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A NEW SPECIES OF *OSTEOCEPHALUS* (ANURA: HYLIDAE) FROM AMAZONIAN ECUADOR AND PERU

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ABSTRACT: A new species of the hylid frog genus *Osteocephalus* from the upper Amazon Basin of Ecuador and Peru is described. It most closely resembles *O. planiceps*, but it differs in the absence of pale stripes on the heels and above the vent, in being smaller, and lacking brown spots on the flanks. The new species, *O. yasuni*, is unique within *Osteocephalus* in having extensive yellow ventral coloration.

Key words: Anura; Hylidae; *Osteocephalus yasuni;* New species; Ecuador; Peru

TRUEB and Duellman (1971) reviewed the genus *Osteocephalus* and recognized five species: *O. buckleyi* (Boulenger, 1882), *O. leprieurii* (Duméril and Bibron, 1841), *O. pearsoni* (Gaige, 1929), *O. taurinus* Steindachner, 1862, and *O. verruciger* (Werner, 1901). Subsequently, Duellman (1974) transferred *Hyla langsdorffii* Duméril and Bibron, 1841, into *Osteocephalus,* and three new species were described—*O. elkejungingerae* (Henle, 1981), *O. subtilis* Martins and Cardoso, 1987, and *O. oophagus* Jungfer and Schiesari, 1995. Duellman and Hoogmoed (1992) transferred *Hyla rodriguezi* Rivero, 1968 to *Osteocephalus,* and five additional species belonging to the *O. rodriguezi* group were described by Ayarzagüena et al. (1992). Ayarzagüena (1992) transferred all the species of the *O. rodriguezi* group to the new genus *Tepuihyla.* Duellman and Mendelson (1995) resurrected two species: *O. planiceps* (Cope, 1874) from the synonymy with *O. taurinus,* and *O. cabrerai* (Cochran and Goin, 1970) from the synonymy with *O. buckleyi.* At present, the genus contains 11 species.

Many unresolved alpha-level taxonomic problems persist within *Osteocephalus.* There are at least three undescribed spe-

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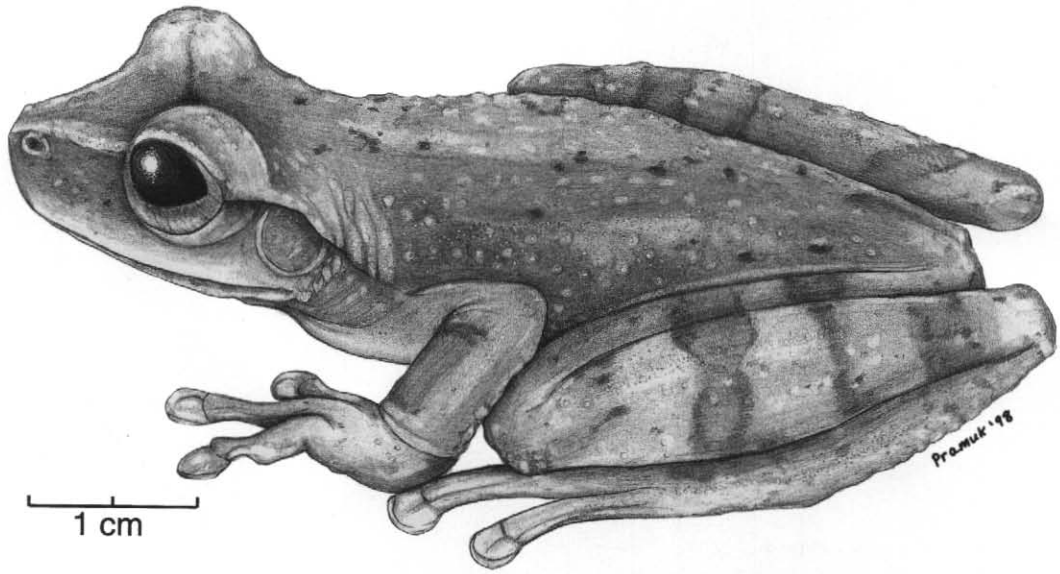

FIG. 1.—*Osteocephalus yasuni*, male (QCAZ 11332). Pencil drawing based on color transparency taken by S. Ron.

