

## Analysis of Energy Expenditure of *Anolis* Lizards in Relation to Thermal and Structural Niches: Phylogenetically Independent Comparisons

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**ABSTRACT.**—Evidence suggests that coevolution of a suite of ecological, behavioral, morphological, and physiological traits has accompanied the elaboration of niches of Caribbean *Anolis* lizards. Yet, information is lacking as to the extent to which energy expenditure is coadapted with the thermal or structural niche. I tested the prediction that body mass and standard metabolic rate (SMR) would covary with the thermal or structural niche of *Anolis* lizards. An analysis of standardized independent contrasts indicated that lizards occupying cooler thermal niches (at higher elevations) had relatively low mass-independent energy costs. Mass-independent SMR at 30°C was significantly related to the species' thermal niche ( $r = 0.88$ ,  $P = 0.02$ ). Other associations with structural niche and body mass were suggested. Possible causes of shifts in energy expenditure with changes in niche are discussed.

Lizards in Caribbean *Anolis* communities occupy a diversity of structural and thermal niches (Schoener, 1969, 1970; Lister, 1976a,b; Losos 1992, 1994; Roughgarden, 1995) and have been described as an array of ecomorphs, morphological types associated with different roles in ecological communities (Williams, 1972, 1983). In Puerto Rico *Anolis gundlachi*, *Anolis krugi*, and *Anolis evermanni* are components of the upland fauna and *Anolis pulchellus*, *Anolis poncensis*, *Anolis cristatellus*, and *Anolis stratulus* are components of the lowland fauna (Rand, 1964; Schoener and Schoener, 1971). There are clear genetic differences among these species (Gorman et al., 1968, 1980, 1983; Wyles and Gorman, 1980; Shochat and Dessauer, 1981; Burnell and Hedges, 1990; Losos, 1990b). Thus, Puerto Rican *Anolis* exhibit interspecific variation in their functional morphology (Losos and Sinervo, 1989; Losos, 1990b,c,d; Beuttell and Losos, 1999) and behavior (Clark and Gillingham, 1990; Kiestler et al., 1975; Losos, 1990b; Leal et al., 1998). There are also interspecific differences in their thermal tolerances (Heatwole et al., 1969; Gorman and Hillman, 1977; Rogowitz, 1996a) and ability to withstand water loss (Heatwole and Veron, 1977; Hillman and Gorman, 1977; Hertz 1980): anoles of the cooler uplands are the least able to tolerate hot, dry conditions (Hertz, 1979; Hertz et al., 1979). In addition, Puerto Rican lizards differ in their habitat selectivity (Lister, 1981; Reagan, 1992), thermal preferences (Rand, 1964; Huey and Webster, 1976), and thermal niche

breadths (range of temperature used for daytime activity; Huey and Webster, 1976; Hertz, 1983, 1992a,b).

Given this genetic, morphological, and behavioral variation, I predicted that energy expenditures would also vary among species. Many of the studies cited above show that *Anolis* species differ in structural niche (using different portions of the tree trunk and adjacent ground area) and thermal niche (using warm-sunny or cool-shaded sites at different elevations). Considering that there likely have been multiple axes of niche diversification among species (Williams, 1972, 1983; Losos, 1994; Roughgarden, 1995), I conjectured that energy expenditures of lizards may have changed during the process of elaboration of thermal or structural niches. Ultimately, the energy expenditures of these lizards should reflect their functional roles in ecological communities. Energy expenditures for maintenance or activity may be increased in environments where there is a high predation risk or a high cost of acquiring or assimilating food. Time and energy budgets may also change as species adapt to thermal or structural niches. Moreover, shifts in different types of energy expenditures, including costs of maintenance and activity, may coincide owing to genetic correlation (Bennett and Ruben, 1979).

In this study, I compared body masses and mass-independent energy expenditures among six Puerto Rican *Anolis* species. I measured standard metabolic rates, which provide a reasonable estimation of costs of maintenance, given that these lizards are typically inactive for long periods of the day in a "sit-and-wait" foraging mode. Note, however, that even during extended periods of inactivity these lizards remain alert

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to conspecifics, predators, and prey in their immediate environment (Roughgarden, 1995; Leal et al., 1998).

#### MATERIALS AND METHODS

*Subjects.*—I selected six Puerto Rican *Anolis* species for study based on known differences in their ecology, morphology, and behavior (see Schwartz and Henderson, 1991; and references cited above). These species have been classified previously by ecomorph type (Williams, 1972, 1983; indicated in parentheses). The robust-bodied *A. gundlachi* (trunk-ground) occupies the lower portion of trees in shaded, montane rain forests of Puerto Rico (Rand, 1964; Lister, 1981, Reagan, 1992). Despite relatively cool temperatures in its upland habitats, these lizards show no preference for relatively warm, sunny sites, even though the occupation of warmer sites has a general effect in lizards of increasing locomotor ability and other measures of ecological performance (Huey and Webster, 1976; Hertz 1981, 1983, 1992b). By contrast, *A. cristatellus* (trunk-ground) actively selects warm, sunny sites of woodlands and forest edges (Rand, 1964; Huey and Webster, 1976; Lister, 1976a; Hertz 1992a,b). The narrowly built *A. stratulus* (trunk-crown) often rests on fine twigs near the crown of trees but can also occur on lower trunks (Rand, 1964; Lister, 1976a; Reagan, 1992). The larger *A. evermanni* (trunk-ground at some sites, trunk-crown at others) forages along rocks in streams at El Verde and frequently occurs on the lower portions of trunks at a height of < 4 m (Schoener and Schoener, 1971; Rand, 1964; Hertz, 1983; Reagan, 1992). Two other species, *A. pulchellus* and *A. krugi* (bush-grass), are slender and streamlined in appearance; these occur on shrubs, grasses, and small trees in lowland and upland areas, respectively (Rand, 1964; Kiester et al., 1975).

I collected *Anolis pulchellus* from shrub-grassland habitat in Rio Piedras, Puerto Rico (30 m elevation) and *A. evermanni*, *A. stratulus*, *A. pulchellus*, *A. krugi*, and *A. cristatellus* from mixed deciduous forest at El Verde, Puerto Rico (350–400 m elevation; Luquillo Experimental Forest). Data for *A. gundlachi*, were obtained in a previous study; lizards were collected in montane rain forest at El Verde (350–400 m, Luquillo Experimental Forest) and El Yunque (900 m) (Rogowitz, 1996a). The standard metabolic rate of *A. gundlachi* was equivalent for lizards obtained at El Verde and El Yunque (Rogowitz, 1996a).

Anoles were held individually in plastic cages (27 × 16 × 12 cm) and provided with drinking water sprayed onto cage walls. Prior to the start of experiments, they were maintained at 30°C for 14 days (Percival environmental chamber, Model I-35LL; lights on at 0600 h EST and off

at 1800 h EST). All lizards were provided with food (crickets, *Acheta domesticus*) until three days before tests began.

*Measurement of Standard Metabolic Rate.*—Standard metabolic rate (SMR) was measured at two test temperatures, 15°C and 30°C, to approximate the range of environmental temperatures in Puerto Rico. The higher of the two temperatures (30°C) is closest to the median body temperature of *Anolis* lizards during daytime activity, which varies from ~34°C at sea level to ~22°C at 800 m (the elevation range over which most species occur; Rand, 1964; Huey and Webster, 1976). At the highest sites occupied by *A. gundlachi* (elevation range: 200 m to 1150 m), body temperatures can be somewhat lower (Hertz, 1992b).

SMR was measured using an open-flow gas exchange system to continuously monitor energy expenditure. All testing occurred during daylight hours under dim illumination. Rates of O<sub>2</sub> consumption were measured for 90 min at each test temperature, following 60 min of adjustment. Lizards were observed through a hole in a blind (a barrier placed so that the lizards could not observe the investigator) to determine whether they were resting or active. Only data for anoles that remained inactive for at least 30 min during the tests were included in the dataset for resting metabolic rate.

