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## A New Species of *Hyalinobatrachium* (Anura: Centrolenidae) from the Highlands of Guyana

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**ABSTRACT.**—A new species of *Hyalinobatrachium* is described from the highlands of Guyana. This is the third centrolenid species reported from Guyana and the second of the genus *Hyalinobatrachium*. The new species is one of 13 *Hyalinobatrachium* found in northeastern South America (Venezuela, Guyana, Surinam, and Guyane); it can be differentiated from *Hyalinobatrachium taylori*, the only other *Hyalinobatrachium* in Guyana, by the color of the bones, which are white, and the color of the dorsum in preservative (lavender vs. cream in the new species). Variation and relationships within the genus in this region are discussed. The tadpole of the new species is described and illustrated.

The family Centrolenidae is remarkably speciose in the Andes Mountains from Colombia to Peru but is relatively poorly represented in the northeastern countries of South America (Venezuela, Guyana, Surinam, and Guyane). Of these, Venezuela possesses the largest number of species (24), followed by Guyana and Surinam (three each, including the species described herein), and Guyane (two). The species described herein is the third species reported from Guyana (for further discussion of the centrolenids of the Guianan Shield, see Noonan and Harvey, 2000; Myers and Donnelley, 1997). The genus *Hyalinobatrachium* is the most speciose centrolenid genus in the Guianan Shield (sensu Hoogmoed, 1979) with this being the 13th species recorded. The identity and relationships of centrolenid frogs have recently been the focus of some speculation (Ruiz-Carranza and Lynch, 1991a, b). Of particular interest to this study is *Hyalinobatrachium orientale*, which was once considered to be a widely distributed species (Cannatella and Lamar, 1986) but is now thought to

represent a complex of similar sibling species (Myers and Donnelley, 1997).

### MATERIALS AND METHODS

Specimens were collected by B. P. Noonan and D. W. Carpenter on 15, 19, and 23 June 1997, in the Pakaraima Mountains near Imbaimadai (05°44'N, 60°18'W). Geographic position was determined using a GPS. Adults were fixed in formalin and preserved in 70% ethanol, whereas eggs and tadpoles were preserved in 10% formalin. Measurements were taken to the nearest 0.1 mm using dial calipers. Coloration of peritonea were determined from color photographs of living specimens and dissection of preserved specimens. Webbing formulae follow Savage and Heyer (1967) as modified by Myers and Duellman (1982). The numbered diagnosis follows the format of Lynch and Duellman (1973) as modified by Ruiz-Carranza and Lynch (1991b), with the addition of characters 14–17. Specimens of the new species were compared to published descriptions of members of the *H. orientale* species group as defined by Ruiz-Carranza and Lynch (1991a) and specimens in the University of Texas at Arlington (UTA) Collection

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FIG. 1. Holotype of *Hyalinobatrachium ignioculus* (HA 722); Snout-vent length = 20.9 mm.

of Vertebrates and the Museum of Natural History, University of Kansas (KU; Appendix 1). The holotype and two paratopotypes of the new species are in the collection of the University of Guyana (HA) and the remaining paratopotypes are in the UTA Collection of Vertebrates.

*Hyalinobatrachium ignioculus*, sp. nov.

*Holotype*.—University of Guyana, Centre for the Study of Biodiversity: HA 722 (field number DWC 91); an adult male (Fig. 1), collected 15 June 1997 by D. W. Carpenter from a small stream on Peters Mountain, 3.6 km north of Imbaimadai in the Pacaraima Mountains, 600 m, Administrative Region 7, Guyana; 05°44'N, 60°18'W (Fig. 2).

*Paratopotypes*.—Guyana: Region 7: UTA 51654–63, adult males; UTA 51664, adult female; all collected at the type locality on the 15, 19, and 23 June, 1997.

