologica, 45(3), 1989, 330–336

A NEW SPECIES OF *ANOLIS* (SAURIA: IGUANIDAE) FROM THE SIERRA DE NEIBA, HISPANIOLA

S. BLAIR HEDGES[1,3] AND RICHARD THOMAS[2]

[1]*Department of Zoology, University of Maryland,*
College Park, MD 20742, USA
[2]*Department of Biology, University of Puerto Rico,*
Rio Piedras, PR 00931, USA

ABSTRACT: *Anolis placidus* is described from cloud forests in the Sierra de Neiba, Dominican Republic (North Island of Hispaniola). It is the seventh member of the twig ecomorph of West Indian *Anolis*. Morphological and electrophoretic data indicate that its closest relative is *A. sheplani* from the South Island of Hispaniola.

Key words: Reptilia; Sauria; Iguanidae; *Anolis placidus* sp. nov.; Hispaniola; Dominican Republic

ANOLIS is the largest genus of amniotes, with over 300 described species [we do not recognize the genera defined in Guyer and Savage (1986) following the recommendations of Williams (1989) and Cannatella and de Queiroz (1989)]. A major center of diversity for this group is the West Indies (124 species; Schwartz and Henderson, 1988) where it has undergone large radiations on each of the four Greater Antilles.

Morphological and ecological convergence is an importance aspect of the West Indian radiations of *Anolis* (Williams, 1969, 1983). Among the different convergent types, the twig ecomorph is one of the most interesting, because it involves an unusual morphology and behavior. These species have short limbs, long snouts usually covered with enlarged scales, a relatively short prehensile tail, and cryptic coloration. Although most species of *Anolis* rely on rapid movement to escape predation, twig species rely on crypsis and will cling, motionless, to a twig or branch when disturbed.

The six described species of twig anoles are found on Jamaica (*A. valencienni*), Hispaniola (*A. darlingtoni, A. fowleri, A. insolitus*, and *A. sheplani*), and Puerto Rico (*A. occultus*). In general, their relationships have not been clearly established. Based on morphology (Williams, 1976, 1983), *A. valencienni* was placed in one group (*sagrei* series); *A. darlingtoni, A. fowleri*, and *A. insolitus* were placed in a second group (*darlingtoni* series); and *A. occultus* and *A. sheplani* in a third group (*occultus* series). New osteological data suggest that *A. occultus* belongs to a separate lineage not closely related to any of the other twig anoles (Williams, 1989). Electrophoretic (Burnell and Hedges, unpublished data) and immunological (Shochat and Dessauer, 1981) data indicate that *A. valencienni* is a member of the Jamaican radiation (*grahami* series). Also, the electrophoretic data suggest that the other twig species are not closely related, with the possible exception of *A. fowleri* and *A. insolitus*.

In this paper, we describe a seventh species of West Indian twig *Anolis*. It occurs in the Sierra de Neiba on the North Island (Hispaniola north of the Cul de Sac/ Valle de Neiba) and shows affinities with *A. sheplani* of the South Island.

In the account below, the following abbreviations are used: KU (Museum of Natural History, University of Kansas), MCZ (Museum of Comparative Zoology, Harvard University), SVL (snout–vent length), and USNM (United States National Museum of Natural History, Smithsonian Institution).

Anolis ***placidus*** sp. nov.

Fig. 1

Holotype.—USNM 286864, an adult male from approximately 10 km N Ca-

---

[3] PRESENT ADDRESS: Department of Biology, 208 Mueller Lab, Penn State University, University Park, PA 16802, USA.

cique Enriquillo (approximately 24 km N Los Pinos), Independencia Prov., Dominican Republic, 1710 m, 29 August 1984, one of a series collected by Richard Thomas and S. Blair Hedges.

Paratypes (10).—USNM 286865–868, MCZ 173209, paratopotypes; USNM 286869–870, MCZ 173208, 13 km N Cacique Enriquillo (27 km N Los Pinos), Elías Piña Prov., 1870 m, 2 July 1986, collected by Richard Thomas and S. Blair Hedges; KU 209776–777, Puesto Pirámide 204, Elías Piña Prov., 1790 m, 21–24 July 1975, collected by Michael H. Strahm and Albert Schwartz; all in the Dominican Republic.