Metabolic chambers used for these investigations (made of Perspex tubing) were sized so that they would be slightly larger than test subjects. Continuous airflow was provided via Teflon tubing affixed to ports at each end of the chambers. Each chamber was water-tight and maintained at the desired test temperature (± 0.1°C) by submergence in a water reservoir (regulated with a temperature controlled water circulator; Fisher, Model 910). Air was pumped through the chamber, dried, and CO<sub>2</sub> absorbed with Drierite and Ascarite, respectively, before passing to a flow meter (Matheson, Model E100) and O<sub>2</sub> analyzer (Applied Electrochemistry, Model S-3A/II). The analyzer was calibrated using precision gas mixtures of O<sub>2</sub>, CO<sub>2</sub>, and N<sub>2</sub> (Matheson Gas). The flow meter was calibrated using a Brooks Vol-U-Meter. A PC computer system was used for all acquisition and analysis of respirometry data (DATACAN V, Sable Systems). Standard metabolic rate (ml O<sub>2</sub>/min) was determined using Equation 4a of Withers (1977) as the lowest mean rate of O<sub>2</sub> consumption per 10-min interval of rest.

*Statistical Analysis.*—Standard least squares regression analysis was performed to examine the influence of body mass on SMR. Because SMR was strongly influenced by body mass, I calculated mass-independent values of SMR (residuals obtained from least-squares regression

of  $\log_{10}$  [SMR] on  $\log_{10}$  [body mass]). I then used ANOVA and Newman-Keuls tests for multiple comparisons of mass-independent SMR among species (significance was accepted at  $P \leq 0.05$ ). These tests were performed using Statistica-Mac (Statsoft). Mean values are given with standard errors (SEM).

*Tests of Association with Thermal or Structural Niche.*—I assigned each species a ranking of thermal niche based on detailed field observations of their body temperatures and thermal preferences (Rand, 1964; Schoener, 1971; Huey and Webster, 1976; and Hertz, 1992b). These thermal niche rankings, from warmest to coolest, were 1, *A. pulchellus*; 2, *A. cristatellus*; 3, *A. stratulus*, *A. evermanni*, *A. krugi*; 4, *A. gundlachi*. I also used an alternate ranking of thermal niche, with only 3 categories (categories 2 and 3 were merged) to evaluate the robustness of conclusions (see Results). The structural niches of *Anolis* species were ranked based on their ecomorph category: 1, grass-bush (*A. krugi*, *A. pulchellus*); 2, trunk-ground (*A. cristatellus*, *A. gundlachi*, *A. evermanni*); and 3, trunk-crown (*A. stratulus*). I also tested an alternate ranking of structural niche, with *A. evermanni* shifted to the trunk-crown category, as this habitat association occurs at some sites (perhaps because of interspecific competition).

I tested for associations of each species' thermal niche and structural niche with body mass and mass-independent SMR. These associations were examined using (1) the traditional approach of standard least-squares regression on raw means and (2) regression through the origin on standardized independent contrasts for each variable. The latter method adjusts data for lack of statistical independence among related members of a clade (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Hansen, 1996). I used the PC computer program PDTREE to obtain standardized independent contrasts and applicable diagnostics (Garland et al., 1992, 1993). Given that only six species were compared ( $N = 5$  contrasts), the contrasts provided are suggestive of relationships, but further testing will be required to provide a definitive analysis. Tests were conducted using phylogeny branch lengths of Losos (1990b) or by assuming equal branch lengths (Garland et al., 1992, 1993). Figure 1 illustrates the phylogeny with branch lengths (Losos, 1990b), which was derived from immunological and electrophoretic data (Gorman et al., 1980, 1983; Wyles and Gorman, 1980; Shochat and Dessauer, 1981).

#### RESULTS

*Species Differences in Energy Expenditure.*—Body masses and standard metabolic rates (SMR) of lizards are shown in Table 1. As ex-

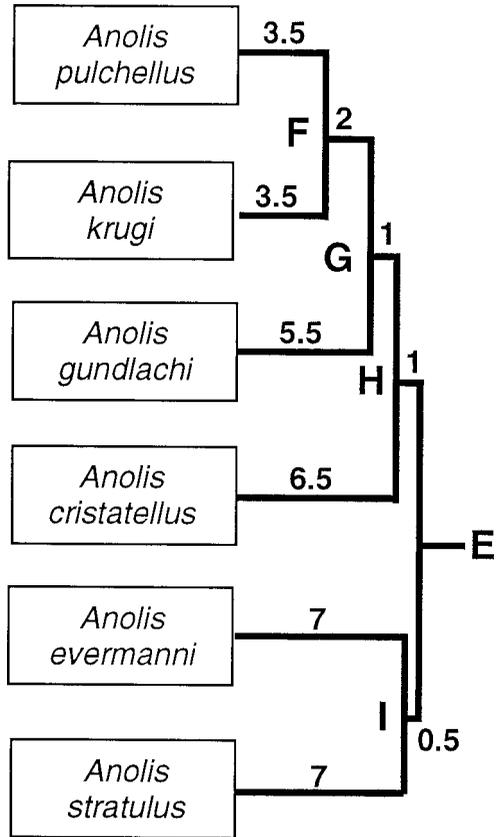


FIG. 1. Phylogenetic relationships with branch lengths for Puerto Rican *Anolis* species (after Losos, 1990b). Contrasts were determined at nodes E, F, G, H, and I.

pected, SMR values were lower at 15°C than 30°C and least for the smallest sized anoles: *A. pulchellus*, *A. krugi*, and *A. stratulus*. Figure 2 shows the influence of body mass on SMR for anoles of each species (also refer to fig. 2 of Rogowitz, 1996a). Coefficients for these relationships are given in Table 2. The general effect of body mass on SMR for all six species is illustrated in Figure 3. Regression of  $\log_{10}$  SMR (ml  $O_2$ /h) on  $\log_{10}$  body mass (g) for all lizards provided the following relationships for *Anolis* at 15°C (Eq. 1) and 30°C (Eq. 2, standard errors in parenthesis):

$$Y = -1.08 (0.044) + 0.61 (0.077) X$$

$$(r^2 = 0.57, \quad P < 0.0001) \quad (1)$$

$$Y = -0.53 (0.032) + 0.74 (0.053) X$$

$$(r^2 = 0.80, \quad P < 0.0001) \quad (2)$$

These results for Puerto Rican anoles agree with SMR values predicted for other squamate reptiles (Andrews and Pough, 1985). Using

TABLE 1. Body mass (g) and standard metabolic rate (SMR, ml O<sub>2</sub>/h) of *Anolis* lizards tested at 15°C and 30°C (mean values, SEM in parenthesis). Data for *Anolis gundlachi* are from Rogowitz (1996a). All results are for inactive, quiescent lizards. For most species, 1–3 lizards were excluded from analysis because they were never quiescent (metabolic rates were variable, with no clear minimum). For *Anolis pulchellus*, data for 11 lizards were excluded (lizards of this species seemed especially alert, judging by eye movements).

Species	15°C			30°C		
	N	Body mass	SMR	N	Body mass	SMR
<i>pulchellus</i>	9	1.6 (0.22)	0.14 (0.023)	7	1.4 (0.29)	0.52 (0.132)
<i>krugi</i>	9	1.5 (0.24)	0.14 (0.020)	11	1.6 (0.24)	0.44 (0.072)
<i>stratulus</i>	7	2.0 (0.18)	0.12 (0.019)	9	2.1 (0.20)	0.51 (0.073)
<i>evermanni</i>	8	4.9 (0.63)	0.28 (0.046)	11	4.6 (0.49)	1.06 (0.088)
<i>crisatellus</i>	10	5.1 (0.68)	0.26 (0.046)	11	5.7 (0.80)	1.31 (0.166)
<i>gundlachi</i>	15	5.9 (0.60)	0.21 (0.027)	14	7.0 (0.59)	0.99 (0.085)

equations of Andrews and Pough (1985), the predicted values for 3-g reptiles are 0.17 ml O<sub>2</sub>/h and 0.62 ml O<sub>2</sub>/h at 15°C and 30°C, respectively. Equations (1) and (2) yield similar values, 0.16 ml O<sub>2</sub>/h and 0.66 ml O<sub>2</sub>/h, respectively. Scaling coefficients for metabolic rates of Puerto Rican anoles at 15°C ( $b = 0.61$ ) and 30°C ( $b = 0.74$ ) are also in the range expected for within-family comparisons (see table 3 of Andrews and Pough, 1985).

