Zoología

THE TADPOLES OF FROGS AND TOADS FOUND IN THE LOWLANDS OF NORTHERN COLOMBIA

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Resumen

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Se han registrado 59 especies nativas y dos especies introducidas de ranas y sapos en las tierras bajas de la región Caribe de Colombia. De estas 61 especies, 54 tienen ciclos de vida que incluyen una etapa larval acuática. Para promover estudios ecológicos sobre estas especies, se ofrece una clave con ilustraciones (de veintinueve especies) que permiten una identificación confiable de la mayoría de renacuajos propios de estas tierras bajas.

Palabras clave: Colombia, Región Caribe, renacuajos.

Abstract

Fifty-nine native species and two introduced species of frogs and toads occur in the lowlands of the Caribbean Region of Colombia. Of these 61 species, 54 have life cycles that include an aquatic larval stage. In order to promote ecological studies on these species, a key and illustrations (of 29 species) are provided to allow confident identification for most tadpoles encountered in these lowlands.

Key words: Caribbean Region, Colombia, tadpoles.

Introduction

Among the most poorly-known components of the amphibian fauna of Colombia are the tadpoles of frogs and toads. This poverty is unfortunate because tadpoles offer unparalleled opportunities to study ecological aspects of the fauna of frogs and toads, including the impact of ecological modifications caused by human intervention in the habitat. The Caribbean Region of Colombia has been defined in various ways and my definition is yet another—this definition is based on my understanding of the distributions of the frogs and toads that occupy part or all of this territory. As defined here, the Caribbean Region extends from the northern coastline (to the north), from the Serranía de Abibe (to the west), from the Serranía de Perijá (to the east), and as far south as the 1000 meter contour in the interandean valleys of the Río Cauca and Río Magdalena and against the Andean cordilleras (Fig. 1). Additionally, there is a small

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Figure 1. The Caribbean Region of Colombia as defined herein. Areas with a pronounced and long dry season (and a much reduced frog fauna) are indicated with coarse stipple. The wetter areas (hatching) of these lowlands harbor more frog species. The black arrow indicates a "disjunct" piece of these lowlands east of the Andes (but this is contiguous habitat fragmented by political boundaries).

fragment of lowlands to the east of the Andes in the Catatumbo drainage (part of the Maracaibo Basin of western Venezuela).

The 1000 meter contour was selected because at about that elevation one finds the uppermost distributions of species otherwise seen in lowland areas and the lowermost records of species distributed in upland areas (**Lynch**, 1998, 1999). Although inserted into the region, the Sierra Nevada de Santa Marta is excluded from the Caribbean Region because of biological discordances (all of the species of frogs and toads found on that massif are endemic to the massif [above 1000 meters elevation] and very few encroach upon the lowlands).

Tadpoles are the larval stage in the development of frogs and toads. Tadpoles usually exhibit very different ecologies from their adults because tadpoles are usually herbivores and are usually aquatic (occupying ponds or sometimes streams). The tadpoles of some species exist very briefly as tadpoles whereas others have substantial durations as tadpoles. Among the tadpoles found in this region, all are exotrophic (they must feed on extraneous materials of the environment in order to obtain sufficient energy to grow), although a few are initially endotrophic (growing using the energy reserves of the yolk). In the normal life cycle, the stages are (1) "egg", (2) embryo, (3) tadpole, (4) metamorphic, (5) juvenile, and (6) adult. During the first two stages, the morphologies are peculiar to an endotrophic existence and few structures characteristic of free-living tadpoles are seen. Once metamorphosis is initiated, structures that were useful as larvae begin to be reabsorbed. In these warm lowlands, stages 1 and 2 are brief (hours or a few days) whereas the larval stage is much longer than the period of reproductive activity of the adults (a few days to as much as several weeks). If one recognizes that there are two transformations (embryo to tadpole and tadpole to metamorphic), one realizes that larval structures need to be acquired and are then lost. None-the-less, during the bulk of the larval period, there is a structural stability only slightly modified by the acquisition of limbs.

Materials and methods

Terminology follows **McDiarmid & Altig** (1999). All tadpoles reported here are housed in the Amphibian collection of the Instituto de Ciencias Naturales (ICN).