Diagnosis.—A small species ($\bar{x}$ SVL = 43 mm males; 44 mm females) of twig *Anolis* with short limbs, long snout, short prehensile tail, and enlarged scales on dorsal surface of head. Of the other six species of West Indian twig anoles (*A. darlingtoni, A. fowleri, A. insolitus, A. occultus, A. sheplani,* and *A. valencienni*), it most closely resembles *A. sheplani* in having a strongly sexually dichromatic dewlap and a series of roughly equally-spaced spinose middorsal scales. It can be distinguished from the latter species in having a larger body size, a relatively wider head, relatively wider rows of digital lamellae, supratemporal and occipital spines present, fixed allelic differences at six allozyme loci (*Adh, Dia, Gpi, Pgm-1, Pgm-3,* and *Xdh-2*), and some modal differences in scalation (see Comparisons below).

Description.—Head: narrow and elongate; head scales large, smooth, smallest anteriorly; nostril circular; nasal scale separated from rostral by 2–3 (modally two; two in holotype) irregularly shaped scales; rostral scale wide, low, in contact with 5–8 scales posteriorly (five in holotype).

Supraorbital semicircles large, weakly convex, rugose laterally, separated by 1–2 (modally two; one in holotype) rows of scales of same size or smaller; a much less distinct row of many small scales along the supraciliary margin on each side, no elongate supraciliary; posterior and interior to the supraciliary row, three or four rows of small scales or granules of which the most interior are largest, surrounding 1–3 (modally two; two in holotype) enlarged scales in the supraorbital disc; canthal ridge of four scales well defined, second canthal longest, diminishing in size anteriorly, anteriormost posterior to nostril and separated by one small scale; loreal rows (below first canthal) 2–3 (modally three; three in holotype) with irregularly shaped scales; temporal scales small, flat, separated from supratemporal region by 1–2 (two in holotype) spines or a ridge; no enlarged supratemporal rows of scales; supratemporal scales variable in size but larger around interparietal; interparietal ovoid, about three times as long as ear opening, separated from supraorbital semicircles by 1–3 (modally two; two in holotype) scales; two clusters of spines (about 10 scales each) posterolateral to interparietal, followed by a single middorsal spine or cluster of spines; ear opening small, elliptical, placed far ventrally, just dorsal to the commissure of the mouth.

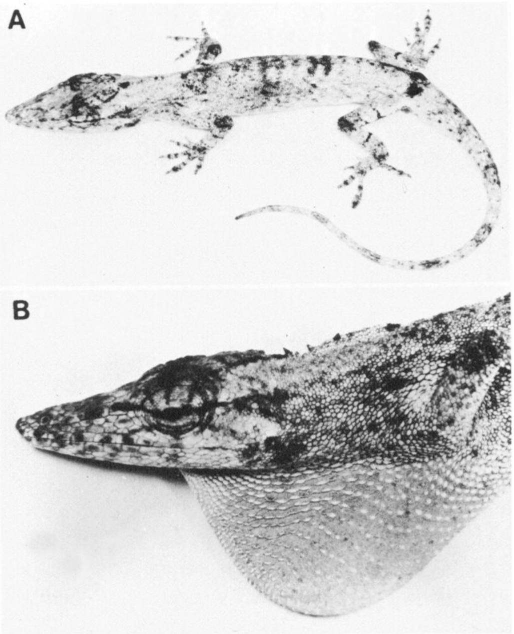

FIG. 1.—Male *Anolis placidus*: (A) body, (B) dewlap. MCZ 173208, paratype.

Suboculars directly in contact with supralabials, anteriorly grading into loreals, posteriorly continuous with the postoculars; 7–9 (eight in holotype) supralabials to center of eye; mental large, semi-divided, wider than deep, in contact with 2–4 (two in holotype) small granular postmental scales; one infralabial and one sublabial in contact with mental on each side; gulars granular, elongate anteriorly, becoming more granular and ovoid posteriorly, gradually merging with the ventral scales.

Trunk: dorsal scales small, granular, slightly larger on flanks, merging with the ventral scales; a middorsal series of individual spinose crest scales, separated by about 2–6 unmodified dorsal scales, continued onto the dorsal caudal midline; ventrals larger than dorsals; smooth, rounded, occasionally in transverse rows.