*Diagnosis*.—The new species is placed in the genus *Hyalinobatrachium* because it possesses a bulbous liver and lacks a humeral spine in males (Ruiz-Carranza and Lynch, 1991a). The following combination of characters distinguish *H. ignioculus* from all other members of the genus: (1) vomerine teeth absent; (2) bones white in life; (3) parietal peritoneum clear; visceral, pericardial and hepatic peritonea white; (4) dorsal color in life pale lime green with many yellow spots; color in preservative cream-yellow with dark melanophores; (5) webbing between outer Fingers III<sub>2</sub>–1½IV; (6) webbing on foot I<sub>1</sub>–2III<sub>1</sub>–2½III<sub>1</sub>–2½IV<sub>2</sub>½–1V; (7) snout truncate in dorsal view, truncate in profile; (8) dorsal skin pustulate, lacking spicules; (9) enameled ulnar fold present along length of forearm and extending onto Finger IV; enameled tarsal fold present along length of tarsus and extending onto Toe V; (10) humeral spines absent; (11) tympanum distinct (in pre-

servative), covered with pustulate, pigmented skin; tympanum directed dorsolaterally with slight posterior inclination; (12) average snout-vent length 21.6 mm in males ( $N = 11$ ), and 23.0 mm in females ( $N = 1$ ); (13) nuptial excrescence clear, Type II; (14) anal decoration present in the form of enameled warts; (15) when adpressed, first finger longer than second; (16) liver bulbous; and (17) eye diameter roughly double width of disc of finger III.

*Hyalinobatrachium ignioculus* is assigned to the *Hyalinobatrachium fleischmanni* species group (Ruiz-Carranza and Lynch, 1991a) based on the presence of white bones, a bulbous liver, white visceral, pericardial, and hepatic peritonea, and the absence of a humeral spine in males. Detailed species comparisons are presented below for the four species of *Hyalinobatrachium* in the Guianan Shield (sensu Hoogmoed, 1979). The remaining species in Venezuela are restricted to the Cordillera Oriental and Cordillera de Merida and are presumably isolated from the species of the Guianan Shield by inhospitable lowlands and/or the Orinoco River. The new species can be distinguished from all species of *Hyalinobatrachium* occurring in the Guianan Shield and the mountains of western Venezuela by the combination of the presence of ulnar and tarsal folds, anal decoration in the form of enameled tubercles, supernumerary tubercles, pigmentation in the pericardium, and the unique red color of the iris in life (Table 1).

The only other species of *Hyalinobatrachium* found in Guyana is *Hyalinobatrachium taylori*, (Fig. 2) which has green bones and white spots on the dorsum in life Ayarzagüena (1992) and a lavender dorsum in preservative (Goin, 1968). These spots in *H. taylori* are retained in preservative on a lavender ground color. The presence of *H. taylori* in Guyana (based solely on the holotype) is in conflict with Frost (1999) who states that the type locality is actually in Surinam, citing personal communication from Hoogmoed. However, Lescure (1975) maps the type locality of *H. taylori* on the New River within the border of Guyana, which is in accordance with the original description (Goin, 1968) though the exact locality was not given in the description. There is currently a border dispute between Guyana and Surinam, with Surinam claiming all land east of the New River. If this side is taken, then it is possible that the type locality is on the east rather than the west bank of the New River and thus lies within Surinam rather than Guyana.

*Description of Holotype*.—An adult male, snout-vent length (SVL) 20.9 mm. Head distinctly wider than body; head length 87% of head width; head length 33% of SVL; snout short, 40% of head length; snout truncate in

