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The California Academy of Sciences Gulf of Guinea Expedition (2001) II. Additions and Corrections to Our Knowledge of the Endemic Amphibians of São Tomé and Príncipe

R. C. Drewes and R. E. Stoelting

Department of Herpetology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA; Email: rdrewes@calacademy.org

We present observations on the São Tomé Island endemic *Hyperolius thomensis* which indicate that it is one of the few African treefrogs known to utilize phytotelmata (tree holes) for breeding. Our field work and observations strongly suggest that this island giant is restricted to primary forest, remnants of which are usually at higher elevations or inaccessible areas of São Tomé Island. Our locality data and field observations in a number of circumstances are not congruent with those of Loumont (1992). An examination of the data associated with her collections housed in the Natural History Museum of Geneva reveals that her data are not specific with regard to individual specimens and dates and, as a result, the status and distribution of the amphibian species on both islands may have been misinterpreted. We note that females of the endemic ranine ranid frog, *Ptychadena newtonii*, attain snout-vent lengths greater than other members of the genus, and that this species should therefore be considered an island giant. We describe and illustrate for the first time the males of Africa's largest treefrog, the Príncipe Island endemic *Leptopelis palmatus*, provide figures illustrating the range of male and female color pattern polymorphism and comment on adult size dimorphism and size at metamorphosis.

The islands of the Gulf of Guinea off the west coast of Africa are a unique chain that includes one geologically recent continental island, Bioko (formerly Fernando Poo), and three oceanic islands, Príncipe, São Tomé and Annobón (Pagalu). Isolated from the African mainland since their orogeny, the three oceanic islands are noted for their highly endemic but poorly known flora and fauna. In 2001, the California Academy of Sciences conducted a multidisciplinary, two-month research expedition to the two geologically oldest islands, Príncipe and São Tomé, which resulted in the collection of voucher specimens and tissues now available for genetic analysis. In an earlier study, Drewes and Wilkinson (2004) presented a more detailed introduction to the geologic history of the two islands, and a popular account of the expeditions' scope and goals is available (Drewes, 2002).

Loumont (1992) attempted the first comprehensive analysis of the entire endemic amphibian fauna of both islands. She recognized three hyperoliid species *Nesionixalus thomensis* endemic to São Tomé, *Leptopelis palmatus* found only on Príncipe, and *Nesionixalus molleri* common on both islands, two ranids, *Ptychadena newtoni* (São Tomé) and *Phrynobatrachus dispar* (common on both), and two species of dermophine caecilians, *Schistometopum thomense* and *S. ephele* of São Tomé. A subsequent morphological study (Nussbaum and Pfrender 1998) indicated that *S. ephele*

is conspecific with *S. thomense*, and we confirmed this decision based on mtDNA analysis (Stoelting, in prep.). In a recent systematic work, Drewes and Wilkinson (2004) returned *N. thomensis* and *N. molleri* to the genus *Hyperolius* Rapp 1842 from which these species were twice removed by Perret (1976, 1988; Loumont 1992).

Although the species that comprise the amphibian fauna of São Tomé and Príncipe have been known to science since the latter half of the 19th Century, these islands have rarely been visited by modern biologists and then usually only briefly. Thus, much of the natural history of these island species including basic data such as the extent of intra-island distributions has remained undocumented. We report data suggesting that the endemic treefrog *Hyperolius thomensis* of São Tomé is a primary forest, high-elevation, tree-hole breeding frog. We describe the male of the Príncipe endemic *Leptopelis palmatus* with comments on adult sexual size dimorphism and metamorph-adult size disparity. We attempt to refine our knowledge of the distributional limits of the amphibian species of São Tomé and Príncipe.

Materials and Methods

The CAS Gulf of Guinea expedition afforded the opportunity to examine localities on both islands in considerable detail and from the perspectives of five academic disciplines: herpetology, ichthyology, mammalogy, entomology and invertebrate zoology. Many sites on both islands were visited and sampled on multiple occasions. Three of the 11 CAS staff members involved in all or part of the 10-week expedition were herpetologists who spent roughly 110 person-days in the field. The availability of transportation and accessibility of many sites, especially on São Tomé, allowed us to conduct a reasonable amount of sampling and observation at night (until 2300 hr or later). All CAS specimens were hand-collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Anuran larvae were retained in formalin. Tissues were taken from selected individuals of all taxa and preserved in 95% ethanol. Latitude, longitude and elevation were recorded with a Garmin 12 Global Positioning System receiver (datum WGS 84). All specimens and tissues are housed in the Department of Herpetology, California Academy of Sciences; associated data can be accessed on-line at *www.calacademy.org/research/herpetology/catalog*. Institutional abbreviations follow Leviton et al. (1985).