cies known from the upper Amazon Basin in Ecuador and Peru that reproduce in bromeliads (Duellman and Mendelson, 1995; K. Jungfer and S. Ron, unpublished data). In the collections at The University of Kansas, there are several specimens from Balta, Peru, which seem to belong to an undescribed species. The males of these Peruvian specimens are characterized by having palmar nuptial callosities. Additionally, two other species are being described (E. Smith, personal communication; M. Martins, cited in Jungfer and Schiesari, 1995) from the upper Amazon Basin of Colombia and midwestern Amazonian Brazil. The fact that many lists of anurans from Amazonian localities (e.g., Duellman and Mendelson, 1995; Lescure, 1982; Zimmerman and Rodrigues, 1990; Zimmerman and Simberloff, 1996) include unidentified species of *Osteocephalus* also reflects the taxonomic problems of the genus.

Herein, we describe a species of *Osteocephalus* that inhabits tropical rainforests in Amazonian Ecuador and Peru. Specimens of this species were identified as *O. planiceps* and *O. leprieurii* in earlier collections. However, when additional collections were made in July 1997 and coloration in life was noted, its distinctiveness from other members of the genus became evident.

MATERIALS AND METHODS

For ease of comparison, we generally follow the format of Trueb and Duellman (1971) for diagnosis and description. Measurements were made (to the nearest 1 mm) using digital calipers from specimens fixed in 10% formalin and preserved in 70% ethanol. Specimens of *Osteocephalus* that we examined are housed in the Natural History Museum of The University of Kansas (KU), Museo de Vertebrados de la Universidad Católica del Ecuador (QCAZ), and Museu Nacional Brazil (MNRJ). Specimens examined are listed in Appendix I. Figure 1 was drawn from a projected color transparency of a living frog. We made osteological descriptions and drawings of the skulls from cleared-and-stained adult females (*O. yasuni* QCAZ 11331; *O. planiceps* QCAZ 5140). Techniques for clearing and double-staining specimens with Alcian Blue and Alizarin Red are modified from the protocol of Taylor and Van Dyke (1985).

Snout–vent length is abbreviated as SVL. Sex was determined by dissection.

Recordings of the call were analyzed using the software Canary™ 1.2.1 for Macintosh at a sampling frequency of 44.1 KHz. Statistical software Minitab 10 Xtra (Minitab, 1995) and Systat 7.0 were used to perform multivariate analyses in order to quantify morphological differences and morphometric overlap among *Osteocephalus yasuni* and the species of *Osteocephalus* that most closely resemble it. The following are the species and number of specimens analyzed (in parentheses): *Osteocephalus yasuni* (17), *O. leprieurii* (10), *O. planiceps* (19), *O. taurinus* (10), and the apparently undescribed *Osteocephalus* from Balta, Departamento Ucayali, Peru (10). Multivariate analyses were applied to eight morphological variables: SVL, head length, head width, eye diameter, tympanum diameter, femur length, tibia length, and foot length. Measurements were made following Duellman's (1970) methodology. All variables were log-transformed. To remove the effect of covarying size from multivariate analyses, linear regressions were performed between all variables and SVL (all P-values < 0.01). The analyses were applied to SVL and the residuals of the regressions with the other variables. To determine patterns of morphometric variation and covariation, principal component analysis (PCA) was employed. Subsequently, a discriminant function analysis (DFA) was performed with the same eight variables to examine interspecific morphological differentiation.

RESULTS

Osteocephalus ***yasuni*** sp. nov.

Holotype.—QCAZ 11336, an adult male collected by Santiago Ron at the Yasuní Scientific Research Station (76° 24′ 19″ W, 00° 40′ 32″ S; altitude 230 m), Provincia del Napo, Ecuador, on 21 July 1997.

Paratopotypes.—QCAZ 10879, 11332 (Fig. 1) adult males; KU 224636–37, QCAZ 11329 adult females; QCAZ 11331 (cleared-and-stained female); collected by Santiago Ron on 15 July, 1997. QCAZ 11334 adult male; collected by Morley Reed on 25 May 1996.