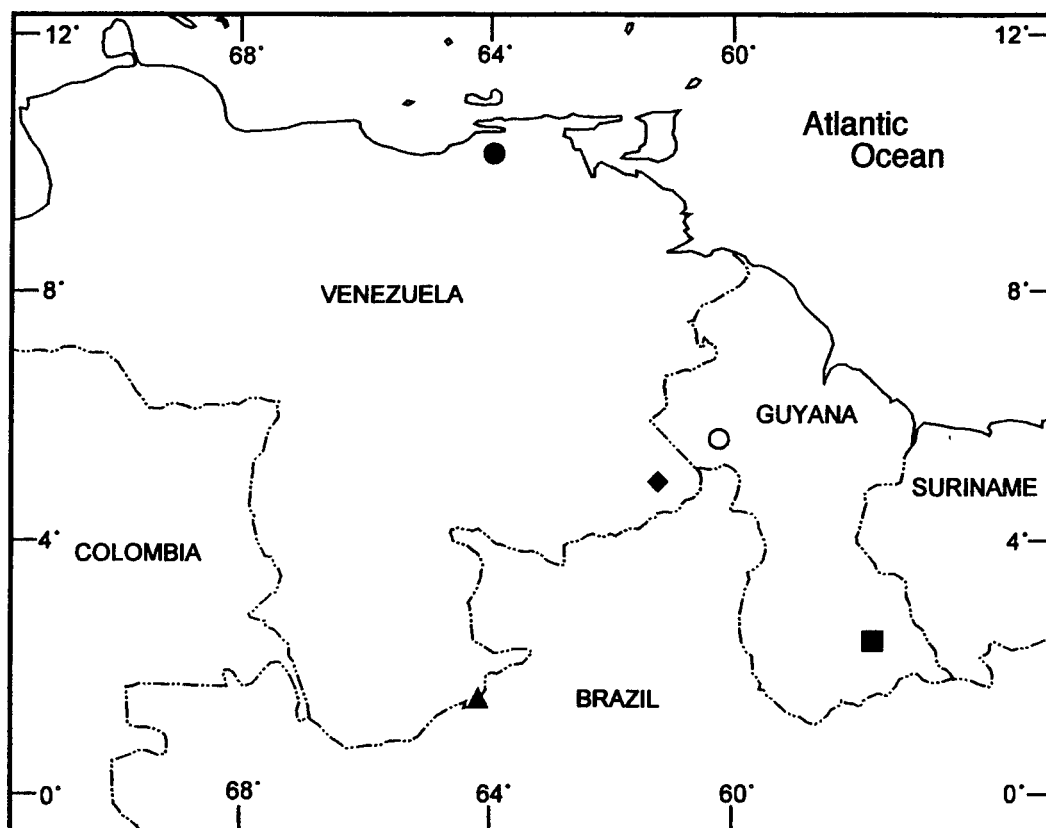


FIG. 2. Map of the Guianan Shield showing the type localities of *Hyalinobatrachium igniocolus* (open circle); *Hyalinobatrachium orientale* (closed circle); *Hyalinobatrachium taylori* (closed square); *Hyalinobatrachium crurifasciatum* (closed triangle); and *Hyalinobatrachium iaspidiense* (closed diamond).

TABLE 1. Comparison of character states of *Hyalinobatrachium* from the Guianan Shield for five characters that serve to quickly distinguish the new species from others in the region, character states that differ from the new species are in bold type.

| Species                          | Iris                    | Pericardial coloration    | Tarsal fold   | Supernumerary tubercles | Anal decoration |
|----------------------------------|-------------------------|---------------------------|---------------|-------------------------|-----------------|
| <b><i>H. igniocolus</i></b>      | yellow with red ring    | white                     | present       | present                 | present         |
| <i>H. antisthenesi</i>           | ?                       | <b>clear</b> <sup>a</sup> | <b>absent</b> | present                 | absent          |
| <i>H. crurifasciatum</i>         | <b>golden</b>           | white                     | present       | present                 | present         |
| <i>H. duranti</i>                | <b>gold</b>             | white                     | <b>absent</b> | <b>absent</b>           | <b>absent</b>   |
| <i>H. fragile</i>                | ?                       | <b>clear</b>              | <b>absent</b> | <b>absent</b>           | <b>absent</b>   |
| <i>H. iaspidiense</i>            | <b>whitish yellow</b>   | <b>clear</b>              | <b>absent</b> | <b>absent</b>           | present         |
| <i>H. loreocarinatum</i>         | <b>whitish gold</b>     | white                     | <b>absent</b> | <b>absent</b>           | <b>absent</b>   |
| <i>H. orientale</i>              | <b>gold to yellow</b>   | <b>clear</b>              | <b>absent</b> | present                 | present         |
| <i>H. ostracodermoides</i>       | ?                       | white                     | <b>absent</b> | <b>absent</b>           | <b>absent</b>   |
| <i>H. pallidum</i>               | <b>gold</b>             | <b>clear</b>              | <b>absent</b> | present                 | <b>absent</b>   |
| <i>H. pleurolineatum</i>         | <b>gold</b>             | white                     | <b>absent</b> | <b>absent</b>           | <b>absent</b>   |
| <i>H. revocatum</i> <sup>b</sup> | <b>silver</b>           | white                     | <b>absent</b> | present                 | present         |
| <i>H. taylori</i> <sup>c</sup>   | <b>reticulated gray</b> | white                     | <b>absent</b> | <b>absent</b>           | present         |

<sup>a</sup> Pericardial coloration determined from preserved specimens, possible artifact of preservation.

<sup>b</sup> Believed to actually belong to the genus *Cochranella* by Ruiz-Carranza and Lynch (1998).