Results and Discussion

I. Reproduction in *Hyperolius thomensis*

In his initial description of the genus *Nesionixalus*, Perret (1976) found 25 large (2.0–2.5 mm) presumably ovarian eggs in each of two of the three females in the type series of *N. thomensis.* In erecting the genus, he suggested that the small number and large size of the eggs might indicate a specialized reproductive mode — "*un cycle biologique particulier!*" Our field data suggest that Perret (1988) was correct. While our observations confirm that *H. molleri* deposits its egg masses above water in typical *Hyperolius* mode (Schiøtz 1999; Fahr 1993; Figure 1 herein;), there is strong inference that *H. thomensis* is one of the few African tree-hole breeding frogs. To date, two bufonids, one microhylid, one petropedetine ranid, and five hyperoliids — *Acanthixalus spinosus, A. sonjae, Callixalus pictus* (possibly)*, Hyperolius mosaicus* and *H. acutirostris* — are known to breed in phytotelmata (Rödel et al., *in press*).

In 10 weeks on São Tomé, we encountered *Hyperolius thomensis* at only two localities. A single, rather small male (CAS 219059; 31.0 mm.) was collected on 14 April 2001 among a group of *H. molleri* males, which were calling from tall grasses along a trail-side ditch on the footpath to Lagoa Amelia above Bom Successo (elevation: 1170+ m.). Our series of 13 adults (CAS

218925–937) was collected on 9 April 2001 within a hole in a buttressed, unidentified tree in primary forest at Macambrara, just west of the site of a large transmission tower at an elevation of 1280 m. This locality is a well-forested ridge top with no open water available. The tree hole was located where two buttresses were joined about 1.7–1.8 m. above the ground. The dimensions of the opening were roughly 7–12 cm wide by 25 cm high. The internal diameter of the hole was about 20 cm, and about 20 cm of stagnant water was in the basin. Two smaller holes were located on the same tree at least 1.7 m above the ground, one of which contained water and egg masses (but no adults); the other was dry.

When initially discovered on 9 April 2001, the first referenced tree hole yielded 11 adult *H. thomensis* — two adult females and nine males, 38 larvae and at least three egg masses adhering to the interior walls of the hole a few centimeters above the water surface. A subsequent visit to the tree on 16 April 2001 resulted in the collection of two more adult males. Of the two females collected, CAS 218925 has ovarian eggs whereas CAS 218934 has none.

We have not attempted to dismantle the egg masses, but each contains from 20–40 large, pigmented eggs. In one mass, the eggs are at the 32-cell stage of development (Gosner 1960, stage 7), and in another the eggs are at yolk plug stage (Gosner stage 11).

The 38 larvae range from Gosner stages 25–41 with the majority around 25–37. A detailed description of the larvae of *Hyperolius thomensis,* along with *H. molleri, Phrynobatrachus dispar* and *Ptychadena newtoni* is in preparation (Drewes and Altig); the *H. thomensis* tadpole has a maximum tooth row formula of 2(2)/3, but a number of individuals lack the second upper row (LTRF 1/3; nomenclature of Altig 1970). Ecomorphogically the larvae most closely fit the exotrophic, lentic, arboreal type 5 of McDiarmid and Altig (1999).

The large number of adults found together along with the various developmental stages of the tadpoles and egg masses suggests that tree-holes are used by multiple individuals at different times; phytotelmata probably represent primary reproductive sites at higher elevations where free water is absent. We assume based on buttress structure and trunk morphologies that there were additional holes that were too high to be surveyed in this tree and in other nearby trees of similar size.

RES returned to the radio tower site with other CAS team members on successive nights from 5–8 May 2001. On 5 May, beginning around 1930 hr, she heard an estimated nine different males calling from about 4.5 m above ground at locations approximately 30–40 m apart. Three locations within the forest where frogs were heard were marked. On 6 May, she and three others returned to the marked spots at about 2130 hr and noted a distinct reduction in calling from the night before. On this second evening, the moon was full, and there was a lack of mist. At one marked spot she heard a male calling from the same perch as on the night before and noted that a few other males seemed to be calling from sites somewhat lower within the canopy than on the previous occasion. Individuals were extremely wary: if disturbed they ceased calling, and then seemed to resume from another spot. On the night of 7 May, numerous frogs were again heard from "all over the radio tower primary forest area [= Macambrara]," but no calls were heard along the road to the lower plantation areas. Finally, on the night of 8 May at around 1900 hr near the original tree from which the *H. thomensis* series was initially collected on 9 April, RES heard, recorded and saw a single individual about 7 m above ground at the juncture of a bifurcating tree trunk. The recording is consistent with the description and sonogram given in Loumont (1992). Upon descending to Bom Successo she noted that no calls were heard in cultivated areas, but a few were heard in a remnant of primary forest between the plantation and Bom Successo.

