DISCOVERY OF THE RICHEST FROG FAUNA IN THE WORLD—AN EXPLORATION OF THE FORESTS TO THE NORTH OF LETICIA

by

John D. Lynch*

Resumen

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A comienzos de 2003 se obtuvieron registros de 97 especies de ranas y sapos en un parche de bosque primario y bosque inundado ubicado aproximadamente 10 kms al norte de Leticia. Sin embargo, hay buenas razones para sospechar que la fauna local consiste en no menos que 123 especies de ranas y sapos, número que supera lo señalado en estudios anteriores realizados en la parte occidental de la cuenca Amazónica. Se sugiere que esta riqueza es más el reflejo del empleo de nuevas metodologías que de la existencia de un "hotspot" biológico.

Palabras clave: Amazónico, Diversidad, Metodología de inventario.

Abstract

Vouchers of 97 species of frogs and toads were obtained in a small section of primary rainforest and flooded forest approximately 10 kms north of Leticia in early 2003. In addition to the 97 species captured, there is good reason to suspect that the actual local fauna consists of no fewer than 123 species of frogs and toads. This local fauna is much larger than previous reports for the western part of the Amazon Basin but probably its size reflects the new methodologies employed rather than a biological "hotspot."

Key words: Amazonian, Diversity, Inventory methodology.

Introduction

Leticia has always been a seldom-visited site perched in the central Amazon. By 2000, only 40 species of frogs and toads (**Cochran & Goin**, 1970; **Duellman**, 1972, 1974, **Flores**, 1987, **Goin & Layne**, 1959, **Heyer**, 1994, **Lynch**, 1979, 1980, 1986, 2002, **Lynch & Lescure**, 1980, **Rivero**, 1991, **Rivero & Serna**, 1984, and **Silverstone**,

* Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

1975, 1976) had been reported from Leticia but I doubted that the fauna had been investigated adequately. Thus, in 2002, I applied for financial support from Conservación Internacional—Colombia to carry out a definitive study of the diversity of frogs and toads in these forests. My team consisted of four undergraduates with a minimum of experience and me. I decided that if we were gong to execute this project, we needed a new methodology for an inventory. At the outset, I knew very little (having collected there only a few times in 20 years)—none-the-less, I was convinced that previous inventories had been managed badly—to allow all participants to carry out "free-searches" was inadequate. Hence, I selected my assistants with a proviso—each had to carry out a specific task and, then, if they wanted, they could join me in nocturnal forays. Long before leaving Bogotá, I had decided that I needed four specialists to back-up my unrestrained nocturnal searches—thus, I assigned to each undergraduate a specific task: (1) To Andrés Duarte, the monitoring of a system of pitfall traps (of 5 gallons, bordered by three drift fences two meters long)—he would need to check each trap three times a day (0600, 1200 and 1800 hrs) and record who had fallen in. This would enable me to sample the terrestrial fauna, a component I had long forgotten in my quest for centrolenids and eleutherodactylines. Years ago, I had recognized my failing of ignoring the ground-fauna. (2) To Jonh Jairo Mueses, another task for which I did not have the patience, to census a single forest pond, night after night, to see who was breeding and who was merely sitting there (with this task, I hoped to show that much of the frog fauna exhibited explosive breeding). (3) To David Sánchez fell the task of collecting tadpoles whenever and wherever he could (largely, daytime work). And, (4) To Adriana Téllez fell the task of sampling the canopy fauna (initially, we planned merely to sample adults and tadpoles in arboreal bromeliads but eventually, we used also felling of primary forest and occasional visits to a canopy platform).