<sup>c</sup> Placement in this genus questionable, see text for discussion.

both dorsal and lateral view; canthus rostralis blunt; loreal region concave; lips not flared; nostrils protuberant; internarial region depressed; eye large, eye diameter 36% of head length; outline of tympanum visible, directed dorsolaterally with slight posterior inclination; tympanic annulus entirely visible, diffusely pigmented with melanophores. Prevomerine dentigerous processes and teeth absent; choanae moderately sized, round, near margin of mouth; tongue round, not notched posteriorly; vocal slits paired, extending from mediolateral base of tongue to angles of jaws.

Humeral spine absent; enameled ulnar fold present (it should be noted that the term enameled used here refers to being covered in a hard, white substance), extending length of Finger IV; forearm larger than upper arm; first finger longer than second (Fig. 3); webbing basal between Fingers I, II, and III, webbing between third and fourth fingers extensive (III2-1½IV); relative lengths of Fingers II < I < IV < III; discs broad, truncate; discs on fingers slightly larger than those on toes; disc on Finger IV approximately 1.6 times larger than tympanum. Low, rounded subarticular tubercles present on first three fingers; supernumerary tubercles low, rounded; palmar tubercle ovoid, raised; thenar tubercle low, elliptical; prepollex not enlarged, prepollical spine not protruding; nuptial pad present, Type II.

Hind limbs slender; length of tibia 56% of SVL; enameled tarsal fold present, extending to tip of Toe V; inner metatarsal tubercle low (Fig. 3), elliptical; outer metatarsal tubercle absent; subarticular tubercles circular, rounded in profile, about as wide as digits; low, rounded supernumerary tubercles present; relative lengths of toes I < II < V < III < IV; toes extensively webbed; webbing formula I 1/2-2III-2 1/2III 1 1/2-2IV2 1/2-1V; discs on toes round; disc on Toe IV approximately 1.3 times larger than tympanum.

Skin on dorsal surfaces pustulate; skin on belly and ventral surfaces of thighs granular; vent directed posteriorly at midlevel of thighs; concealed by dermal fold; flanked by irregular enameled warts.

*Color in Life.*—Dorsum (including eyelid) light lime green with numerous yellow spots, giving appearance of a green "net" over a yellow ground color; color extending length of the leg; skin on humeral area and Toes I-III transparent, but forearm and fourth finger patterned as dorsum. Fine melanophores found in green areas, the expression and darkness of which seem to vary between active and dormant periods; ventral surfaces cream; parietal peritoneum clear; pericardial, visceral, and hepatic peritonea white; iris yellow with small dark flecks similar

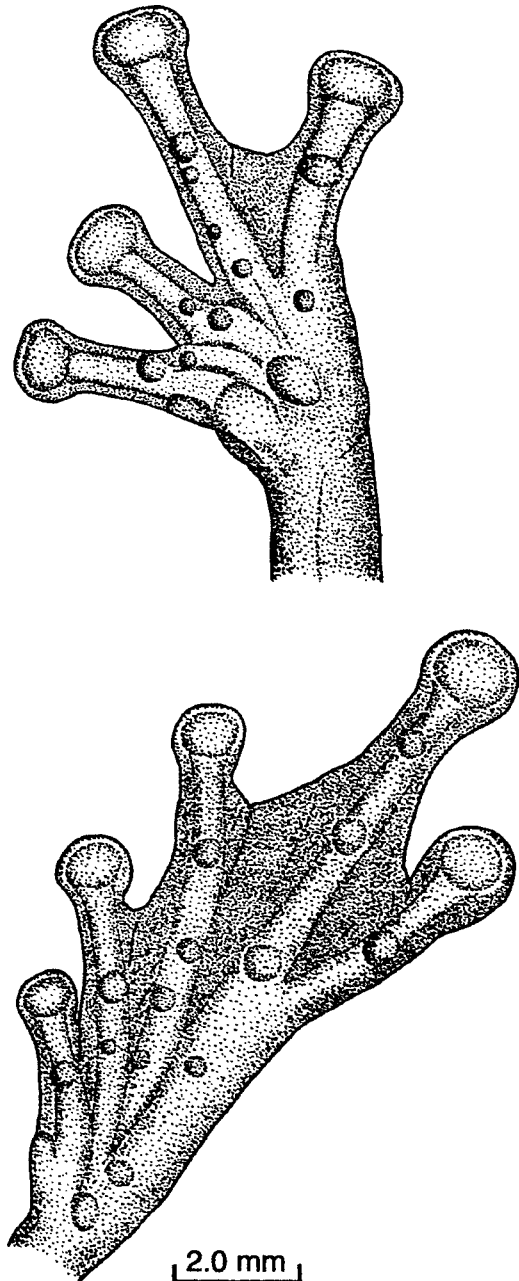


FIG. 3. Palmar and plantar view of the left hand and foot of *Hyalinobatrachium igniocolus* (HA 722).

to melanophores on dorsum, and a distinct, red ring, that may or may not be complete, encircling the pupil; bones white.