Diagnosis.—A moderate-sized species of *Osteocephalus* having the following combination of characters: (1) size, skin texture, and intensity of yellow ventral coloration sexually dimorphic; maximum SVL in males 55.7 mm, in females 61.6 mm; (2) skin on dorsum in males bearing numerous nonspinous tubercles, all about equal in size; (3) skin on flanks granular; (4) hand-webbing formula (following Savage and Heyer, 1967) of **II**2^-—3^+**III**3^-—2.5**IV**; foot-webbing formula of **I**1^+—2^-**II**1^+—2^-**III**1^+—2^-**IV**2^+—1^-**V**; (5) dorsum brown, usually with scattered dark spots and/or irregular dark marks; (6) venter varying from yellow to creamy yellow (yellow coloration especially intense in groin) with fine brown reticulations on throat; (7) narrow, cream labial stripe confluent with suborbital cream mark; (8) flanks brown near the dorsum becoming yellow or creamy yellow ventrally; (9) dermal roofing bones of the skull exostosed; (10) sphenethmoid exostosed; (11) nasals contacting medially; (12) anteromedial margin of frontoparietal at midlevel of orbit; (13) frontoparietal fontanelle covered; (14) neopalatine not serrate; (15) parasphenoid lacking odontoids; (16) zygomatic ramus of the squamosal extending approximately one-third distance to maxillary arch; (17) transverse process of Presacral Vertebra III about equal in length to sacral diapophysis; (18) bones white; (19) iris coppery bronze with irregular black reticulations and reddish-brown median horizontal streak; (20) paired lateral vocal sacs located behind jaw articulation.

Osteocephalus yasuni is unique within the genus because of its extensive yellow ventral coloration (creamy yellow in females). The only other member of *Osteocephalus* that has yellow coloration on the venter (though only restricted to the belly) is *O. langsdorffii* (Duellman, 1974). However, *O. langsdorffii* has a geographically distant range (Atlantic forests of Brazil and northeastern Argentina; Frost, 1985), is larger (up to 99 mm), and has scalloped dermal folds on the outer edges of the hands and feet (Duellman, 1974; Lutz, 1973). The ventral colorations of the other *Osteocephalus* vary between tan and

white, with the exception of *O. cabrerai* that is pinkish gray (Duellman and Mendelson, 1995). *Osteocephalus yasuni* most closely resembles *O. planiceps*, from which it differs by the combination of the following characters: (1) smaller size (Table 1); (2) absence of brown spots on the flanks (Fig. 2); (3) absence of pale stripes on heels and above cloacal opening; (4) white bones (green in *O. planiceps*); (5) irregular black reticulations in the iris [straight, black lines radiating from the pupil in *O. planiceps* (Fig. 3)]; (6) fine brown reticulations on throat (throat with brown spots or immaculate in *O. planiceps*); (7) ventral coloration varying from yellow to creamy yellow (cream in *O. planiceps*); and (8) call (call diagram is shown in Fig. 6). *Osteocephalus yasuni* differs from *O. subtilis* by lacking a black iris (Martins and Cardoso, 1987), from *O. pearsoni* by lacking dark spots on flanks (Trueb and Duellman, 1971), from *O. cabrerai* by lacking a row of tubercles on the ventrolateral edges of tarsi, and from *O. verruciger* by lacking black spots on the venter (Trueb and Duellman, 1971). *Osteocephalus yasuni* differs from *O. buckleyi, O. leprieurii, O. oophagus, Osteocephalus* sp. (sensu Duellman and Mendelson, 1995), and *O. taurinus* by having irregular black reticulations in a bronze iris instead of straight, black lines radiating from the pupil (Fig. 3). *Osteocephalus yasuni* also differs from *O. leprieurii* by lacking well-defined transverse brown marks on the dorsum and by the absence of pale stripes on the heels and around the cloacal opening. These two species also differ in their cranial morphology; *O. yasuni* lacks the frontoparietal fenestra that is present in *O. leprieurii* (Trueb and Duellman, 1971). *Osteocephalus taurinus* also has green bones (white in *O. yasuni*), is larger (Table 1), and has more extensive webbing on the hands (**II**1.5—2.5**III**2$^+$—2 **IV**) than *O. yasuni*. *Osteocephalus oophagus* has a single, median, subgular vocal sac (double and lateral in *O. yasuni*) and more extensive webbing between the fingers (**II**1.5—3 **III**2.5—2$^+$**IV**; Jungfer and Schiesari, 1995) than does *O. yasuni*. *Osteocephalus yasuni* differs from *O. buckleyi* by the ab-

TABLE 1.—Ranges, means (bold characters) and standard deviations (in parentheses) of five species of *Osteocephalus*. SVL = snout–vent length; FOOT = foot length; HL = head length; HW = head width; ED = eye diameter; TD = tympanum diameter; TL = tibia length; FL = femur length. All measurements in mm.

