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Description of the Tadpoles of *Gastrophryne pictiventris* and *Nelsonophryne aterrima* (Anura: Microhylidae), with a review of Morphological Variation in Free-Swimming Microhylid Larvae

MAUREEN A. DONNELLY,¹ RAFAEL O. de SÁ,²
AND CRAIG GUYER³

ABSTRACT

The tadpoles of *Gastrophryne pictiventris* and *Nelsonophryne aterrima* are described based on material collected in Costa Rica and Panama, respectively. The tadpole of *G. pictiventris* resembles those of the other species of *Gastrophryne*. The tadpole of *N. aterrima* differs from other New World microhylid tadpoles in location of the vent

tube (medial), the spiracular opening (ventral to the gut), and eyes (dorsolateral). The unique configuration of mouthparts in *N. aterrima* is described. Morphological variation in microhylid tadpoles is reviewed and six larval characters are analyzed cladistically for 10 New World microhylid genera.

RESUMEN

Se describen en este trabajo los renacuajos de *Gastrophryne pictiventris* y *Nelsonophryne aterrima* con base en material colectado en Costa Rica y Panamá. Los renacuajos de *G. pictiventris* son semejantes a los de las demás especies de *Gastrophryne*. Los renacuajos de *N. aterrima* se diferencian de los demás renacuajos microhílidos del Nuevo Mundo, en la localización del tubo clo-

acal (media), el opérculo (ventral al estómago), y los ojos (dorsolaterales). Se describe también la configuración única de las partes bucales de *N. aterrima*. Por último, se revisa la variación morfológica en los renacuajos microhílidos y se efectúa un análisis cladístico usando seis caracteres larvales para los diez géneros de esta familia en el Nuevo Mundo.

¹ Boschenstein Research Fellow, Department of Herpetology and Ichthyology, American Museum of Natural History.

² Department of Zoology, University of Texas, Austin, Texas 78712-1064.

³ Department of Zoology and Wildlife Science, Auburn University, Auburn Alabama 36849.

INTRODUCTION

Frogs in the family Microhylidae exhibit one of three modes of development: direct development, nonfeeding (= endotrophic, Altig and Johnston, 1989) tadpoles that hatch late in development in terrestrial nests, and free-swimming, feeding (= exotrophic, Altig and Johnston, 1989) tadpoles that hatch from eggs deposited in water (Parker, 1934). Species in the subfamilies Cophylinae, Dyscophinae, Phrynomerinae, Scaphiophryninae, and most species in the subfamily Microhylinae are characterized by the third mode of development (Duellman and Trueb, 1986). Orton (1953) distinguished among four types of anuran larvae based on mouthparts and position of the spiracle. Her Type II larvae with a single midventral spiracle and unkeratinized mouthparts are characteristic of microhylids. All New World microhylids are placed in the subfamily Microhylinae (Frost, 1985), and tadpoles have been described for only 15 of 36 New World species (Altig and Johnston, 1986). Presumably the New World genera represent a monophyletic group within the subfamily (Zweifel, 1986), although Wassersug and Pyburn (1987) argued that *Otophryne robusta* should be placed in its own subfamily (Otophryninae) mainly based on larval morphology.

Carvalho (1954) suggested that the genus *Gastrophryne* is more closely related to *Hypopachus* than it is to the Asian *Microhyla* as previously proposed by Parker (1934). The *Gastrophryne*-*Hypopachus* affinity was subsequently supported by Nelson (1972) based on several characters, including tadpole morphology. Nelson (1969) indicated that the tadpoles of *Nelsonophryne* [= *Glossostoma*, Frost, 1987] are more similar to those of Asian microhylids than they are to other New World taxa. Altig and Johnston (1986) summarized larval features of *N. aterrima* but a detailed description is not available. Here we describe the tadpoles of two Neotropical microhylids, *Gastrophryne pictiventris* and *Nelsonophryne aterrima*, using material collected in Costa Rica and Panama, respectively. Based on a review of the literature, we summarize known variation in mouthparts, tail shape, spiracle position, and breeding patterns observed in the five subfamilies of microhylids charac-

terized by free-swimming larvae. We also analyzed six tadpole characters for 10 New World microhylid genera cladistically.

THE TADPOLE OF *GASTROPHRYNE PICTIVENTRIS*

The tadpoles of *Gastrophryne pictiventris*, collected by MAD and CG at the La Selva Biological Reserve (Heredia Province: 2.6 km SE of Puerto Viejo de Sarapiquí) in north-eastern Costa Rica, were in a shallow, temporary pool that formed in a fallow cacao grove after several days of heavy rains. The tadpoles were collected on July 28, 1982, one specimen (CRE 6706) being preserved on August 1, 1982, and five (CRE 6717) on August 21, 1982. The description of the tadpole of *G. pictiventris* is based on two stage 33 (Gosner, 1960) specimens; the *G. pictiventris* tadpoles are deposited in the Costa Rican Expeditions (CRE) collection at the University of Miami. We also examined tadpoles of *G. carolinensis* (AMNH 50556, 129941), *G. elegans* (KU 145983), *G. olivacea* (AMNH 52550, 77341-43, 85405, 88986), and *G. usta* (KU 145984-87). All tadpoles were measured to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope.

DESCRIPTION: Values are means. Body length 7.75 mm, body width 6.15 mm, body depth 4.45 mm, total length 20.45 mm. Body depressed (body width/body depth = 1.38); snout rounded in dorsal outline, acuminate in profile (fig. 1). Nares dorsal, not opened. Eyes lateral, visible above and below; diameter 0.75 mm; interocular plane (from tip of snout to center of pupil) 2.9 mm behind snout. Spiracle tube medial, ventral to vent tube; spiracle tube length 1.1 mm; opening 0.7 mm wide.

Caudal musculature moderately robust anteriorly, gradually tapering posteriorly to tail tip; height adjacent to body 1.6 mm. Tail length 62% of total length. Maximum tail height 24% of total length. Fins subequal in height; dorsal fin height 1.5 mm at greatest tail height, not extending onto body; ventral fin height 2.05 mm at greatest tail height. Tip of tail fin rounded (fig. 1).

Mouth Terminal. Upper lip 2.7 mm wide

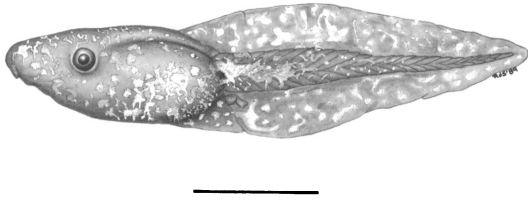


Fig. 1. Lateral view of stage 33 (Gosner, 1960) tadpole of *Gastrophryne pictiventris* (CRE 6714). Bar = 5.0 mm.

with pendant labial flaps; flaps occupy 85% of the breadth of the upper lip (the medial 15% lacks flaps); medial edges of flaps parallel, diverging ventrally; flap margins cover lower lip; flap edges smooth. Lower lip spatulate; medial infralabial prominence aligned with medial notch between labial flaps (fig. 2A).

Color in preservative, dorsal body brown or mottled brown and white; brown laterally with irregularly shaped white spots; venter brown anteriorly with scattered white spots, spots larger posteriorly. Caudal musculature brown; white stripe present on caudal musculature. Fins transparent with brown spots on dorsal and ventral fin edges. Labial flaps dark brown.

COMPARISONS AMONG GASTROPHRYNE TADPOLES

We examined stage 33 tadpoles of *Gastrophryne carolinensis*, *G. olivacea*, *G. usta*, and the stage 37 tadpole of *G. elegans*. All *Gastrophryne* tadpoles have: depressed bodies (width > depth), medial spiracles that open near the vent tube, lateral eyes, closed nares (nares open in late stages), terminal mouths lacking keratinized mouthparts, upper lip with labial flaps separated by medial notch, spatulate lower lip, and a light stripe on the anterior caudal musculature. Tadpole measurements are summarized in table 1.