I used mass-independent values of SMR to compare energy expenditure among *Anolis* species. Figure 4 illustrates the significant interspecific variation in mass-independent SMR at 15°C ( $P = 0.06$ ) and 30°C ( $P < 0.0003$ , ANOVA). The two forest species, *A. gundlachi* and *A. stratulus*, had the lowest mass-independent metabolic rates. At 15°C *A. gundlachi* had a lower mass-independent SMR than *A. pulchellus* ( $P = 0.023$ ), *A. krugi* ( $P = 0.011$ ) or *A. evermanni* ( $P = 0.026$ ; Newman-Keuls comparisons). At 30°C *A. gundlachi* had a lower mass-independent SMR than *A. pulchellus* ( $P = 0.001$ ), *A. cristatellus* ( $P = 0.007$ ), or *A. evermanni* ( $P = 0.013$ ), and *A. stratulus* had a lower mass-independent SMR than *A. pulchellus* ( $P = 0.021$ ).

*Association with Thermal or Structural Niche.*—Table 3 summarizes the tests of association of mass-independent SMR and body mass with thermal and structural niches of *Anolis* species. For simplicity, I refer to statistically independent contrasts as “contrasts” and mass-independent SMR as “SMR<sub>i</sub>.” Contrasts for SMR<sub>i</sub> at 30°C (a temperature appropriate for activity) were positively correlated positively with contrasts for species’ thermal niche. Correlations were significant both in tests that incorporated phylogeny branch lengths ( $r = 0.88$ ,  $P = 0.02$ ) and equal branch lengths ( $r = 0.89$ ,  $P = 0.02$ ; Table 3). In tests using alternate rankings for the thermal niche (see Materials and Methods), contrasts for SMR<sub>i</sub> at 30°C were also significantly correlated with contrasts for species’ thermal niche (tests with phylogeny branch lengths:  $r = 0.89$ ,  $P =$

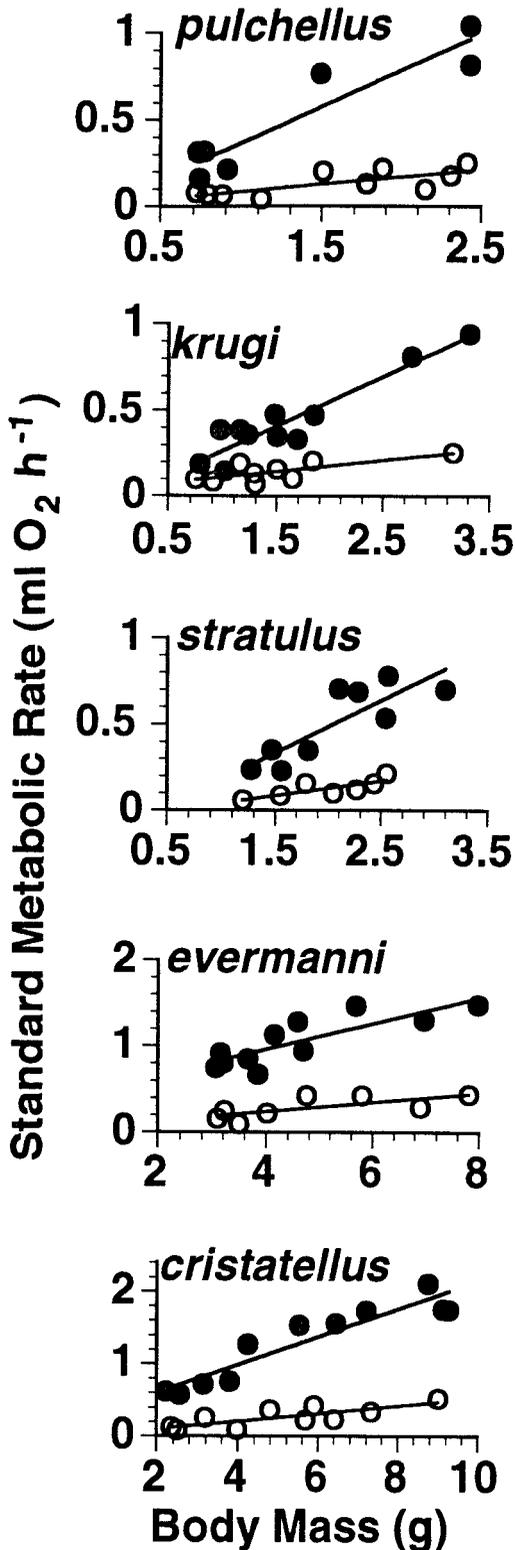
0.02; tests with equal branch lengths:  $r = 0.85$ ,  $P = 0.03$ ).

Figure 5 illustrates the association between species’ thermal niche and SMR<sub>i</sub> at 30°C. A higher metabolic rate was associated with the use of a warmer thermal niche. The large values at nodes F and G (see Fig. 1) are noteworthy. The large influence at node F illustrates that the lowland species *A. pulchellus* had a higher SMR<sub>i</sub> and occupied warmer sites than the upland *A. krugi*. The large effect at node G illustrates that the two grass-bush anoles (*A. pulchellus*, *A. krugi*) had a higher SMR<sub>i</sub> and occupied warmer sites than the montane species *A. gundlachi*. Lizards of the latter species occur over a broad range of elevations, including relatively high (and colder) sites in cloud forest where the grass-bush anoles do not occur.

Several other associations were suggested (refer to correlation coefficients in Table 3), but few other significant relationships ( $P \leq 0.05$ ) were detected in tests of contrasts or raw mean values. All tests for an association between species’ thermal niche and SMR<sub>i</sub> at 15°C were nonsignificant. Also, there was no clear relationship between SMR<sub>i</sub> and structural niche (correlation with mass-independent SMR was detected only at 15°C and only when equal phylogeny branch lengths were assumed, Table 3). Mean body mass was not significantly related to the species’ thermal or structural niche.

## DISCUSSION

Results suggest that the energy requirements of *Anolis* lizards may have shifted as species differentiated and elaborated different thermal niches. Species with a relatively high metabolic rate at 30°C (a temperature that permits foraging and other activity) occupied the warmest thermal niches. Although SMR<sub>i</sub> at 30°C was strongly related to the species’ thermal niche ( $r = 0.88$ ,  $P = 0.02$ , from standardized independent contrasts), SMR<sub>i</sub> was not significantly associated with the species’ structural niche. Thus,



the thermal niche appears to be a better predictor of species differences in energy expenditure than the structural niche.

The buildup of anoline fauna in the Caribbean has been complex, with species assortment by habitat, diet, and thermal environment contributing to trait divergence and convergence (Schoener, 1969, 1970; Roughgarden et al., 1983; Roughgarden, 1995; Losos, 1990a, 1992, 1994; Miles and Dunham, 1996). There have been major evolutionary shifts in morphology and behavior, which could have coincided with changes in energy requirements, given that structural, behavioral and ecomorphological traits covary in *Anolis* species (Williams, 1972, 1983; Losos, 1990a-c).

Several factors could have acted to modify the energy expenditures of lizards over evolutionary time. Changes in time-energy budgets may modify the fitness of lizards in different kinds of thermal environments (Adolph and Porter, 1993). Thus, lizards occupying cooler, higher elevation sites are more likely encounter temperatures that limit foraging activity and energy (food) assimilation, which in turn could affect growth rates, maturation times, survival, or reproductive output. Prey capture efficiencies and hence dietary intake may also decrease at lower temperatures owing to thermal effects on lizard mobility (Bennett, 1980; Huey, 1983). At the same time lizards occupying cooler sites in shaded forest may incur a "cost" associated with having a body temperature that is suboptimal for escaping from predators or executing other kinds of activity (Huey and Slatkin 1976; Huey, 1983).