Our extensive field work on São Tomé leads us to the conclusion that *H. thomensis* is a high-elevation, primary forest, tree-hole breeding species, which is not consistent with collecting localities given in Loumont (1992).

II. Localities and Distributions

We were puzzled by our inability to confirm some of the *H. thomensis* localities cited in Loumont's paper and by the absence of supporting data that one would normally expect to see (e.g., specific collecting dates, voucher numbers associated with sonograms, and behavioral observations). Published sonograms of male advertisement calls by *H. thomensis* that were supposedly collected at Java and Colonia Açoreana indicate that they were recorded from captive males calling in plastic bags (as were the recordings of *Phrynobatrachus dispar* and *H. molleri* [Loumont, p. 40]). However, there are no individual voucher numbers provided with these sonograms, and it is not clear from which specimens these calls were recorded, nor where they were made — on-site, in the town of São Tomé or in Geneva. Although the sonogram of *H. thomensis* is accurate based on our recordings and observations noted above, we assume that Loumont failed to note calling sites, times and specific dates because she did not collect nor observe these specimens in the field. Additional inconsistencies lead us to believe that much of her hyperoliid material was brought to her by local collectors.

Loumont indicated that specimens of *H. thomensis* were found in São Tomé town (coastal), Colonia Açoreana (coastal), Java (600 m), and Monte Café (680 m) under banana leaves, and in mossy hollows in old walls, close to small reservoirs of water; these represent the entirety of the microhabitat information provided by Loumont (*op. cit*., p. 51) for this species. We sampled the abandoned plantation at Java on several occasions but found no evidence of *H. thomensis*, although *H. molleri* adults, tadpoles and egg masses were readily found in such microhabitats. No suitable sites were found in the town of São Tomé in spite of many days of searching there and at many other coastal and lowland localities. We did not survey Monte Café (500+ m below the CAS Macambrara site), but in October-November 2003, a private collector camped for three days at Pousada Boa Vista while actively looking for *H. thomensis* and other endemics. Pousada Boa Vista is above Monte Café on the same road, ca. 800 m. Five *H. thomensis* were brought to him by a local boy who indicated they came from a site about an hour away and stated that they were "very hard to find." (Daniel Hofer, pers. commun.). The CAS expedition did not survey the coastal locality of Colonia Açoriana *per se* but worked many similar sites along the east and southeast coasts (Micondó, vicinity of Rio Angobó, Sao Joao, vicinity of Dona Augusta).

The Natural History Museum in Geneva kindly provided by electronic mail all of the field data associated with Loumont's collections of *H*. (as *Nesionixalus*) *thomensis* and also of *Leptopelis palmatus* (Príncipe Id.). Loumont's collection dates with respect to nearly all of these specimens are recorded inclusively rather than as individual dates. For instance, Loumont's data for 21 "*Nesionixalus" thomensis* contain but one specific date: 10.07.1988 for two specimens from Java. Two specimens from Monte Café bear the date 7.1988. Four more from Java are recorded as 1.1990, and the remaining specimens from São Tomé town, Gulf of Guinea, Monte Café, Agua Cascada, Colonia Açoreana and Java all bear the collection date 1.12.1989–31.12.1990, a 13-month period. The Agua Cascada specimen (MHNG 2492.084) and the two from "Golfe de Guinée (MHNG 2492.081–082) were not included in her publication, but the MHNG data sheets indicate the same collecting date as the others: 1.12.1989–31.12.1990. Similarly, all *Leptopelis palmatus* taken from three separate localities on Príncipe Island are cataloged as having been collected from 1.12.1989–31.1.1990. In her materials and methods section, Loumont (1992) stated that field work took place in early July 1988 and in January 1990. If this is accurate then any and all specimens taken during December of 1989 must have been collected by someone else prior to her arrival.

We conclude that Loumont did not publish nor archive individual collection dates or more specific locality site data because she did not know them, and that she relied on local collectors for

collection of the specimens and for their general locality data. Data such as "Golfe du Guinée" is consistent with the broad and technically correct information a researcher might record for a valuable specimen if more precise locality data was unknown or had been lost. Similarly suspect is the collection locality of Colonia Açoreana. Colonia Açoreana is a lowland site on the southeastern coast at about 200 m and surrounded by old plantations and secondary growth; however, the topography inland rises to above 600 m within 6 km of the town where primary growth likely still persists. We think it is reasonable that a local collector bringing specimens to São Tomé city would probably indicate "Colonia Açoreana" as the point of capture for animals that had perhaps been collected at an un-named locality high in the mountains above that town.

