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## RESPONSES TO CHEMICAL FOOD STIMULI BY AN HERBIVOROUS ACTIVELY FORAGING LIZARD, *DIPSOSAURUS DORSALIS*

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**ABSTRACT:** The abilities of the desert iguana, *Dipsosaurus dorsalis*, to detect food odors and to discriminate them from non-food odors were demonstrated by presenting chemical stimuli on cotton-tipped applicators to lizards. The stimuli were from two plant food species, an insect food species, deionized water (odorless control), and cologne (pungency control). Tongue-flick attack score, a measure of squamate response strength to chemical food stimuli that combines effects of biting and tongue-flicks before biting, differed greatly among conditions. Tongue-flick attack score was significantly greater for all food stimuli than for the two controls, which did not themselves differ. The same pattern of results was found for total number of tongue-flicks in one minute. For tongue-flicks before biting, the only significant difference was a greater response to carrot than water. Lizards bit only applicators bearing food stimuli. Significantly more bit and at shorter latencies when responding to plant odors than to either control, and significantly more bit in response to carrot than cricket stimuli. These results falsify the wide belief that a major group of lizards, the Iguania, is insensitive to food stimuli. Relationships between diet, foraging mode, and reliance on chemical cues in feeding are discussed.

*Key words:* Squamata; *Dipsosaurus*; Food odor; Foraging mode

THE senses an animal uses in prey acquisition must be closely adapted to diet and the means of obtaining food. Among lizards, the vast majority of species are insectivores or carnivores that employ one of two foraging modes. Widely (or actively) foraging lizards tend to eat prey that are distributed patchily, hidden, and/or sedentary, whereas ambush (sit-and-wait) foragers are more likely visually to detect prey that are active on the surface (Anderson and Karasov, 1988; Huey and Pianka, 1981; Magnusson et al., 1985). The prediction that actively foraging species, which appear to locate hidden food by tongue-flicking, rely more on chemical senses in locating food (Regal, 1978) has been verified. Six families of active foragers for which data are available detect prey by chemosensory means; species in two families of ambush foragers do not (Cooper, 1989*a,b*, in press *a,b*; Cooper and Vitt, 1989).

Although most lizards in the family Iguanidae are ambush foragers, the diet, foraging behavior, and tongue-flicking rate of lizards in the informal subfamily Iguaninae suggest that these lizards might use chemical cues to detect and recognize odors

of foods. Most iguanids are insectivorous, but iguanines are primarily herbivores (Iverson, 1982) and must actively seek plant food. Iguanines presumably detect plant food visually, as do other iguanids (e.g., Burghardt, 1964), but chemical cues could be important for testing food qualities. A further hint that chemical cues may be important in the feeding behavior of iguanines is that *Iguana iguana* has a higher tongue-flicking rate than insectivorous iguanids (Burghardt et al., 1986).

The desert iguana, *Dipsosaurus dorsalis*, is an actively foraging iguanine that is primarily herbivorous (Minnich and Shoemaker, 1970). Individuals often tongue-flick immediately before feeding in natural habitats. (Krekorian, 1989). A higher tongue-flicking rate in the presence of a novel food item (a raisin) than a paper control (Krekorian, 1989) suggests that the desert iguana can detect chemical food stimuli. However, the results are not conclusive, because the paper control almost certainly differed from the raisin in non-chemical ways detectable to the lizards (e.g., ultraviolet dyes in paper may be visible to the lizards—Alberts, 1989; texture, reflectivity, mass, moisture content). Al-

though the data indicate probable detection of chemical food stimuli, chemical discrimination among various foods and between foods and other odorous substances was not investigated.

We tested the ability of *D. dorsalis* to detect chemical food stimuli and distinguish them from control stimuli. Plant and insect odors were used because *D. dorsalis* occasionally consumes insects (Minnich and Shoemaker, 1970; Norris, 1953). The results are compared to previous findings on iguanids from two other subfamilies and to findings for other lizards to assess the probable influences of diet, foraging mode, and tongue-flicking rate on utilization of chemosensory cues in feeding in desert iguanas. Finally, broad preliminary hypotheses about the probable relationships between chemical discrimination of prey, lizard systematics, diet, and foraging mode are presented to suggest areas for future investigation.