*Color in Preservative.*—Venter chalky white and semitransparent; dorsum cream with dark flecks present in all patterned areas described above; melanophores maintain circular shape of yellow spots (which lack melanophores) ob-

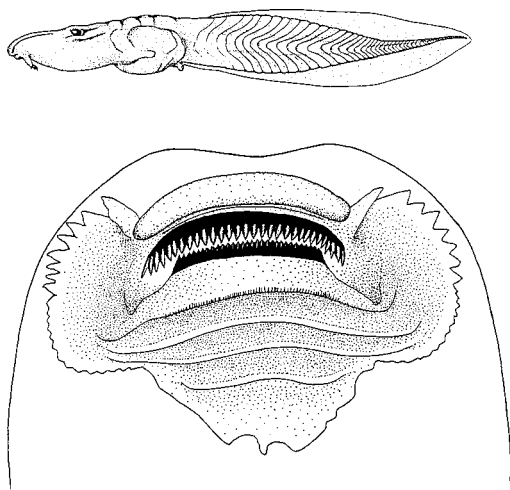


FIG. 4. Lateral aspect and mouthparts of the tadpole of *Hyalinobatrachium ignioculus* (UTA-51904).

served in life in absence of contrasting green color. Parietal peritoneum clear; pericardium, visceral, and hepatic peritonea white; bones white.

*Variation.*—Measurements in mm of holotype followed by mean and range of male paratopotypes in parentheses: SVL 20.9 (21.6, 20.8–23.0); head width 7.5 (8.2, 7.5–8.6); head length 6.5 (7.1, 6.5–7.2); snout length 2.7 (2.8, 2.6–3.1); eye diameter 2.5 (2.5, 2.4–2.7); hand length 6.2 (6.6, 6.0–7.2); tibia length 12.2 (12.1, 11.4–12.7). Measurements in millimeters of the single adult female paratopotype are as follows: SVL 23.0; head width 8.7; head length 7.7; snout length 3.0; eye diameter 2.5; hand length 7.2; tibia length 13.2.

Although guanophores are undoubtedly present in the pericardium of all specimens in life and in preservative, a small portion of the heart of some specimens appears reddish in preservative (after 18 months) and is visible through the ventral surface. Variation in webbing of outer fingers and feet is as follows: outer Fingers III(1 1/2–2)–(1 3/4–2)IV; Toes I(1–1 1/2)–2II(1–1+)–(2–2 1/2)III(1–1 1/2)–(2–2+) IV(2+–3)–1V

*Eggs and Tadpoles.*—Males of this species apparently guard nesting sites, and may use them multiple times (this was observed in several instances). As many as three clutches, at varying stages of development, were found on the underside of a leaf with a single calling male. Color of eggs was not noted. One of these clutches (UTA 51903) contained 11 eggs, and a second clutch containing 10 eggs was kept alive until two larvae (other eight eggs damaged in field, not preserved) hatched (UTA 51904–5). One of these larvae was preserved immediately (UTA 51904) and is illustrated in Figure 4 (total length

= 13.1 mm). The second tadpole was raised in captivity to a total length of 23.6 mm (UTA 51905). This description will center on UTA 51904 to avoid reporting any artifacts of captivity, although some structures are not formed or are undetectable in UTA 51904; in such situations, descriptions were made from UTA 51905 and are noted as such below. Both specimens are in developmental Stage 25 (operculum fully developed, no limb buds apparent; Gosner, 1960).