Differences in thermal preferences (Rand, 1964; Hertz 1992a,b); thermal niche breadths (temperature ranges for daily activity; Huey and Webster, 1976; Hertz, 1983), or thermal and hydric tolerances (Hillman and Gorman, 1977; Hertz, 1979; Hertz et al., 1979) could also contribute to species differences in energy costs. Thus, the montane forest lizard *A. gundlachi* is a stenothermic thermoconformer (with a body temperature that reflects its cool, shaded environment; Huey and Webster, 1976; Hertz, 1981, 1983, 1992), has a poor tolerance to high temperature (Heatwole et al., 1969; Hertz et al., 1979; Rogowitz, 1996a) and has a relatively low SMR<sub>1</sub> (this study). By comparison, *A. cristatellus* is eurythermic and preferentially occupies

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FIG. 2. Standard metabolic rates of *Anolis* lizards at 15°C (open symbols) and 30°C (closed symbols). For each species, the influence of body mass (g) on metabolic rate (ml O<sub>2</sub>/h) was determined by least-squares regression (coefficients are given in Table 2).

TABLE 2. Regression coefficients describing the influence of body mass (g) on SMR (ml O<sub>2</sub>/h) of Puerto Rican *Anolis* species at 15°C and 30°C. Intercept (a) and slope (b) are indicated (SEM in parenthesis).

Species	15°C		30°C	
	a	b	a	b
<i>pulchellus</i>	0.06 (0.022)	0.04 (0.005)	0.27 (0.072)	0.13 (0.014)
<i>krugi</i>	0.04 (0.025)	0.04 (0.005)	0.29 (0.085)	0.13 (0.016)
<i>stratulus</i>	0.06 (0.023)	0.03 (0.005)	0.27 (0.075)	0.13 (0.014)
<i>evermanni</i>	0.06 (0.017)	0.03 (0.004)	0.23 (0.064)	0.13 (0.013)
<i>crystalellus</i>	0.07 (0.020)	0.03 (0.005)	0.28 (0.061)	0.12 (0.013)

warm, sunny sites (Rand, 1964; Huey and Webster, 1976; Hertz 1992a,b), has a greater tolerance to warm temperature (Heatwole et al., 1969; Gorman and Hillman, 1977; Hertz et al., 1979), and has a higher SMR<sub>i</sub> (this study). These associations may be coincidental, or they may reflect a coadaptation of energy costs with thermal characteristics of habitats. Costs for maintenance and activity may increase at sites where lizards are active over a relatively broad or high temperature range as a possible consequence of attempting to avoid hyperthermia or predation.

Previous studies indicate that locomotor capacities of lizards (which reflect their abilities to escape from predators) may also be coadapted with thermal niches. Thus, higher maximal sprint speeds have been reported for lizards that are routinely active at warmer environmental temperatures (van Berkum, 1986; Huey and Bennett, 1987; van Damme and Vanhooydonck, 2001). Nonetheless, an association between performance and thermal niche is not always evident (Hertz et al., 1983; Garland et al., 1991; Martins and Garland, 1991).

A noteworthy result of the present study is that two anoles that routinely occupy forested sites with dense canopy cover, *A. gundlachi* and *A. stratulus*, had relatively low SMR<sub>i</sub> values compared with other species (Fig. 4). The fact that both species had low metabolic rates suggests that a lower maintenance cost may be associated with their occupation of dense forested habitat.

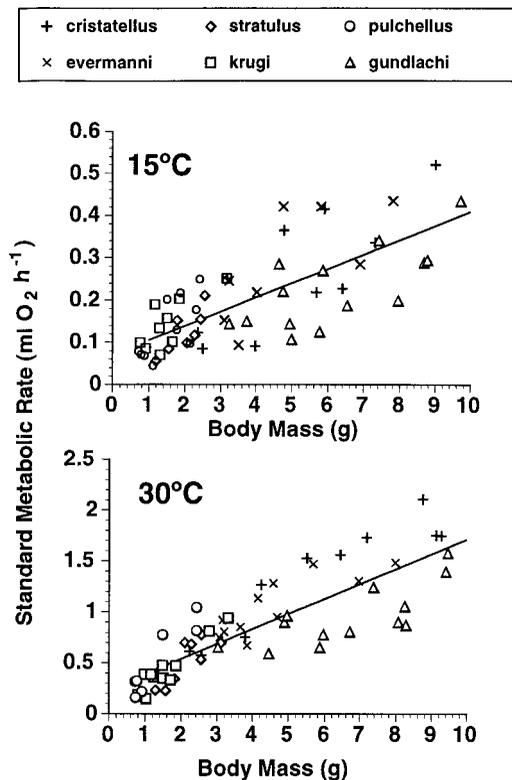


FIG. 3. Influence of body mass on standard metabolic rates of *Anolis* lizards at 15°C and 30°C (combined data for *Anolis pulchellus*, *Anolis krugi*, *Anolis evermanni*, *Anolis stratulus*, *Anolis cristatellus*, and *Anolis gundlachi*).

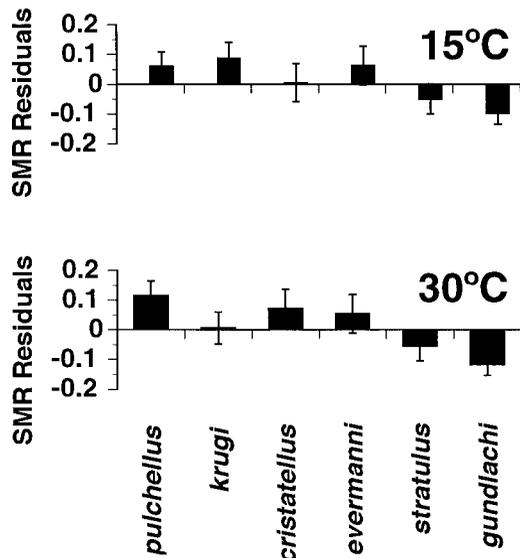


FIG. 4. Mass-independent standard metabolic rates (SMR residuals) of *Anolis* lizards at 15°C and 30°C (means  $\pm$  SEM). Residuals were obtained from least square regression of  $\log_{10}$ SMR (ml O<sub>2</sub>/h) on  $\log_{10}$ body mass (g).

TABLE 3. Association of thermal and structural niches of Puerto Rican *Anolis* species with standard metabolic rate (SMR, mass-independent values for 15°C or 30°C) and body mass. Correlation coefficients ( $r$ ) and probability values ( $P$ ) are shown for tests of standardized independent contrasts (contrasts) and raw mean values (means). "Standard" and "alternate" methods were used to rank thermal and structural niches (see Materials and Methods). Contrasts were obtained using branch lengths for the phylogeny (Losos, 1990b) or by assuming equivalent branch lengths (values in brackets).

	Standard ranking		Alternate ranking	
	$r$	$P$	$r$	$P$
Association with thermal niche				
SMR at 15°C (contrasts)	.043 [0.43]	0.39 [0.40]	0.60 [0.57]	0.21 [0.24]
SMR at 30°C (contrasts)	<b>0.88 [0.89]</b>	<b>0.02 [0.02]</b>	<b>0.89 [0.85]</b>	<b>0.02 [0.03]</b>
Body mass (contrasts)	0.44 [0.40]	0.38 [0.42]	0.66 [0.62]	0.15 [0.19]
SMR at 15°C (means)	0.11	0.83	0.24	0.65
SMR at 30°C (means)	0.17	0.74	0.15	0.77
Body mass (means)	0.48	0.33	0.72	0.11
Association with structural niche				
SMR at 15°C (contrasts)	<b>0.71 [0.81]</b>	<b>0.11 [0.05]</b>	0.44 [0.45]	0.39 [0.37]
SMR at 30°C (contrasts)	0.64 [0.62]	0.17 [0.19]	0.20 [0.38]	0.70 [0.45]
Body mass (contrasts)	0.13 [0.06]	0.81 [0.91]	0.40 [0.41]	0.43 [0.42]
SMR at 15°C (means)	0.86	0.03	0.56	0.25
SMR at 30°C (means)	0.69	0.13	0.48	0.34
Body mass (means)	0.28	0.59	0.37	0.47

Conversely, habitats with less cover may require anoles, such as the grass-bush *A. pulchellus*, to maintain a high maintenance cost (e.g., for antipredator vigilance, maintaining awareness of predators).