#### METHODS

Desert iguanas were captured in Riverside County, California and were transported to the laboratory at the University of California where the experiment was conducted. Eight male and eight female iguanas were marked for individual recognition by painting numbers in black ink on their dorsolateral surfaces. Lizards used in the experiment were long-term (over a year) captives that had been used previously in studies of pheromonal communication (Alberts, 1989, in press). They were thoroughly acclimated to laboratory conditions and the experimenter's presence. Lizards were kept in two large group enclosures (120 × 45 × 45 cm) before and between trials. Each enclosure was filled with a 0.15 m layer of sand and was equipped with rocks for basking and several small shelters. Windows afforded a natural light cycle, which was supplemented by 12 h fluorescent lighting. During daylight hours, heat was provided in each enclosure by a single infrared bulb suspended above the cage and by a hot rock at each end of the cage. Three times per week, the lizards were fed to satiation. They were maintained on a diet of mixed vegetables (grated carrots, turnips, yellow squash, broccoli, zucchini, spinach) occa-

sionally supplemented by a commercial reptile vitamin and either *Oxalis* or *Taraxacum* flowers when available. In addition, they were fed and readily ate crickets (*Acheta domesticus*) on two occasions. Water was obtained solely from food, but the lizards appeared to be fully hydrated.

To determine whether desert iguanas can detect chemical food stimuli or discriminate them from chemical stimuli from nonfood sources, responses of the desert iguanas to several chemical stimuli presented on cotton-tipped applicators were recorded. These stimuli were from carrot, creosote (*Larrea tridentata*) leaves, cricket, deionized water, and Mennen Skin Bracer, Spice Scent. Carrots constituted a large part of the laboratory diet; creosote flowers form a large part of the diet in the natural habitat (Mautz and Nagy, 1987; Norris, 1953). The water served as an odorless control for response to the applicator and experimental situation; the cologne was a pungency control: i.e., a control for responses to highly odorous stimuli lacking dietary or social relevance. Previous studies established that lizards detect cologne rapidly but stop tongue-flicking sooner than when responding to pheromonal or food stimuli (Cooper and Vitt, 1986, 1989). Stimuli were prepared as follows: the deionized water and cologne stimuli by dipping swabs in them; carrot stimuli by rubbing the swab over the moist end of a freshly cut carrot; cricket stimuli by dipping the swab in deionized water, then rolling it on a cricket's back; and creosote stimuli by dipping the swab in water, then rolling it over a few creosote leaves. Concentrations of odorants may have varied among stimuli produced by this method but are realistic, because concentrations of surface odorants presumably vary naturally among odor sources.

Before a trial, the experimenter removed the lizard from its group enclosure and placed it in a 60 × 30 × 30 cm glass terrarium with a paper substrate. After a lizard had been in the terrarium for 4–5 min, the trial was begun. To begin a trial, the experimenter slowly approached a lizard and placed the cotton tip of an applicator bearing one of the stimuli 1 cm anterior to the lizard's snout. Tongue-flicks to the applicator were counted for 60 s.

Attacks on the applicator and their latencies were also recorded. In other studies of this sort, trials had been terminated at the time of initial attack (e.g., Burghardt, 1970; Cooper and Vitt, 1989), but in this study, tongue-flicks were recorded after a bite as well as before it during the entire 60 s trial. This allowed us to observe potentially food-related responses throughout a fixed interval, thus avoiding a lack of comparability in duration for tongue-flicks between trials with and without biting. All trials were conducted 24–28 October 1988 at an air temperature of 32 C between 1100 and 1330 h PST when the lizards were fully active. Although the air temperature was well below the mean body temperature of active desert iguanas in summer (42 C: Norris, 1953), the lizards were still warmed from exposure to the infrared source in the home cage when tested. That they attempted to feed during the trials demonstrated their responsiveness. The lizards were not fed for three days before the first trial but were fed after testing on days 1, 3, and 5. Thus, the hunger level may have been somewhat less on days 2 and 4, but examination of the raw data revealed no indication that this affected responses.