Gastrophryne pictiventris tadpoles have deeper bodies than the other four species, and the lowest ratio of body width to body depth (body width/body depth: *G. elegans* = 2.58, *G. olivacea* = 2.00, *G. usta* = 1.88, *G. carolinensis* = 1.63, *G. pictiventris* = 1.38). The absolute tail length in *G. pictiventris* is greater than all species except *G. elegans*; the ratio

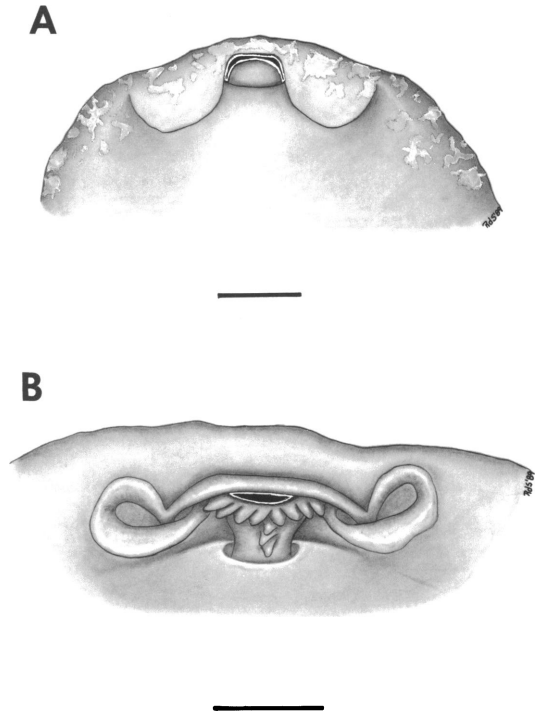


Fig. 2. A: Mouthparts of stage 33 tadpole of *Gastrophryne pictiventris* (CRE 6714). B: Mouthparts of stage 37 tadpole of *Nelsonophryne aterima* (AMNH 98434). Bars = 1.0 mm

of tail length/total length is largest in *G. pictiventris* (table 1).

In *Gastrophryne carolinensis* and *G. usta*, the dorsal and ventral fin heights are approximately equal. The dorsal fin is higher than the ventral fin in *G. elegans*, whereas the ventral fin is higher than the dorsal fin in *G. pictiventris*. The tip of the tail is rounded in *G. elegans* and *G. pictiventris*, rounded or pointed in *G. olivacea* and *G. carolinensis*, and pointed in *G. usta*.

With the exception of *Gastrophryne elegans*, all *Gastrophryne* tadpoles are brown or mottled dorsally; brown (*G. carolinensis*) or mottled laterally (brown and white in *G. olivacea* and *G. pictiventris*, brown and gray in *G. usta*), and mottled ventrally. The tail stripe is gray in *G. elegans*, and white in the other species. The fins are tan in *G. elegans* and transparent in the other species. All *Gastrophryne* tadpoles have irregularly shaped brown blotches on the fins that are adjacent to the caudal musculature in *G. olivacea*, *G.*

TABLE 1

Measurements (mm) of *Gastrophryne* Tadpoles

(All specimens are stage 33 except *G. elegans* (stage 37). The species are indicated by the following abbreviations: Gc = *G. carolinensis*, Go = *G. olivacea*, Gp = *G. pictiventris*, Gu = *G. usta*, and Ge = *G. elegans*)

Species	N	Body length	Body depth	Body width	Tail length	Total length	Tail L/total L
Gc	2	6.25	2.80	4.40	10.0	16.25	.6150
Go	1	7.90	3.00	6.00	—	—	—
Gp	2	7.75	4.45	6.15	12.7	20.45	.6215
Gu	3	9.10	3.60	6.73	11.7	20.80	.5600
Ge	1	11.20	3.30	8.50	16.0	27.20	.5882

carolinensis, and *G. usta* and near the fin edges in *G. elegans* and *G. pictiventris*.

THE TADPOLE OF
NELSONOPHRYNE ATERRIMA

Tadpoles of *Nelsonophryne aterrima*, housed in the American Museum of Natural History (AMNH), were collected in Panama (Panama: Colce; Continental Divide N El Copé, 600 m) on October 3, 1977 by Charles W. Myers and Alan P. Jaslow. Nine tadpoles (AMNH 98434) were taken from a small puddle at the edge of a logging road and preserved. Others were reared in the laboratory through metamorphosis; one of the metamorphs (AMNH 98435) was preserved. The description of the tadpole of *N. aterrima* is based on nine stage 37 (Gosner, 1960) specimens. All tadpoles were measured to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope.

DESCRIPTION: Values are means. Body length 14.14 mm, body width 9.52 mm, body depth 7.27 mm, total length 44.26 mm. Body depressed (body width/body depth = 1.31); snout truncate in dorsal outline, rounded in profile (fig. 3). Nares dorsal, not opened. Eyes dorsolateral, directed laterally; diameter 0.94 mm; interocular plane 2.99 mm behind snout; interorbital distance (between center of pu-

pils) 3.99 mm. Nasolacrimal groove distinct, extends laterally from nares and curves posteroventrally to the anteroventral margin of the orbit. Spiracle ventral; opens 10.82 mm from snout at center of intestinal coil; opening 1.38 mm wide, slitlike without a tube. Vent tube medial, in ventral fin, directed posteroventrad, opens at ventral edge of fin.

Caudal musculature moderately robust anteriorly, gradually tapering posteriorly to the tail tip; height adjacent to body 3.32 mm; height at greatest tail height 3.11 mm. Tail length 68% of total length. Tail height 17.8% of total length. Fins subequal in height; dorsal fin height 2.48 mm at greatest tail height, not extending onto body; ventral fin height 2.30 mm at greatest tail height. Tip of tail fin rounded (fig. 3).

Mouth Terminal. Upper lip slightly concave, 1.78 mm wide; smooth except at lateral margins; no labial flaps (fig. 2B). Lateral margins of oral apparatus expanded into auricle-like flaps (fig. 2B); flap margins crenulate, dorsal margin erect, lateral margin flush with snout, ventral margin pendant; distance between lateral margins of left flap and right flap 3.07 mm. Lower lip spatulate; lip projects ventrally; margin of lower lip with 8–12 conical papillalike structures; large papilla on ventromedial surface of lower lip; papilla width 0.16 mm, papilla length 0.33 mm (fig. 2B).

In preservative, dorsal color light brown; lateral body lighter than dorsum; ventral skin transparent. Caudal musculature white; caudal fins transparent.

Altig and Johnston (1986) summarized larval features of *Nelsonophryne aterrima* based on an unpublished manuscript by Craig E. Nelson. Our description (first value in paren-

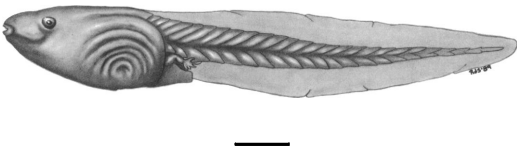


Fig. 3. Lateral view of stage 37 tadpole of *Nelsonophryne aterrima* (AMNH 98434). Bar = 5.0 mm

theses) differs from that summary (second value in parentheses) in: total tadpole length (44 mm in stage 37 vs. 21 mm in stage 36), spiracle location (single, midventral at center of belly vs. single, midventral, near the vent tube), and eye location (dorsolateral vs. lateral).

Nelsonophryne aterrima is the only Central American microhylid with almost completely webbed toes (Carvalho, 1954).⁴ The metamorph (snout-to-vent length = 11.3 mm) of *N. aterrima* (AMNH 98435) has webbed toes, and a small tail bud (1.2 mm long). In preservative, the dorsum is light brown, the dorsal surface of the limbs are tan, and the venter is light tan. The tail bud is dark brown outlined by white. The toe webbing is transparent.

DISCUSSION AND REVIEW OF MORPHOLOGICAL VARIATION IN MICROHYLID TADPOLES

Five subfamilies in the Microhylidae (152 species) are characterized by free-swimming tadpoles; descriptions of tadpoles are available for 59 of the 152 species (see Appendix 1: Cophylinae, three species; Dyscophinae, three species; Microhylinae, 49 species; Phrynomerinae, three species; Scaphiophryninae, one species). Comparisons among tadpoles are difficult because descriptions vary in the type and amount of information presented.