Dewlap: large, present in both sexes but smaller in females, inset; scales large and arranged in rows, larger than throat scales and about the same size as ventrals; marginal dewlap scales crowded and about the same size as throat scales adjacent to dewlap.

Limbs and digits: limbs short, tibial length shorter than distance from tip of snout to center of eye; 14–18 (18 in holotype) lamellae under phalanges II and III of fourth toe; scales of limbs smooth dorsally, granular ventrally, those on anterior surface of limb slightly enlarged; supradigital scales smooth.

Tail: laterally compressed with shallow groove on each side extending about ½ length of tail (anteriorly); a median series of spinose and keeled scales, their apices directed posteriorly, separated from each other by about 2–4 smaller keeled dorsal caudal scales; two enlarged postanal scales in males; scales behind vent and around base of tail smooth; 4–5 (four in holotype) ventral rows of strongly keeled scales.

Coloration (in life): general coloration pale gray with black and brown lichenate markings (darker gray or brown when active or disturbed); 3–4 faint dark brown or black crossbands or blotches on body, 5–7 more distinct brown bands on tail; two black blotches above pelvic region; middorsal spines black; about eight narrow dark brown lines radiating from eye; temporal blotch and blotch posteroventral to ear opening black; narrow bands on legs brown; dewlap in males, pale peach anteriorly and centrally, grading to light yellow-green posteriorly; in females, dark brown with a cream border.

Measurements (holotype in parentheses).—SVL 39.4–45.3 (45.3), $\bar{x} = 42.9$ mm males; 41.1–45.9, $\bar{x} = 43.5$ mm females; tail 39.0–49.9 (49.9), $\bar{x} = 44.7$ mm males; 39.3–47.0, $\bar{x} = 42.7$ mm females; live weight 0.8–1.4, $\bar{x} = 1.0$ g males ($n = 4$); 0.9–1.4, $\bar{x} = 1.1$ g females ($n = 3$).

Comparisons.—*Anolis placidus* is a member of the twig ecomorph of *Anolis*, and therefore the relevant comparisons are with those six species. Although it is recognized that most are morphologically convergent (Williams, 1983), they are the species most likely to be confused with *A. placidus*. From *A. darlingtoni*, *A. fowleri*, and *A. valencienni*, the twig "giants" (SVL = 70–80 mm), it can be distinguished by smaller size and inset dewlap. Of the three other small (dwarf) species of twig anoles (*A. insolitus*, *A. occultus*, and *A. sheplani*), it most closely resembles *A. sheplani* in having a strongly sexually dichromatic dewlap and a series of roughly equally-spaced spinose middorsal scales, each separated by about 2–6 unmodified scales.

From its closest relative, *A. sheplani*, it can be distinguished by a larger body size ($\bar{x}$ SVL = 43 mm males, 44 mm females in *A. placidus*; 38 mm males, 39 mm females in *A. sheplani*), a relatively wider head (Fig. 2), relatively wider rows of digital lamellae, the presence of supratemporal and occipital spines, and fixed allelic differences at six allozyme loci (*Adh*, *Dia*, *Gpi*, *Pgm-1*, *Pgm-3*, and *Xdh-2*; see below). Scale characters which can distinguish most *A. placidus* from most *A. sheplani* are: modally three (2–3) loreal scale rows below the first canthal [modally two (2–3) in *A. sheplani*], modally two (1–2) scales between supraoccular semicircles at narrowest point [modally one (0–2) in *A. sheplani*], modally two (1–3) scales between interparietal and supraoccular semicircles [modally one (0–2) in *A. sheplani*], modally two (1–3) enlarged scales in supraorbital disk (one in *A. sheplani*), and modally two (2–3) scales between nasal and rostral [modally three (2–3) in *A. sheplani*] (Fig. 2). The most consistent scale difference involves the loreal rows: all specimens of *A. placidus* have three loreal rows below the first canthal, although in one specimen, there are two rows on one side of the head. Likewise, all specimens of *A. sheplani* have two loreal rows, although in three of those specimens, there are three rows on one side. In combination, these modal scale differences clearly distinguish all specimens of *A. placidus* from *A. sheplani.*

Electrophoresis.—Although *A. placidus* can be distinguished morphologically from *A. sheplani,* it is similar enough that its taxonomic status might be questioned. Genetic distance (Nei, 1972) provides an independent criterion for deciding whether or not two allopatric populations should be recognized as conspecific or different species (Thorpe, 1982). Fixed differences (no shared alleles) between populations, as opposed to allelic frequency differences, suggest that gene flow is restricted or absent.