General tadpole anatomy

The head and body are united in a single unit but are readily distinguished from the tail. The tail consists in three units: the caudal musculature down the center and

the dorsal fin above the caudal musculature and the ventral fin below it. The dorsal fin may or may not extend onto the body. On the head/body, the nostrils (if formedpresent in most tadpoles) are near the anterior tip of the unit and posterior to these are the eyes (lateral or dorsal [dorsolateral]). Near the anterior end of the head/body is the mouth which normally lies within the oral disc. This structure can be terminal or subterminal (or rarely ventral) to the head (Fig. 2). Within the oral disc are various structures (Fig. 3, although some tadpoles lack all of these): (1) two keratinized jaw sheaths, one above and the other below the mouth; (2) tooth row ridges, bearing keratinized teeth [these exist as rows above, or anterior to, the jaw sheaths, the A rows, and below, or posterior to, the jaw sheaths, the P rows; tooth rows are each numbered anterior—posterior]; and (3) one or more rows of papillae along the borders of the oral disc [these may completely surround the oral disc or be interrupted anterior or be interrupted both anterior and posterior]. Some tadpoles have their mouths open permanently (alive as well as preserved) whereas others can close their jaws so that few oral structures, except the most lateral papillae, are visible (alive,



Figure 2. Outline drawing of a "typical" tadpole as seen from the left side of body showing certain structures mentioned in text.



Figure 3. Drawings of the mouth with retracted jaws (A) and after applying pressure on the throat of a tadpole of *Scinax rostratus* (ICN 45692). The open mouth (B) is labeled for certain structures mentioned in the text.

except briefly, when respiring, as well as preserved). To open the mouth, use a pin to apply pressure to the throat just behind the mouth (Fig. 3).

Tadpoles possess internal gills (and lungs) and water enters the mouth carrying both foodstuffs and oxygen. The water taken into the mouth exits the tadpole through an operculum (the spiracle). In most of the tadpoles in the Caribbean Region, the spiracle is located on the left side of the tadpole and most have a spiracle about half-way up the body. Tadpoles of two species have a ventral spiracle, located on the posterior part of the abdomen. In one species in the region, there are two spiracles, one on each side of the body.

The frog and toad community of the Caribbean Region

These lowlands are reasonably well-known although surely we have much to learn about the details of most distributions. That said, published records for frogs and toads of the Caribbean Region are few (Cochran & Goin, 1970; Cuentas et al., 2002; Duellman, 1970; Kluge, 1979; Nelson, 1972; Renjifo & Lundberg, 1999; Ruthven, 1922; Silverstone, 1975). In general, this region suffers a very marked dry season (when activity of frogs and toads is severely reduced) and brief rainy seasons (when frogs and toads are very obvious). That said, there are a few sectors of the Caribbean Region, as defined here, that are notably humid with only a brief dry season (that may not even be apparent, judging from frog activity). These wetter areas are located near the margins of the region (western border, the northern foothills of the Cordillera Central and Cordillera Occidental) and in the Middle Magdalena.

The frog and toad fauna of these lowlands is reasonably well-known (the most recently described species was named in 1961). However, there remain small and vexing taxonomic problems (some with solutions underway): A large toad called Leptodactylus pentadactylus is apparently undescribed (Ron Heyer and Rafael de Sá, pers. *comm.*, have a description in press); the alpha level taxonomy of the toads of the Bufo typhonius group remains to be done (Claudia Vélez is working on this particular problem); the identity of Hypsiboas "albomarginatus" for the Caribbean coast remains to be resolved; and the small frogs of the genus Colostethus remain confusing and require someone to bring order to the existing chaos (Taran Grant assures me that he is working on this problem). For much of these lowlands, the local frog fauna consists of no more than 25-27 species-but along the wetter perimeters, the local fauna expands (Fig. 1).