Loumont indicated that most of her localities were within two ecological zones on both islands: a lower altitude zone from 0–500 m, where *Ptychadena*, *Phrynobatrachus* and *Leptopelis* are found, and a middle montane zone (500–1000 m) where "*espéces parasylvicoles"* (species of disturbed-forest/secondary forest?) such as *Nesionixalus* (= *H. thomenis and H. molleri*) occur but they may also descend to the lower plains. She mentions three other zones from which she had no specimens: the northeast savannah on São Tomé (grassland with baobab trees [*Adansonia digitata*] in the rain shadow of Pico do São Tomé, the primary site of 16th Century sugar production by the Portuguese), the areas adjacent to the central peak (from 1500 to 2000 m), and the forests of middle elevation on the southern exposures of both islands which are inaccessible by road.

During our stay there, the local inhabitants and expatriates on São Tomé were consistent in telling us that amphibians were not found above 500 or 600 m, but Schiøtz (1999) wrote that *Hyperolius* (as *Nesionixalus*) *molleri* occurs between 500–1000 m, evidently following Loumont (1992). Below, we provide species distributions based on our own data for specimens collected at altitudinal extremes, our interpretation of Loumont's (1992) data and records by J. Baillie (1999).

Hyperolius thomensis Bocage, 1886. This frog is the largest member of the genus *Hyperolius* and an island giant. *H. thomensis* is an endemic to São Tomé Island and restricted to remnants of primary forest which are usually at higher elevations above 800 m. The five type specimens lost in the Lisbon fire included a male and female from Roça Saudade (800 m), a male and female from "Ile São Tomé" (exact provenance unknown), and a single female from the Rio Quiza (= Rio Quija, A. Gascoigne, pers. commun.), a river in the southwestern part of the island with headwaters at 900 m. Specific localities documented by voucher specimens include CAS 219059, above Bom Sucesso on trail to Lagoa Amelia (ca. 1170 m) and CAS 218925–218937, in the tree hole on primary-forested ridge at Macambrara (1280 m.). Probable localities (viz Loumont, 1992) are forest remnants on slopes above Monte Café and Java, and inland from Colonia Açoreana. We reject the capital city of São Tomé as a locality for this species. It is likely that this species still exists wherever primary forest remains, especially on the steep terrain of relatively inaccessible southern slopes of the island.

Hyperolius molleri Bedriaga, 1892. A common *Hyperolius* on both São Tomé and Príncipe islands, this species appears to be a classic "farmbush" species, *sensu* Schiøtz (1967). It breeds in still or very slow-moving water; egg masses are deposited on overhanging vegetation (Fig. 1). On São Tomé, *H. molleri* occurs at sites near sea level adjacent to São Tomé town such as at Praia Melão (CAS

FIGURE 1. Egg mass of *Hyperolius molleri*. São Tomé: Quisinda. Photograph by D. Lin

219068–219069), is common in both low and mid-elevation abandoned and functioning plantations such as those at Caxueira (CAS 218848–218891) and Java (218974–218994), and specimens were found calling from bushes on the banks of Lagoa Amelia in primary forest at 1412 m (CAS 219048–219050).

On Príncipe, *H. molleri* was found in the same microhabitats as on São Tomé. CAS 219203–219208 were collected while calling from vegetation near pooling areas of a small stream at sea level, just in from our campsite on the beach at Baia das Agulhas on the southwestern coast. Another series was taken at about 150 m near the town of Santo Antonio while males called from vegetation overhanging eddies of the slow-moving Ribeira Doutor. Notably, RES did not encounter *H. molleri* at higher elevations during her ascent of Pico do Príncipe.

Leptopelis palmatus (Peters, 1868). Endemic to Príncipe Island, this species has hitherto been considered a lowland treefrog based on three localities reported by Loumont (1992), who suggested it was found up to 300 m. CAS 219370–219383 and 219397–219401 were collected at about 620 m on the central massif of Pico do Príncipe; BMNH 2000.58 was taken at approximately 700 m during a daytime descent from Pico do Príncipe by Jonathan Baillie in 1999. (Baillie, personal communication) Because this collection is the basis for the first description of the male of this species, it is treated in further detail in Section III, below.

Ptychadena newtoni (Bocage,1886). This São Tomé endemic may be the only true lowland amphibian species *sensu* Loumont (1992); all of her collection localities are in the northern lowlands of São Tomé Island (north of a line between São Tomé town and Diogo Vaz on the northwest coast), well below 150 m. We collected two series of adults in town (CAS 219248–219263 in an undeveloped lot, and CAS 219313–219317 in a swampy area of Agua Grande). We also collected a series of *P. newtoni* tadpoles (CAS-RCD 13682) together with *Phrynobatrachus dispar* larvae in a road-side puddle at Java (595 m), which would constitute an altitude record for these species. At this site, no adults were seen. A description of the *P. newtoni* tadpole and others is in progress. *P. newtoni* is the only endemic amphibian species of São Tomé and Príncipe that may be endangered. Since Loumont's visit, many low-lying areas in the vicinity of São Tomé town have been drained for housing. We visited a number of sites at which we were told this species used to be common; in most cases, the areas were dry.