COPHYLINAE: Parker (1934) postulated that species in this subfamily would have a short larval stage or direct development based on large ovarian egg size. Blommers-Schlösser (1975) described breeding behavior and tadpoles of *Anodonthyla boulengerii*, *Platypelis* [= *Platyhyla*] *grandis*, and *Plethodontohyla notosticta*. Water-filled holes (in trees) and phytotelmes are used for breeding in *A. boulengerii* and *P. notosticta*. Insofar as known, the eggs are attended by the male parent; male attendance of eggs may prevent fungal infection. The tadpoles of the three arboreal cophylines hatch before limb-bud emergence, are nonfeeding, have rounded tail tips, and

lack spiracles. Mouthparts have been described for *P. grandis* (Blommers-Schlösser, 1975); the mouth is terminal, the opening is circular and glandular.

Altig and Johnston (1989) classified anuran larvae according to the sources of energy used during development. Exotrophic larvae are free-swimming, feeding tadpoles that are subdivided into 18 ecomorphological guilds. Endotrophic larvae gain developmental nutrition from parental sources, and they are subdivided into six developmental guilds. In this classification scheme, all the tadpoles of species in the subfamily Cophylinae are endotrophic and belong to the nidicolous developmental guild (Altig and Johnston, 1989).

SCAPHIOPHRYNINAE: The only tadpole known in this subfamily is *Pseudohemismus granulorum* [= *granulosus*]. This tadpole has a mediosinistral (= paragyrid, Altig and Johnston, 1986) spiracle, unperforated nares, and complete marginal papillae (Blommers-Schlösser, 1975). Wassersug (1984) reported that *P. granulorum* has keratinized mouthparts but only the lower beak is serrated. The tadpole of *P. granulorum*, like other microhylid tadpoles, is a microphagous suspension feeder. The tadpole scrapes the substrate with the lower jaw and feeds on suspended particles (Wassersug, 1984). *Pseudohemismus* tadpoles are interesting from a systematic standpoint because they have a mosaic of microhylid and ranid features (Blommers-Schlösser, 1975; Wassersug, 1984). The implications for higher-level anuran systematics have been discussed most recently by Wassersug (1984). The tadpoles of *P. granulorum* were collected in a shaded temporary pool.

DYSCOPHINAE: Tadpoles of three species have been described: *Dyscophus insularis* [= *quinquelineatus*] (Blommers-Schlösser, 1975), *Calluella guttulata* (Smith, 1917; Bourret, 1942; Parker, 1934; Savage, 1952), and *C. yunnanensis* (Liu and Hu, 1961). In these dyscophine tadpoles, the mouth is terminal, the upper lip is slightly concave and does not bear labial flaps, the spatulate lower lip is contractile, and the spiracle is medial. The spiracle opens under a flap or sheath of transparent skin near the gut in *D. insularis* and opens near the vent in *C. guttulata*. The tail tip is rounded and the fins are approximately the same height in *D. insularis*. The tail tip

⁴ Zimmerman and Bogart (1988) described sexual dimorphism in the amount of webbing in *Chiasmocleis shudikarensis*; males have fully webbed toes and females have slightly webbed toes.

is pointed and the ventral fin is higher than the dorsal fin in *C. guttulata* and *C. yunnanaensis*. Blommers-Schlösser (1975) collected tadpoles of *D. insularis* in a shallow temporary pool.

PHRYNOMERINAE: This subfamily contains four species; tadpoles have been described for *Phrynomerus annectens* (Gradwell, 1974), *P. bifasciatus* (Power, 1926 [= *Phrynomantis bifasciata*]; Wager, 1965), and *P.* [= *Phrynomantis*] *microps* (Lamotte, 1964). In the three species, the mouth is terminal, the lower lip is spatulate, and the spiracle is medial. The lips of *P. bifasciatus* lack flaps, *P. annectens* has labial flaps on either side of the infralabial prominence on the lower lip, and *P. microps* has a large pendant flap on the upper lip. The spiracle opens near the gut in *P. annectens* and near the vent in *P. bifasciatus* and *P. microps*. The tip of the tail is pointed in *P. annectens* and thin and whiplike in *P. bifasciatus* and *P. microps*. These species breed in temporary pools.

MICROHYLINAE: Microhyline tadpoles exhibit considerable morphological variation in mouth location, spiracle location, shape of the spiracular opening, tail morphology, and mouthparts. The tadpole of *Gastrophryne pictiventris* is similar to tadpoles of other species in the genus; the most distinctive tadpole in the genus is *G. elegans* (Nelson and Altig, 1972). Carvalho (1954) and Nelson (1972) suggested that *Gastrophryne* is more closely related to *Hypopachus* than it is to *Microhyla*. Zweifel (1986) showed a close relationship between *Gastrophryne* and *Ctenophryne*; the relationship of these genera to *Hypopachus* and *Dermatonotus* is unresolved in Zweifel's cladogram. Unfortunately, the tadpole of *Ctenophryne* has not been described (fide Zweifel and Myers, 1989).

All New World microhyline tadpoles have terminal mouths. Among Old World microhylines, 21 species have terminal mouths and 11 have dorsoterminal mouths (table 2). With the exception of *Otophryne robusta* (Pyburn, 1980; Wassersug and Pyburn, 1987), the known New World microhylines lack keratinized mouthparts. *Pseudohemisus granulolum* has keratinized jaw sheaths (Wassersug, 1984) and *Ramanella* [= *Kaloula*] *variegata* occasionally has a "horny rim" on the lower lip (Rao, 1918: 44). The upper lip

has pendant flaps separated by a medial notch in *Dermatonotus muelleri* (Vizotto, 1967; Cei, 1980), *Elachistocleis bicolor* (Williams and Gudynas, 1987), *E. ovalis* (Griffiths and Carvalho, 1965; Kenny, 1969), *E. surinamensis* (Kenny, 1969), *Gastrophryne carolinensis* (Parker, 1934; Orton, 1946; Altig, 1970), *G. elegans*, *G. usta* (Nelson and Altig, 1972), *G. olivacea* (Altig, 1970), and *G. pictiventris*. *Hamptophryne boliviana* has a "fleshy upper lip" (Duellman, 1978: 191) that is similar to that of *Gastrophryne* (R. Altig, personal commun.). Thibaudeau and Altig (1988) described development of the oral apparatus in *H. boliviana* and *G. carolinensis* and they indicated that the mouthparts of the two are similar. *Stereocyclops incrassatus* appears to have pendant flaps on the upper lip, but a detailed description of mouthparts is not available. *Hypopachus* tadpoles also have pendant flaps with scalloped or papillate margins on the upper lip; these flaps overlap medially in *H. variolosus* [= *caprimimus*] (Taylor, 1942) and abut on the midline in *H. barberi* (= *simus*) (Stuart, 1941, 1943). Although Nelson (1972) stated that Asian *Microhyla* do not have flaps on the upper lip, five Old World microhylines have been reported as having fleshy upper lips with lobes: *Chaperina fusca* (Inger 1956, 1966, 1985), *Microhyla borneensis* (Inger, 1966, 1985), *M. palmipes* (Mertens, 1929), *M. perparva*, and *M. petrigena* (Inger and Frogner, 1979; Inger, 1985).