One of us (SBH) therefore examined these two species and *A. insolitus,* the other Hispaniolan dwarf twig anole, at 38 protein loci. Details of the methodology are presented elsewhere (Hedges, 1986). Five individuals of each species were examined: *A. insolitus* (USNM 286903–904, and three tissue vouchers), *A. placidus* (USNM 286865–868, MCZ 173209), and *A. sheplani* (USNM 286891–893, and two tissue vouchers).

In the account below, alleles are indicated as S (slow), M (medium), or F (fast), depending on relative mobility. All three species were identical at the following nine loci: *Acp, Apep, Ck-1, Glud, Icd-1, Ldh-2, Lgl-1, Pt-2,* and *Pt-4.* There were fixed differences at six loci [*Adh* (M, F = *A. sheplani*/S = *A. placidus*), *Dia* (F/S), *Gpi* (S/M, F), *Pgm-1* (S/F), *Pgm-3* (F/S), and *Xdh-2* (F/S)] and frequency differences at four other loci [*Dpep* (F:1.0/S:0.1, M:0.6, F:0.3), *Icd-2* (S:1.0/S:0.6, F:0.4), *Mpi* (S:1.0/S:0.9, F:0.1), and *Xdh-1* (S:0.6, F: 0.4/S:0.8, F:0.2)] between *A. sheplani* and *A. placidus* resulting in a *D* (Nei, 1972) of 0.20. Both *A. sheplani* and *A. placidus* differed (no shared alleles) from *A. insolitus* at 23 loci: *Aat-1, Aat-2, Adh, Ak, Ck-2, Cr, Gpd, Gpi, Icd-2, Ldh-1, Lgl-2, Mdh-1, Me-1, Me-2, Pgd, Pk, Pt-1, Pt-3, Pt-5, Pt-6, Pt-7, Sod,* and *Xdh-1.* There were three additional fixed differences (*Dpep, Mpi,* and *Pgm-1*) and no frequency differences between *A. insolitus* and *A. sheplani* resulting in a *D* of 1.15. There were three additional fixed differences (*Dia, Pgm-3,* and *Xdh-2*) and frequency differences at three loci (*Dpep, Mpi,* and *Pgm-1*) between *A. insolitus* and *A. placidus* resulting in a *D* of 1.34. The large genetic distance between *A. insolitus* and *A. sheplani* agrees with the results of a study using only slow-evolving loci (Burnell and Hedges, unpublished data) where those two species were not found to be closely related (*A. placidus* was not examined in that study). The genetic distance between *A. sheplani* and *A. placidus* (0.20) is typical of closely related species (Thorpe, 1982) and provides supporting evidence for recognizing them as different species. Also, the six fixed differences can be added to the scale characters as diagnostic differences separating the two taxa. In the above comparison, sequential electrophoresis (Coyne, 1982)

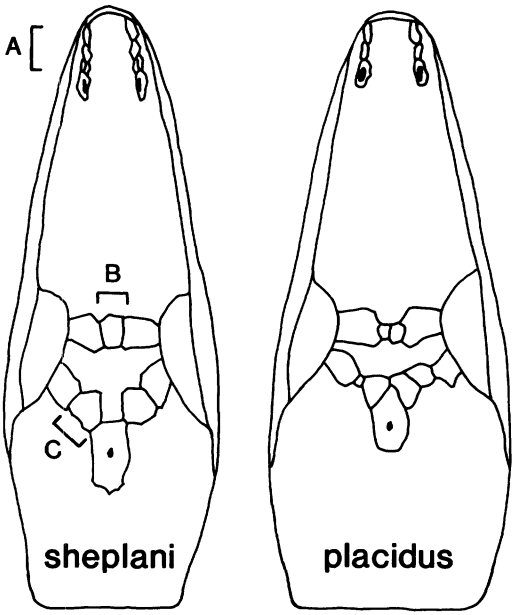

FIG. 2.—Head profiles and scalation in *Anolis sheplani* (USNM 194015) and *A. placidus* (MCZ 173208) illustrating differences. (A) scales between naris and rostral, (B) scales between supraorbital semicircles, and (C) scales between supraorbital semicircles and interparietal.