Initially, I had constructed an expected fauna, using all published accounts and records for the Amazon basin (**Acosta**, 2000, **Ardila R & Ruiz C**, 1997, **Duellman**, 1973, **Lutz & Kloss**, 1952, **Myers & Carvalho**, 1945, and **Ruiz C *et al.*,** 1996) and my estimates of the distributional areas for Amazonian species. My initial construct was too ambitious—I imagined a fauna of more than 130 species of frogs and toads. Furthermore, I assigned each species to one of four habitat contingencies: (A) terrestrial, (B) aquatic, (C) canopy, and (D) inhabitant of the understory. In many cases, my assignments were based on my experiences collecting the frogs—in other cases, my failures to find them (a mixture of positive and negative evidence).

We set out to conduct a five-pronged inventory. Four prongs covered each of the assigned tasks and the fifth was my free search of microhabitats (aided by my students, each of whom decided that finding frogs was more enjoyable than sleep). Our fieldwork was carried out between Dec. 24, 2002, and March 31, 2003, essentially at three localities (Km 10 and Km 11, along the only road in the department, the Leticia—Tarapacá road, and along the northern shores of Lago Yahuarcaca). We also explored other nearby localities but these three appear to cover the entire fauna—two in *tierra firme* forest (Km 10 and 11) and one in *varzea* (Lago Yahuarcaca).

In retrospect, I erred in constructing the team—I should have included a specialist to care for amplectant pairs of frogs (and to recover the tadpoles produced by them). Likewise, I underestimated how complex was the canopy—I should have included one, or more, persons to conduct nightly searches, using climbing equipment. But, we all learn from our mistakes.

Before this project began, the storied locality for the Amazon Basin was the study reported by **Duellman** (1978) for Santa Cecilia, in eastern Ecuador—a locality that eventually yielded 86 species (**Duellman**, 1990). Looking at the general trend of diversity across the Amazon Basin (low to the east, but building to the west), one might imagine a fauna of 60 or 70 species for Leticia. In a bit over 90 days, I and my students managed to secure preserved vouchers for 96 species of frogs and toads—in the following year, I added species number 97 to the fauna and we now have 98 documented.

A frog fauna of 96 or 98 species is truly impressive but is not a testimony to our efficiency. Furthermore, when one reflects upon previous records from nearby sites (Benjamin Constant, in Brasil, or Puerto Nariño, in Colombia, or, Leticia, itself), the local frog fauna swells considerably—to 123 species—and this number, however impressionable, does not include species that live there but that no one has ever seen.

Materials and Methods

All specimens preserved from this study reside in the collection of Amphibians in the Instituto de Ciencias Naturales. The methods employed were five: (1) **The free-search method**: nocturnal surveys inspecting the understory as well as being directed towards calling males; this technique varied nearly every night—some nights were confined to pond-free forest trails, others to lake edges, others to marshes and ponds within the forest and, only occasionally, with attention to terrestrial

individuals. (2) **Pit-fall traps**: these were five-gallon buckets buried in the forest soil and armed with three two-meter long drift fences (set at 120°) and revised three times per day for 15 days and then moved to another patch. (3) **Census of a single forest pond**: nightly visits with counts of individuals/ species and notes on their activities with daytime measures of depth and extent of the pond. (4) **Tadpole searches**: this was a daytime activity, searching any body of water for tadpoles within the areas being searched for adults. (5) **Canopy fauna**: three sub-methods were used—in order of use—(a) inspection of individual bromeliads, between six and 13 meters above the forest floor, enclosed within a gunny sack and lowered to ground-level, (b) harvesting the frogs sitting at night on trees felled during the day, and (c) visual inspection of frogs from a platform 34 meters above the forest floor (Km 11).

Results

Although the distances between collecting sites were minor, we sampled two very distinctive assemblies within the Amazonian rainforests—(A) the *varzea* or seasonally flooded forest and (B) the *tierra firme* forests; accordingly, I will separate the results using this initial filter.

Varzea: During December 2002—March 2003, it was not possible to walk in these forests (between the Quebrada Yahuarcaca and Lago Yahuarcaca) because they were under two to six meters of water—in that time frame, we sampled the canopy fauna using boats and native climbers. In January, July, and September 2004 (and in July 2005), I sampled these forests during low water. I also had sampled these forests in July 2001. Some additional data for this class of forest comes from the relatively nearby Parque Nacional Natural de Amacayacu (sampled in September 1985 and April 2001).