Body ovoid, short (29% of total length), longer than wide (body length/body width = 1.8), depth less than width; snout rounded in dorsal and lateral view; eyes dorsolateral (pupils visible in dorsal view); dorsal surface flattened, sloping anteroventrally between eyes and snout; oral disc ventral; belly flat; nostrils about one-third of distance between eyes and snout; nostrils not protuberant, directed anterolaterally; spiracle sinistral, on longitudinal axis of body, directed posteriorly; spiracular tube short; anal tube short, medial (from UTA 51905). Caudal musculature robust; caudal fins extremely low, expanding distally as caudal musculature narrows; tip of tail pointed.

Oral disc large with well-developed posterior and lateral folds (Fig. 4); posterior fold strongly fringed; jaw sheath wide, heavily serrated. Labial teeth in three weakly keratinized lower rows; labial tooth row formula 0/3. Labial papillae large and irregular on ventral and lateral edges, greatly reduced in size along dorsal edge. Oral disc emarginate below level of third tooth row.

In preservative, dorsal and lateral surfaces of body covered with dark brown melanophores; ventral skin transparent (heart visible), UTA 51905 with a few melanophores present on ventral surface; eyes dark brown, lens visible as milky spot in eye; caudal musculature white, with dark brown melanophores (UTA 51905 only); caudal fin clear, dorsal fin clear, both with dark brown melanophores in UTA 51905.

Few centrolenid tadpoles have been described, and only two from northern South America. Mijares-Urrutia (1990) described the tadpole of *Centrolene andinum*, which differs from the new species in having the eyes barely visible, having anterior tooth rows, and lacking a heavily serrated beak. Myers and Donnelly (1997) briefly described the tadpole of *Hyalinobatrachium crurifasciatum*, which differs from the new species in having a poorly keratinized beak and mouthparts.

*Etymology.*—The species name is a noun in apposition and is derived from the Latin words *ignis*, meaning fire, and *oculus*, meaning eye. The name refers to the distinctive red color of part of the iris.

*Distribution and Ecology.*—*Hyalinobatrachium ignioculus* is known only from the type locality on Peters Mountain, 3.6 km north of Imbaimadai, Region 7, Guyana (Fig. 2). Peters Mountain reaches approximately 900 m in elevation at the peak, is covered in evergreen sclerophyllous forest, and is situated in the highland savanna of western Guyana. The fast-flowing stream where *H. ignioculus* was found is a tributary of the Mazaruni River and varies between 0.1 and 1.0 m depth and 1.0 and 2.0 m width at the type locality. This stream has a smooth rock and/or sandy bottom, and its banks are steep and about 3.0–4.0 m high. The creek is heavily shaded by the forest canopy.

Individuals of *H. ignioculus* were active by night along the stream bank on leaves between 1.0 and 6.0 m above the surface of the water. Males began calling with the onset of darkness but rarely called after 2000 h. Calling males were always found on the undersides of leaves and were often occupying a leaf with one or more clutches of eggs (which were attached to the underside of the leaf). The area was not visited during the day, so it is not known whether the males guard sites during the day. The call consisted of a single, flat note that could be heard for a considerable distance (calls were not recorded). Calling males (and egg clutches) were rarely in or over "splash zones" but were commonly found over relatively tranquil sections of the stream. A single female (UTA 51664) was found on the top of a leaf above the stream.

#### DISCUSSION

The new species is presumably a member of the Guianan *Hyalinobatrachium orientale* species complex, which belongs to the more formal *H. fleischmani* species group of Ruiz-Carranza and Lynch (1991a). The discovery of this and other members of this complex point to the existence of an assemblage of similar sibling species, some of which were considered synonyms by Cannatella and Lamar (1986). With the discovery in recent years of specimens that differ considerably from *H. orientale* and a better understanding of the relationships of centrolenids in general, the true identity of *H. orientale* has again come into question (Myers and Donnelley, 1997; D. C. Cannatella, pers. comm.). Preliminary evidence alluded to by Gorzula and Señaris (1999[1998]) indicates some morphological and behavioral differences between the populations of *H. orientale* (sensu Cannatella and Lamar, 1986).