The lower lip is spatulate (lower lip U-shaped, infralabial prominence present) in 12 New World and 20 Old World microhylines (table 3). *Microhyla achatina* and *M. heymonsi* are the only members of the family that have enlarged flaps on the lower labium and both have an infralabial prominence. The infralabial prominence in the lower lip is aligned with the medial notch in the upper lip in *Elachistocleis bicolor* (Williams and Gudynas, 1987), *E. ovalis* (Griffiths and Carvalho, 1965; Kenny, 1969), *E. surinamensis* (Kenny, 1969), *Gastrophryne carolinensis* (Orton, 1946), *G. elegans*, *G. usta* (Nelson and Altig, 1972), *G. olivacea* (Altig, 1970), *G. pictiventris*, and *Hypopachus barberi* (Stuart, 1943). Thibaudeau and Altig (1988) observed development of oral flaps by stage 25 and the adult configuration of mouthparts

TABLE 2
Mouth Location in Paletropical Microhylines
(See Appendix 1 for references)

Terminal	Dorsoterminal
<i>Chaperina fusca</i>	<i>Kaloula medilineata</i>
<i>Glyphoglossus molossus</i>	<i>Metaphrynella</i>
<i>Kalophrynus pleurostigma</i>	<i>pollicaris</i>
<i>Kaloula baleata</i>	<i>Microhyla achatina</i>
<i>K. borealis</i>	<i>M. berdmorei</i>
<i>K. conjuncta</i>	<i>M. heymonsi</i>
<i>K. pulchra</i>	<i>M. inornata</i>
<i>K. rugifera</i>	<i>M. okinavensis</i>
<i>K. verrucosa</i>	<i>M. pulchra</i>
<i>Microhyla annectens</i>	<i>M. rubra</i>
<i>M. borneensis</i>	<i>M. zeylanica</i>
<i>M. butleri</i>	<i>Ramanella palmata</i>
<i>M. ornata</i>	
<i>M. palmipes</i>	
<i>M. perparva</i>	
<i>M. petrigena</i>	
<i>Ramanella montana</i>	
<i>R. triangularis</i>	
<i>R. variegata</i>	
<i>Uperodon globulosus</i>	
<i>U. systoma</i>	

TABLE 3
Microhylines with Spatulate Lower Lips
(See Appendix 1 for references)

Old World	New World
<i>Glyphoglossus molossus</i>	<i>Dasylops schirchi</i>
<i>Kaloula borealis</i>	<i>Elachistocleis bicolor</i>
<i>K. conjuncta</i>	<i>E. ovalis</i>
<i>K. pulchra</i>	<i>E. surinamensis</i>
<i>K. rugifera</i>	<i>Gastrophryne</i>
<i>K. verrucosa</i>	<i>carolinensis</i>
<i>Metaphrynella pollicaris</i>	<i>G. elegans</i>
<i>Microhyla achatina</i>	<i>G. olivacea</i>
<i>M. berdmorei</i>	<i>G. pictiventris</i>
<i>M. butleri</i>	<i>G. usta</i>
<i>M. heymonsi</i>	<i>Hypopachus barberi</i>
<i>M. inornata</i>	<i>H. variolosus</i>
<i>M. okinavensis</i>	<i>Nelsonophryne</i>
<i>M. ornata</i>	<i>aterrima</i>
<i>M. palmipes</i>	
<i>M. perparva</i>	
<i>M. petrigena</i>	
<i>M. pulchra</i>	
<i>M. zeylanica</i>	
<i>Ramanella variegata</i>	
<i>Uperodon globulosus</i>	

by stage 44. They suggested that the oral flaps of microhylids are homologous with the oral discs of most tadpoles and with the labial folds of rhinophrynids. Carvalho (1954) and Nelson (1972) argued that similarity in tadpole morphology indicated a close relationship between *Gastrophryne* and *Hypopachus*—but the tadpoles of *Gastrophryne* also resemble those of *Elachistocleis*, *Dermatonotus*, *Hamptophryne*, and *Stereocyclops*.

Nelson (1969) stated without elaboration that *Nelsonophryne* tadpoles are morphologically similar to Asian *Microhyla* tadpoles. *Nelsonophryne aterrima* has features that are unique among the New World taxa but have been observed in some Asian microhylines: (1) location of the vent tube (in the ventral fin), (2) dorsolateral eyes, and (3) spiracle location (midventral, opens at gut). The vent tube is in the ventral fin in *Chaperina fusca* (Inger, 1966, 1985), *Microhyla achatina* (Smith, 1916), *M. annectens* (Inger, 1966), *M. borneensis* (Inger, 1985), *M. ornata* (Flower, 1899; Ferguson, 1904⁵; Liu, 1950),

M. palmipes (Mertens, 1929), and *M. zeylanica* (Kirtisinghe, 1957).

The eyes are dorsolateral in *Chaperina fusca* (Inger, 1956, 1966), *Kalophrynus pleurostigma* (Berry, 1972), *Kaloula conjuncta* (Alcala, 1962), *K. borealis* [= *Cacopoides tornieri*] (Okada, 1931), *Metaphrynella* [= *Phrynella*] *pollicaris* (Berry, 1972), *Ramanella palmata* (Kirtisinghe, 1958) and *Uperodon globulosus* [= *globulosum*] (Bhaduri and Daniel, 1956). Eye location may or may not vary in *Kaloula pulchra*. Kirtisinghe (1958) reported that the eyes are dorsolateral whereas other descriptions state that the eyes are lateral (Smith, 1916; Annandale, 1917; Heyer, 1971; Schmidt, 1978). We did not examine specimens of *K. pulchra* to determine if this discrepancy is the result of different interpretations by the authors or if this variation in eye location is real.

The position of the spiracle varies among microhyline tadpoles; the spiracle opens ventral to the gut in 14 species and opens near the vent in 30 species (table 4). In 19 microhylines, the spiracle opens into a flap or sheath of transparent skin (table 4). Although Nelson (1972) reported that only *Microhyla but-*

⁵ Ferguson described tadpoles of *Microhyla rubra* that were actually *M. ornata* according to Rao (1915).

TABLE 4
Spiracle Location in Microhylina Tadpoles with Ventral Spiracles
 (Asterisk indicates New World species. See Appendix 1 for references)

Spiracle opens ventral to gut	
Flap present	Flap absent
<i>Glyphoglossus molossus</i>	<i>Chaperina fusca</i>
<i>Microhyla achatina</i>	<i>Kalophrynus</i>
<i>M. borneensis</i>	<i>pleurostigma</i>
<i>M. heymonsi</i>	<i>Microhyla berdmorei</i>
<i>M. okinavensis</i>	<i>Nelsonophryne</i>
<i>M. palmipes</i>	<i>aterrima</i> *
<i>M. perparva</i>	<i>Ramanella</i>
<i>M. pulchra</i>	<i>triangularis</i>
<i>Ramanella variegata</i>	
Spiracle opens near vent	
Flap present	Flap absent
<i>Kaloula conjuncta</i>	<i>Chiasmocleis anatipes</i> *
<i>K. rugifera</i>	<i>Dermatonotus muelleri</i> *
<i>K. verrucosa</i>	<i>Gastrophryne</i>
<i>Microhyla annectens</i>	<i>carolinensis</i> *
<i>M. butleri</i>	<i>G. elegans</i> *
<i>M. ornata</i>	<i>G. olivacea</i> *
<i>M. petrigena</i>	<i>G. pictiventris</i> *
<i>M. rubra</i>	<i>G. usta</i> *
<i>M. zeylanica</i>	<i>Hamptophryne</i>
<i>Ramanella montana</i>	<i>boliviana</i> *
	<i>Hypopachus barberi</i> *
	<i>H. variolosus</i> *
	<i>Kaloula baleata</i>
	<i>K. borealis</i>
	<i>K. mediolineata</i>
	<i>K. pulchra</i>
	<i>Microhyla inornata</i>
	<i>Metaphrynella pollicaris</i>
	<i>Ramanella palmata</i>
	<i>Stereocyclops</i>
	<i>incrassatus</i> *
	<i>Uperodon globulosus</i>
	<i>U. systoma</i>

leri has the spiracle near the anus, six other *Microhyla* tadpoles prove to have the spiracle in the same location (table 4). Duellman (1978) described paired ventral spiracles in *Chiasmocleis anatipes* but the spiracle is single and midventral (W. E. Duellman, personal commun. to R. Altig). Sinistral spiracles are known in five New World microhylines; *Otophryne robusta* has an elongate spiracle (Pyburn, 1980; Wassersug and Pyburn, 1987), the spiracle opens near the

vent in *Dasypops schirchi* (Cruz and Peixoto, 1978), *Elachistocleis bicolor* (Williams and Gudynas, 1987), *E. ovalis* (Griffiths and Carvalho, 1965; Kenny, 1969), and *E. surinamensis* (Kenny, 1969). The location of the spiracular opening varies in different populations of *Kalophrynus pleurostigma* (Berry, 1972) and *Kaloula pulchra* (Smith, 1916; Anandale, 1917; Parker, 1934; Kirtisinghe, 1958; Inger, 1966; Heyer, 1971; Schmidt, 1978), and the shape of the spiracular opening varies in *Stereocyclops incrassatus* (Griffiths and Carvalho, 1965).