If we restrict our inspection to the site near Leticia (Yahuarcaca), the frog fauna consists of only 27 species (25 as vouchered specimens, neither *Bufo marinus* nor *Pipa pipa* was preserved). The preserved samples include two dendrobatids (*Epipedobates femoralis, E. hahneli*), 18 hylids (*Dendropsophus brevifrons, D. haraldschultzi, D. leucophyllatus, D. rossalleni, D. triangulum, D. sp.* [grupo *microcephala*], *Hypsiboas lanciformis, H. punctatus, H. raniceps, H. sp, Scarthyla goinorum, Scinax garbei, S. ruber, S. sp.* [grupo *rostratus*], *Sphaenorhynchus carneus, S. dorisae, S. lacteus, Trachycephalus venulosus*), and five leptodactylids (*Adenomera hylaedactyla, Eleutherodactylus zimmermannae, Leptodactylus bolivianus, L. leptodactyloides, L. petersi*).

Collections made in the flooded forests in the Parque Nacional Natural Amacayacu add one toad (*Bufo roqueanus*), four hylids (*Dendropsophus koechlini, Hypsiboas fasciatus, H. geographicus, Osteocephalus yasuni*), one leptodactylid (*Hydrolaetatre schmidti*), and one microhylid (*Hamptophryne boliviana*).

Of the species we collected in these two sites in the *varzea,* most are common frogs, known for decades from this part of Colombia (and elsewhere). Only four species can be viewed as rare— *Dendropsophus koechlini,* a species not previously known for Colombia (this represents its northernmost locality), *D. rossalleni* is a species rarely collected and we only found a single individual (secured during a treefall—suggesting that it is a canopy species), *Hyspsiboas raniceps,* a species not previously known from Colombia but very abundant in the *gramalote* (this represents its westernmost locality but the species is also widely distributed in southern Brasil and northern Argentina, **Cei**, 1980), and *Eleutherodactylus zimmermannae,* an uncommon frog living in arboreal bromeliads in Colombia (this represents its westernmost locality). Of the 33 species documented for the flooded forests, only seven are restricted to the flooded forests (that is, we failed to find them in our more extensive explorations of the *tierra firme* forests): *Dendropsophus koechlini, D. rossalleni, Hyspsiboas raniceps, H. sp.* (at present known only from tadpoles), *Scarthyla goinorum, Scinax sp.* and *Leptodactylus bolivianus.* However, the rarity of the two *Dendropsophus* in our collections (single individuals of each) must be taken into account—neither may be confined to such forests.

Tierra firme: Most of our collections in these forests were made in the *resguardas* of the *Uitotos* at sites locally called Km 7, Km 10, and Km 11. Additionally, we sampled at Kms 13.5, 18.5, 21, and 23. The additional sites did not yield species not found in the small area beside the Río Tacana, seven to eleven kilometers north of Leticia (along the Leticia—Tarapacá road), aside from *Lithodytes lineatus* (only found at Km 23) and *Physalaemus petersi* (only found at Km 18.5). In our collections, some species are known from only one of the sites within the *Uitoto resguardas* but most were found at each of the three sites (although we spent less time at Km 7, the *comunidad Jitoma*).

