

MATERIALS AND METHODS

Tadpoles were preserved in 10% formalin. In our descriptions, we use the terminology of Altig (1970) and Altig and McDiarmid (1999). Tadpoles were staged with Gosner's (1960) developmental table. Drawings were made using a stereomicroscope with a camera lucida. Museum codes follow those of Leviton et al. (1985) and Frost (2006). Specimens examined are listed in Appendix 1.

Most measurements were taken to the nearest 0.1 mm using a stereomicroscope equipped with an ocular micrometer, although for *N. aequatorialis*, tail length, body length, and body width were measured with digital calipers. Recorded measurements include: body length (distance from the tip of the snout to the body terminus, which is the junction of the posterior body wall with the tail axis); tail length (distance from the body terminus to the absolute tip of tail); total length (sum of body length and tail length); body width (measured at the widest point right behind the eyes); body height (at level of eye); eye diameter; interorbital distance (measured between the centers of the pupils); internarial distance (measured between the centers of the nares indicated by less pigmentation when closed); distance between tip of snout and naris (from center of naris to middle of snout); and distance between naris and eye (from the center of naris to the anterior edge of the eye); spiracle tube width (at level of opening); tail muscle height at (1) junction of the body wall with the ventral margin of the tail muscle and (2) at midtail length; and overall tail height (at midlength of tail). Additional measurements for *M. carpish* include posterior labium width (greatest, measured ventrally between terminal ends), and posterior labium length (greatest, measured ventrally). Natural history observations of *M. carpish* and *N. aequatorialis* were recorded by P. J. Venegas and E. Arbeláez, respectively. The description of coloration in life for *N. aequatorialis* is based on photos taken by L. Coloma.

RESULTS

Tadpole of Melanophryne carpish.—The following description is based on an individual at Stage 28 (MTD 46546) and one individual at Stage 27 (MTD 46563) in parentheses. The tadpole is illustrated in Figure 1.

Body ovoid in lateral profile. Dorsal surface of body flat. Body depressed, with midbody height being only about 37% of body length; quadrangular in dorsal and ventral aspects. Body 34.7% (34.3%) of total length of tadpole; greatest body height in its posterior third;

greatest body width at midlength of body. Gills relatively large. Snout truncate, sloping posteriorly in lateral aspect; broadly rounded in dorsal and ventral aspects. Eyes small (approximately 5% body length; 12.5% body height at level of eyes); positioned dorsal on anterior fourth of body, facing dorsolaterally; in dorsal aspect, eyes noticeably medial to lateral margin of body, with interocular distance being about 51% of body width at this level; eyes not visible in ventral aspect. Nares dorsal, closed. Nasolacrimal groove indistinguishable. Spiracle broader than long, with short tube; at greatest width, tube about one-third of greatest body width, flat, located midventral, without evident medial subdivision of tube; spiracular aperture oval, located ventral to about midlength of intestinal coil in posterior quarter of body length. Vent tube medial, incorporated into ventral fin with aperture directed downward.

Caudal musculature moderately robust throughout anterior three-quarters of length; in posterior quarter of length, musculature curves dorsally, and gradually tapers to tail tip. Tail length 65.3% (65.7%) of total length and $1.94 \times$ body length; maximum tail height 10.9% (11.7%) of total length. Dorsal fin originating at caudal musculature; fins nearly straight and parallel throughout most of tail length dorsal and ventral fins about equal in height; at midlength of tail, heights of dorsal and ventral fins less than that of caudal musculature; greatest heights of fins in posterior quarter of tail. Tail tip subacuminate and dorsal to the longitudinal midline of the lateral aspect.

Mouth terminal. Unpigmented jaw sheaths present (Fig. 1D, E). Margins of upper and lower jaw sheaths smooth. Upper jaw sheath with small, median acuminate protuberance. Lower jaw broadly arcuate, rather than U-shaped. Papillae and tooth rows absent. Anterior labium medially incomplete, arises as low, ridge of flesh dorsal (anterior) to the paramedial portion of the upper jaw; labium curves ventrolaterally around dorsal margin of upper jaw and gradually increases in depth (anterior-posterior length) reaching its maximum at its union with the lower labium anterolaterally. Posterior labium spatulate, with sinuous, transversely oriented margin.