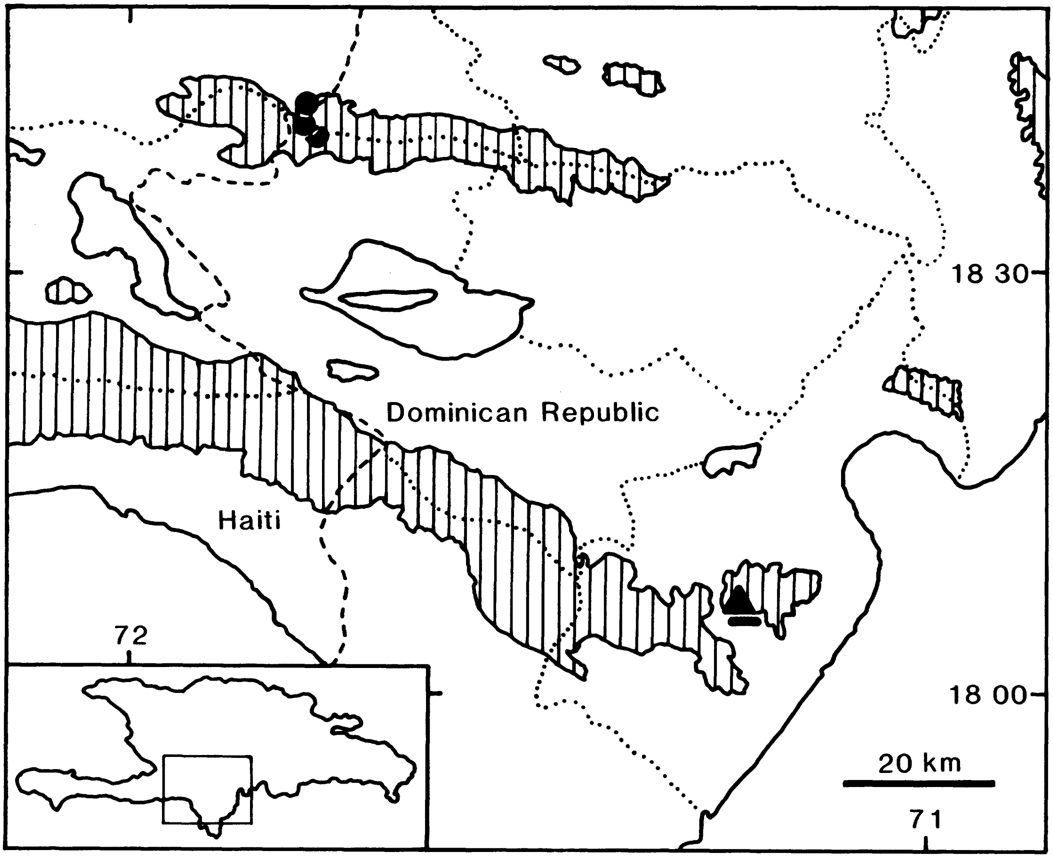

FIG. 3.—Southern Hispaniola, showing locality records for *Anolis placidus* (circles) in the Sierra de Neiba and *A. sheplani* (triangles) in the Sierra de Baoruco. Dashed line is border between Haiti and the Dominican Republic, dotted lines are political subdivisions (approximate) within those countries, and vertical lines indicate areas above 1000 m.

was not used, and therefore it is likely that there are additional allelic differences between *A. placidus* and *A. sheplani*.

Distribution.—Known from only three localities (Fig. 3) in the Sierra de Neiba, Dominican Republic (Hispaniola): the type locality (Independencia Prov.), 13 km N Cacique Enriquillo (27 km N Los Pinos), and Puesto Pirámide 204 (Elías Piña Prov.). Altitudinal range 1710–1900 m.

Etymology.—Latin: *placidus*, quiet, still; in allusion to the cryptic behavior of this species and other twig anoles—clinging (motionless) to twigs or branches when disturbed.

Natural history.—*Anolis placidus* occurs in cloud forests near the crest of the Sierra de Neiba (Dominican Republic). Only one road crosses the mountain range, close to the border with Haiti, and the three known localities for *A. placidus* are along this road.