Species list using current family groups—BUFONIDAE: *Bufo castenoticus, B. ceratophrys, B. marinus, B. roqueanus, B. sp., B. sp.,* (both *Bufo sp* appear to be undescribed and are under study by Claudia Vélez), *Dendrophryniscus minutus.* CENTROLENIDAE: *Cochranella ametarsia* (Fig. 2), *C. sp., Hyalinobatrachium*

sp. DENDROBATIDAE: *Colostethus trilineatus, Dendrobates ventrimaculatus, Epipedobates femoralis, E. hahneli, E. trivittatus.* HYLIDAE (novel taxonomy follows **Faivovich *et al.***, 2005): *Cruziohyla craspedopus, Dendropsophus bokermanni, D. brevifrons, D. haraldschultzi, D. leucophyllatus, D. marmoratus, D. minutus, D. parviceps, D. rhodopeplus, D. riveroi, D. sarayacuensis, D. triangulum, D. sp.* (*microcephalus* group), *Hemiphractus proboscideus, H. scutatus, Hypsoboas "albopunctulata", H. boans, H. calcaratus, H. fasciatus, H. geographicus, H. granosus, H. hobbsi, H. lanciformis, H. microdermus, H. ornatissimus, H. punctatus, Nyctimantis rugiceps* (Fig. 3), *Osteocephalus cabrerai, O. deridens, O. heyeri, O. planiceps, O. taurinus, O. yasuni, Phyllomedusa bicolor, P. tarsius, P. tomopterna, P. vaillanti, Scinax cruentommus, S. funereus, S. garbei, S. ruber, Sphaenorhynchus carneus, S. dorisae, S. lacteus, Trachycephalus coriaceus* (Fig. 6), *T. resinifictrix, T. venulosus.* LEPTODACTYLIDAE: *Adelophryne adiastola* (Fig. 1), *Adenomera hylaedactyla, Ceratophrys cornuta, Edalorhina perezi, Eleutherodactylus acuminatus, E. altamazonicus, E. carvalhoi, E. croceoinguinis, E. malkini, E. nigrovittatus, E. ockendeni, E. peruvianus, E. sulcatus, E. zimmermannae, Ischnocnema quixensis, Leptodactylus diedrus, L. knudseni, L. leptodactyloides, L. pentadactylus, L. petersi, L. rhodomystax, L. stenodema, Lithodytes lineatus, Physalaemus petersi, Phyllonastes myrmecoides* (Fig. 4). MICROHYLIDAE: *Chiasmocleis bassleri, C. ventrimaculata, C. sp., Hamptophryne boliviana, Syncope carvalhoi* (Fig. 5). PIPIDAE: *Pipa pipa.*

Most of these species were not found in inventory work in the flooded forest, suggesting very strongly that within a few kilometers, one moves from one frog fauna to another. Against this argument are several species which are very abundant in the flooded forest but present (and rare) in the *tierra firme* forests.

Six named species are vouchered for Leticia (records published or not) but we did not collect them: *Hydrolaetare schmidti, Leptodactylus fuscus, L. mystaceus, Pseudopaludicola ceratophyes, Pipa snethlageae,* and *Rana palmipes.* Four others are vouchered (and published) for Benjamin Constant in Amazonas, Brasil and surely occur at Leticia: *Bufo dapsilis, Cochranella ritae, Hemiphractus helioi,* and *Eleutherodactylus ventrimarmoratus*. For twelve other species, vouchers exist for nearby localities (Amacayacu, Calderón, Isla Santa Sofia, Loretoyacu, Puerto Nariño, or Tarapacá) and they too are expected for this local fauna: *Atelopus pulcher, Colostethus faciopunctulatus,Ctenophryne geayi, Eleutherodactylus aaptus, E. conspicillatus, E. lanthanites, E. lythrodes, E. vilarsi, Hypsiboas hutchinsi, Leptodactylus discodactylus, L. riveroi,* and *Osteocephalus mutabor.* Lastly, I suspect that *Adenomera andreae, Dendropsophus miyatai,* and *Hypsiboas tuberculosus* occur in the local fauna as well although the nearest published (or known to me) records are more distant.