It is possible that predation pressure selects for lizards with a greater metabolic capacity to support locomotor (escape) activity and a greater maintenance cost in certain environments (assuming genetic covariance of energy costs; see Bennet and Ruben, 1979). Under this coevolutionary scenario, energy requirements of lizards would be predicted to increase in environments with a greater diversity or abundance of

predators. Few data are available to test this hypothesis, however, avian species are the primary predators of *Anolis* lizards in Puerto Rico and elsewhere in the Caribbean (Wunderle, 1981; Roughgarden, 1995; Reagan, 1996) and avian species richness and density both decline at higher elevations in Puerto Rico (Snyder et al., 1986). Thus, by inference, the lower energy expenditure of anoles occupying forest sites at high elevation in Puerto Rico, such as *A. gundlachi*, may be related to a decreased risk of predation. Less predation risk at higher elevations may also help explain why the montane species *A. gundlachi* does not actively seek warm, sunny sites that would permit a greater locomotor (escape) performance (Huey and Webster, 1976; Huey and Slatkin 1976; Hertz, 1992b).

Malaria, which occurs in some *Anolis* populations (Schall and Vogt, 1993), is unlikely to have affected the metabolic rates of anoles. Studies of *Sceloporus occidentalis* indicate that malarial parasitism causes no significant change in SMR (Schall et al., 1982). Also, acclimatory processes have negligible effect on the energy expenditures of anoles. In studies of *crisatellus*, *gundlachi*, and *sagrei*, Rogowitz, (1996a,b) found no evidence of acclimatory shifts in SMR with changes in latitude or altitude (or compensation after exposure to a higher or lower temperature). It appears that there has been insufficient time or seasonal environmental variation for acclimatory mechanisms to have evolved in anole species (Rogowitz, 1996a,b).

Energy costs of lizards may ultimately de-

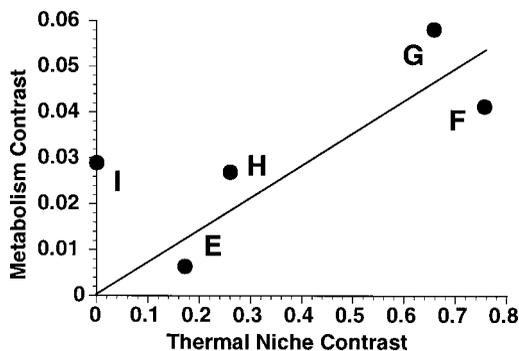


FIG. 5. Association between thermal niche and mass-independent SMR at 30°C. Symbols refer to nodes in Figure 1. Absolute values of contrasts were used here (but not in Table 3) to illustrate relative effects of contrasts. A contrast of zero implies no evolutionary change.

pend on a complex of factors related to thermal, structural, and resource axes of niches. The fact that several correlation coefficients were large but nonsignificant in this study, including contrasts for body mass versus thermal niche ( $r = 0.66$ , Table 3) and for  $SMR_t$  at 30°C versus structural niche ( $r = 0.64$ ), suggests that additional associations may be detected in a broader study of anoline species.

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## A New Species of *Hyalinobatrachium* (Anura: Centrolenidae) from the Highlands of Guyana

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**ABSTRACT.**—A new species of *Hyalinobatrachium* is described from the highlands of Guyana. This is the third centrolenid species reported from Guyana and the second of the genus *Hyalinobatrachium*. The new species is one of 13 *Hyalinobatrachium* found in northeastern South America (Venezuela, Guyana, Surinam, and Guyane); it can be differentiated from *Hyalinobatrachium taylori*, the only other *Hyalinobatrachium* in Guyana, by the color of the bones, which are white, and the color of the dorsum in preservative (lavender vs. cream in the new species). Variation and relationships within the genus in this region are discussed. The tadpole of the new species is described and illustrated.

The family Centrolenidae is remarkably speciose in the Andes Mountains from Colombia to Peru but is relatively poorly represented in the northeastern countries of South America (Venezuela, Guyana, Surinam, and Guyane). Of these, Venezuela possesses the largest number of species (24), followed by Guyana and Surinam (three each, including the species described herein), and Guyane (two). The species described herein is the third species reported from Guyana (for further discussion of the centrolenids of the Guianan Shield, see Noonan and Harvey, 2000; Myers and Donnelley, 1997). The genus *Hyalinobatrachium* is the most speciose centrolenid genus in the Guianan Shield (sensu Hoogmoed, 1979) with this being the 13th species recorded. The identity and relationships of centrolenid frogs have recently been the focus of some speculation (Ruiz-Carranza and Lynch, 1991a, b). Of particular interest to this study is *Hyalinobatrachium orientale*, which was once considered to be a widely distributed species (Cannatella and Lamar, 1986) but is now thought to

represent a complex of similar sibling species (Myers and Donnelley, 1997).

### MATERIALS AND METHODS

Specimens were collected by B. P. Noonan and D. W. Carpenter on 15, 19, and 23 June 1997, in the Pakaraima Mountains near Imbaimadai (05°44'N, 60°18'W). Geographic position was determined using a GPS. Adults were fixed in formalin and preserved in 70% ethanol, whereas eggs and tadpoles were preserved in 10% formalin. Measurements were taken to the nearest 0.1 mm using dial calipers. Coloration of peritonea were determined from color photographs of living specimens and dissection of preserved specimens. Webbing formulae follow Savage and Heyer (1967) as modified by Myers and Duellman (1982). The numbered diagnosis follows the format of Lynch and Duellman (1973) as modified by Ruiz-Carranza and Lynch (1991b), with the addition of characters 14–17. Specimens of the new species were compared to published descriptions of members of the *H. orientale* species group as defined by Ruiz-Carranza and Lynch (1991a) and specimens in the University of Texas at Arlington (UTA) Collection

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FIG. 1. Holotype of *Hyalinobatrachium ignioculus* (HA 722); Snout-vent length = 20.9 mm.

of Vertebrates and the Museum of Natural History, University of Kansas (KU; Appendix 1). The holotype and two paratopotypes of the new species are in the collection of the University of Guyana (HA) and the remaining paratopotypes are in the UTA Collection of Vertebrates.

*Hyalinobatrachium ignioculus*, sp. nov.

*Holotype*.—University of Guyana, Centre for the Study of Biodiversity: HA 722 (field number DWC 91); an adult male (Fig. 1), collected 15 June 1997 by D. W. Carpenter from a small stream on Peters Mountain, 3.6 km north of Imbaimadai in the Pacaraima Mountains, 600 m, Administrative Region 7, Guyana; 05°44'N, 60°18'W (Fig. 2).

*Paratopotypes*.—Guyana: Region 7: UTA 51654–63, adult males; UTA 51664, adult female; all collected at the type locality on the 15, 19, and 23 June, 1997.

*Diagnosis*.—The new species is placed in the genus *Hyalinobatrachium* because it possesses a bulbous liver and lacks a humeral spine in males (Ruiz-Carranza and Lynch, 1991a). The following combination of characters distinguish *H. ignioculus* from all other members of the genus: (1) vomerine teeth absent; (2) bones white in life; (3) parietal peritoneum clear; visceral, pericardial and hepatic peritonea white; (4) dorsal color in life pale lime green with many yellow spots; color in preservative cream-yellow with dark melanophores; (5) webbing between outer Fingers III2–1½IV; (6) webbing on foot I1–2III1–2½III1–2½IV2½–1V; (7) snout truncate in dorsal view, truncate in profile; (8) dorsal skin pustulate, lacking spicules; (9) enameled ulnar fold present along length of forearm and extending onto Finger IV; enameled tarsal fold present along length of tarsus and extending onto Toe V; (10) humeral spines absent; (11) tympanum distinct (in pre-

servative), covered with pustulate, pigmented skin; tympanum directed dorsolaterally with slight posterior inclination; (12) average snout-vent length 21.6 mm in males ( $N = 11$ ), and 23.0 mm in females ( $N = 1$ ); (13) nuptial excrescence clear, Type II; (14) anal decoration present in the form of enameled warts; (15) when adpressed, first finger longer than second; (16) liver bulbous; and (17) eye diameter roughly double width of disc of finger III.