Nelsonophryne aterrima, *Dasypops schirchi* (Cruz and Peixoto, 1978), and *Otophryne robusta* (Pyburn, 1980; Wassersug and Pyburn, 1987) are the only New World microhylina tadpoles with distinct nasolacrimal grooves (= rostral groove in *O. robusta*). Nasolacrimal grooves also occur in the Asiatic species *Kaloula borealis* (Okada, 1931; Pope, 1931), *K. conjuncta* (Alcala, 1962), *K. rugifera* (Liu, 1950), *K. verrucosa* (Liu, 1945, 1950), *Metaphrynella pollicaris* (Berry, 1972), *Microhyla butleri* (Pope, 1931), *M. inornata* (Wang et al., 1989), *M. ornata* (Liu, 1950), *M. palmipes* (Mertens, 1929), *Ramanella* [= *Kaloula*] *triangularis* (Rao, 1918), and *R. variegata* (Rao, 1918; Kirtisinghe, 1957).

The combination of unusual labial structures and lower lip structure of *Nelsonophryne aterrima* is unique among tadpoles in the subfamily; some Paleotropical and Neotropical microhylines have similar oral structures but no species has the same configuration of mouthparts. The upper lip of *N. aterrima* lacks labial flaps. *Dasypops schirchi* (Cruz and Peixoto, 1978) and *Otophryne robusta* (Pyburn, 1980; Wassersug and Pyburn, 1987) are the only other New World microhylines lacking labial flaps. Among Old World taxa, the upper lip lacks flaps in *Glyphoglossus molossus* (Smith, 1917; Parker, 1934; Savage, 1952), *Kaloula borealis* (Okada, 1931), *K. rugifera* (Liu, 1950), *K. verrucosa* [= *macroptical*]⁶ (Liu, 1945, 1950), *Metaphrynella pollicaris* (Berry, 1972), *Microhyla achatina* (Smith, 1916; Parker, 1934), *M. annectens* (Inger, 1966), *M. okinavensis* (Okada, 1931, 1966; Parker, 1934), *M. heymonsi* (Parker, 1934; Liu and Hu, 1961; Griffiths,

⁶ See Liu and Hu (1961: 289).

1963), *M. pulchra* (Smith, 1916; Pope, 1931; Parker, 1934), *M. zeylanica* (Kirtisinghe, 1957), and *Uperodon globulosus* (Bhaduri and Daniel, 1956). In *M. zeylanica*, the lateral margins of the mouth are expanded and five conical papillae occur on the lower lip (Kirtisinghe, 1957). Several bluntly pointed papillae border the lower lip of *M. okinavensis* [= *fissipes*] (Okada, 1931, 1966), and three soft papillae occur on the lower lip of *Metaphrynella pollicaris* (Berry, 1972). The only other New World microhylina with a papilla-like structure on the lower lip is *Dasypops schirchi* (Cruz and Peixoto, 1978). Two microhylina tadpoles, *Microhyla achatina* and *M. heymonsi* (Parker, 1934; Liu and Hu, 1961; Griffiths, 1963), have a lower lip that can be elevated and expanded to form an "inverted funnel" (= umbelliform, Altig and Johnston, 1989). The two species have knob-like prominences on the lateral margins of the mouth opening, medial to the edges of the flap. Pope (1931) suggested that the funnel was an adaptation to feeding on the surface of clear mountain pools but *M. heymonsi* also occurs in swampy areas in the lowlands (Parker, 1934). Tadpoles with umbelliform mouthparts are also known in the Dendrobatidae (*Colostethus nubicola*), Pelobatidae (*Megophrys montana*), and Hylidae (*Phyllomedusa guttata*) (Orton, 1953; Duellman and Trueb, 1986).

In his earliest treatment of seven species of frogs in the genus *Microhyla*, Parker (1928: 477) noted that "except in *M. berdmorei*, the tail ends in a whip-like flagellum." He hypothesized that the vibration of the flagellum enabled tadpoles to maintain their position in the water column as they feed. Parker (1934) described tadpoles of an additional five species of *Microhyla* in his monograph. Nine species of *Microhyla* have a long flagellum at the end of the caudal fin: *M. annectens* (Inger, 1966), *M. borneensis* (Inger, 1966, 1985), *M. butleri* (Pope, 1931), *M. inornata* (Parker, 1934; Wang et al., 1989), *M. pulchra* (Rao, 1915; Pope, 1931), and *M. rubra* (Parker, 1934; Kirtisinghe, 1957). The flagellum is short in *M. achatina* (Smith, 1916; Annandale, 1917), *M. okinavensis* (Okada, 1931), and *M. ornata* (Flower, 1899; Parker, 1934). The tadpole of *Nelsonophryne aterima* has a rounded tail tip. Fourteen micro-

TABLE 5

Microhylina Tadpoles with Pointed Tail Tips
(VF = ventral fin height, DF = dorsal fin height. Data for fin height not available for *Chiasmocleis anatis*. Asterisk indicates New World species. See Appendix 1 for references)

VF > DF	VF = DF
<i>Glyphoglossus molossus</i>	<i>Elachistocleis ovalis</i> *
<i>Dermatonotus muelleri</i> *	<i>Gastrophryne usta</i> *
<i>Microhyla berdmorei</i>	<i>Hypopachus variolosus</i> *
<i>M. heymonsi</i>	<i>Kaloula borealis</i>
<i>M. inornata</i>	<i>K. conjuncta</i>
<i>M. palmipes</i>	<i>K. mediolineata</i>
<i>M. perparva</i>	<i>Stereocyclops</i>
<i>M. petrigena</i>	<i>incrassatus</i> *
<i>M. zeylanica</i>	<i>Uperodon globulosus</i>
	<i>U. stoma</i>
VF < DF	
<i>Elachistocleis bicolor</i> *	
<i>E. surinamensis</i>	
<i>Ramanella montana</i>	

hylina tadpoles also have rounded tail tips: *Chaperina fusca* (Inger, 1985), *Dasypops schirchi* (Cruz and Peixoto, 1978), *Gastrophryne elegans* (Nelson and Altig, 1972), *G. pictiventris*, *Hypopachus barberi* (Stuart, 1943), *Kaloula baleata* (Parker, 1934; Bourret, 1942), *K. borealis* (Pope, 1931), *K. rugifera* (Liu, 1950), *K. verrucosa* (Liu, 1945, 1950), *Metaphrynella pollicaris* (Berry, 1972), *Otophryne robusta* (Wassersug and Pyburn, 1987), *Ramanella palmata* (Kirtisinghe, 1958), *R. triangularis*, and *R. variegata* (Rao, 1918). Most microhylina tadpoles have pointed tail tips (table 5). Four species vary in tail tip morphology. *Gastrophryne carolinensis* (Parker, 1934; Orton, 1946; Wright and Wright, 1949), *G. olivacea* (personal obs.), *Kalophrynus pleurostigma* (Berry, 1972), and *Kaloula pulchra* (Smith, 1916; Annandale, 1917; Parker, 1934; Heyer, 1971) have a pointed tail tip or a rounded tip. Tail-tip shape of *Hamptophryne boliviana* has not been described.

Nelson (1972) also described tail morphology and stated that *Microhyla* tadpoles have ventral fins that are deeper than the dorsal fins. The ventral fin is much higher than the dorsal fin in *M. pulchra* and *M. rubra*. The ventral fin is higher than the dorsal fin in *M. annectens*, *M. borneensis*, *M. in-*

ornata, *M. ornata*, *Chaperina fusca*, *Kaloula baleata*, *K. pulchra*, *Kalophrynus pleurostigma*, *Ramanella variegata*, *Gastrophryne olivacea*, *G. pictiventris*, and *H. barberi*. The ventral fin is only slightly higher than the dorsal fin in *M. achatina*, *M. butleri*, and *M. okinavensis*. The fin heights are approximately equal in *Dasypops schirchi*, *Metaphrynella pollicaris*, *Kaloula rugifera*, *K. verrucosa*, *R. palmata*, and *G. carolinensis*. The dorsal fin is higher than the ventral fin in *K. borealis*, *R. triangularis*, *G. elegans*, *Nelsonophryne aterrima*, and *Otophryne robusta*.