Discussion

The documented frog fauna of this patch of forest centered on the *Uitoto* communities at Kms 10 and 11 consists of 27 species captured in seasonally flooded forests and 94 species captured in *tierra firme* forests with 23 shared species (Table 1) as well as six other species documented for "Leticia" or "forests near Leticia" by others (104 species in total). However, for an additional 19 species (Table 2), I am convinced that they too form part of this fauna because there are locality records nearby (within 50 km within forests that appear the same to me). Although every species must have a distributional limit somewhere, 50 kms strikes me as a trivial distance within the *hyalea* when our new records offer distributional extensions of as much as 800—1000 kms, especially for hylids, re-inforcing the criticism of **Heyer *et al.*** (1999) about generalizations drawn from the known distributions for frogs of that family. Thusly, I consider the fauna to contain no fewer than 123 species of frogs and toads of which we collected nearly 80% in three months of fieldwork.

And, What of my "New" methodology to do inventories? It contained two elements: (1) forced, permanent, attention towards four submethodologies and the liberal application of a general methodology and (2) assignment of every known or suspected species to one of four habitat contingencies (aquatic, canopy, terrestrial, or understory).

In terms of (1), we had excellent success as measured in terms of collecting efficiency. Of an enormous local frog fauna estimated at 123 species, we required fewer than 100

Table 1. The 98 species of frogs and toads vouchered (in the collections of the ICN) for the forests just to the north of Leticia.

Family	Varzea	Shared	Tierra firme
Bufonidae	1	1	7
Centrolenidae	0	0	3
Dendrobatidae	2	2	5
Hylidae	18	15	48
Leptodactylidae	5	4	25
Microhylidae	0	0	5
Pipidae	1	1	1
Totals	27	23	94

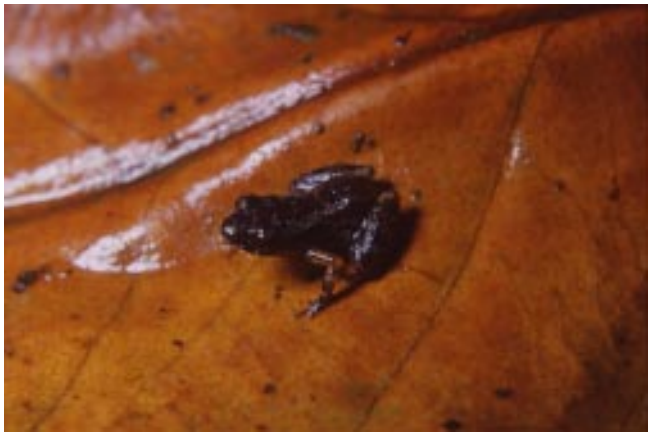

Figura 1. *Adelophryne adiastola.* ICN 50253, Km 10, carr. Leticia—Tarapacá. A rare, miniature frog species.

Figura 2. *Cochranella ametarsia.* ICN 50846, Km 10. A rare species found in the canopy.

Figura 3. *Nyctimantis rugiceps.* ICN 50660, Km 10. First record for Colombia for this canopy species.

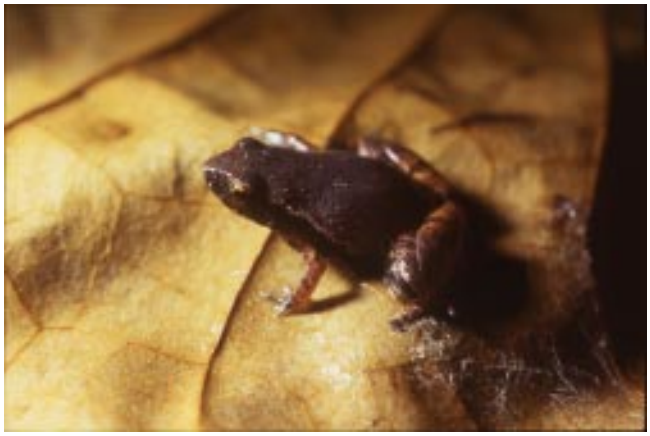

Figura 4. *Phyllonastes myrmecoides.* ICN 46195, Km 13.8. First record for Colombia for this miniature species found in leaf-litter.