Species	*n*	SVL	FOOT	HL	HW	ED	TD	TL	FL
O. leprieurii	10	46.7–60.9	17.8–24.8	14.5–18.9	15.7–20.0	4.6–5.9	3.4–4.0	25.2–33.7	20.0–28.5
		56.52 (3.69)	**22.11** (1.77)	**17.52** (1.22)	**19.05** (1.26)	**5.20** (0.42)	**3.64** (0.23)	**30.9** (2.19)	**26.31** (2.05)
O. planiceps	19	40.8–89.2	16.8–35.6	12.6–29.7	13.5–25.7	4.2–7.4	2.6–5.7	23.5–46.2	22.0–42.5
		63.2 (11.7)	**26.7** (5.31)	**20.2** (4.06)	**20.4** (3.29)	**5.71** (0.846)	**4.27** (0.80)	36.6 (6.37)	**33.4** (5.80)
O. sp.	10	47.7–58.1	19.8–25.7	13.9–18.2	14.5–19.4	4.4–5.9	3.1–4.2	27.3–36.9	22.5–30.0
		52.5 (3.84)	**22.8** (1.84)	**15.8** (1.51)	**16.8** (1.71)	**5.16** (0.48)	**3.82** (0.35)	**31.5** (3.17)	**26.4** (2.58)
O. taurinus	10	68.6–103.9	27.6–40.3	19.7–27.9	22.0–30.2	5.3–7.9	4.1–6.0	36.6–51.3	29.7–47.6
		82.5 (10.83)	**33.54** (4.46)	**23.85** (2.81)	**26.41** (2.89)	**6.75** (0.86)	**5.02** (0.64)	**43.6** (5.43)	**39.7** (5.58)
O. yasuni	17	42.6–61.6	16.7–27.2	14.1–20.4	14.7–21.2	4.4–6.2	2.7–4.2	24.3–36.5	21.9–34.3
		52.7 (5.50)	**22.6** (2.84)	**17.2** (1.89)	**17.8** (1.95)	**5.47** (0.565)	**3.55** (0.384)	**31.0** (3.57)	**28.4** (3.22)

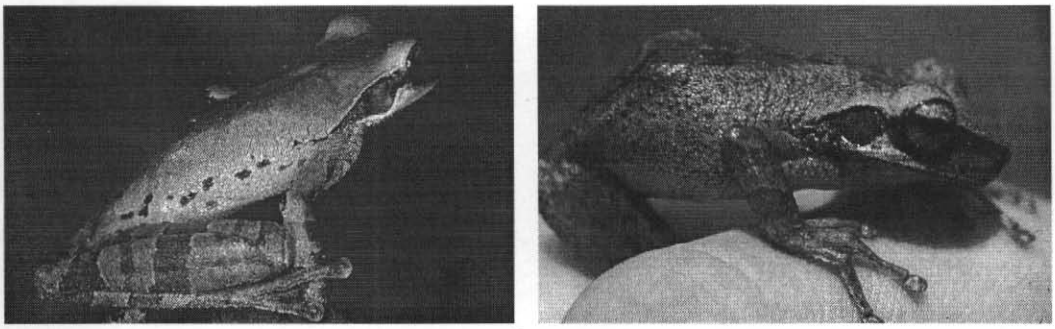

FIG. 2.—Left: *O. planiceps* (QCAZ 11322, adult female, SVL = 60.4 mm). Right: *Osteocephalus yasuni* (QCAZ 10879, adult male, SVL = 47.35 mm). Note dark spots on the flank of *O. planiceps* (absent in *O. yasuni*). Color transparencies by S. Ron.

sence of aerolate skin on the flanks (granular in *O. yasuni*) and by having nasals meeting medially (nasals widely separated in *O. buckleyi*; Trueb and Duellman, 1971). *Osteocephalus elkejungingerae* is smaller (maximum SVL 22 mm; Henle, 1981) and has a dull red iris (Duellman and Mendelson, 1995) in contrast to the bronze iris of *O. yasuni* (Henle, 1981).

The generic placement of *Osteocephalus yasuni* is based on the absence of diagnostic features that can associate it with the other hyline genera bearing paired lateral vocal sacs that inflate behind the jaw articulation (i.e., *Argenteohyla, Phrynohyas,* and *Trachycephalus;* see discussion).