All microhylines with free-swimming larvae, except *Microhyla butleri*, *Hamptophryne boliviana*, and *Otophryne robusta*, breed in temporary pools or ponds that form after heavy rains. *Microhyla butleri* tadpoles were found in relatively permanent ponds (Parker, 1934). Pope (1931: 593) collected *M. butleri* tadpoles in "more permanent ponds at the bottom of excavations, NOT in any and every small, temporary pool and mud hole inhabited by larvae of *pulchra* and *ornata*." *Hamptophryne boliviana* breeds in "relatively large forest ponds and swamps" (Crump, 1974: 24). *Otophryne robusta* eggs and recently hatched larvae have been found in terrestrial sites near streams (Pyburn, 1980; Gorzula, 1985). In several species, metamorphosis is completed in less than two weeks. Pope (1931) suggested that rapid growth of tadpoles is an adaptation that allows these frogs to inhabit areas of limited and irregular rainfall.

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 microhyline relationships, makes interpretation and polarization of larval characters difficult. Among New World microhylines, the tadpoles of *Nelsonophryne aterrima*, *Dasypops schirchi*, and *Otophryne robusta* share some characters and differ from those of *Chiasmocleis*, *Dermatonotus*, *Elachistocleis*, *Hamptophryne*, *Hypopachus*, *Gastrophryne*, and *Stereocyclops*.

Zweifel (1986) assumed that the New World genera were a monophyletic group within the

subfamily; the relationship between *Otophryne* and *Nelsonophryne* is unresolved and both are primitive to other New World genera in his cladogram. *Nelsonophryne* has a primitive foot structure (webbed toes and rounded toe tips) and a derived pelvic girdle (loss of clavicles and procoracoids) (Zweifel, 1986). Many Old World microhylines have webbed toes (Parker, 1934), whereas most of the New World taxa have free toes or rudimentary webs (Parker, 1934; Carvalho, 1954; but see Zimmermann and Bogart, 1988). Reduction of girdle elements has been observed in almost all microhylid subfamilies, in Old World microhyline genera, and in several of the American genera (Zweifel, 1986).

We reanalyzed Zweifel's data (1986: tables 2: 19 and 3: 20) with the phylogenetic package PAUP (Swofford, 1985). The PAUP subroutine Global Branch Swapping and MULTIPARS (for identifying multiple most parsimonious trees) were employed to obtain the best estimate(s) of phylogeny. We used a hypothetical outgroup to root the tree (primitive character states for characters 1–8), *Dermatonotus* and *Hypopachus* were considered as a single taxon, and multistate characters 3 through 8 were unordered. In one analysis, *Synapturanus* was coded as having character "C" for character 5 following Carvalho (1954), and in another, character 5 was coded as "E" following Zweifel (1986). In both analyses, more than 50 equally parsimonious trees of 29 steps were found. We generated strict consensus trees (CONTREE option of PAUP) based on 50 of these trees. When *Synapturanus* is coded following Carvalho, the consensus tree is identical to Zweifel's cladogram (1986: fig. 12: 18). When *Synapturanus* is coded according to Zweifel, *Nelsonophryne* clusters with *Hypopachus* and the consistency information of the consensus tree is reduced (0.266 vs. 0.335).

We also analyzed the tadpole characters (see table 6 and Appendix 2) with Zweifel's data for 10 New World taxa (14 characters total; six tadpole characters + Zweifel's eight characters) using the same PAUP subroutines. Eighteen equally parsimonious trees of 30 steps were found. The strict consensus tree (fig. 4A) can be contrasted with a modification of Zweifel's cladogram (fig. 4B)—this modified cladogram retains the original to-

TABLE 6
Tadpole Characters Analyzed
(Character state assignments indicated by number
in parentheses)

1. Eyes lateral (0)	Eyes dorsolateral (1)
2. Upper lip lacking flap (0)	Upper lip bearing flap (1) Upper lip with scalloped flaps (2)
3. Spiracle ventral to gut (0)	Spiracle near vent (1) Spiracle sinistral (2)
4. Nasolacrimal groove present (0)	Nasolacrimal groove absent (1)
5. Lower lip papilla present (0)	Lower lip papilla absent (1)
6. Vent tube in fin (0)	Vent tube free of fin (1)

pology but it only includes taxa for which there are descriptions of tadpoles. The two cladograms in figure 4 are entirely consistent, with only changes in resolution between them. The combined data sets show a resolved relationship between *Dasypops* and *Elachistocleis*, but the relationship of *Stereocyclops*, *Dermatonotus*, and *Hypopachus* is unresolved when the tadpole characters are included with Zweifel's data (see fig. 4).

Six tadpole characters vary among but not within species (table 6), and we analyzed these data to see how these characters clustered New World microhylids. Because there is no phylogenetic hypothesis of relationships for microhylines, we analyzed the data matrix for the New World taxa (Appendix 2) using 11 Old World microhylid taxa as outgroups to polarize the characters described in table 6 (see Appendix 2). Each PAUP analysis searched for the most parsimonious trees with global branch swapping. Tadpole characters 2 and 3 were run as unordered, and *Chiasmocleis*, *Dermatonotus*, *Gastrophryne*, *Hamptophryne*, and *Stereocyclops* were considered to be one taxon (see Appendix 2). We analyzed the data with and without *Otophryne* as part of the ingroup when the outgroup was an Old World microhylid, and we used *Otophryne* as an outgroup in one analysis because Wassersug and Pyburn (1987) suggested that this species should be in its own subfamily. The results are summarized in table 7 and figure 5.

In most of the trees summarized in figure 5, the tadpole characters suggest a clade con-

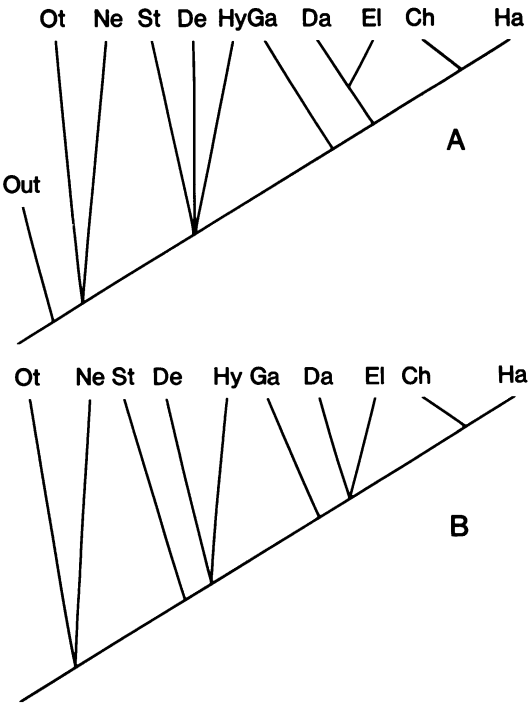


Fig. 4. A: Strict consensus tree based on tadpole characters and Zweifel's data (1986: table 2) for New World microhylines with tadpoles. B: A modification of Zweifel's cladogram (1986: fig. 18) that retains topology but only includes taxa that have described tadpoles. The New World microhylids are indicated by the following abbreviations: Out = hypothetical outgroup, Ot = *Otophryne*, Ne = *Nelsonophryne*, St = *Stereocyclops*, De = *Dermatonotus*, Hy = *Hypopachus*, Ga = *Gastrophryne*, Da = *Dasypops*, El = *Elachistocleis*, Ch = *Chiasmocleis*, and Ha = *Hamptophryne*.

taining *Hypopachus*, five of the New World genera, and *Elachistocleis*—with *Hypopachus* + the five usually as sister taxa. *Hypopachus* differs from these genera in upper lip flaps; the flap edges are distinctly scalloped. *Elachistocleis* shares several characters with the other six genera and differs from them only in spiracle location. In some of the cladograms in figure 5, the relationships of *Otophryne*, *Nelsonophryne*, and *Dasypops* are uncertain. In several cases, *Nelsonophryne* does fall out unambiguously as the sister taxon to the rest of the ingroup. This arrangement differs from that of Zweifel (1986) wherein *Dasypops* clusters with *Elachistocleis* (fig. 4B). When *Phrynomerus* species are