Using the existing classifications, there are records for four species of toads (Bufonidae) although only two occur throughout the region. The family Centrolenidae (glassfrogs) is poorly represented but five species have one or more records within the region. The family Dendrobatidae is represented by a single widely distributed (in the region) species and peripheral records of seven others. The family Hylidae is a dominant family with 23 species but ten of these are best termed peripheral species. The family Leptodactylidae is likewise a dominant family with 14 species but five of these are peripheral. The two Microhylidae and the single native Ranidae are widespread within the region. The only Pipidae species is of restricted distribution. Beyond these 59 species of native frogs and toads, two species have been introduced into the region (Eleutherodactylus johnstonei, native to the Lesser Antilles but introduced as a "pet" and Rana catesbeiana, native to the eastern United States but introduced in hopes of exploiting it as a source of frog legs). The Eleutherodactylus (five native species occur periphally in the region) have no tadpoles (direct development) and need not concern us further but Rana catesbeiana is like other species of that genus and does have tadpoles (it is a biological plague in the valley of the Río Cauca and in certain localities on the western slopes of the Cordillera Oriental in Cundinamarcaand, being here to stay [unfortunately], it is also included here). Of the remaining native species, all have tadpoles except for one species of Cryptobatrachus (Hylidae, direct development, found in a few localities in the foothills of the Sierra Nevada de Santa Marta).

Identification of tadpoles

The accounts given below are presented as a textual "key" containing a minimum of "couplets." Within each couplet, the state of current knowledge is summarized with the intent of allowing rapid and secure identifications for the majority of the 54 tadpole species encountered within the region. I have attempted to use morphology wherever convenient rather than depending upon labile features of the color patterns which are subject to much environmentally induced variation (tadpoles found in turbid waters have very subdued color patterns whereas those from clear waters have more pronounced color patterns).

A. Tadpoles lacking jaw sheaths, tooth rows and papillae: Only three species of frogs in the region having tadpoles conform to this description. These are classified as the families Microhylidae (*Chiasmocleis panamensis* and *Relictivomer pearesi*) and Pipidae (*Pipa parva*) and are pelagic tadpoles that swim slowly high in the water column. All have lateral eyes (meaning that the eyes can be seen even in ventral view) and terminal mouths. Most microhylid tadpoles are very similar in terms of structure (**Wild**, 1995) and the differences between the tadpoles of the two microhylids that are distributed over the entire Caribbean Region are mostly in their coloration. Each has a pair of labial flaps that cover the mouth and each lacks nostrils until very late in their development (Fig. 4).

The only pipid of the region has tadpoles (Fig. 5). They initiate their development within individual pits in the highly vascularized skin of the dorsum. The free-living



Figure 4. Tadpole of *Relictivomer pearesi* (ICN 48993) in dorsal and lateral views; mouthparts of same.



Figure 5. Tadpole of *Pipa parva* (ICN 33602) in dorsal and lateral views; mouthparts of same.

tadpoles have a wide mouth as seen in anterior view. Within the region, this species is restricted to the Catatumbo Basin.

A'. Tadpoles with jaw sheaths: All other tadpoles (51 species, including the introduced *Rana catesbeiana*) found in the Caribbean Region have keratinized jaw sheaths (families Centrolenidae, Dendrobatidae, Hylidae, Leptodactylidae, and Ranidae).

B. Lacking rows of keratinized teeth: Of the 51 species having jaw sheaths in the Caribbean Region, only three lack rows of keratinized teeth (all three are species of the hylid genus *Dendropsophus*). The tadpoles of *D. microcephalus* are distinctive because their oral disks lack papillae (Fig. 6). The tadpoles of *D. ebraccatus* and *D. subocularis* have papillae on the lateral and ventral borders of the oral disk (Fig. 7). The tadpole of *D. ebraccatus* has an incomplete white stripe from below the eye onto the body and anterior part of the tail whereas that of *D. subocularis* lack such a stripe but has irregular tan vertical bars on the caudal fins. **Duellman** (1970) provides a description and illustrations for *D. subocularis*. These three tadpoles have lateral eyes.

One other species may fall in this contingency. Adults of a small *Colostethus* are available for the Middle Magdalena (border between Antioquia and Santander) which appears to be allied with *C. nubicola*. The *C. nubicola* complex is under revision by T. Grant and C. W. Myers and the taxonomy will change. Among the species



Figure 6. Tadpole of *Dendropsophus microcephalus* (ICN 49350) in dorsal and lateral views; mouthparts of same.