Each of 16 lizards responded to all five stimuli. Order of presentation of stimuli was randomized, because insufficient lizards were available for complete counterbalancing. Nevertheless, the sequences used did not depart substantially from those that would have been obtained by incomplete counterbalancing. Numbers of trials with food stimuli on days 1–5 were 10, 11, 10, 10, and 7. Lizards were tested only once per day, the sequence of lizards tested on a given day being random. Data analyzed include the tongue-flick attack score (see below), pre-attack tongue-flicks (which includes all tongue-flicks if the lizard does not attack the swab), total tongue-flicks, latency to attack, and number of bites. Tongue-flick attack score is the best available index of overall response strength to chemical food stimuli in this experimental paradigm, because it accounts for both chemosensory investigation and feeding responses mediated by the chemical senses. Because a bite is a stronger feeding response than any number of tongue-flicks, a lizard that bites always receives a higher

tongue-flick attack score than one that does not (Cooper and Burghardt, in press). If a lizard does not bite the swab, tongue-flick attack score is the number of tongue-flicks emitted in the test interval; if it does bite, tongue-flick attack score is the maximum number of preattack tongue-flicks emitted by any lizard in the study during a single trial for any stimulus plus {maximum trial duration – latency to attack in seconds} (Burghardt, 1970; Cooper and Burghardt, in press).

Primary analyses were done by non-parametric Friedman Two-way ANOVA by Ranks, because logarithmic transformation did not remove heterogeneity (Hartley's test: Winer, 1962) from the tongue-flick attack score data. Multiple comparison tests followed procedures described in Hollander and Wolfe (1973). Additional planned comparisons were made using the Wilcoxon Signed-ranks Matched-pairs Test. Multiple comparison tests were two-tailed except comparisons of responses to chemical food stimuli and controls. The effect of day of testing was examined by Friedman Two-way ANOVA of tongue-flick attack score by day rather than by condition. Biting frequencies were compared by McNemar's Test. (Siegel, 1956).  $\alpha = 0.05$ .

## RESULTS

All lizards tongue-flicked applicators in all conditions and several bit applicators bearing chemical food stimuli. Tongue-flick attack score differed greatly among stimuli (Fig. 1), producing a highly significant condition effect ( $X^2 = 27.94$ ,  $df = 4$ ,  $P < 0.001$ ). Multiple comparisons showed that the iguanas responded more strongly to carrot, creosote, and cricket stimuli than to water ( $P < 0.001$ , 0.001, and 0.01, respectively) or cologne ( $P < 0.001$  for each comparison). Responses to the two control stimuli did not differ significantly, nor did responses elicited by the three chemical food stimuli differ from each other. The ranges (as well as variances noted above in Methods) of tongue-flick attack score differed greatly among conditions, being 1–77 for carrot, 1–76 for creosote, 2–78 for cricket, 1–12 for deionized water, and 1–11 for cologne.

There were no obvious differences

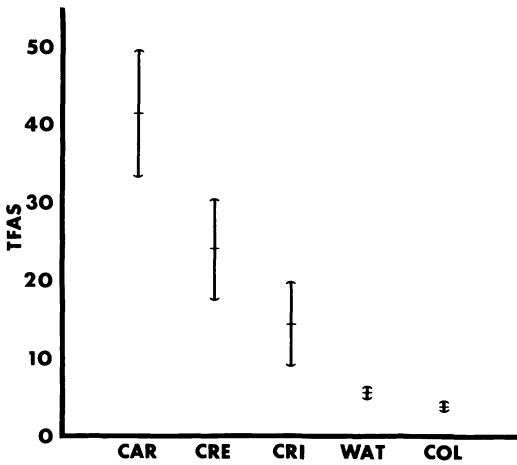


FIG. 1.—Tongue-flick attack scores (TFAS) for *Dipsosaurus dorsalis* in response to chemical stimuli derived from carrot (CAR), creosote (CRE), cricket (CRI), deionized water (WAT), and cologne (COL). Means are indicated by horizontal bars; bracketed vertical bars represent  $\pm 1$  SE.

among conditions in pre-attack tongue-flicks (Table 1). The main stimulus effect was significant ( $X^2_r = 11.08$ ,  $df = 4$ ,  $P < 0.05$ ). Pairwise comparisons among controls and food stimulus conditions revealed only one significant difference: a lower level of pre-attack tongue-flick in response to cologne than carrot ( $P < 0.01$ ) was indicated by the ordinal analysis despite the small difference in means.