Figura 5. *Syncope carvalhoi.* ICN 51769, Km 7.5, *Comunidad Jitoma.* The smallest species found in these forests—relatively common in leaf-litter.

Figura 6. *Trachycephalus coriaceus.* ICN 50664, Km 10. First record for Colombia for this canopy species.

Table 2. Species anticipated but not yet known (in the ICN collections) for Leticia and their estimated habitat contingency.

Anticipated species lacking vouchers	
Adenomera andreae	terrestrial
Atelopus pulcher	terrestrial
Bufo dapsilis	terrestrial
Cochranella ritae	canopy
Colostethus faciopunctulatus	terrestrial
Dendropsophus miyatai	canopy
Eleutherodactylus aaptus	underbrush
Eleutherodactylus conspicillatus	terrestrial or underbrush
Eleutherodactylus lanthanites	terrestrial or underbrush
Eleutherodactylus lythrodes	underbrush
Eleutherodactylus ventrimarmoratus	canopy
Eleutherodactylus vilarsi	terrestrial or underbrush
Hemiphractus helioi	terrestrial
Hypsiboas hutchinsi	canopy with tadpoles in streams
Hypsiboas tuberculosus	canopy
Leptodactylus discodactylus	terrestrial
Leptodactylus riveroi	terrestrial
Osteocephalus mutabor	canopy
Ctenophryne geayi	terrestrial
Species known for the site but which we failed to collect	
Hydrolaetare schmidti	aquatic
Leptodactylus fuscus	terrestrial
Leptodactylus mystaceus	terrestrial
Pipa snethlegae	aquatic
Pseudopaludicola ceratophyes	terrestrial
Rana palmipes	terrestrial near streams

days to secure specimens of 98 of those. Cuzco Amazonico (**Duellman**, 2005) and Santa Cecilia (**Duellman**, 1978, 1990) represent lesser faunas requiring much more human investment (as measured in person months).

I do not think the data acquired are suggestive that Leticia is an extraordinarily rich "hotspot" in the western Amazon. It is possible to forge lists of species for which Leticia represents the northernmost locality, the easternmost locality, the westernmost locality, and the southernmost locality but this zoogeographic "analysis" presupposes the existence of discrete geographic communities of frogs and toads. My expectation is that other localities in the western part of the Amazon Basin are equally (or more rich) as rich as Leticia but were sampled with less effective methodologies.

In terms of (2), we lack a means of making a meaningful comparison. On the one hand, we do have my informed/ uninformed guesses of the habitat contingency for the 134 species so classified. Now, armed with data collected, I claim not 134 but only 123 species and between 15 and 16% of those remain to be documented. My original classification of species into contingencies received a good deal of revision (mostly removing species from the understory habitat [where I had found them previously] and re-assigning them to an unexplored habitat [the canopy]). The material basis for this reclassification was the unpublished undergraduate thesis of one of my students (**Téllez**, 2004) and she will report her results separately.

I have continued to do violence with my unsupported assignments evident in Table 2 (about species with which I have zero experience). Of these, I assign two to the aquatic contingency (now and originally, yet they elude me and my assistants). Of the remaining, I assign (now and originally), 12 to the terrestrial contingency and three others to a mixture of habitats (terrestrial and/ or understory). Once again, the few data I have are for certain species from as far away as 300 kilometers (not exactly close, even for the *hyalea*). The morphological data as well as the extrapolations based on reproductive biologies suggest to me that these species are classified correctly. Only two species are exclusive to the understory (the ecological contingency I've explored off and on for nearly 40 years). The expected canopy fauna now