Figure 7. Tadpole of *Dendropsophus ebraccatus* (ICN 14373) in dorsal and lateral views; mouthparts of same.

of that complex in Colombia, at least one has tadpoles with an umbelliform mouth (an expanded oral disc used for sweeping foodstuffs from the surface of the water; this disc has papillae located within it, lacks lateral emarginations, and lacks teeth). The tadpoles of the species from Puerto Berrio have not been collected to date.

B'. With rows of keratinized teeth (all with jaw sheaths and papillae): The remaining 47 species (including the introduced *Rana catesbeiana*) having tadpoles conform to this description. These have tooth row formulae of at least 1/2 (one anterior and two posterior rows) but most (45 species) have a labial tooth row formula of 2/3 (or greater).

C. Eyes lateral on body: Tadpoles with lateral eyes tend to be somewhat or exclusively pelagic in their habits. The tadpoles with lateral eyes (and complex oral disks) in the region are all treefrogs (Hylidae) and pertain to the genera *Agalychnis, Dendropsophus, Phyllomedusa, Pseudis, Scinax,* and *Trachycephalus.* There is one other species with lateral eyes but its classification was not been changed by **Faiviovich et al.** (2005) owing to lack of material—it is currently still called "*Hyla vigilans.*" These 11 species all have tooth row formulae of 2/3 except for *Dendropsophus columbianus* and *Trachycephalus venulosus.*

The tadpole of *T. venulosus* is easily recognized because it has a formula of 3/6 and because there is a dark longitudinal stripe along the upper part of the caudal musculature (Fig. 8). The tadpole is able to close the mouth, obscuring its tooth rows and jaw sheaths.



Figure 8. Tadpole of *Trachycephalus venulosus* (ICN 45833) in dorsal and lateral views; mouthparts of same.

Tadpoles of Agalychnis and Phyllomedusa have the spiracle located very low on the side of the body (almost midventral). Additionally, they are distinctive in that the dorsal fin of the tail is much smaller and lower than the ventral fin. To date, tadpoles of the two Agalychnis known from the region have not been collected (or not identified). Each is of very restricted distribution. Agalychnis callidryas is known from extreme northern Depto. Bolivar in Colombia but potentially is distributed from there west to Panamá. The species is well known from southern Mexico to eastern Panamá and its tadpole has been described (Duellman, 1970, 2001). The other Agalychnis appears to be undescribed and is found along the eastern margin of the Middle Magdalena (Deptos. Boyacá and Cundinamarca). By way of contrast, Phyllomedusa venusta (Fig. 9) is relatively abundant perhaps over the entire region (as far south as Chaparral, Tolima). It is uncommon in collections, perhaps because when not breeding, it occupies the top layer of the forest, far from casual encounters. These tadpoles can close the mouth and obscure their 2/3 dental formulae.

Tadpoles of frogs of the genus *Scinax* are like the above in being able to close their mouths, obscuring their mouth parts. Within the region, four species of *Scinax* have been identified (*S. elaeochrous*, *S. rostratus*, *S. ruber*, and *S. xsignatus*) but only the tadpole of *S. rostratus* is distinctive. The tadpole of *S. rostratus* has relatively low caudal fins and the P3 contains very large teeth and lies outside of the oral disk defined by the marginal papillae (Fig. 10).



Figure 9. Tadpole of *Phyllomedusa venusta* (ICN 45850) in dorsal and lateral views; mouthparts of same.

Figure 10. Tadpole of *Scinax rostratus* (ICN 48967) in dorsal and lateral views; mouthparts of same.

In the other species, the labial papillae are complete across the posterior lip and the teeth of the P3 are the same size as teeth in other tooth rows. The P1 (first tooth row posterior to the jaw sheaths) is divided medially in *S. ruber* and S. x-signatus but is complete in S. elaeochrous (**Duellman**, 1970). The caudal fins are high in S. ruber and S. x-signatus but relatively low in S. elaeochrous. Just as the adults are difficult to distinguish, the tadpoles of S. ruber (Fig. 11) and S. x-signatus (Fig. 12) are very similar. At least to me, the tadpoles of S. x-signatus appear to have deeper caudal fins than do those of S. ruber. Previous reports of S. boulengeri from this region of Colombia are all based on specimens now identified as S.