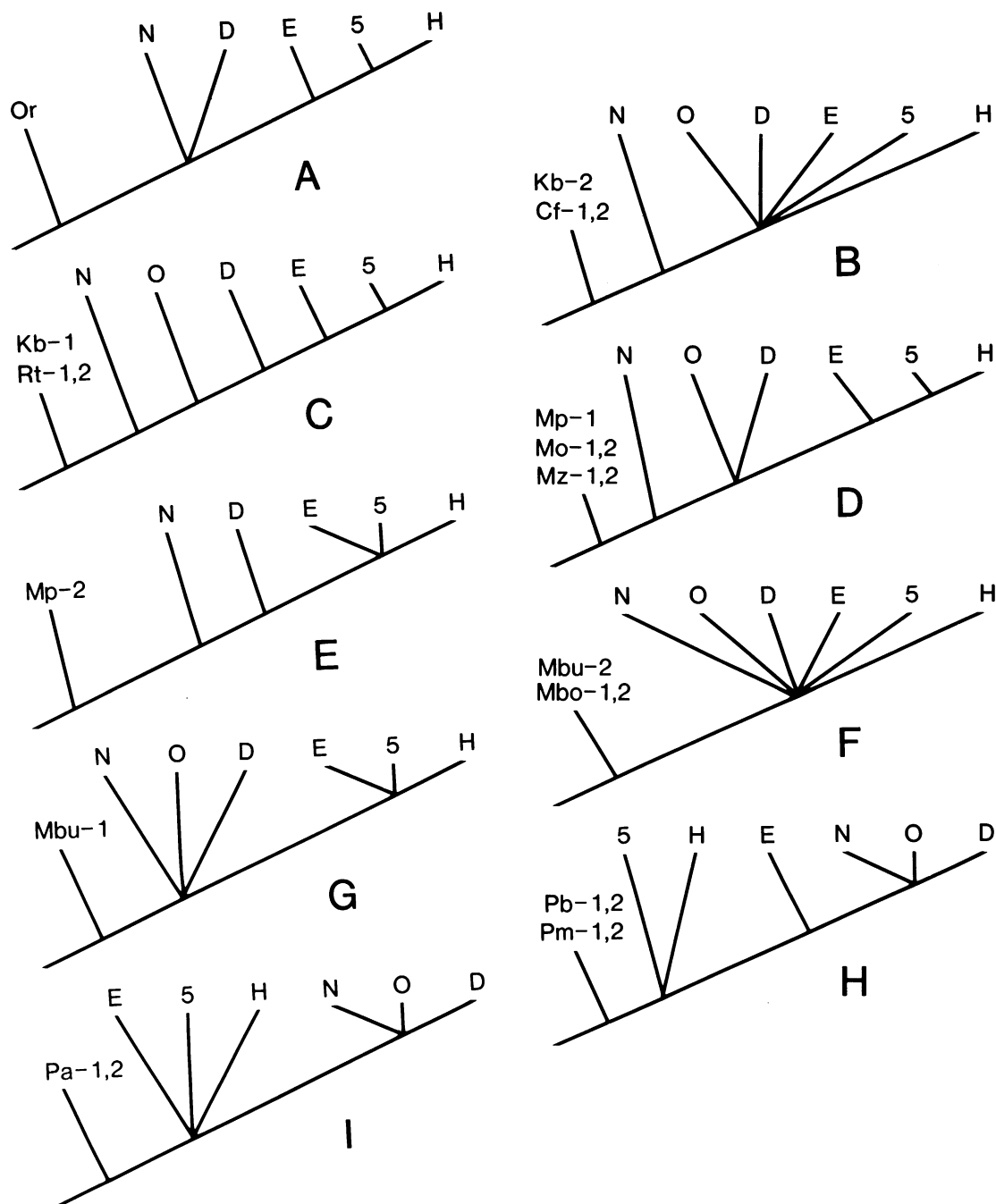


Fig. 5. Trees based on tadpole characters. The outgroup taxa codes are in table 7. The New World ingroup taxa are indicated by the following abbreviations: D = *Dasypops*, E = *Elachistocleis*, H = *Hypopachus*, N = *Nelsonophryne*, O = *Otophryne*, 5 = *Gastrophryne*, *Chiasmocleis*, *Dermatonotus*, *Synapturanus*, and *Hamptophryne*.

used as the outgroup (fig. 5H and 5I), *Otophryne*, *Nelsonophryne*, and *Dasypops* form a monophyletic group relative to the other

New World genera. The topology of the trees changes slightly when *Microhyla butleri* and *Metaphrynella pollicaris* are used as the out-

TABLE 7

Summary of Tree Statistics Generated with PAUP
(The codes are abbreviations for outgroups used in fig. 5. The number 1 following a taxon indicates that *Otophryne* was included as part of the ingroup in the analysis, the number 2 indicates that it was not included with other New World genera. CI is the consistency index for individual trees)

Outgroup	Code	Num- ber of trees	Num- ber of steps	CI
<i>Chaperina fusca</i> -1	Cf-1	7	11	0.727
<i>C. fusca</i> -2	Cf-2	5	10	0.800
<i>Kaloula borealis</i> -1	Kb-1	1	10	0.800
<i>K. borealis</i> -2	Kb-2	6	10	0.800
<i>Metaphrynella</i>				
<i>pollicaris</i> -1	Mp-1	2	10	0.800
<i>M. pollicaris</i> -2	Mp-2	3	9	0.889
<i>Microhyla</i>				
<i>borneensis</i> -1	Mbo-1	17	11	0.727
<i>M. borneensis</i> -2	Mbo-2	12	10	0.800
<i>M. butleri</i> -1	Mbu-1	8	10	0.800
<i>M. butleri</i> -2	Mbu-2	12	10	0.800
<i>M. okinavensis</i> -1	Mo-1	2	10	0.800
<i>M. okinavensis</i> -2	Mo-2	1	9	0.889
<i>M. zeylanica</i> -1	Mz-1	2	10	0.800
<i>M. zeylanica</i> -2	Mz-2	1	10	0.800
<i>Phrynomerus</i>				
<i>annectens</i> -1	Pa-1	10	10	0.800
<i>P. annectens</i> -2	Pa-2	7	9	0.889
<i>P. bifasciatus</i> -1	Pb-1	6	9	0.889
<i>P. bifasciatus</i> -2	Pb-2	3	8	1.000
<i>P. microps</i> -1	Pm-1	6	8	0.889
<i>P. microps</i> -2	Pm-2	3	8	1.000
<i>Ramanella</i>				
<i>triangularis</i> -1	Rt-1	1	9	0.889
<i>R. triangularis</i> -2	Rt-2	1	9	0.889
<i>Otophryne robusta</i>	Or	2	9	0.889

group and *Otophryne* is excluded from the ingroup (fig. 5E and 5F); in all other cases, exclusion of *Otophryne* does not change topology or the number of character state changes (table 7).

Although there is disagreement about the phylogenetic significance of larval characters in anuran systematics (Noble, 1927; Orton, 1953, 1957; Griffiths, 1963; Hecht, 1963; Griffiths and Carvalho, 1965; Tihen, 1965; Starrett, 1968, 1973; Kluge and Farris, 1969; Sokal, 1975), tadpoles do have characters that are undoubtedly phylogenetically informative. Before the utility of larval characters can be fully evaluated, detailed, stage-specific de-

scriptions of microhylid tadpoles should be completed. We feel that the relationships described by these larval characters are tentative because there are several other possible outgroups that could be used to polarize characters, and the number of taxa exceeds the number of characters. It is also difficult to interpret the characters because of the lack of information for several microhylid taxa. Ontogenetic data from developmental series may be more useful than the outgroup method for polarizing characters because the systematic relationship among microhylines and the relationships of microhylids among other frogs families is debatable (Orton, 1953, 1957; Griffiths, 1963; Tihen, 1965; Inger, 1967; Starrett, 1968, 1973; Kluge and Farris, 1969; Lynch, 1973; Savage, 1973; Trueb, 1973; Blommers-Schlösser, 1975; Sokal, 1975; Wassersug, 1984; Duellman and Trueb, 1986).

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APPENDIX 1
Published Descriptions of Microhylid Tadpoles
Asterisk indicates New World taxon.