From the south, the border road begins its ascent of the Sierra de Neiba in La Descubierta and passes north through Los Pinos and Angel Felix. From there, it turns to the west and approaches the Haitian border at Cacique Enriquillo (1300 m), a military outpost, before ascending to the northeast, eventually reaching a limestone plateau at an elevation of 1700–1900 m. The road passes by another military outpost (Puesto Pirámide 204) just before the steep descent on the north slope. *Anolis placidus* was taken in cloud forest at three localities on that limestone platform, which forms the crest of the Sierra de Neiba.

All specimens except one were collected

at night while sleeping 1–3 m above the ground on vines and twigs of bushes or trees next to the road. When collected, they remained tightly fastened to the twig and often had to be pried loose. One individual (KU 209776) was found hopping across the road during a heavy rain in the late afternoon. In daylight, we observed captive specimens (collected the previous night) "squirrelling": orienting their bodies on the opposite side of the twig from a disturbance such as a moving hand. In other *Anolis* species, squirrelling usually involves moving around the trunk or large branch of a tree, but in *A. placidus*, the animal rotates around the twig. In doing so, it keeps its body exactly opposite the disturbance but without visible movement of the limbs. A similar behavior was noted for *A. insolitus* (Williams and Rand, 1969).

Remarks.—*Anolis placidus* may occur throughout the Sierra de Neiba in suitable habitat. However, its close relative, *A. sheplani*, does not appear to be continuously distributed in the Sierra de Baoruco. We have searched suitable habitat in several areas on the eastern (S of La Guazara) and western (Los Arroyos to El Aguacate) ends of that range unsuccessfully. A major difficulty in defining the ranges of these and other species restricted to montane areas in Hispaniola is the limited number of roads accessing the upper elevations. Other nearby areas where twig anoles have not yet been found, but may occur, are the Massif de la Selle and the Sierra Martin Garcia.

The close morphological and electrophoretic similarity between *A. placidus* and *A. sheplani* indicates that they are sister species. However, the relationship of this pair of species to other *Anolis* is unclear. Based on this, *A. sheplani* and *A. placidus* are best placed in their own series, the *sheplani* series.

Acknowledgments.—For collecting permits and general support, we thank G. Hermatin, E. Magny, P. Paryski, R. Pierre-Louis, and F. Sergile (Haiti); S. and Y. Incháustegui (Dominican Republic), and E. Cardona (Puerto Rico). A. Schwartz kindly loaned us comparative material and G. Zug allowed us to examine the holotype of *A. sheplani*. C. Hass, R. Highton, A. Schwartz, and E. Williams offered helpful comments on the manuscript. Support for the field and laboratory (electrophoresis) work was provided by the National Science Foundation (grant BSR-83-07115 to R. Highton).

LITERATURE CITED

CANNATELLA, D. C., AND K. DE QUEIROZ. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? Syst. Zool. 38:57–69.

COYNE, J. A. 1982. Gel electrophoresis and cryptic protein variation. Isozymes: Current Topics Biol. Med. Res. 6:1–32.

GUYER, C., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35:509–531.

HEDGES, S. B. 1986. An electrophoretic analysis of Holarctic hylid frog evolution. Syst. Zool. 35:1–21.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–291.

SCHWARTZ, A., AND R. W. HENDERSON. 1988. West Indian amphibians and reptiles: A checklist. Milwaukee Publ. Mus. Contrib. Biol. Geol. 74:1–264.

SHOCHAT, D., AND H. C. DESSAUER. 1981. Comparative immunological study of albumins of *Anolis* lizards of the Caribbean islands. Comp. Biochem. Physiol. 68A:67–73.

THORPE, J. P. 1982. The molecular clock hypothesis: Biochemical evolution, genetic differentiation, and systematics. Ann. Rev. Ecol. Syst. 13:139–168.

WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Q. Rev. Biol. 44:345–389.

———. 1976. West Indian anoles: A taxonomic and evolutionary summary. 1. Introduction and a species list. Breviora 440:1–21.

———. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard Ecology. Harvard University Press, Cambridge.