Figure 11. Tadpole of *Scinax ruber* (ICN 45652) in dorsal and lateral views; mouthparts of same.



Figure 12. Tadpole of *Scinax x-signatus* (ICN 48977) in dorsal and lateral views; mouthparts of same.

rostratus. Scinax ruber is distributed throughout the region whereas the other species are known from a smaller part of the region (the western part and extending southward into the Middle Magdalena).

The tadpole (Fig. 13) of *Dendropsophus columbianus* can be found below 1000 m in the valley of the Río Cauca although the species is normally found at greater elevations. As in other species of this group, the mouth is permanently open and there are small papillae laterally and posteriorly. The oral disk contains 1/2 tooth rows although the A1 is not always visible. Unlike, "*Hyla*" vigilans tadpoles, the tadpole of *D. columbianus* has a mottled pattern on the tail (not vertical bands).

The tadpole of "*Hyla*" vigilans (Fig. 14) resembles young tadpoles (see Fig. 15) of *Pseudis paradoxa* in coloration (black vertical bars on the tail) but retain this pattern so long as they are tadpoles. Their head/body remains globular and is not deeper than long. A detailed description of the tadpole of "*Hyla*" vigilans is given by **Suárez Mayorga & Lynch** (2001).

The tadpole of *Pseudis paradoxa* is remarkable due to its upper size limits and due to the strong ontogenetic changes in coloration. Young (small) tadpoles have strong black vertical bars on the tail but larger tadpoles become uniformly black except for scattered cream spots (Fig. 15). The mouths of these tadpoles are terminal and appear incapable of being closed. Larger tadpoles of *P. paradoxa* develop a pair of longitudinal troughs between the eyes (Fig. 16).

C'. Eyes dorsolateral (or dorsal) on body (never visible from beneath): Tadpoles of thirty-six species (in-



Figure 13. Tadpole of *Dendropsophus columbianus* (ICN 45837) in dorsal and lateral views; mouthparts of same.

cluding the introduced *Rana catesbeiana*) from the region can be thus described. Additionally, as is evident in this key, all have a single sinistral spiracle, jaw sheaths, at least **2/2** tooth rows, and labial papillae. These tadpoles include all bufonids, all centrolenids, all dendrobatids,



Figure 14. Tadpole of "*Hyla*" vigilans (ICN 44541) in dorsal and lateral views; mouthparts of same.



Figure 15. Young tadpoles of *Pseudis paradoxa* (ICN 48981) in dorsal and lateral views showing early coloration.



Figure 16. Larger tadpoles of *Pseudis paradoxa* (ICN 48979) in dorsal (showing longitudinal furrows) and lateral views; mouthparts of ICN 48981.

the hylids of the genera *Hypsiboas* and *Smilisca*, all leptodactylids having tadpoles, and the ranids (introduced or native).

D. Labial papillae with obvious dorsal gap (space) and posterior (gap); papillae restricted to marginal papillae: This condition is seen in the four "true" toads (genus *Bufo*) of the region and in two leptodactylids (*Pleurodema* and *Pseudopaludicola*). In all other species, the labial papillae form a complete series along the posterior margin of the oral disc (or there are no labial papillae). *Bufo granulosus* and *B. marinus* are widely distributed in the region (they occur seemingly at every locality and are abundant toads) whereas the other two *Bufo* are distributed only in wetter facies of the region. *Pleurodema brachyops* is most abundant along the coast and does not penetrate the Middle Magdalena nor the interior valleys. *Pseudopaludicola pusilla* occurs widely in the region but has its southern distributional border in the Middle Magdalena (it is not known from the valley of the upper Río Cauca). One of the vexing problems with these six species is that the tadpoles of two of them (*Bufo* granulosus and *Pseudopaludicola pusilla*) are very small, making observation of the details of the mouthparts even more trying.