Loumont (1999) records a female *P. newtoni* of 76 mm, snout-vent length. To our knowledge this is the largest known *Ptychadena* specimen. This indicates that together with *Hyperolius thomensis*, and *Leptopelis palmatus*, there are three examples of anuran island gigantism inhabiting the Gulf of Guinea Islands.

Phrynobatrachus dispar (Peters, 1870). This species was originally described from Príncipe Island; a second species, *Phrynobatrachus feae* (Boulenger, 1906) also from Príncipe, was described later. The differences between descriptions are rather minor, and Loumont (1992) concluded that the latter is a synonym of the former. The CAS expedition took tissue samples from a number of populations on both islands but has not yet sequenced them. We treat these taxa as one, *Phrynobatrachus dispar. P. dispar* is a nearly ubiquitous frog in suitable wet areas in disturbed as well as near-pristine conditions on both islands. CAS 218918–218919 and 219064–219077 were collected at 700 m in aqueduct tunnels of the Rio Contador on the west side of São Tomé Island; CAS 219047 was taken from the edge of Lagoa Amelia at 1412 m. On Príncipe Island *P. dispar* was collected by RES at 620 m (CAS 219385–219393) in a tributary of the Ribeira Banzu, and on the top of Pico do Príncipe at 948 m (CAS 219393–219394). Baillie (1999) records the species as very common on the top of Pico Mesa, ca. 530 m.

Schistometopum thomense (Bocage,1873). The endemic São Tomé caecilian is perhaps the most unlikely amphibian inhabitant of the island from a dispersal point of view. Wholly fossorial,

it might be expected to occur principally in the lowlands, but such is not the case. Two specimens were collected on the west side of the island in a vertical rock crevice along the Rio Contador culvert at 700 m. (CAS 218914–218915), and a series (CAS 219324–219334) was found in a cultivated field above the arboretum at Bom Sucesso, ca 1180 m. J. Measey (personal communication) has collected specimens of *S. thomense* within 100 m of the Lagoa Amelia crater rim (which would be at about 1300 m).

III. The male of *Leptopelis palmatus*

Prior to the CAS Gulf of Guinea expedition, the Príncipe endemic treefrog *Leptopelis palmatus* (Peters, 1868) was represented in collections by the female holotype (ZMB 6067: "île de Principe"), eight females from three lower-elevation localities reported by Loumont (1992) and deposited in the MHNG, and two males and a female in the collections of BMNH collected by J. Baillie in 1999. Loumont (1992) published a table of measurements of the females including MHNG 2491.82 from Bela Vista with a snout-vent length of 110 mm, indicating that *Leptopelis palmatus* attains a greater snout-vent length than any other African treefrog species. She included a photograph of one of the females (1992, fig. 7; museum number not given) which illustrated the dorsal pattern described as marbled ("*un aspect marbré"*); she described the other specimens as being dark green or black with a number of light patches. A photograph by Loumont of what appears to be the same specimen is presented in Schiøtz (1999, fig. 570), which together with the aforementioned comprise the only published images of *L. palmatus* to date excepting three on-line images by Baillie (1999). Figure 2 illustrates the range of color pattern variation we observed in females. Figure 2A is a 108 mm SVL individual collected in at Tchipique, a locality in the northwestern part of Príncipe Island; Figure 2B is 88 mm SVL from the Rio Papagaio a central island locality. BMNH 2000.58, the smallest mature female known (oviducal eggs present) exhibits a dark brown pattern on a beige background which we interpret as cryptic.

Our series of eleven adult male *L. palmatus* was collected by the second author (RES) over 17–18 May 2002 on the massif of Pico do Príncipe along a tributary of the Ribeira Banzu at about 620 m elevation. The same locality yielded two females, three juveniles and three post-metamorphs (Appendix I). The locality is a small cascading stream in primary forest dominated by saplings and tree ferns (the endemic *Cyathea camerooniana* var. *currori*). The specimens were collected from 1800–0030 hr on the 17 May and 1800–2000 hr on 18 May. The males were perched on leaves or branches of saplings or leaves of tree ferns from 1.0–1.5 m above ground, although the larger