Measurements (mm).—Those of the Stage-28 individual are followed by those of the Stage-27 tadpole in parentheses. Body length 10.2 (8.5), body width 6.4 (5.4), body height 2.7 (2.8), total length 29.4 (24.8), eye diameter 0.5 (0.4), interorbital distance 3.5 (3.1), internarial distance 3.5 (3.2), snout-naris distance 1.8 (1.8), naris-eye distance 1.4 (1.4), width lower labium width 2.3 (2.1), lower lip plate length 0.6 (0.5), spiracle

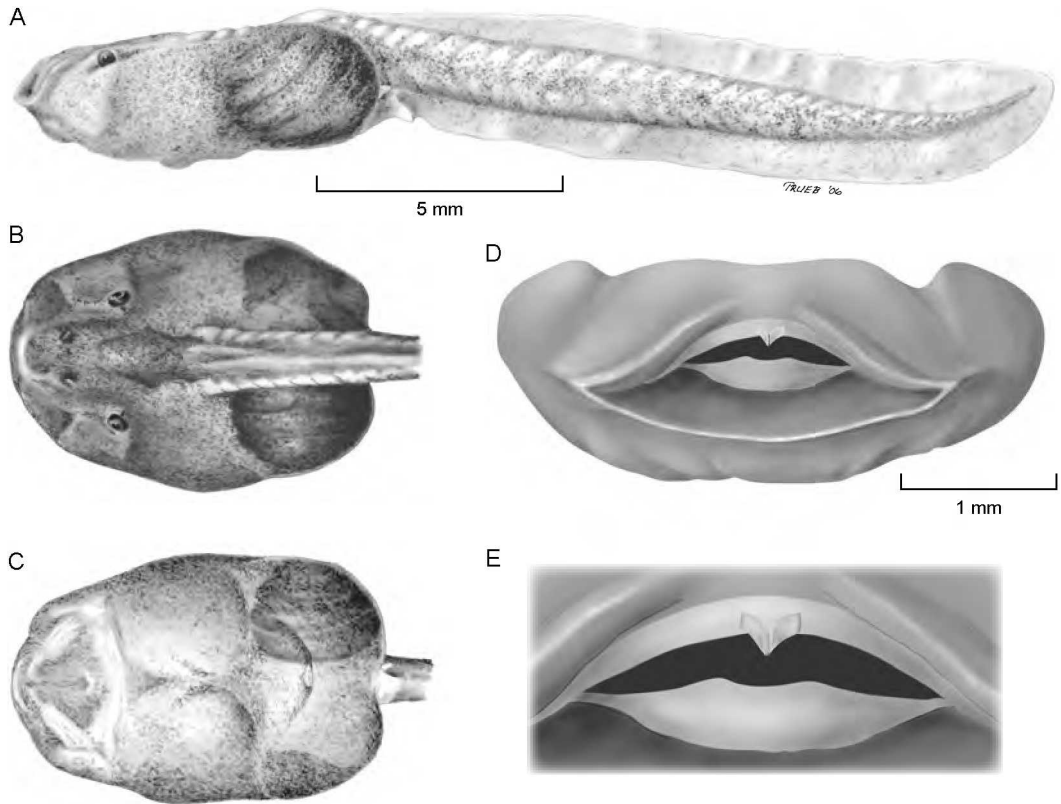


FIG. 1. Tadpole of *Melanophryne carpish*, Stage 28 (MTD 46546), in lateral (A), dorsal (B), and ventral (C) views. The oral apparatus is shown in D, with an enlargement of the jaws and sheaths in E.

tube width 3.7 (3.3), width spiracle opening 1.2 (0.8), tail muscle height 1: 1.2 (1.3), tail muscle height 2: 1.4 (1.3), tail height 3.2 (2.9), tail length 19.2 (16.3)

Coloration.—In life, tadpole pale brown dorsally, parts of intestines yellowish-cream, tail musculature pale brown, fins transparent. In preservative, jaw sheaths creamy white.

Distribution and natural history.—The tadpoles were collected by P. Venegas in the Departamento de San Martín, Provincia de Mariscal Caceres, Laguna de Los Cóndores (6°50'49"S, 77°41'40"W, 2,870 m), Peru, on 25 November 2003. The habitat is very humid montane forest as characterized by Duellman and Pramuk (1999). The forest at the collecting site is dense, with many terrestrial and arboreal bromeliads and little evidence of human impact. Four tadpoles were observed swimming at night in the center of an arboreal bromeliad; the plant was about 50 cm tall and located about 80 cm above the ground on the trunk of a bush. Two of the tadpoles were collected. The same bromeliad had been observed by day, but larvae were not seen; therefore, we speculate that the

tadpoles may hide between the leaf axils during the day and become active at night.