Description of holotype.— Adult male 55.7 mm SVL, tibia length 34.2 mm, foot length 25.1 mm, head length 16.2 mm, head width 18.1 mm, eye diameter 5.6 mm, tympanum width 3.2 mm; body wider than head; head longer than wide; diameter of tympanum slightly greater than half diameter of eye; head flat between orbits, slightly concave in intercanthal region; snout truncate in profile and in dorsal view; nostrils slightly elevated, internarial region flat; canthus rostralis slightly rounded; loreal region concave; tympanum distinct, rounded; elevated supratympanic fold from midlevel of eye to area above tympanum, descending to insertion of arm; wrinkles originating from supratympanic fold extending toward midline; axillary membrane weak, extending half length of humerus. Fingers with moderately large discs, that of third finger about one-third diameter of tympanum; nuptial pads absent; distal subarticular tubercle on Finger IV weakly bifid; palmar supernumerary tubercles present; webbing between Fingers I and II basal; webbing formula for hand: **II**2^{-}—3^{+}**III**3^{-}—2.5**IV**; relative lengths of adpressed fingers III > IV

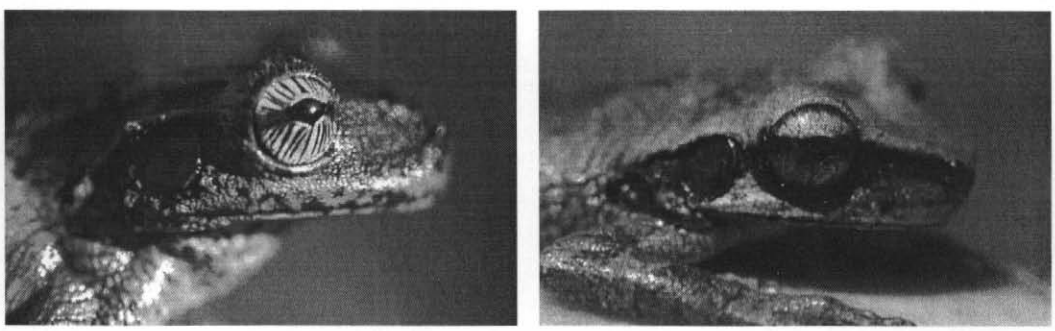

FIG. 3.—Left: *Osteocephalus taurinus* (QCAZ 11289, adult female, SVL = 84.1). Right: *O. yasuni* (QCAZ 10879, adult male, SVL = 47.3 mm). Note differences in the iris pattern. Color transparencies by S. Ron.

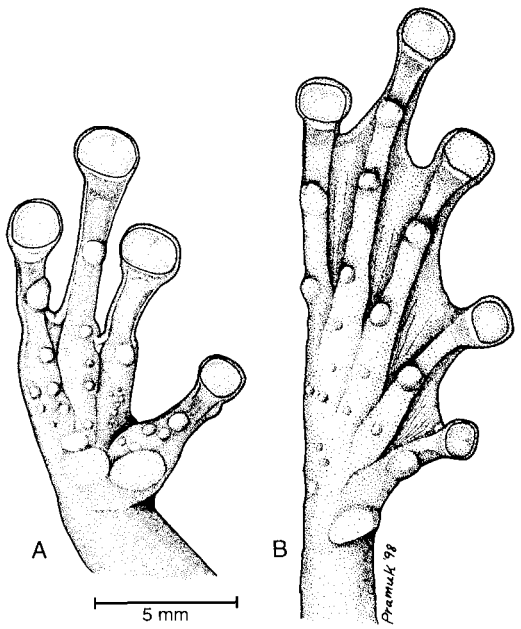

FIG. 4.—Ventral view of the (A) right hand and (B) right foot of the holotype of *Osteocephalus yasuni* (QCAZ 11336).

> II > I (Fig. 4A). Tarsus extending past the tip of snout when limb is adpressed against the body. Inner metatarsal tubercle present, outer metatarsal tubercle absent. Foot webbing formula: **I**1$^+$—2$^-$**II**1$^+$—2$^-$**III**1$^+$—2$^-$**IV**2$^+$—1$^-$**V**. Relative lengths of toes IV > V > III > II > I (Fig. 4B).