More total tongue-flicks were elicited by the chemical food stimuli than by either of the control stimuli (Table 1). Total tongue-flicks differed significantly among conditions ( $X^2_r = 15.46$ ,  $df = 4$ ,  $P < 0.01$ ). Greater response was given to carrot, creosote, and cricket than to cologne ( $P < 0.001$  each) or deionized water ( $P < 0.01$  each). In addition, more total tongue-flicks were elicited by creosote stimuli than by cricket stimuli ( $P < 0.01$ ). The remaining differences were not significant.

TABLE 2.—Latency to attack in seconds and number of *Dipsosaurus dorsalis* attacking cotton-tipped applicators bearing chemical stimuli from three foods and two control substances.

	Latency to attack			Number of individuals attacking
	$\bar{x}$	1 SE	Range	
Carrot	34.19	25.91	5–60	9
Creosote	48.25	4.78	6–60	5
Cricket	54.00	4.16	4–60	2
Deionized water	60.00	0	60–60	0
Cologne	60.00	0	60–60	0

Latency to attack was lower in response to carrot, cricket, and creosote stimuli than to the other stimuli (Table 2). Despite relatively large latency differences among conditions, especially between stimuli from the two plant species and the two control stimuli, the overall difference among conditions was not significant ( $X^2_r = 4.75$ ,  $df = 4$ ,  $P > 0.10$ ). When the analysis was restricted to the 12 lizards that bit at least one applicator, the differences approached, but still did not attain, significance ( $X^2_r = 8.73$ ,  $df = 4$ ,  $0.05 < P < 0.10$ ). The lack of overall significance is presumably due to the high frequency of tied ranks. Because comparisons between chemical food stimuli and controls were planned a priori, Wilcoxon Signed-ranks Matched-pairs tests were conducted to examine these paired differences. Latency was significantly less in response to carrot stimuli than to water or cologne ( $T = 0$ ,  $n = 9$ ,  $P < 0.005$ , one-tailed) and marginally less to creosote stimuli than to either control stimulus ( $T = 0$ ,  $n = 5$ ,  $P < 0.05$  each, one-tailed). Latency to attack did not differ between cricket stimuli and either control stimulus ( $T = 0$ ,  $n = 2$ ,  $P > 0.10$  each).

The iguanas bit only applicators bearing chemical food stimuli, the most frequently bitten being carrot stimuli (Table 2). McNemar's Test of Differences among

TABLE 1.—Tongue-flicking responses of *Dipsosaurus dorsalis* to chemical stimuli from three foods and two control stimuli. Pre = number of pre-attack tongue-flicks; Tot = number of pre-attack plus post-attack tongue-flicks; SE = one standard error of the mean.

	Carrot		Creosote		Cricket		Deionized water		Cologne	
	Pre	Tot	Pre	Tot	Pre	Tot	Pre	Tot	Pre	Tot
$\bar{x}$	5.00	7.75	8.00	8.81	6.25	6.31	5.68	5.68	3.88	3.88
SE	1.13	1.26	1.54	2.20	1.01	1.00	0.81	0.81	0.71	0.71
Range	1–14	1–19	1–22	1–22	2–13	2–13	1–12	1–12	1–11	1–11

pairs of conditions showed that carrot stimuli evoked attack more frequently than either water or cologne [ $P$  (nine of nine values)  $< 0.002$  each, one-tailed] or cricket stimuli [ $P$  (seven of seven values)  $< 0.016$ , two-tailed]. Creosote stimuli also elicited more bites than did water or cologne [ $P$  (five of five values)  $= 0.031$  each, one-tailed]. None of the remaining differences approached significance.

Tongue-flick attack score varied with trial, being  $22.12 \pm 7.57$  ( $\bar{x} \pm SE$ ) for trial one,  $31.06 \pm 8.22$  for the second,  $19.56 \pm 6.13$  for the third,  $11.44 \pm 3.96$  for the fourth, and  $5.56 \pm 1.34$  for the last. Tongue-flick attack score varied significantly over trials ( $X^2 = 11.79$ ,  $df = 4$ ,  $P < 0.01$ ). The only significant difference between pairs of trials was that tongue-flick attack score was greater for trial 2 than for trial 5 ( $P < 0.01$ ). This analysis is only approximate, because number of lizards tested with each stimulus varied slightly over trials due to randomization. Although these results give no clear evidence of habituation, the trend reinforces the necessity for randomization or counterbalancing in experiments of this sort using repeated measures (randomized blocks) designs.