includes six species in Table 2 (originally only three of them). Then, in the absence of relevant data, I had assumed that species of the *leucophyllatus* and *parviceps* groups of *Dendropsophus* were species of the understory—because I had caught many of them there (in the lowest three meters of this very deep forest). In December of 1999, esconced along the Río Puré immediately before it leaves Colombia bound for Brasil and the Río Japurá, I learned otherwise—*Dendropsophus parviceps* is an abundant canopy species (any day, there are 100s of individuals concealed there but descending, in mass, to breed explosively at ground level and, perhaps to be captured by a visiting herpetologist for one night or so). I have now generalized these observations (in large part due to our harvests of frogs of these groups from the crowns of trees cut down) and now view all species now assigned to the *D. leucophyllatus* (excepting *D. triangulum*) and the *D. parviceps* groups as canopy species, rarely visiting the zone frequented by herpetologists. In the Amazon, centrolenids are heard frequently, but very high, in the canopy. Given that they reproduce at ground level (so far as we know), we have a chance to catch them. *Cochranella ritae* has been caught (to my knowledge) only four times (1950 [the holotype], 1967 [the holotype of *Centrolenella resplendens*], 1971 [a juvenile from San Miguel de Sucumbios] and 1994 [another juvenile in Amazonas, Colombia])—and its rarity is because it normally occupies a stratum we don't visit. At Leticia, we did relatively well with centrolenids by cutting down palm trees up to 45 meters tall.

My original expectations fare even worse when we consider species now documented for these forests but that I had never imagined lived there (*Dendropsophus koechlini, Eleutherodactylus croceoingunis, Hypsiboas raniceps, Nyctimantis rugiceps, Osteocephalus deridens, O. heyeri, O. planiceps, O. yasuni*,and *Trachycephalus coriaceus*—these are not necessarily rare species in our collections yet others, long known, have yet to be documented in our inventory (Table 2).

What do we make of this admission? In spite of all our efforts (1999-2005, but especially Dec. 2002—March 2003), certain species remain very rare at our collecting sites. All of our efforts have secured only single specimens of *Cruzihyla craspedopus* (plus a suspected egg mass), *Ceratophrys cornuta, Edalorhina perezi* (elsewhere in these forests in the Upper Amazon, much more commonly found), *Dendropsophus koechlini, D. minutus, D. rossalleni* (if my identification of tadpoles in the *tierra firme* forests is incorrect), *Phyllomedusa tarsius, Eleutherodactylus nigrovittatus,* and *Physalaemus petersi*)—these nine species (9% of the total found or 7% of the anticipated + known fauna) are not a trivial component—a single "missed" night (for a *fiesta* of whatever nature) could have changed the list of documented (and/or anticipated) species.

What conclusions might I draw from this "experiment"? The lowland faunas of wet forests are much more complex than I had ever imagined (**Lynch**, 1979) and, to dissect them, even more complicated. Lastly, I now am very skeptical of just how good is our database for lowland sites in general. Years ago, prior to dedicating myself to the Andean fauna (which I knew to be understudied), I had assumed that the lowland faunas were well studied. The fauna at Leticia calls all of these assumptions into question. Ignoring this lowland fauna, the richest lowland frog fauna (each sample site is in the biogeographic Chocó) for Colombia is that of the Naval Base at Malaga or that in the immediate environs of Quibdó (**Lynch**, 1998, **Lynch & Suárez Mayorga**, 2004)—perhaps 70 to 80 species—modest in comparison with Leticia (104 to 123 species). Ignoring these three sites, there is simply nothing comparable—many localities (Andean as well as lowland) with only 20 to 30 species vouchered (reinforcing my opinion, voiced above, that the lowlands have been poorly documented). This criticism cannot be extended to the Andean faunas because, for them, alpha diversity (species number) is notably lower than for lowland sites (**Duellman**, 1988) whereas beta diversity (geographic replacement of species) is very notable (in lowland sites, beta diversity is modest or non-existent). This last point is evident when we compare species lists for Leticia and Santa Cecilia (broad overlap in lists) but to see beta diversity we need to compare "equivalent" sites separated by trenchant barriers (such as the Andean cordilleras)—Leticia and Malaga share only two species of amphibians (both frogs) out of two lists that include about 200 species of frogs.

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