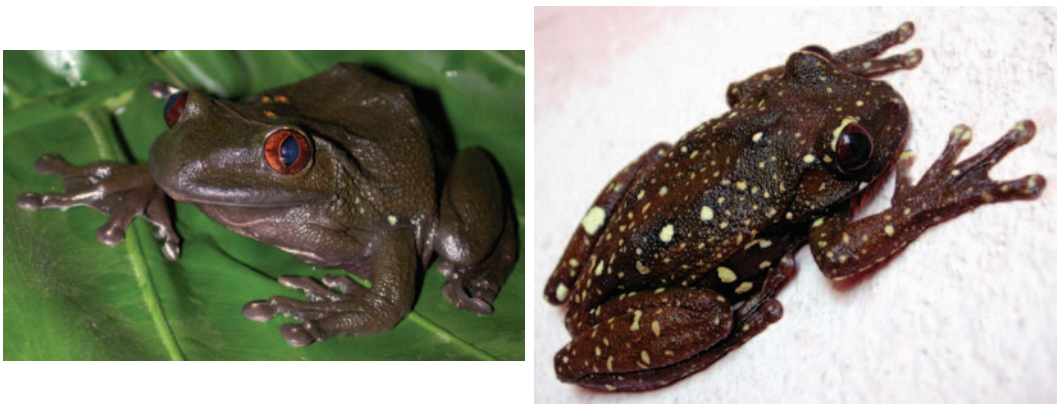

FIGURE 2. (A) CAS 219177, female *Leptopelis palmatus*. Príncipe: Tchipique, near Sundi. Photograph by D. Lin; (B) CAS 219351, female *L. palmatus*. Príncipe: Rio Papagaio. Photograph by J. Ledford.

female (CAS 219401) was found on the ground beneath a rocky overhang near a pool at the base of a small waterfall. A small post-metamorph, CAS 219370, was found perched on the same leaf as an adult male. RES collected an area about 10 m out from both banks of the stream along approximately 30 m of its length and found the tree frogs remarkably numerous: she saw three times as many specimens as she collected (ca. 60 seen). On both nights RES heard calls of *Phrynobatrachus dispar* which were numerous in the leaf litter near the stream, but did not hear any advertisement call attributable to *L. palmatus* males.

Description of males

Adult male *Leptopelis palmatus* specimens are less than half the snout-vent length of females (male mean = 41.4 mm — Appendix I; female mean = 93.8 mm, n = 12, including data from Loumont, 1992). *L. palmatus* males are remarkably polymorphic for color pattern; male color patterns include individuals with uniform bright green dorsum, slightly darker green with random mustard blotches or faint blackish vermiculations, pinkish maroon with indistinct olive blotches and occasional dull-orange spots, mottled light brown and white, and light brown individuals with fairly distinct partial "X"-shaped patterns on the dorsum and distinct thigh bands. (Fig. 3). The dorsal and lateral skin of all specimens is heterogeneous and rough, as in females. The male ventrum is not dark as in females, but ranges from off-white to lightly mottled gray.

In larger females, there is a conspicuous fold of skin extending across the head between the posterior margins of the tympani. This structure is quite obvious in Peters' drawing of the holotype (1868), in Loumont's photographs (1992, in Schiøtz 1999) and in our own Figure 2A. This feature was not discussed in Perret's examination of the type (1973). It is absent in all male specimens and also absent in smaller CAS females (219351; 219401) photographed in life.

The irises of all males (and females) are a deep ruby-red in life, in contrast to the gold iris of *L. rufus* (Schiøtz, 1999) with which *L. palmatus* was compared in an earlier study by Perret (1973) (Figs. 2–3). This ruby iris color is most similar both in hue and extent to that of live specimens of *Leptopelis parkeri* of East Africa. As suggested by the figures in Schiøtz (1999), whereas many species of *Leptopelis* have reddish coloration in the dorsal quarter to fifth of the iris, only a few appear to consistently have red irises, and these are of a lighter shade than *L. palmatus*, e.g. *L. kivuensis* and Nigerian *L. boulengeri*.

The tympanum in males is conspicuous and measures a little less than one-half the diameter of the eye as in the female (Perret 1973). The eyes are large and protruding, their horizontal diameter nearly equal to the interorbital distance.

The toes of the males are nearly as fully webbed as in females, but the proximal side of the terminal phalanx of toe IV is free. The fingers of males are less webbed than those of the females; the area between toes IV and III is about one-half webbed, that between III and II about one-quarter webbed (for comparison, see figure of holotype in Boulenger [1882:136]). Males possess poorly defined pectoral glands discernible as light patches posterior to the posterior edge of the insertion of the forelimbs.

Dissection of the gular regions of three males (CAS 219373; 219377 and 219400) revealed that *L. palmatus* males lack a vocal sac; there is no elaboration of the *m. interhyoideus*. Vocal sac openings are absent. This is a unique condition within the genus *Leptopelis* although there have been few studies that include these characters (e.g., Drewes 1984, for 11 species).