Tadpoles (Figs. 17-18) of the two widely distributed species (the two common Bufo) are easily distinguished by color pattern (the caudal musculature of *B. marinus* is bicolored—dark above, cream below—and the caudal



Figure 17. Tadpole of *Bufo granulosus* (ICN 48942) in dorsal and lateral views; mouthparts of same.



Figure 18. Tadpole of *Bufo marinus* (ICN 48940) in dorsal and lateral views; mouthparts of same.

musculature of *B. granulosus* bears dark saddles). Structurally, they can be distinguished based on the length of the P3 relative to the P2 (very short in *B. granulosus*, long in *B. marinus*). In the other two *Bufo* (*B. haematiticus* and one or more species of the *Bufo typhonius* species group) found in the region (each peripherally), the gap in the A2 is broader than those illustrated here. **McDiarmid & Altig** (1990) provide a detailed description for the tadpole of *B. haematiticus*. The species of the *Bufo typhonius* group that occur in the region are in dire need of taxonomic attention (**Vélez**, 1995). One or two of these occur in the lowlands of the Pacific and one or both encroaches onto the southwestern edge of the Caribbean Region. One, two, or three species occur principally on the Andean slopes but descend below 1000 meters.

The median gap in the A2 of *Pleurodema brachyops* (Fig. 19) and *Pseudopaludicola pusilla* (Fig. 20) is much broader (nearly as wide as the length of either A2 segment) than the "broad" gaps in *Bufo haematiticus* and *Bufo* of the *typhonius* group or the narrow gaps seen in *Bufo granulosus* (Fig. 17) or *B. marinus* (Fig. 18). These two leptodactylids are easily distinguished because *Pleurodema brachyops* has a labial tooth row formula of 2/3 and the marginal papillae partially overlap the A1 (Fig. 19) whereas in *Pseudopaludicola pusilla* (Fig. 20), the labial tooth row formula is 2/2 and the marginal papillae partially overlap the A1.

D'. Labial papillae complete along lateral and posterior borders of oral disc: Twenty-nine species of frogs and toads (five centrolenids, seven dendrobatids, eight



Figure 19. Tadpole of *Pleurodema brachyops* (ICN 48983) in dorsal and lateral views; mouthparts of same.

hylids, seven leptodactylids, and two ranids) of the region have (or are expected to have) tadpoles with this morphology. Tadpoles of two species (*Hypsiboas "albomarginatus"* and *H. phantasmagorius*) are unknown and the adults hardly better known. Adding to our difficulty is the instability of the taxonomy for the dendrobatids currently residing in *Colostethus*.

E. Four or more tooth rows anterior to jaw sheaths and posterior to jaw sheaths: This condition is seen in *Ceratophrys calcarata* and the only native ranid (*Rana* vaillanti). Tadpoles of *C. calcarata* have papillae surrounding the oral disc and can develop as many as six tooth rows anterior to the jaw sheaths and seven posterior to them (Fig. 21) whereas in *R. vaillanti* the tooth row



Figure 20. Tadpole of *Pseudopaludicola pusilla* (ICN 45519) in dorsal and lateral views; mouthparts of same.



Figure 21. Tadpole of *Ceratophrys calcarata* (ICN 45732) in dorsal and lateral views; mouthparts of same.

formulae vary between 4/4 and 5/4 (**Acosta**, 2000) and papillae are absent from the anterior border of the oral disc (Fig. 22).

E'. No more than two tooth rows anterior to jaw sheaths: The five centrolenids, seven dendrobatids, six *Hypsiboas*, two *Smilisca*, five *Leptodactylus*, one *Physalaemus*, and *R. catesbeiana* conform to this component (27 species).

F. No gap in any tooth row: Among species found in the Caribbean Region having 2/3 tooth rows, the only species exhibiting this condition is the abundant *Leptodactylus insularum*. The species occurs throughout the region but is not endemic to it (Fig. 23 shows the condition for another species of *Leptodactylus*, *L. colombiensis*).