Remarks.—Each of the four known adult specimens of *M. carpish* was found in undisturbed habitat, and each was associated closely with either a terrestrial or an arboreal bromeliad; the gravid female (MTD 45614) was found in the center of a water-filled bromeliad on 10 July 2003 at the type locality (Cordillera de Carpish, Huánuco) and contained 83 eggs of $\bar{x} = 1.6 \pm 0.1$ mm diameter ($N = 10$). At the locality at which the tadpoles were observed and collected, an adult male *M. carpish* (MHNSM 19471) was collected under a terrestrial bromeliad on 25 November 2003 (Venegas, 2005). Because no other microhylid species is known from the Laguna de Los Cóndores locality or elsewhere in the Andes of northern Peru, we are reasonably confident in referring these tadpoles to *M. carpish*. The distance between the two localities is 364 km (airline). If we are correct in assuming that these tadpoles feed while undergoing development in bromeliads, then *M. carpish* would be the first known microhylid to have Reproductive Mode 4, in which eggs are de-

posited in and feeding tadpoles develop in water in tree holes or aerial plants; this mode also occurs in some leptodactylids, bufonids, and hylids (Duellman and Trueb, 1986).

Tadpole of Nelsonophryne aequatorialis.—The following description is based on a Stage-37 individual (QCAZ 29070), which is illustrated in Figure 2.

Body oval in lateral aspect. Dorsal surface of body rounded. Body not depressed, with mid-body height being about 50% of body length; oval in dorsal and ventral aspects. Body about 38% total length of tadpole; greatest body height and width at midlength of body. Snout rounded in lateral profile; broadly rounded to flat in dorsal aspect; narrowly rounded in ventral view. Eyes moderate in size (approximately 8% body length; 18% body height at level of eyes); located in anterior third of body, facing lateral-dorsolaterally; in dorsal aspect, eyes near lateral margin of body, with interocular distance being about 71% of body width at this level; eyes not visible in ventral aspect. Nares dorsal, closed. Nasolacrimal groove moderately distinct; extending from developing olfactory capsule posterolaterally to anterior margin of eye. Spiracle tube width about equal to length, with greatest tube width about half greatest body width; spiracle flat, midventral, with medial subdivision evident anterior to the gut, forming tubes each of which connect with a gill; spiracular aperture a transverse slit located well posterior to mid-length of intestinal coil in posterior quarter of body length. Vent tube medial, incorporated into the ventral fin with aperture directed downward.

Caudal musculature moderately robust throughout anterior half of length; in posterior half of length, musculature straight and gradually diminishing to slender tip. Tail length about 64% total length and $1.64 \times$ body length; maximum tail height 20% of total length. Dorsal fin originating at caudal musculature; shallowly convex dorsal margin, with highest part of dorsal fin at about two-thirds posterior on the tail being two to three times height of dorsal fin at posterior margin of body. Size, shape, and symmetry of ventral fin similar and complementary to that of dorsal fin. At midlength of tail, heights of dorsal and ventral fins greater than that of caudal musculature. Tail tip rounded and in the longitudinal midline of the lateral aspect.

Mouth terminal. Jaw sheaths absent. Anterior lip complete as a shallow, broadly arcuate ridge of flesh that is continuous with a well-developed labial flap (anterior labium) on each side of mouth. Anterior and posterior labia unite at corner of "labial flap" anteroventral to mouth; posterior labium extends from corner of

"labial flap" to corner of mouth. Oral surfaces of anterior and posterior labia lie adjacent to one another, forming a double-layered "labial flap." Transverse distance between corners of labial flaps about twice width of lower jaw.

Measurements (mm).—Body length 13.6, body width 8.9, body height 6.1, total length 39.0, eye diameter 1.4, interorbital distance 7.0, internarial distance 1.0, snout–naris distance 2.0, naris–eye distance 2.5, spiracle tube width 2.7, width spiracle opening 2.3, tail muscle height 1: 2.6, tail muscle height 2: 2.4, tail height 7.3, tail length 25.4.

Coloration.—In life, a tadpole at Stage 41 pale brownish-olive dorsally, anterior half of body brownish-orange laterally, posterior half of body brownish-olive laterally; fins transparent with few brown reticulations; anterior half of tail muscle brown laterally, its posterior half pale brown to unpigmented toward posterior end; iris gold with black reticulations. In preservative, dark brown dorsally, pale brown laterally, and pale gray ventrally. Fins with few dark brown reticulations.

Variation.—A tadpole of Stage 41 (QCAZ 29068) has the following measurements (mm): body length 14.4, body width 8.2, body height 5.3, total length 40.7, eye diameter 1.4, interorbital distance 6.5, internarial distance 1.2, snout–naris distance 2.1, naris–eye distance 2.4, spiracle tube width 1.9, width spiracle opening not visible, tail muscle height 1: 2.7, tail muscle height 2: 2.4, tail height 8.5, tail length 26.3. In a Stage-42 tadpole (QCAZ 29069), the body length is 13.2, body width 6.5, and total length 36.2. The largest total length of 42.5 mm was measured for two tadpoles of Stage 40 (QCAZ 29071).