#### DISCUSSION

##### *Chemical Detection and Discrimination of Food*

Desert iguanas readily detected chemical food stimuli, confirming a previous report (Krekorian, 1989). Our results show that desert iguanas not only detect foods chemically, but (1) respond to them as if they were food, (2) do not so respond to odorous and odorless nonfoods, and (3) respond differentially among food types. Results for tongue-flick attack score, total tongue-flicks, number of attacks, and latency consistently indicated stronger responses to odors of food than of control stimuli. Only pre-attack tongue flicks did not reveal stronger response to food odors, because their numbers were limited when food stimuli elicited attacks at short latency. Evidence for differential response to chemical cues among food types was that (1) cricket stimuli elicited fewer bites than carrot stimuli and (2) cricket stimuli elicited fewer total tongue-flicks than creosote

stimuli. The two plants may be preferred to crickets, consistent with infrequent inclusion of insects in the diet (Minnich and Shoemaker, 1970; Norris, 1953). Similar variation in chemoreceptive responses to preferred and nonpreferred foods has been documented in garter snakes of the genus *Thamnophis* (Arnold, 1981; Burghardt, 1969). A less likely possibility is that stimulus concentrations were lower for crickets than plant foods.

##### *Diet, Foraging Mode, Systematics and Chemical Detection of Food*

*Dipsosaurus dorsalis* is not an ambush forager, but neither is it a typically active forager. Differences in food characteristics between this primarily herbivorous species and insectivorous active foragers undoubtedly affect foraging movements and use of chemical cues. However, two prey features of plants that are typical for prey of widely foraging species suggest a possible common selective basis for movement while foraging: they are sedentary and may be patchily distributed. Despite these commonalities, actively foraging insectivorous lizards are more likely to use chemical cues for initial detection of hidden prey than are iguanines, which presumably detect most food visually and use chemical cues to assess important food qualities such as chemical defenses, edibility, ripeness, and nutritive content. Both iguanines and typical active foragers may identify potential food items by chemosensory examination subsequent to visual detection.

Present results support the hypothesis that foraging mode and use of chemical cues to detect and identify potential food items are tightly linked in lizards. Iguanidae is the first family of lizards in which chemical detection and discrimination of food have been examined in lizards having both contrasting diets and foraging styles. The three insectivorous iguanid ambush foragers that have been studied, including two sceloporines (*Sceloporus jarrovi*, Simon et al., 1981; *S. malachiticus*, Cooper, 1989a) and an anoline (*Anolis carolinensis*, Cooper, 1989a), do not use chemical cues either to detect or to identify food before attack, but the herbivorous desert iguana, which is an active forager, does (Krekorian, 1989; this paper).

Iguanidae is now considered polyphyletic and will likely soon be divided into multiple families (Etheridge and de Queiroz, 1988). Thus, the observed differential use of chemical cues among members of three subfamilies may reflect phylogenetic inertia rather than adaptations to foraging mode (Huey and Bennett, 1986) and diet that evolved de novo in each species. Indeed, the conservatism in foraging mode in most families of lizards suggests that evolutionary events effecting major shifts in foraging style and diet are quite rare and constitute adaptive revolutions strongly affecting future trophic relationships, including predator as well as prey suites (Huey and Pianka, 1981) and life history (Anderson and Karasov, 1988).

A relationship between the lizard divisions Ascalabota and Autarchoglossa (sensu Camp, 1923) and use of chemical senses has long been noted in lizards. An important early hypothesis was that autarchoglossan lizards use chemical cues during foraging and social behavior, but that ascalabotans, including iguanids, do not (Evans, 1961). This hypothesis has been falsified as a general rule for social behavior (e.g., Alberts, 1989; Duvall, 1979) and must now be abandoned for feeding behavior. Beyond the ability of desert iguanas to discriminate prey odors, additional bits of evidence suggesting that Evans' (1961) hypothesis is not valid for predatory behavior include prey odor detection by *D. dorsalis* (Krekorian, 1989) and the geckos *Coleonyx brevis* (Dial, 1978) and *C. variegatus* plus prey odor discrimination in *C. variegatus* (Dial et al., 1989).