Unfortunately, Gorzula and Señaris (1999[1998]) have introduced additional confusion regarding the identity of *H. orientale*. In their coverage of the centrolenid fauna of the region, they include *H. taylori* based on three specimens in

the Museum of Natural History, University of Kansas, collected by W. E. Duellman and S. Gorzula. They go on to state that Ayarzagüena (1992) and Señaris and Ayarzagüena (1993) also reported this taxon from the Gran Sabana and Auyán-tepui. Duellman is indicated as identifying the three KU specimens as *H. taylori*, even though these specimens are described as *H. orientale* by Duellman himself in his 1997 report of the amphibians of the La Escalera region (Duellman, 1997). It seems that Gorzula and Señaris (1999[1998]) are reporting these specimens as *H. taylori* on the basis of identification made in the field by Duellman and Gorzula (W. E. Duellman, pers. comm.). The authors further state that "other material of this species from the same area (La Escalera) has been examined by Ayarzagüena (1992)" but in fact Duellman (1997) reports the bones of the KU specimens as being white, and Ayarzagüena (1992) reports the bones of *H. taylori* as green. Gorzula and Señaris (1999[1998]) also describe the dorsum in preservative as being lavender (which follows Goin's, 1968, original description) including the two specimens from La Escalera he examined. The two KU specimens were examined and found to have cream colored dorsums and white bones (though green bones may fade to white in preservative, so Duellman's 1997 description of these specimens must be trusted). Thus, there are either two species of *Hyalinobatrachium* in the La Escalera region, one with green bones and one with white bones. Alternatively, Ayarzagüena (1992) misreported the color of the bones of *H. taylori* or at least those of specimens from Auyán-tepui and the Gran Sabana. If Ayarzagüena (1992) was correct and *H. taylori* does indeed have green bones, then this taxon can no longer be considered a member of the *H. fleischmani* species group, because this group is defined by the presence of white bones (Ruiz-Carranza and Lynch, 1991a). However, if the bones are actually white, this taxon is still unique in having a lavender dorsum in preservative.

*Hyalinobatrachium iaspidiense* (Ayarzagüena, 1992) appears to be the species whose geographic distribution is physically closest to the type locality of *H. ignioculus*. This species differs markedly from the new species in lacking pigmentation in the pericardium, a tarsal fold, supernumerary tubercles, and anal ornamentation. Additionally, the iris of *H. iaspidiense* is whitish yellow compared to yellow with a red ring in the new species.

The most recently described species in the *H. fleischmani* group is *Hyalinobatrachium crurifasciatum*, which was discovered in 1989 at Pico Tamacuari in Amazonas, Venezuela. The main difference between *H. crurifasciatum* and *H. orien-*

*tale* is that the former has green bands on the limbs, a golden iris, and ulnar and tarsal folds, all of which are absent in *H. orientale*. *Hyalinobatrachium crurifasciatum* also appears to be the most phenotypically similar species in the region to *H. ignioculus*; differing in having a golden iris, green limb bands in life, smooth skin on the dorsum, and a larger adult size in males (SVL 22.0–24.0 compared to 20.8–23.0;  $t_{0.05} = 2.65$ ;  $P < 0.01$ ). The relationships of the Guianan *Hyalinobatrachium* remain poorly understood and will likely remain so until a detailed phylogenetic analysis of the group is done. It is hoped that work in progress by the senior author (BPN) will elucidate the origins and patterns of speciation not only within this group but of the entire family.

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#### APPENDIX 1

##### Comparative Material Examined

*Hyalinobatrachium antisthenesi*, KU 133467–79, 167336–59, 185766–7; *Hyalinobatrachium bergeri*, KU 182363 (holotype), 162248–9, 162251–55, 162257, 182364–8 (paratypes); *Hyalinobatrachium chirripoi*, KU 36865 (holotype), 36862–4 (paratypes), 36866–70 (paratypes); *Hyalinobatrachium colymbiophylum*, KU 23812 (holotype), 32939–42, 65238, 77526, 77535–39, 103819, 116425–35; *Hyalinobatrachium eurygnathum*, KU 93220–23; *Hyalinobatrachium lemur*, KU 211768 (holotype), 211769 (paratype); *Hyalinobatrachium munozorum*, KU 118054 (holotype), 105251 (paratype), 123225 (paratype), 150620 (paratype), 152488–9, 154749, 155493–6, 172167–9, 175215, 175504, 197028–9, 217295–7; *Hyalinobatrachium orientale*, KU 133481, 167360–68, 167370–3, 181126–7, 185768–9, 224499–03; *Hyalinobatrachium pulveratum*, KU 85476, 116493; *Hyalinobatrachium pellucida*, KU 143298 (holotype); *Hyalinobatrachium talamancae*, KU 30887 (holotype), 32936–8, 140018; *Hyalinobatrachium uranoscopum*, KU 74310–1, 93226–7, 93229–30.