Distribution and natural history.—The description is based on a larval series collected in a pasture at an elevation of 2,535 m by L. Coloma and colleagues on 29 April 2005. These tadpoles were found in a canal that connected pools in the pasture.

One of us (EA) studied tadpoles of *N. aequatorialis* at four sites in the vicinity of Cuenca, Ecuador. The study sites, at elevations of 2,350 and 2,860 m, are highly disturbed by cattle ranching and agriculture. Eggs of *N. aequatorialis* were found during the rainy season in December and February. The pigmented eggs are 5 mm in diameter and were attached individually to plants, branches, or stones at least 30 cm below the water surface. Tadpoles were found in permanent or temporary bodies of quiet or slowly running water 12–140 cm deep in open areas, and contained many aquatic

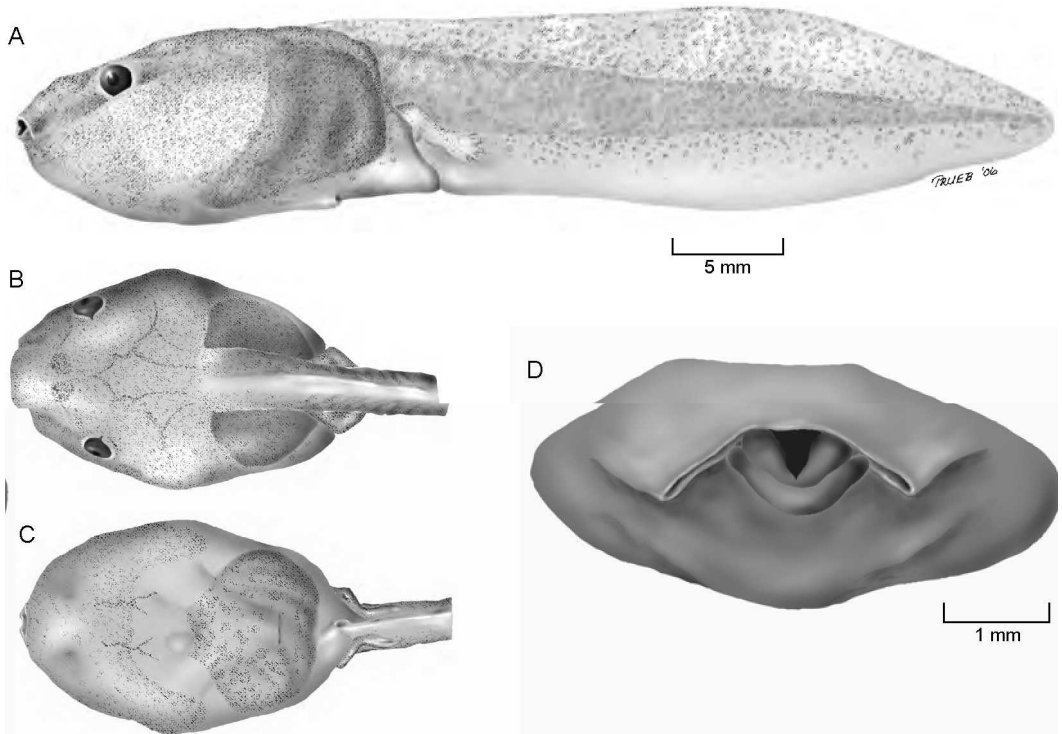


FIG. 2. Tadpole of *Nelsonophryne aequatorialis*, Stage 28 (QCAZ 29070), in lateral (A), dorsal (B), and ventral (C) views. The oral apparatus is shown in D.

remained motionless, floating amidst the vegetation.

In captivity, one female *N. aequatorialis* laid 13 eggs. The larvae hatched in 3–4 days, and metamorphosis was completed between 102 and 124 days; in nature, between 105 and 135 days were required. No parental care was observed.

Tadpoles of *N. aequatorialis* co-occur with larvae of *Gastrotheca litonensis*. Dragonfly larvae and tadpoles of *Gastrotheca* sp. were observed feeding on tadpoles of *N. aequatorialis*. Adult *N. aequatorialis* are known from elevations of 2,500–3,615 m in the Andes of Ecuador (Lynch, 1986; Duellman, 1999) and have been recorded for pastures, grassland, agricultural fields, and degraded secondary habitats (IUCN et al., 2004). Although individuals have been collected near small pools, the breeding habits of the species were unknown (IUCN et al., 2004).