F'. Broad gap in A2 (as broad as, or broader than, the length of either A2 segment): All centrolenids have a very broad A2 gap (much broader than the length of either A2 segment and sometimes as broad as the jaw sheaths). **Starrett** (1960) described and illustrated the tadpoles of one *Centrolene,* two *Cochranella,* and two *Hyalinobatrachium* (all under the generic name *Centrolenella*). At least using that sample, the genera are not readily distinguishable using tadpoles. All have a labial tooth row formula of 2/3. There are no gaps other than that of the A2 in



Figure 22. Tadpole of *Rana vaillanti* (ICN 45529) in dorsal and lateral views; mouthparts of same.

tooth rows and the P3 is 60 to 80 % the length of other rows (ignoring the A2). Tadpoles of this family live in streams and have greatly elongated tails (tail length 2.2— 2.6 X body length). The upper lip is bare and the labial papillae scarcely overlap the lateral-most extent of the A1. In the collections of the ICN, there are no free-living tadpoles of centrolenids captured from this region.

Four other species from the region have a broad gap in the A2 (this gap is as broad as the length of an A2 segement or slightly narrower)—*Leptodactylus fragilis* (Fig. 24), *L.* "*pentadactylus,*" *Physalaemus pustulosus* (Fig. 25), and *Rana catesbeiana* (the last introduced, Fig. 26). Of these, the tadpole of *L. fragilis* has the P3 about as broad as the P2



Figure 23. Tadpole of *Leptodactylus colombiensis* (ICN 14363) in dorsal and lateral views; mouthparts of same.



Figure 24. Tadpole of *Leptodactylus fragilis* (ICN 49005) in dorsal and lateral views; mouthparts of same.



Figure 25. Tadpole of *Physalaemus pustulosus* (ICN 43249) in dorsal and lateral views; mouthparts of same.



Figure 26. Tadpole of *Rana catesbeiana* (ICN 45809) in dorsal and lateral views; mouthparts of same.

whereas in the other three species the P3 is only about ¹/₂ the length of the P2. **Heyer** (1970) provides a detailed description and illustrations of *L. "pentadactylus."* The P3 is shorter than the P2 in *Leptodactylus "pentadactylus"* and in *Rana catesbeiana* and about the same length as the P2 in *Leptodactylus fragilis* and *Physalaemus*. Laterally, the oral disc of *Rana catesbeiana* is emarginated (Fig. 26) whereas it is not in *Leptodactylus "pentadactylus."* This same character allows distinction of *Leptodactylus fragilis* (Fig. 24) and *Physalaemus pustulosus* (Fig. 25).

F". Narrow gap in A2 (much narrower than the length of either A2 segment): This condition is seen in the remaining species from the region for which the tadpole is known (*Colostethus palmatus, C. pratti, C. wayuu, Dendrobates truncatus, Hypsiboas boans, H. crepitans, H. pugnax, H. rosenbergi, Leptodactylus fuscus, and L. poecilochilus.* Tadpoles remain unknown for two *Hypsiboas* (*"albomarginatus"* and *phantasmagorius*) and for *C. inguinalis, C. ruthveni,* and an apparently undescribed species—each is expected to exhibit this condition.

G. Narrow gap in P1: The tadpoles of the *Hypsiboas* found in the region, of two species of *Leptodactylus* found in the region, and the two *Smilisca* all share the condition of having narrow gaps in the A2 and the P1. In the *Hypsiboas* and *Smilisca*, the lateral margins of the oral disc are emarginated whereas the lateral margins of the oral discs of *Leptodactylus* do not show emarginations. I have not been able to identify tadpoles of *Leptodactylus* poecilochilus in the collections available to me but **Heyer** (1970) provides a detailed description and illustrations of *L. poecilochilus*.

The four *Hypsiboas* for which the tadpoles are known are distinctive in that the dorsal caudal fin is obviously deeper than is the ventral caudal fin (Figs. 27-29). In each of these species, the "mature" tadpole has four posterior tooth rows (the other species of contingency F" in this region have only three posterior tooth rows) but very young tadpoles of these *Hypsiboas* exhibit labial tooth



Figure 27. Tadpole of *Hypsiboas boans* (ICN 45530) in dorsal and lateral views; mouthparts of same.