Male advertisement call

The advertisement call of male *L. palmatus* has never been recorded nor analyzed; however,

FIGURE 3. *Leptopelis palmatus*. A composite of adult males and one juvenile from Príncipe: Ribeiro Banzu (CAS 219371–219383, 219400). Photographs by J. Ledford.

we were assured by the local inhabitants of Príncipe Island that males do call, and the presence of well-developed tympani in both males and females tends to confirm the fact. On the evenings of 5/17 and 5/18, REL heard multiple calls of *Phrynobatrachus dispar* but no calls referable to *Leptopelis*. Males did not call in captivity during transfer back to Santo Antonio. In 1999, the male call was described by Jonathan Baillie in his on-line account of his dissertation field research on Príncipe Island. The following is an excerpt from his account dated 1 September 1999:

> In the dark we took flashlights and cameras to try and find the frogs responsible for the loud night chorus. *Phrynobatrachus dispar* was also common in the small streams. . . . If you listen closely you can hear the soft repetitive peep-peep-peep of this tiny frog. The more noticeable croaking noise, more like a pop bottle being continuously opened, belongs to the tree frog (*Leptopelis palmatus*) that is found in high densities (we saw about 50 that night) on the branches and vines in close proximity to the stream.

This "popping" sound had been described to us by locals earlier in Príncipe's only town, Santo Antonio, and it is consistent with the non-resonant call that might be associated with males lacking a vocal sac. If this call is correctly assigned, it is very different from the call described onomatopoetically by Schiøtz (1999:256) for *Leptopelis rufus*: "a series — about ten long cries [of] 'yiin.'" Baillie's account and personal communications suggest that the campsite near which these observations were made was probably the same site at which RES collected the CAS series of *L. palmatus,* or at least very close to it (Baillie's local guide, Monauna, a former parrot hunter, also guided the CAS party nearly two years later). On 5 Sept, Baillie again heard *L. palmatus* advertisement calls at about 700 m in the forest of Morro de Leste, a ridge approximately 3 km ENE of Pico do Príncipe, but could not locate any individual frogs (Baillie 1999).

Island effects

Female *Leptopelis palmatus* are both the largest of that hyperoliid genus and the largest known African treefrog. They are also among the few anuran island giants that have mainland congeners including *Hyla vasta* and *Eleutherodactylus inoptatus*, both of Hispaniola (Cochran 1941; Zug et al. 2001). The two islands of São Tomé and Príncipe have a number of endemics that are classic examples of island gigantism (Carlquist 1965). On São Tomé, some of these include the largest treefrog of the hyperoliid genus *Hyperolius* (*H. thomensis,* Drewes and Wilkinson 2004), the largest member of the widespread African ranid genus *Ptychadena*, *P. newtoni,* the largest nectariniid sunbird, *Dreptes thomenis* (Cheke and Mann 2001), and the giant two-meter begonia, *B. baccata* (Plana et al., 2004). Both islands share the endemic gecko, *Hemidactylus greefiii*, which is the largest African member of that genus (Loveridge 1947). Although it is an obvious and frequently documented phenomenon, island gigantism is not well understood; release from competition for resources and predation have been suggested as causative factors.

Our series of male *Leptopelis palmatus* exhibit what appears to be non-fixed color pattern polymorphism. Some non-cryptic, arboreal African treefrogs, notably populations of the *Hyperolius viridiflavus* complex, exhibit striking inter- and intrapopulational variation in color pattern, which has led to a proliferation of taxonomic names (Schiøtz 1971). Within such populations, this variation can usually be assigned to one of a number of phases. For instance, Schiøtz (1967), described in *Hyperolius* a PhJ or juvenile phase exhibited by all juveniles and some adult males and a PhF, the female phase, exhibited by all adult females and some males. In our series of male *L. palmatus*, color and pattern are seemingly random, and there appears to be no selection for crypsis (Fig. 3). We know of no other African treefrog with this magnitude of color pattern variation. Females are dull green, brown or black, whether marbled or not (Figs. 2A–B). We considered the possibility of a sexual difference in microhabitat which might account for the less variable, more subdued coloration in females. Although all of the CAS males were collected in arboreal situations, two of the CAS females, 219177, the largest, most heavy-bodied specimen (Fig. 2A), and CAS 219401 were found — at different localities — on the ground in moist areas protected by overhangs (Appendix, Table 1). BMNH 2000.58 was found on the forest floor. The other two females, CAS 219399 and 219351, were collected while perched. Unfortunately, our sample of females is

limited to five as there are no habitat data associated with the eight females Loumont deposited in Geneva (MHNG).