DISCUSSION

In what might have seemed at the time to be a mild hyperbole, Donnelly et al. (1990:10) observed that “Microhylid tadpole morphology varies within subfamilies, among genera within subfamilies, within genera, among species

within genera, and in some cases, among individuals of the same species. The known variation in the family exceeds that described by Orton (1953). This variation, and the lack of a phylogenetic hypothesis of both New World and Old World microhylid relationships, make the interpretation and polarization of larval characters difficult.” Nearly two decades later, these words have proven to be more prescient than Donnelly and her coauthors might have imagined. Although new taxa of microhylids continue to be discovered, our understanding of their evolutionary relationships has advanced little. Likewise, there has been little progress in our knowledge of the larval anatomy of microhylids or of their diversity.

Reprise of some larval characters.—In reviewing the literature describing microhylid tadpoles, we noted some potentially confusing character descriptions. In their review of larval morphological characters, Donnelly et al. (1990) discussed the distribution of the nasolacrimal grooves in microhylid larvae, noting their absence in most New World taxa and sporadic occurrence in some Old World taxa. We assume that the nasolacrimal “groove” of Donnelly et al. is the nasolacrimal duct, which originates from one of the nasal sacs of the olfactory organ

and extends posteriorly to open at the margin of the eye in all transformed anurans (except some pipids) for which descriptions of the nasal organ exist. We suspect that all microhylid larvae possess nasolacrimal ducts that begin to develop near metamorphosis. The developing ducts may or may not be pigmented; if pigmented, they would be evident, as they are in *Nelsonophryne* (Donnelly et al., 1990; this study), *Dasylops schirchi* (Cruz et al., 1978), and *Otophryne pyburni* (Pyburn, 1980; Wassersug and Pyburn, 1987) in the New World and several taxa in the Old World. The more appropriate character description is: nasolacrimal duct pigmented or not. McDiarmid and Altig (1999) use the term nasolacrimal duct [= lacrimal duct or gland; = orbitonasal line] and stated that it connects the corner of the eye with the naris, which describes the superficial appearance of the structure in the developing larva but not its actual anatomical relationships in the metamorphosed frog.

The lower jaw of larval anurans is composed of a pair of Meckel's cartilages that are separated medially by a pair of stout lower labial cartilages [= infrarostral cartilages]. In most anuran larvae, these cartilages are transversely oriented, with a slight anterior convexity; usually they bear a keratinous sheath and are recognized as the lower horny beak or jaw or mandible of the tadpole. The lower labial cartilages of many microhylid larvae are slender, arcuate elements that together form a strongly convex and anterodorsally oriented \cap -shape (e.g., *Kaloula pulchra* [Haas, 2003:fig. 20]; *Elachistocleis bicolor* [Lavilla and Langone, 1995:fig. 1]; *Hamptophryne boliviana* [de Sá and Trueb, 1991:fig. 6]) that resembles a funnel or spout (*H. boliviana* [Duellman, 1978:fig. 45a]) when viewed from an oral perspective. This configuration is the infralabial prominence defined by Thibaudeau and Altig (1988) as the U- or V-shaped medial protrusion of the lower jaw typical of many microhylid tadpoles. Donnelly et al. (1990) described a U-shaped infralabial prominence as being a "spatulate lower lip." If we accept McDiarmid and Altig's (1999) contention that the "lip" is the labium (i.e., fleshy structure[s] surrounding or adjacent to the larval mouth), the terminology of Donnelly et al. is particularly confusing, because the tadpole of *M. carpish*, in fact, has a spatulate posterior labium (or lower lip) that lies posterior (i.e., below) to the lower jaw.

Donnelly et al. (1990) described an "upper lip" with or without "flaps" of different kinds. Following the reasoning of McDiarmid and Altig (1999), we agree that the flaps are derived from the labium [= lip] around the mouth, and that the "upper lip" of Donnelly et al. (1990) is

simply the anterior end of the snout above the mouth. If present, labial flaps can be complete or incomplete; incomplete flaps seem to be represented by retention or development of lateral portions of the labia, and absence or lack of development of medial portions of the labia. Donnelly et al. (1990) described this incomplete anterior/dorsal labial flap as having a "medial notch."

The "lips" or labia arise from the oral pad, which surrounds the stomodeum (Altig and McDiarmid, 1999). The margins of the pad become undercut in a regional sequence to form the labia; the ventrolateral labium forms first, followed by the anterolateral labium and the ventromedial labium. Based on the description of the development of *Spea intermontanus* (Hall et al., 1997:fig. 10), the dorsomedial labium is the last to appear; the failure of the development of this part of the dorsal labium accounts for the so-called medial notch or divided anterior labium. In taxa having labial papillae, these structures arise from marginal crenulations that appear along the edges of the developing labia.