Species	Reference(s)
Subfamily: Cophylinae	
<i>Anodonthyla boulengerii</i>	Blommers-Schlösser, 1975
<i>Platypelis grandis</i>	Blommers-Schlösser, 1975
<i>Plethodontohyla notosticta</i>	Blommers-Schlösser, 1975
Subfamily: Dyscophinae	
<i>Calluella guttulata</i>	Smith, 1917; Parker, 1934; Bourret, 1942; Savage, 1952
<i>C. yunnanensis</i>	Liu and Hu, 1961
<i>Dyscophus insularis</i>	Blommers-Schlösser, 1975
Subfamily: Microhylinae	
<i>Chaperina fusca</i>	Bourret, 1942; Savage, 1952; Inger, 1956, 1966, 1985
<i>Chiasmocleis anatis*</i>	Duellman, 1978
<i>Dasypops schirchi*</i>	Cruz and Peixoto, 1978
<i>Dermatonotus muelleri*</i>	Vizotto, 1967; Ceil, 1980
<i>Elachistocleis bicolor*</i>	Williams and Gudynas, 1987
<i>E. ovalis*</i>	Griffiths and Carvalho, 1965; Kenny, 1969
<i>E. surinamensis*</i>	Kenny, 1969
<i>Gastrophryne carolinensis*</i>	Parker, 1934; Orton, 1946; Altig, 1970; Thibaudeau and Altig, 1988
<i>G. elegans*</i>	Nelson and Altig, 1972
<i>G. olivacea*</i>	Altig, 1970
<i>G. pictiventris*</i>	this paper
<i>G. usta*</i>	Nelson and Altig, 1972
<i>Glyphoglossus molossus</i>	Smith, 1917; Parker, 1934; Bourret, 1942; Savage, 1952
<i>Hamptophryne boliviana*</i>	Duellman, 1978; Thibaudeau and Altig, 1988
<i>Hypopachus barberi*</i>	Stuart, 1941, 1943
<i>H. variolosus*</i>	Taylor, 1942; Altig, 1970
<i>Kalophrynus pleurostigma</i>	Parker, 1934; Bourret, 1942; Inger, 1956, 1966, 1985; Berry, 1972
<i>Kaloula baleata</i>	Parker, 1934; Bourret, 1942; Inger, 1966
<i>K. borealis</i>	Okada, 1931; Pope, 1931; Parker, 1934
<i>K. conjuncta</i>	Alcala, 1962
<i>K. mediolineata</i>	Heyer, 1971
<i>K. pulchra</i>	Smith, 1916; Annandale, 1917; Parker, 1934; Bourret, 1942; Kirtisinghe, 1958; Inger, 1966; Heyer, 1971; Schmidt, 1978
<i>K. rugifera</i>	Liu, 1940, 1950; Liu and Hu, 1961
<i>K. verrucosa</i>	Liu, 1945, 1950
<i>Metaphrynella pollicaris</i>	Berry, 1972
<i>Microhyla achatina</i>	Smith, 1916; Annandale, 1917; Rao, 1918; Parker, 1928, 1934; Neuhäus, 1949
<i>M. annectens</i>	Inger, 1966
<i>M. berdmorei</i>	Annandale, 1917; Smith, 1924; Parker, 1928, 1934; Bourret, 1942; Inger, 1966
<i>M. borneensis</i>	Inger, 1966, 1985
<i>M. butleri</i>	Flower, 1899 ^a ; Smith, 1917; Annandale, 1917; Parker, 1928, 1934, Pope, 1931; Bourret, 1942; Liu and Hu, 1961

^a The "transparent" tadpoles of Flower (1899: 903–905) are *Microhyla butleri* (Smith, 1917: 268) not *M. berdmorei* (Annandale, 1917: 151; Rao, 1918: 42).

APPENDIX 1
Continued

Species	Reference(s)
<i>M. heymonsi</i>	Parker, 1928, 1934; Pope, 1931; Bourret, 1942; Neuhaus, 1949; Liu and Hu, 1961; Griffiths, 1963
<i>M. inornata</i>	Smith, 1924; Parker, 1934; Bourret, 1942; Heyer, 1971; Wang et al., 1989
<i>M. okinavensis</i>	Okada, 1931, 1966; Parker, 1934
<i>M. ornata</i>	Flower, 1899; Ferguson, 1904; Smith, 1917; Rao, 1918; Parker, 1928, 1934; Pope, 1931; Liu, 1940, 1950; Bourret, 1942; Kirtisinghe, 1957; Liu and Hu, 1961; Heyer, 1971; Kuramoto, 1973; Khan, 1982; Wang et al., 1989
<i>M. palmipes</i>	Mertens, 1929; Parker, 1934; Neuhaus, 1949
<i>M. perparva</i>	Inger and Frogner, 1979; Inger, 1985
<i>M. petrigena</i>	Inger and Frogner, 1979; Inger, 1985
<i>M. pulchra</i>	Smith, 1916; Parker, 1928, 1934; Pope, 1931; Bourret, 1942
<i>M. rubra</i>	Rao, 1915, 1918; Parker, 1928, 1934; Kirtisinghe, 1957
<i>M. zeylanica</i>	Kirtisinghe, 1957
<i>Nelsonophryne aterrima</i> *	this paper
<i>Otophryne robusta</i> *	Pyburn, 1980; Wassersug and Pyburn, 1987
<i>Ramanella montana</i>	Ferguson, 1904 ^b ; Parker, 1934
<i>R. palmata</i>	Kirtisinghe, 1958
<i>R. triangularis</i>	Rao, 1918; Parker, 1934
<i>R. variegata</i>	Rao, 1918; Parker, 1934; Kirtisinghe, 1957
<i>Stereocyclops incrassatus</i> *	Griffiths and Carvalho, 1965
<i>Uperodon globulosus</i>	Bhaduri and Daniel, 1956
<i>U. systoma</i>	Ferguson, 1904; Kirtisinghe, 1957; Mohanty-Hejmadi, et al. 1979
Subfamily: Phrynomerinae	
<i>Phrynomerus annectens</i>	Gradwell, 1974
<i>P. bifasciatus</i>	Power, 1926; Wager, 1965
<i>P. microps</i>	Lamotte, 1964
Subfamily: Scaphiophryninae	
<i>Pseudohemisus granulorum</i>	Blommers-Schlösser, 1975; Wassersug, 1984

^b Ferguson (1904) described a series of tadpoles of *Callula obscura* from India. Parker (1934: 92) assigned this series to *Ramanella montana*; *R. obscura* occurs in Sri Lanka (Parker, 1934; Frost, 1985).

APPENDIX 2
Data Matrix for Tadpole Characters Described in
Table 6

Asterisk indicates outgroup taxa. *Otophryne robusta* was included as part of the ingroup for 11 of the 23 analyses.

Taxon	Characters					
	1	2	3	4	5	6
<i>Chaperina fusca</i> *	1	1	0	1	1	0
<i>Kaloula borealis</i> *	1	0	1	0	1	1
<i>Metaphrynella pollicaris</i> *	1	0	1	0	0	1
<i>Microhyla borneensis</i> *	0	1	0	1	1	0
<i>Microhyla butleri</i> *	0	0	1	0	1	1
<i>Microhyla okinavensis</i> *	0	0	0	1	0	1
<i>Microhyla zeylanica</i> *	0	0	0	1	0	0
<i>Phrynomerus annectens</i> *	0	1	0	1	1	1
<i>Phrynomerus bifasciatus</i> *	0	0	1	1	1	1
<i>Phrynomerus microps</i> *	0	1	1	1	1	1
<i>Ramanella triangularis</i> *	0	0	0	0	1	1
<i>Otophryne robusta</i> *	0	0	2	0	1	1
<i>Chiasmocleis</i>	0	1	1	1	1	1
<i>Dasypops</i>	0	1	2	0	0	1
<i>Dermatonotus</i>	0	1	1	1	1	1
<i>Elachistocleis</i>	0	1	2	1	1	1
<i>Gastrophryne</i>	0	1	1	1	1	1
<i>Hamptophryne</i>	0	1	1	1	1	1
<i>Hypopachus</i>	0	2	1	1	1	1
<i>Nelsonophryne</i>	1	0	0	0	0	0
<i>Stereocyclops</i>	0	1	1	1	1	1

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