In a recent taxonomic revision, Ascalabota has been abandoned and a number of families have been removed from Autarchoglossa, which now forms a part of a new taxon called Scleroglossa. Geckos are placed with all former autarchoglossans in Scleroglossa; the remaining families constitute Iguania (Estes et al., 1988). An updated modification of Evans' (1961) hypothesis is that iguanians do not detect prey or identify prey by the chemical senses, which use visual cues for these functions, but that scleroglossans do. The updated hypothesis accommodates use of chemical cues for detection and identification of food

by geckos. It is also consistent with the finding that the only agamid lizard studied, *Calotes mystaceus*, did not chemically detect food before biting (Cooper, 1989a). However, food odor discrimination by desert iguanas falsifies the revised hypothesis.

With the demise of the systematic hypothesis in its general form, the available evidence suggests that foraging mode is the primary factor accounting for the difference in use of chemical cues in food acquisition by desert iguanas and carnivorous iguanians and for the presence of prey odor discrimination in other lizards tested. However, only a single species has been examined in most families of lizards and none have been studied in a few others. Although general observations of many more species suggest that the results obtained thus far are typical for many species in the groups of lizards involved, it is important to regard the proposed relationship as an hypothesis demanding much more testing.

Another limitation of the hypothesis regarding foraging mode and use of chemical senses in feeding is that we have adopted the syndrome hypothesis of foraging modes, which states that there are only two polarized foraging modes that are species-specific (McLaughlin, 1989). In reality, (1) a spectrum of foraging modes exists, having the two modes identified here at opposite extremes (Pianka, 1973; Regal, 1978), (2) individuals undoubtedly differ somewhat in the degree of foraging movement within a species, and (3) individuals in some species that usually ambush may actively search for prey when sufficiently hungry (Chiszar et al., 1981). Despite these limitations, a recent study confirms that the foraging movements of lizards have the predicted dichotomous pattern, with variation in the degree of foraging movement within each mode (McLaughlin, 1989). Lizards neatly fall into broad taxonomic groups that differ so greatly in foraging behavior that it is usually easy to categorize them as active or sit-and-wait foragers without collecting quantitative data on movement. Thus categorical data are adequate for the initial examination of broad relationships between foraging mode and use of the chemical senses in feeding.

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## A NEW SPECIES OF *MIXOPHYES* (ANURA: LEPTODACTYLIDAE) AND FIRST RECORD OF THE GENUS IN NEW GUINEA

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**ABSTRACT:** *Mixophyes hihiorlo* sp. nov. is described from Namosado at an elevation of 900 m in the Southern Highlands Province of Papua New Guinea. In comparison with congeners, it is a large species (males 69-75 mm SVL, females 85-90 mm SVL) with long legs and small eyes, extensive toe webbing, and a narrow midvertebral stripe. Additionally it is distinguished by details of its karyotype and osteology. *Mixophyes* has not been recorded previously in New Guinea.

**Key words:** Anura; *Mixophyes hihiorlo*; New Guinea; New species; Karyology; Morphology; Osteology

IN contrast to Australia, the leptodactylid<sup>1</sup> fauna of New Guinea is relatively depauperate. Only four genera are known, three of which are represented by single species from the southern lowland savannah of New Guinea and adjacent areas of northern Australia. The fourth genus, *Lechrodus*, with three endemic New Guinean species and a single Australian species, is widely distributed in rain forest and wet sclerophyll forest in both regions. Two other rain forest leptodactylid genera, *Mixophyes* and *Taudactylus*, are found in northern Australia but not as yet in New Guinea (Frost, 1985; Menzies, 1975).

In November 1985, biologists from the South Australian Museum found an undescribed species of leptodactylid frog referable to *Mixophyes* in midmontane rain forest in the Southern Highlands Province of Papua New Guinea. We herein describe the species.

### MATERIALS AND METHODS

Specimens reported here are deposited in the Australian Museum, Sydney (AMS), the South Australian Museum, Adelaide (SAMA), and the University of Papua New Guinea, Port Moresby (UPNG). Measurements were taken with vernier calipers from formalin-fixed, alcohol-preserved specimens after the method of Tyler (1968). Measurements taken were snout-vent length (SVL), tibia length (TL), head length

<sup>1</sup> The use of Leptodactylidae instead of Myobatrachidae follows the argument of Tyler (1979).

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