*Hyalinobatrachium ignioculus* is assigned to the *Hyalinobatrachium fleischmanni* species group (Ruiz-Carranza and Lynch, 1991a) based on the presence of white bones, a bulbous liver, white visceral, pericardial, and hepatic peritonea, and the absence of a humeral spine in males. Detailed species comparisons are presented below for the four species of *Hyalinobatrachium* in the Guianan Shield (sensu Hoogmoed, 1979). The remaining species in Venezuela are restricted to the Cordillera Oriental and Cordillera de Merida and are presumably isolated from the species of the Guianan Shield by inhospitable lowlands and/or the Orinoco River. The new species can be distinguished from all species of *Hyalinobatrachium* occurring in the Guianan Shield and the mountains of western Venezuela by the combination of the presence of ulnar and tarsal folds, anal decoration in the form of enameled tubercles, supernumerary tubercles, pigmentation in the pericardium, and the unique red color of the iris in life (Table 1).

The only other species of *Hyalinobatrachium* found in Guyana is *Hyalinobatrachium taylori*, (Fig. 2) which has green bones and white spots on the dorsum in life Ayarzagüena (1992) and a lavender dorsum in preservative (Goin, 1968). These spots in *H. taylori* are retained in preservative on a lavender ground color. The presence of *H. taylori* in Guyana (based solely on the holotype) is in conflict with Frost (1999) who states that the type locality is actually in Surinam, citing personal communication from Hoogmoed. However, Lescure (1975) maps the type locality of *H. taylori* on the New River within the border of Guyana, which is in accordance with the original description (Goin, 1968) though the exact locality was not given in the description. There is currently a border dispute between Guyana and Surinam, with Surinam claiming all land east of the New River. If this side is taken, then it is possible that the type locality is on the east rather than the west bank of the New River and thus lies within Surinam rather than Guyana.

*Description of Holotype*.—An adult male, snout-vent length (SVL) 20.9 mm. Head distinctly wider than body; head length 87% of head width; head length 33% of SVL; snout short, 40% of head length; snout truncate in

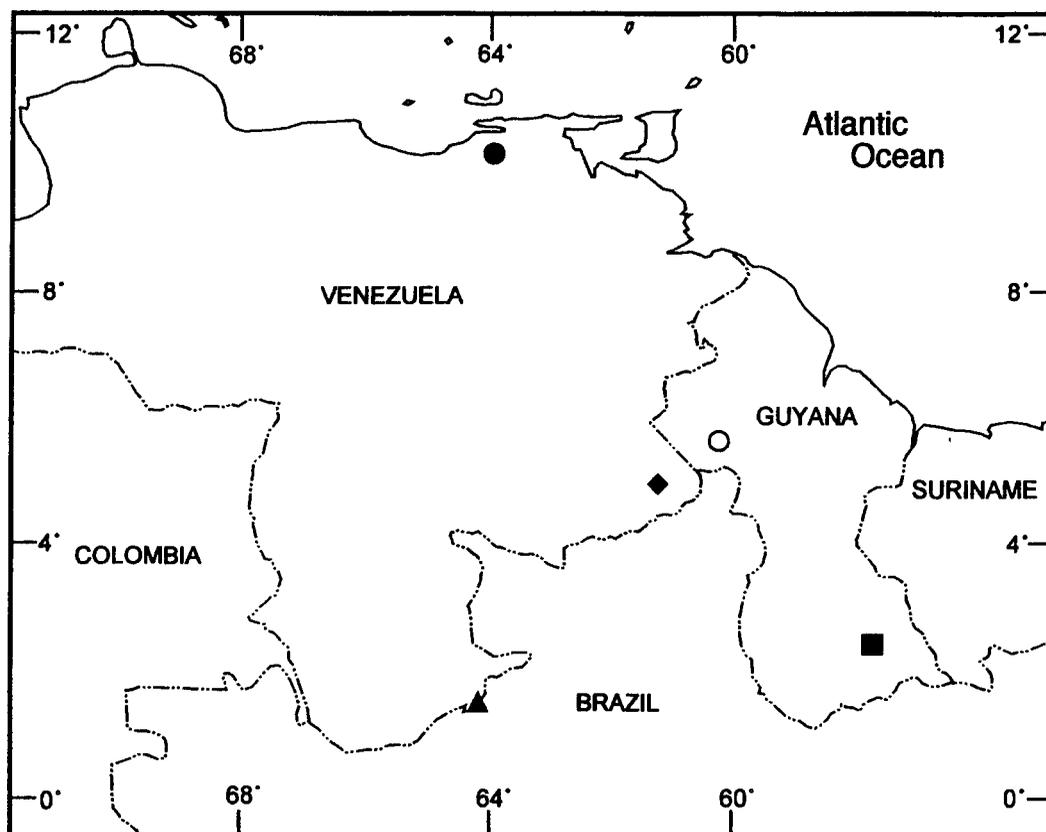


FIG. 2. Map of the Guianan Shield showing the type localities of *Hyalinobatrachium igniocolus* (open circle); *Hyalinobatrachium orientale* (closed circle); *Hyalinobatrachium taylori* (closed square); *Hyalinobatrachium crurifasciatum* (closed triangle); and *Hyalinobatrachium iaspidiense* (closed diamond).

TABLE 1. Comparison of character states of *Hyalinobatrachium* from the Guianan Shield for five characters that serve to quickly distinguish the new species from others in the region, character states that differ from the new species are in bold type.

Species	Iris	Pericardial coloration	Tarsal fold	Supernumerary tubercles	Anal decoration
<b><i>H. igniocolus</i></b>	yellow with red ring	white	present	present	present
<i>H. antisthenesi</i>	?	<b>clear</b> <sup>a</sup>	<b>absent</b>	present	absent
<i>H. crurifasciatum</i>	<b>golden</b>	white	present	present	present
<i>H. duranti</i>	<b>gold</b>	white	<b>absent</b>	<b>absent</b>	<b>absent</b>
<i>H. fragile</i>	?	<b>clear</b>	<b>absent</b>	<b>absent</b>	<b>absent</b>
<i>H. iaspidiense</i>	<b>whitish yellow</b>	<b>clear</b>	<b>absent</b>	<b>absent</b>	present
<i>H. loreocarinatum</i>	<b>whitish gold</b>	white	<b>absent</b>	<b>absent</b>	<b>absent</b>
<i>H. orientale</i>	<b>gold to yellow</b>	<b>clear</b>	<b>absent</b>	present	present
<i>H. ostracodermoides</i>	?	white	<b>absent</b>	<b>absent</b>	<b>absent</b>
<i>H. pallidum</i>	<b>gold</b>	<b>clear</b>	<b>absent</b>	present	<b>absent</b>
<i>H. pleurolineatum</i>	<b>gold</b>	white	<b>absent</b>	<b>absent</b>	<b>absent</b>
<i>H. revocatum</i> <sup>b</sup>	<b>silver</b>	white	<b>absent</b>	present	present
<i>H. taylori</i> <sup>c</sup>	<b>reticulated gray</b>	white	<b>absent</b>	<b>absent</b>	present

<sup>a</sup> Pericardial coloration determined from preserved specimens, possible artifact of preservation.

<sup>b</sup> Believed to actually belong to the genus *Cochranella* by Ruiz-Carranza and Lynch (1998).

<sup>c</sup> Placement in this genus questionable, see text for discussion.

both dorsal and lateral view; canthus rostralis blunt; loreal region concave; lips not flared; nostrils protuberant; internarial region depressed; eye large, eye diameter 36% of head length; outline of tympanum visible, directed dorsolaterally with slight posterior inclination; tympanic annulus entirely visible, diffusely pigmented with melanophores. Prevomerine dentigerous processes and teeth absent; choanae moderately sized, round, near margin of mouth; tongue round, not notched posteriorly; vocal slits paired, extending from mediolateral base of tongue to angles of jaws.

Humeral spine absent; enameled ulnar fold present (it should be noted that the term enameled used here refers to being covered in a hard, white substance), extending length of Finger IV; forearm larger than upper arm; first finger longer than second (Fig. 3); webbing basal between Fingers I, II, and III, webbing between third and fourth fingers extensive (III2-1½IV); relative lengths of Fingers II < I < IV < III; discs broad, truncate; discs on fingers slightly larger than those on toes; disc on Finger IV approximately 1.6 times larger than tympanum. Low, rounded subarticular tubercles present on first three fingers; supernumerary tubercles low, rounded; palmar tubercle ovoid, raised; thenar tubercle low, elliptical; prepollex not enlarged, prepollical spine not protruding; nuptial pad present, Type II.