Figure 28. Tadpole of *Hypsiboas crepitans* (ICN 20710) in dorsal and lateral views; mouthparts of same.



Figure 29. Tadpole of *Hypsiboas pugnax* (ICN 49353) in dorsal and lateral views; mouthparts of same.



Figure 30. Tadpole of *Leptodactylus fuscus* (ICN 49641) in dorsal and lateral views; mouthparts of same.

row formulae of 2/3 (Figs. 27-29 and see **Duellman**, 1970:251-252, for illustrations of *H. rosenbergi*). The two *Smilisca* (Figs. 31-32) differ in the length of the tail relative to the body; in *S. sila* (a stream dwelling tadpole), the tail is more than twice the length of the body whereas in *S. phaeota* (a pond dwelling tadpole) the tail is less than twice the length of the body. "Long" tails are seen in *H. crepitans* and *H. pugnax* whereas *H. boans* and *H. rosenbergi* have shorter tails (see Figs. 27-29). Tadpoles of *Hypsiboas boans* have submarginal papillae.



Figure 31. Tadpole of *Smilisca phaeota* (ICN 45737) in dorsal and lateral views; mouthparts of same.



Figure 32. Tadpole of *Smilisca sila* (ICN 45521) in dorsal and lateral views; mouthparts of same.

G'. P1 lacking gap: The dendrobatids (*Colostethus* and *Dendrobates*) found in the region (Figs. 33-34) are difficult to distinguish individually (except perhaps by coloration)—but I am hampered because my samples are



Figure 33. Tadpole of *Colostethus palmatus* (ICN 45562) in dorsal and lateral views; mouthparts of ICN 19739.



Figure 34. Tadpole of *Dendrobates truncatus* (ICN 40749) in dorsal and lateral views; mouthparts of same.

minimal—and all are distinctive in lacking any gaps in any of the posterior tooth rows.

Discussion

Of the 59 native species, only two (Colostethus inguinalis and Dendrobates truncatus) are endemic to the Colombian Caribbean Region (and C. inguinalis is restricted to a small subset where wet conditions obtain, Grant, 2004) although Phyllomedusa venusta is nearly so (also known from just across the Panamanian border). If we ignore political boundaries and instead focus on biological boundaries, this region extends to the east into coastal Venezuela and the list of endemic taxa rises slightly (the leptodactylids Ceratophrys calcarata and *Pseudopaludicola pusilla*). Of these five species, the only one having a distribution that encompasses this entire region (except the Catatumbo drainage) is D. truncatus. At any rate, a level of endemics of only four or five species out of a fauna of nearly 60 is trivial and does not provide support for proposals such as that of Morrone (2001).

Much of this fauna consists of species having only peripheral presence within the region. These peripherally distributed species conform to two components: (A) species found normally at greater altitudes on the Andean slopes but whose lowermost distributional records encroach upon the zone and (B) species frequently termed "Chocoan" because part of their distribution area lies within the usually recognized Biogeographic Chocó (Lynch & Suárez Mayorga, 2004). The species found in the relatively dry parts (stippled zone, Fig. 1) represent less than half of the species recorded from the zone and some of these are distributed as well within the wetter parts of these lowlands.

The tadpole community of this region (and of its two ecological zones) is primarily a community found in lentic (standing) waters (51 species, plus *Hypsiboas crepitans*, normally, and occasionally *Rana vaillanti*). Tadpoles of lentic habitats occupy puddles, temporary ponds, and permanent ponds (*ciénagas*). Few of these tadpoles normally occupy flowing water. The exceptions are *Bufo haematiticus*, *Hypsiboas boans*, occasionally *H. crepitans*, *H. rosenbergi*, *Smilisca sila*, and *Rana vaillanti*—these occupy low gradient streams. The lentic water community is divided ecologically into a pelagic subcommunity (*Agalychnis*, *Chiasmocleis*, *Dendropsophus*, "*Hyla vigilans*, *Phyllomedusa*, *Pipa*, *Relictivomer*, and *Trachycephalus*) and a benthic subcommunity (all remaining tadpoles, including species found in streams).

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