Sexual size dimorphism is the rule among *Leptopelis* species, and, based on specimens collected, *L. palmatus* exhibits the greatest disparity between adult male and female snout-vent lengths of any species of the genus. Schiøtz (1999) provides male and female snout-vent maxima for 33 of the 44 species of *Leptopelis* he recognized and in most species, males range from 8–20 mm smaller in snout-vent length than females. Table 2 (see Appendix) is a compilation of maximum male and female snout-vent lengths recorded from the seven *Leptopelis* species in which the females are greater than 20 mm in length than the males. Our data indicate that the largest known *L. palmatus* male is only 41% of the snout-vent length of the largest female. Mean male size is 45% of mean female SVL. The only other species in which males are less than half as long as females is the widespread West African mainland species, *L. macrotis* at 45% (based on SVL maxima). In addition, we are unaware of any other anuran species that exhibits such as marked range of SVL among adult females (Appendix I).

There is a full order of magnitude difference in *L. palmatus* between post-metamorphic size (10.5–11.3 mm, Gosner stages 45, 46 — Table 2 in Appendix) and potential adult size (MHNG female 2491.82–110 mm; Loumont 1992). Nothing is known of the breeding biology of *L. palmatus*, and the larvae have yet to be discovered. Small size at metamorphosis can be interpreted as an indication that the water in which early development takes place is ephemeral (this would seem unlikely on Príncipe which has high rainfall especially in the forested higher elevations) or that predation on developing larvae is high. Baillie (1999) noted abundant crabs of about 9 cm in diameter feeding in the river at night at the same elevation (and presumably at the same *L. palmatus* collection site; see above), and these may be a significant predator on small frogs. CAS 219370 (11.0 mm) was perched on the same leaf as an adult *L. palmatus* male (field number not noted), about 1.5 m above ground, suggesting both resource availability for individuals at both sizes and perhaps avoidance of predation by crabs. However, RES observed no crabs during her visit to the site. The CAS *Leptopelis palmatus* were removed and taken to lower elevation for photography, processing and removal of tissue; as a result an examination of stomach contents was not informative.

Reduction of predation pressure may well be a factor in the extreme variation in color and pattern observed among *L. palmatus* males (at least for the known sample which was collected at densely-forested higher elevations). Color pattern variation appears much reduced in females suggesting that females are under a different selection regime.

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Appendix

TABLE 1. *Leptopelis palmatus* specimens collected on Príncipe Island by the CAS Gulf of Guinea Expedition including three specimens from the BMNH. Sexual maturity was determined by dissection in male specimens greater than 33 mm SVL.

Sex	*Museum*	*Catalog number*	*Locality*	*Snout-vent length (mm)*
Males	CAS	219371	Ribeira Banzu*	44.2
		219372		45.6
		219373		38.4
		219374		34.7
		219377		41.8
		219378		42.8
		219379		44.5
		219380		43.35
		219381		42
		219382		41.2
		219400		35
	BMNH***	2000.59	“Pico de Principe” 600 m*.	43.8
		2000.60		41.4
juv.	CAS	219375		23
		219376		21.9
		219383		22
metamorphs		219370		11.0 – Gosner stage 45
		219397		10.5 – Gosner stage 46
		219398		11.6 – Gosner stage 46
Females		219399		105
		219401		69.2
		219177	Tchipique	108
		219351	Rio Papagaio	88.8
	BMNH***	2000.58	“Pico de Principe” 700 m**	63.99 (oviducal eggs)

* We are reasonably certain that these localities are equivalent in spite of differences in our GPS coordinates(see text): CAS = 01 35 20.7 N, 007 22 46.3 E; Baillie (1999) = 01 37 11N, 007 22 52 E.

** This specimen was collected on the forest floor by Baillie at about 700 m during his first descent from Pico do Príncipe. The precise locality is unknown but if the estimate of elevation is correct, this is the highest known specimen (Baillie personal communication).

*** Non–CAS Specimens examined: BMNH 2000.58. Female. Pico do Principe, Principe, 700 m. Sept 1, 1999. col. J.E.M. Bailie; BMNH 2000.59-60. Males. Pico do Principe, Principe 600 m. Sept. 1, 1999. col. J.E.M. Baillie.

TABLE 2. Size disparity between male and female *Leptopelis* in species where females are greater than 20 mm in snout-vent length than males; comparative snout-vent maxima taken from Schiøtz, 1999.

Species	*Maximum male SVL (mm)*	*Maximum female SVL (mm)*	*Maximum male SVL as % of max. female SVL*
Leptopelis palmatus	45.6	110	41
L. macrotis	46	84	45
L. millsoni	49	87	56
L. vermiculatus	50	85	58
L. boulengeri	48	81	59
L. occidentalis	43	71	60