———. 1989. A critique of Guyer and Savage (1986): Cladistic relationships among anoles (Sauria: Iguanidae). In press. *In* C. A. Woods (Ed.), Biogeography of the West Indies: Past, Present, and Future. Sand Hills Crane Press, Gainesville, Florida.

WILLIAMS, E. E., AND A. S. RAND. 1969. *Anolis insolitus*, a new dwarf anole of zoogeographic importance from the mountains of the Dominican Republic. Breviora 326:1–21.

Accepted: 18 November 1988
Associate Editor: John Iverson

APPENDIX I

Specimens Examined

Anolis darlingtoni (2).—HAITI: Dept. de la Grande Anse, 11.2 km S, 1.9 km E (airline) Marché Léon, 1360 m, USNM 286898–899.

Anolis fowleri (2).—DOMINICAN REPUBLIC: Peravia Prov., 13 km NW La Horma, 1770 m, USNM 266303–304.

Anolis insolitus (9).—DOMINICAN REPUBLIC: Elías Piña Prov., N slope of Loma Nalga de Maco, 1270 m, USNM 286884–887; La Vega Prov., 10.5 km NW La Horma, 1645 m, USNM 286903–904; 13.2 km NW La Horma, 1770 m, USNM 286888–889.

Anolis occultus (4).—PUERTO RICO: El Yunque, vic. of University of Puerto Rico Biology House, USNM 286827–830.

Anolis sheplani (11).—DOMINICAN REPUBLIC: Barahona Prov., 19.7 km SE Cabral, 1007 m, KU 209770–774 (paratypes); 20.8 km SE Cabral, 976 m, KU 209769 (paratype), USNM 194015 (holotype), USNM 194016–017 (paratypes), USNM 286891–893; 18 km SW Cabral, 818 m, KU 209775.

Anolis valencienni (2).—JAMAICA: Trelawny Parish, vic. of Quick Step, 395 m, USNM 286860.

Herpetologica, 45(3), 1989, 336–343

A BIOCHEMICAL AND MORPHOLOGICAL STUDY OF *RANA* (ANURA: RANIDAE) FROM THE CHIMBU PROVINCE, PAPUA NEW GUINEA

S. C. DONNELLAN[1], M. ADAMS[1], AND K. P. APLIN[2]

[1]*Evolutionary Biology Unit, South Australian Museum,*
Adelaide, Australia, 5000
[2]*School of Zoology, University of New South Wales,*
Kensington, Australia, 2033

ABSTRACT: Allozyme electrophoresis was used to delineate species boundaries among 46 specimens of *Rana* from seven locations in the Chimbu and Central provinces of Papua New Guinea. The study revealed five genetic groups, most of which are sympatric. These correspond to a minimum of five biological species. Discriminant function analysis of external meristics differentiated these species and provided a means of identifying further specimens from the Chimbu Province.

Key words: *Rana*; New Guinea; Electrophoresis; Discriminant function; Taxonomy

FROGS of the genus *Rana* from Papua New Guinea are remarkably conservative at the morphological level. Nevertheless, the existence of considerable variation in ecological parameters and male call indicate that a number of species is involved (Menzies, 1975).

The most recent attempt at a taxonomic revision of *Rana* in Papua New Guinea is that of Menzies (1987). His field studies revealed "ecospecies" of *Rana* distinguishable by habitat and call of the male, and subsequent discriminant function analysis of specimens assigned to these "ecospecies" seemed to confirm specific status of many of these forms. Menzies (1987) recognized 10 species of *Rana* in mainland Papua New Guinea and provided a key for identification.

However, there are some problems with this analysis. Following discriminant function analysis, there was overlap among some species suggesting that identification based on "ecotype" may not be totally adequate, or that additional cryptic species may be involved. Moreover, as Menzies (1987) pointed out, no species can be identified using morphological characters alone, and ecological data are necessary for positive identification. Unfortunately, male *Rana* are difficult to catch in a way that unequivocally associates a specimen with a call.

Clearly a full understanding of the species-level taxonomy of *Rana* in New Guinea requires some method for assigning specimens of either sex to biological species. Allozyme electrophoresis has the potential for providing such definition (Richardson et al., 1986).

During 1984, we obtained frozen tissues from 46 specimens of *Rana* collected in the Chimbu Province. While allozyme electrophoresis of such a small sample from such a limited geographic area could not possibly totally solve the taxonomic prob-