Comparisons among microhylid larvae.—It seems reasonably clear that in tadpoles of *Gastrophryne pictiventris* (Donnelly et al., 1990:fig. 2A) and *Gastrophryne carolinensis* (Altig and McDiarmid, 1999:fig. 3.11C, D), and probably *Altigius alios* (Wild, 1995:fig. 4), the lower labium fails to differentiate. Thus, margination of the anterolateral parts of the oral pad produces the characteristic "flaps" of skin on either side of the simple mouth with a protruding lower jaw or infralabial prominence. (We note that if a lower labium is absent, it is somewhat misleading to say that an "infralabial" prominence is present.)

In *N. aterrima* (Donnelly et al., 1990:fig. 2B), it seems that there is a reduced upper labium and highly modified lower labium. The upper labium and lateral part of the lower labium form the "auricle-like flap" with an erect dorsal margin, lateral margin flush with snout, and pendant lower margin described by Donnelly et al. (1990:4). In the region of the mouth, the lower labium is represented by a series of papillae subtending the lower jaw; two or three larger papillae are arranged in a longitudinal midline series below the transverse series of papillae along the lower jaw. *Nelsonophryne aequatorialis* has a much simpler labial arrangement than its congener. Both upper and lower labia are present lateral to the mouth (Fig. 2D). They are configured as a triangular flap of folded skin, with the upper layer representing the anterior labium and the lower layer the posterior labium. Ornamentation in the form of crenulations or papillae is absent. In view of

the variation noted in labial structures, it would seem prudent to review these across microhylids and reevaluate their status and phylogenetic utility.

The oral apparatus of *M. carpish* is somewhat unusual among those known for New World microhylids. The jaws seem to be keratinized, but unpigmented (Fig. 1D, E), and in this feature, resemble the jaws of *Otophryne pyburni*; the latter, however, is distinguished by its possession of highly modified jaw sheaths with hypertrophied serrations that resemble fanglike "teeth" associated with both the upper and lower jaws (Pyburn, 1980; Wassersug and Pyburn, 1987). Among the Old World taxa, the scaphiophryne, *Scaphiophryne calcarata*, has keratinized jaw sheaths (Wassersug, 1984) and *Ramanella variegata* has been reported occasionally to have a "horny rim" on the lower lip (Rao, 1918:44). The lower jaw of *M. carpish* does not protrude in a prominent spout or funnel shape; the jaw is transverse in its orientation and bears a broad, shallow medial concavity (Fig. 1D, E). The upper jaw is slender and broadly arched. In one specimen (MTD 46546), there is a peculiar medial protuberance that seems to be composed of a pair of tiny keratinous structures (Fig. 1E); we speculate that this structure fell off the upper jaw of the second specimen. The upper labium is incomplete medially; it is a simple, ridgelike structure that is lowest medially and that gradually increases in width toward its lateral terminus with the lower labium. The lower labium is an unornamented, spatulate shelf that protrudes anteriorly and unites the lateral ends of the anterior labia.

Adult *N. aequatorialis* and *N. aterrima* share a number of external morphological and osteological features (Carvalho, 1954; Lehr and Trueb, 2007). The Ecuadorian *N. aequatorialis* seems to be the higher elevation (2,500–3,615 m), southern Andean counterpart to the northern *N. aterrima*, which occurs at lower elevations (20–1,500 m) northward from northwestern Ecuador to Costa Rica (Savage, 2002). Both species deposit their eggs in ephemeral bodies of water and have similar-sized larvae with similar body proportions. Based on the measurements and illustrations provided here and by Donnelly et al. (1990), it is apparent that the eyes of the tadpole of *N. aequatorialis* are placed more dorsally on the body and separated by a substantially greater interocular distance (71% body width vs. 42% body width) than in the tadpole of *N. aterrima*. In addition, a spiracular tube with a clear anterior subdivision forming two tubes is evident in *N. aequatorialis*, whereas the spiracle is a simple slit in *N. aterrima*. But the single greatest difference in

the larvae of the two taxa is in the configurations of the oral apparatus. In both species there are remnants of the anterior and posterior labia. These structures are represented by an "auricle-like flap" and ventromedial row of papillae in *N. aterrima* (Donnelly et al., 1990) and by a simple, triangular fold of skin on either side of the mouth in *N. aequatorialis*.