Hind limbs slender; length of tibia 56% of SVL; enameled tarsal fold present, extending to tip of Toe V; inner metatarsal tubercle low (Fig. 3), elliptical; outer metatarsal tubercle absent; subarticular tubercles circular, rounded in profile, about as wide as digits; low, rounded supernumerary tubercles present; relative lengths of toes I < II < V < III < IV; toes extensively webbed; webbing formula I 1/2-2III-2 1/2III 1 1/2-2IV2 1/2-1V; discs on toes round; disc on Toe IV approximately 1.3 times larger than tympanum.

Skin on dorsal surfaces pustulate; skin on belly and ventral surfaces of thighs granular; vent directed posteriorly at midlevel of thighs; concealed by dermal fold; flanked by irregular enameled warts.

*Color in Life.*—Dorsum (including eyelid) light lime green with numerous yellow spots, giving appearance of a green "net" over a yellow ground color; color extending length of the leg; skin on humeral area and Toes I-III transparent, but forearm and fourth finger patterned as dorsum. Fine melanophores found in green areas, the expression and darkness of which seem to vary between active and dormant periods; ventral surfaces cream; parietal peritoneum clear; pericardial, visceral, and hepatic peritonea white; iris yellow with small dark flecks similar

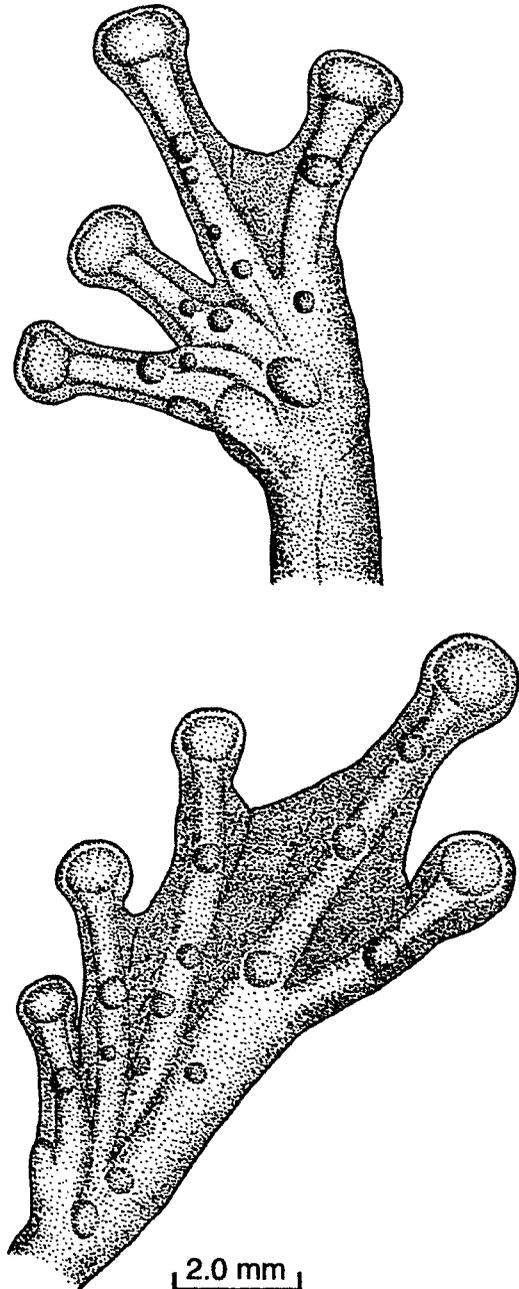


FIG. 3. Palmar and plantar view of the left hand and foot of *Hyalinobatrachium igniocolus* (HA 722).

to melanophores on dorsum, and a distinct, red ring, that may or may not be complete, encircling the pupil; bones white.

*Color in Preservative.*—Venter chalky white and semitransparent; dorsum cream with dark flecks present in all patterned areas described above; melanophores maintain circular shape of yellow spots (which lack melanophores) ob-

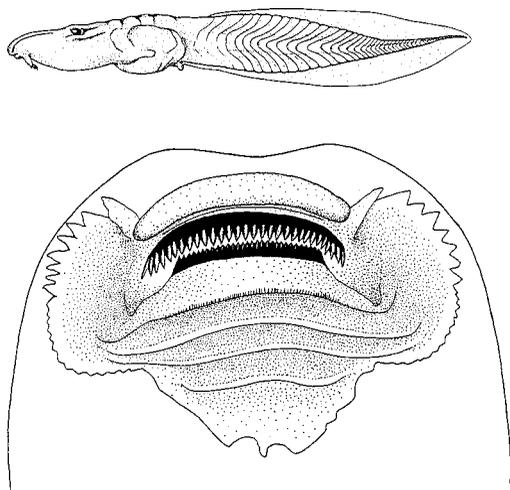


FIG. 4. Lateral aspect and mouthparts of the tadpole of *Hyalinobatrachium ignioculus* (UTA-51904).

served in life in absence of contrasting green color. Parietal peritoneum clear; pericardium, visceral, and hepatic peritonea white; bones white.

*Variation.*—Measurements in mm of holotype followed by mean and range of male paratopotypes in parentheses: SVL 20.9 (21.6, 20.8–23.0); head width 7.5 (8.2, 7.5–8.6); head length 6.5 (7.1, 6.5–7.2); snout length 2.7 (2.8, 2.6–3.1); eye diameter 2.5 (2.5, 2.4–2.7); hand length 6.2 (6.6, 6.0–7.2); tibia length 12.2 (12.1, 11.4–12.7). Measurements in millimeters of the single adult female paratopotype are as follows: SVL 23.0; head width 8.7; head length 7.7; snout length 3.0; eye diameter 2.5; hand length 7.2; tibia length 13.2.

Although guanophores are undoubtedly present in the pericardium of all specimens in life and in preservative, a small portion of the heart of some specimens appears reddish in preservative (after 18 months) and is visible through the ventral surface. Variation in webbing of outer fingers and feet is as follows: outer Fingers III(1 1/2–2)–(1 3/4–2)IV; Toes I(1–1 1/2)–2II(1–1+)–(2–2 1/2)III(1–1 1/2)–(2–2+) IV(2+–3)–1V

*Eggs and Tadpoles.*—Males of this species apparently guard nesting sites, and may use them multiple times (this was observed in several instances). As many as three clutches, at varying stages of development, were found on the underside of a leaf with a single calling male. Color of eggs was not noted. One of these clutches (UTA 51903) contained 11 eggs, and a second clutch containing 10 eggs was kept alive until two larvae (other eight eggs damaged in field, not preserved) hatched (UTA 51904–5). One of these larvae was preserved immediately (UTA 51904) and is illustrated in Figure 4 (total length

= 13.1 mm). The second tadpole was raised in captivity to a total length of 23.6 mm (UTA 51905). This description will center on UTA 51904 to avoid reporting any artifacts of captivity, although some structures are not formed or are undetectable in UTA 51904; in such situations, descriptions were made from UTA 51905 and are noted as such below. Both specimens are in developmental Stage 25 (operculum fully developed, no limb buds apparent; Gosner, 1960).

Body ovoid, short (29% of total length), longer than wide (body length/body width = 1.8), depth less than width; snout rounded in dorsal and lateral view; eyes dorsolateral (pupils visible in dorsal view); dorsal surface flattened, sloping anteroventrally between eyes and snout; oral disc ventral; belly flat; nostrils about one-third of distance between eyes and snout; nostrils not protuberant, directed anterolaterally; spiracle sinistral, on longitudinal axis of body, directed posteriorly; spiracular tube short; anal tube short, medial (from UTA 51905). Caudal musculature robust; caudal fins extremely low, expanding distally as caudal musculature narrows; tip of tail pointed.