Natural history notes.—Three modes of development have been reported for microhylid frogs—direct development; endotrophic tadpoles that hatch from terrestrial nests; and free-swimming, exotrophic tadpoles that hatch from eggs deposited into water (Parker, 1934; Donnelly et al., 1990). Duellman and Trueb (1986) characterized five different reproductive modes (Modes 1, 6, 15, 17, 18) for Microhylidae. The only other Neotropical microhylid besides *M. carpish* that uses bromeliads for reproduction is *Syncope antenori* (Krügel and Richter, 1995), but larvae of *S. antenori* are nonfeeding and depend on internal yolk reserves. *Melanophrhynchus carpish* is the first known microhylid in which eggs and feeding tadpoles develop in water in tree holes or aerial plants, Reproductive Mode 4 as defined by Duellman and Trueb (1986). Tadpoles of *M. carpish* seem to be suited for life in the unstable and nutrient-poor environment offered by aerial plants. The long, flat body with large gills seeming would allow the larva to cope with low oxygen levels in its habitat; the long, well-muscled tail with narrow fins transports additional oxygen. The spatulate labium may direct food into the mouth. *Melanophrhynchus carpish* larvae are more active at night than by day; this may be a behavioral adaptation that allows the larvae to take advantage of the higher levels of oxygen in the cooler water at night. Given the oral apparatus structure of the larvae of *M. carpish*, it seems likely that these tadpoles are feeding actively. They may be feeding opportunistically on invertebrates, or perhaps there is parental care in which females deposit infertile eggs as food items for the larvae, as do some hylids and dendrobatids.

The discovery of the larvae of these two genera of microhylids and the contribution they have made to our understanding of the morphology of microhylid larvae emphasizes just how much we have to learn about the diversity and natural history of this cosmopolitan group of anurans, and the importance of seemingly simple morphological observations to our understanding of the evolutionary history of a group of organisms.

Acknowledgments.—For loan of material, we thank L. Coloma (QCAZ), J. H. Córdova (MHNSM), and Darrel Frost (AMNH). L. Coloma kindly provided photos of tadpoles of

N. aequatorialis. We thank W. E. Duellman and R. Altig for their critical comments on the manuscript and J. M. Guayasamin for providing a Spanish translation of the Abstract. The research was supported by a postdoctoral grant given to EL by the Alexander von Humboldt-Foundation. A National Science Foundation grant (EF 0334928 to LT) provided valuable research support to EL and LT. PJV thanks the Environmental Fund Peru for financial support of his fieldwork and R. Wagter for logistic support. EA thanks L. Coloma, E. Segovia, and the technical personal of the Zoológico Amaru for their support.

LITERATURE CITED

- ALTIG, R. 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26: 180–207.
- ALTIG, R., AND G. F. JOHNSON. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3:81–109.
- ALTIG, R., AND R. W. MCDIARMID. 1999. Body plan: development and morphology. In R. W. McDiarmid and R. Altig (eds.), *Tadpoles. The Biology of Anuran Larvae*, pp. 24–51. University of Chicago Press, Chicago.
- CARVALHO, A. L. DE. 1954. A preliminary synopsis of the genera of American microhylid frogs. *Occasional Papers of the Museum of Zoology, University of Michigan* 555:1–19.
- CRUZ, C. A., A. DA GONÇALVES, AND O. L. PEIXOTO. 1978. Notas sobre o girino de *Dasylops schirchi* Miranda-Ribeiro (Amphibia, Anura, Microhylidae). *Revista Brasileira de Biologia* 38:297–299.
- DE SÁ, R. O., AND L. TRUEB. 1991. Osteology, skeletal development, and chondrocranial structure of *Hamptophryne boliviana*. *Journal of Morphology* 209:311–330.
- DONNELLY, M. A., R. O. DE SÁ, AND C. GUYER. 1990. Description of the tadpoles of *Gastrophryne pictiventris* and *Nelsonophryne aterrima* (Anura: Microhylidae), with a review of morphological variation in free-swimming microhylid larvae. *American Museum Novitates* 2976:1–19.
- DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication, Museum of Natural History, University of Kansas* 65:1–352.
- . 1999. Distribution patterns of amphibians in South America. In W. E. Duellman (ed.), *Patterns of Distribution of Amphibians: A Global Perspective*, pp. 255–328. John Hopkins University Press, Baltimore, MD.
- . 2005. Cusco Amazónico. *The Lives of Amphibians and Reptiles in an Amazonian Rainforest*. Comstock Publishing Associates, Ithaca, NY.
- DUELLMAN, W. E., AND J. PRAMUK. 1999. Frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae) in the Andes of northern Peru. *Scientific Papers, Natural History Museum, University of Kansas* 13:1–78.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. John Hopkins University Press, Baltimore, MD.
- FROST, D. R. 2006. *Amphibian Species of the World: An Online Reference*. Version 4 (17 August 2006). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.php>. American Museum of Natural History, New York.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identifications. *Herpetologica* 16:183–190.
- HAAS, A. 2003. Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* 19:23–89.
- HALL, J. A., J. H. LARSEN JR., AND R. E. FITZNER. 1997. Postembryonic ontogeny of the Spadefoot Toad, *Scaphiopus intermontanus* (Anura: Pelobatidae): external morphology. *Herpetological Monographs* 11:124–178.
- IUCN, CONSERVATION INTERNATIONAL, AND NATURESERVE. 2004. *Global Amphibian Assessment*. <www.globalamphibians.org>. Accessed on 24 January 2006.
- KRÜGEL, P., AND S. RICHTER. 1995. *Syncope antenori*—a bromeliad breeding frog with free-swimming, nonfeeding tadpoles (Anura, Microhylidae). *Copeia* 1995:955–963.
- LAVILLA, E. O., AND J. A. LANGONE. 1995. Estructura del condrocráneo y esqueleto visceral de larvas de *Elachistocleis bicolor* (Valenciennes, 1838) (Anura: Microhylidae). *Cuadernos de Herpetología* 9:45–49.
- LEHR, E., AND L. TRUEB. 2007. Diversity among New World microhylid frogs (Anura: Microhylidae) morphological and osteological comparisons between *Nelsonophryne* (Günther 1901) and a new genus from Peru. *Zoological Journal of the Linnean Society* 2007:583–609.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- LYNCH, J. D. 1986. Origins of high Andean herpetological fauna. In F. Vuilleumier and M. Monasterio (eds.), *High Altitude Tropical Biogeography*, pp. 478–499. Oxford University Press, New York.
- MCDIARMID, R. W., AND R. ALTIG. 1999. *Tadpoles. The Biology of Anuran Larvae*. University of Chicago Press, Chicago.
- ORTON, G. L. 1953. The systematics of vertebrate larvae. *Systematic Zoology* 2:63–75.
- PARKER, H. W. 1934. *A monograph of the frogs of the family Microhylidae*. British Museum (Natural History), London.
- PYBURN, W. F. 1980. An unusual anuran larva from the Vaupés region of southeastern Colombia. *Papeis Avulsos de Zoologia (São Paulo)* 33: 231–238.
- RAO, C. R. N. 1918. Notes on the tadpoles of Indian Engystomatidae. *Records of the Indian Museum (Calcutta)* 11:31–38.