Oral disc large with well-developed posterior and lateral folds (Fig. 4); posterior fold strongly fringed; jaw sheath wide, heavily serrated. Labial teeth in three weakly keratinized lower rows; labial tooth row formula 0/3. Labial papillae large and irregular on ventral and lateral edges, greatly reduced in size along dorsal edge. Oral disc emarginate below level of third tooth row.

In preservative, dorsal and lateral surfaces of body covered with dark brown melanophores; ventral skin transparent (heart visible), UTA 51905 with a few melanophores present on ventral surface; eyes dark brown, lens visible as milky spot in eye; caudal musculature white, with dark brown melanophores (UTA 51905 only); caudal fin clear, dorsal fin clear, both with dark brown melanophores in UTA 51905.

Few centrolenid tadpoles have been described, and only two from northern South America. Mijares-Urrutia (1990) described the tadpole of *Centrolene andinum*, which differs from the new species in having the eyes barely visible, having anterior tooth rows, and lacking a heavily serrated beak. Myers and Donnelly (1997) briefly described the tadpole of *Hyalinobatrachium crurifasciatum*, which differs from the new species in having a poorly keratinized beak and mouthparts.

*Etymology.*—The species name is a noun in apposition and is derived from the Latin words *ignis*, meaning fire, and *oculus*, meaning eye. The name refers to the distinctive red color of part of the iris.

*Distribution and Ecology.*—*Hyalinobatrachium ignioculus* is known only from the type locality on Peters Mountain, 3.6 km north of Imbaimadai, Region 7, Guyana (Fig. 2). Peters Mountain reaches approximately 900 m in elevation at the peak, is covered in evergreen sclerophyllous forest, and is situated in the highland savanna of western Guyana. The fast-flowing stream where *H. ignioculus* was found is a tributary of the Mazaruni River and varies between 0.1 and 1.0 m depth and 1.0 and 2.0 m width at the type locality. This stream has a smooth rock and/or sandy bottom, and its banks are steep and about 3.0–4.0 m high. The creek is heavily shaded by the forest canopy.

Individuals of *H. ignioculus* were active by night along the stream bank on leaves between 1.0 and 6.0 m above the surface of the water. Males began calling with the onset of darkness but rarely called after 2000 h. Calling males were always found on the undersides of leaves and were often occupying a leaf with one or more clutches of eggs (which were attached to the underside of the leaf). The area was not visited during the day, so it is not known whether the males guard sites during the day. The call consisted of a single, flat note that could be heard for a considerable distance (calls were not recorded). Calling males (and egg clutches) were rarely in or over "splash zones" but were commonly found over relatively tranquil sections of the stream. A single female (UTA 51664) was found on the top of a leaf above the stream.

#### DISCUSSION

The new species is presumably a member of the Guianan *Hyalinobatrachium orientale* species complex, which belongs to the more formal *H. fleischmani* species group of Ruiz-Carranza and Lynch (1991a). The discovery of this and other members of this complex point to the existence of an assemblage of similar sibling species, some of which were considered synonyms by Cannatella and Lamar (1986). With the discovery in recent years of specimens that differ considerably from *H. orientale* and a better understanding of the relationships of centrolenids in general, the true identity of *H. orientale* has again come into question (Myers and Donnelley, 1997; D. C. Cannatella, pers. comm.). Preliminary evidence alluded to by Gorzula and Señaris (1999[1998]) indicates some morphological and behavioral differences between the populations of *H. orientale* (sensu Cannatella and Lamar, 1986).

Unfortunately, Gorzula and Señaris (1999[1998]) have introduced additional confusion regarding the identity of *H. orientale*. In their coverage of the centrolenid fauna of the region, they include *H. taylori* based on three specimens in

the Museum of Natural History, University of Kansas, collected by W. E. Duellman and S. Gorzula. They go on to state that Ayarzagüena (1992) and Señaris and Ayarzagüena (1993) also reported this taxon from the Gran Sabana and Auyán-tepui. Duellman is indicated as identifying the three KU specimens as *H. taylori*, even though these specimens are described as *H. orientale* by Duellman himself in his 1997 report of the amphibians of the La Escalera region (Duellman, 1997). It seems that Gorzula and Señaris (1999[1998]) are reporting these specimens as *H. taylori* on the basis of identification made in the field by Duellman and Gorzula (W. E. Duellman, pers. comm.). The authors further state that "other material of this species from the same area (La Escalera) has been examined by Ayarzagüena (1992)" but in fact Duellman (1997) reports the bones of the KU specimens as being white, and Ayarzagüena (1992) reports the bones of *H. taylori* as green. Gorzula and Señaris (1999[1998]) also describe the dorsum in preservative as being lavender (which follows Goin's, 1968, original description) including the two specimens from La Escalera he examined. The two KU specimens were examined and found to have cream colored dorsums and white bones (though green bones may fade to white in preservative, so Duellman's 1997 description of these specimens must be trusted). Thus, there are either two species of *Hyalinobatrachium* in the La Escalera region, one with green bones and one with white bones. Alternatively, Ayarzagüena (1992) misreported the color of the bones of *H. taylori* or at least those of specimens from Auyán-tepui and the Gran Sabana. If Ayarzagüena (1992) was correct and *H. taylori* does indeed have green bones, then this taxon can no longer be considered a member of the *H. fleischmani* species group, because this group is defined by the presence of white bones (Ruiz-Carranza and Lynch, 1991a). However, if the bones are actually white, this taxon is still unique in having a lavender dorsum in preservative.

*Hyalinobatrachium iaspidiense* (Ayarzagüena, 1992) appears to be the species whose geographic distribution is physically closest to the type locality of *H. ignioculus*. This species differs markedly from the new species in lacking pigmentation in the pericardium, a tarsal fold, supernumerary tubercles, and anal ornamentation. Additionally, the iris of *H. iaspidiense* is whitish yellow compared to yellow with a red ring in the new species.

The most recently described species in the *H. fleischmani* group is *Hyalinobatrachium crurifasciatum*, which was discovered in 1989 at Pico Tamacuari in Amazonas, Venezuela. The main difference between *H. crurifasciatum* and *H. orien-*

*tale* is that the former has green bands on the limbs, a golden iris, and ulnar and tarsal folds, all of which are absent in *H. orientale*. *Hyalinobatrachium crurifasciatum* also appears to be the most phenotypically similar species in the region to *H. ignioculus*; differing in having a golden iris, green limb bands in life, smooth skin on the dorsum, and a larger adult size in males (SVL 22.0–24.0 compared to 20.8–23.0;  $t_{0.05} = 2.65$ ;  $P < 0.01$ ). The relationships of the Guianan *Hyalinobatrachium* remain poorly understood and will likely remain so until a detailed phylogenetic analysis of the group is done. It is hoped that work in progress by the senior author (BPN) will elucidate the origins and patterns of speciation not only within this group but of the entire family.

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## APPENDIX 1

## Comparative Material Examined

*Hyalinobatrachium antisthenesi*, KU 133467–79, 167336–59, 185766–7; *Hyalinobatrachium bergeri*, KU 182363 (holotype), 162248–9, 162251–55, 162257, 182364–8 (paratypes); *Hyalinobatrachium chirripoi*, KU 36865 (holotype), 36862–4 (paratypes), 36866–70 (paratypes); *Hyalinobatrachium colymbiophylum*, KU 23812 (holotype), 32939–42, 65238, 77526, 77535–39, 103819, 116425–35; *Hyalinobatrachium eurygnathum*, KU 93220–23; *Hyalinobatrachium lemur*, KU 211768 (holotype), 211769 (paratype); *Hyalinobatrachium munozorum*, KU 118054 (holotype), 105251 (paratype), 123225 (paratype), 150620 (paratype), 152488–9, 154749, 155493–6, 172167–9, 175215, 175504, 197028–9, 217295–7; *Hyalinobatrachium orientale*, KU 133481, 167360–68, 167370–3, 181126–7, 185768–9, 224499–03; *Hyalinobatrachium pulveratum*, KU 85476, 116493; *Hyalinobatrachium pellucida*, KU 143298 (holotype); *Hyalinobatrachium talamancae*, KU 30887 (holotype), 32936–8, 140018; *Hyalinobatrachium uranoscopum*, KU 74310–1, 93226–7, 93229–30.