- SAVAGE, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, between Two Seas. University of Chicago Press, Chicago.
- THIBAudeau, D. G., AND R. ALTIG. 1988. Sequence of ontogenetic development and atrophy of the oral apparatus of six anuran tadpoles. *Journal of Morphology* 197:63–69.
- VENEGAS, P. 2005. Geographic distribution: Anura: *Phrynopus carpish*. *Herpetological Review* 36:76.
- WASSERSUG, R. J. 1984. The *Pseudohemisus* tadpole: a morphological link between microhylid (Orton type 2) and ranoid (Orton type 4) larvae. *Herpetologica* 40:138–149.
- WASSERSUG, R. J., AND W. F. PYBURN. 1987. The biology of the Pe-ret' Toad, *Otophryne robusta* (Microhylidae), with special consideration of its fossorial larva and systematics relationships. *Zoological Journal of the Linnean Society* 91:137–169.
- WILD, E. R. 1995. New genus and species of Amazonian microhylid frog with a phylogenetic analysis of New World genera. *Copeia* 1995:837–849.
- APPENDIX 1
- Specimens Examined*
- Preserved larvae.*—*Ctenophryne geayi*: PERU: MADRE DE DIOS: Cuzco Amazónico. 15 km east of Puerto Maldonado, 200 m: KU 216011–16 (7 lots).
- Nelsonophryne aterrima*: PANAMA: COLCE: Continental Divide north of El Copé, 600 m: AMNH 98434 (5 of a lot of 9, Stage-37 larvae).
- Nelsonophryne aequatorialis*: ECUADOR: AZUAY: Cuenca, predio de la Universidad del Azuay, (–29.151.944 Lat., 7.900.566 Long.), 2,535 m: QCAZ 29068 (1 tadpole, Stage 41), 20969 (1 tadpole, Stage 42), 29070 (1 tadpole, Stage 37), 29071 (2 lots of 7/8 larvae, Stages 37–40/39–42).
- Melanophryne carpish*: PERU: SAN MARTÍN: Mariscal Cáceres: Laguna de los Cóndores (06°50'49"S, 77°41'40"W), 2,870 m: MTD 46546 (1 tadpole, Stage 28), 46563 (1 tadpole, Stage 27).
- Adult specimens.*—*Melanophryne carpish*: PERU: HUÁNUCO: Cordillera de Carpish (09°43'58.2"S, 76°06'41.9"W), 2,750 m: MTD 45614 (cleared and stained), was found in July in the center of a water-filled bromeliad about 1 m above ground during the afternoon; SAN MARTÍN: Huallaga: Juanjui: Laguna de los Cóndores (06°50'49"S, 77°41'40"W), 2,870 m: MHNSM 19471, was found in November on the ground below a terrestrial bromeliad (Venegas, 2005).

Accepted: 10 May 2007.