Skin on dorsum granular; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short. Tongue round. Nine and 12 teeth present on the left and right vomers, respectively. Vocal slits parallel to the posterolateral margin of the mandible. Deflated vocal sac forming everted pouch (width about two-thirds diameter of tympanum), dangling loosely beneath supratympanic fold.

Color of holotype in preservative.—Dorsum dark brown with irregular gray patches and scattered, dark gray spots; venter cream, with fine brown reticulations on throat; dorsal surfaces of limbs brown with darker brown, transverse bars; ventral surfaces of limbs reddish brown; sides of head dark brown with narrow, pale cream labial stripe confluent with a suborbital pale cream mark; flanks brown dorsally changing to cream ventrally; bones white. Testes white.

Color of holotype in life.—(Santiago Ron, field notes, 21 July 1997). Dorsum brown with dark brown marks; dorsal surfaces of limbs brown with darker brown bars; flanks brown dorsally, becoming yellow ventrally. Venter yellow, with more intense color in inguinal region and with fine brown reticulations on throat; ventral surfaces of limbs reddish brown, with small yellow spots on thighs (most numerous medially); sides of head dark brown with narrow, pale cream labial stripe confluent with a suborbital cream mark. Dark brown interorbital line present. Iris coppery bronze with irregular, black reticulations and reddish-brown median horizontal streak; bones white.

Etymology.—The specific name *yasuni* is derived from the name of the Yasuní National Park, the largest protected area in Ecuador and type locality for the new species. According to the Pleistocene refuge hypothesis, the Yasuní National Park is located within the "Napo Refuge" (Haffer, 1987; Prance, 1979). The area contains a highly diverse biota; for this reason, its conservation is of vital importance.

Variation.— The following characters pertain to live specimens. An adult male (QCAZ 11337) has several irregularly placed, pale brown spots on dorsum. In females, the venter is creamy yellow with coloration intensifying toward the groin. The dark interorbital line present in the holotype is absent (QCAZ 5139) or diffuse (QCAZ 10879) in two male specimens. The fine brown reticulations on throat are absent in QCAZ 10879 and QCAZ 11334. One juvenile (QCAZ 11470) has dorsal surfaces of finger discs reddish tan, lateral part of head pale brown, and pale labial stripe absent.

The largest male in the type series has a SVL of 55.7 mm, and the largest female, 61.9 mm. Although females attain a noticeably larger size than males, there is little variation in size proportions between the sexes, except that the tympani of females are slightly larger than those of males (Table 2). Measurements and proportions (following those of Duellman,

TABLE 2.—Size and proportions of males and females of *Osteocephalus yasuni* (means in parentheses). Measurements in mm. Abbreviations as in legend of Table 1.

Sex	n	SVL	HL/SVL	HW/SVL	TD/ED	TL/SVL	FL/SVL
Males	7	43.97–55.72 (49.09)	0.310–0.369 (0.320)	0.307–0.356 (0.333)	0.584–0.799 (0.571)	0.533–0.600 (0.575)	0.401–0.451 (0.431)
Females	13	42.63–61.93 (55.11)	0.307–0.350 (0.328)	0.312–0.370 (0.312)	0.572–0.826 (0.670)	0.536–0.661 (0.594)	0.385–0.483 (0.430)

1970) are given in Tables 1 and 2. The hand- and foot-webbing formulae, and relative lengths of adpressed toes and fingers are not variable among individuals (e.g., toe-webbing formula, relative lengths of adpressed fingers, foot-webbing formula, and relative lengths of toes, are the same for all the individuals of the type series).

The skin on the dorsum of most males has scattered, nonkeratinized tubercles. However, one calling male from Yasuní (QCAZ 11333, SVL = 47.26 mm), and two from the Iquitos region (the only two specimens known from Peru) have numerous keratinized tubercles on the dorsum. The dorsum of females is smooth. Nuptial excrescences were absent in all males examined, with the exception of those having keratinized tubercles on the dorsum. The number of vomerine teeth varies among individuals; for example QCAZ 11329 has 11 and 13 teeth, and QCAZ 10879 has 13 and 10 teeth on the right and left vomers, respectively.

Osteological comparisons.— Osteological characters were observed and drawn from cleared-and-stained specimens of *Osteocephalus yasuni* (QCAZ 11331) and *O. planiceps* (QCAZ 5140). Dorsal and ventral views of the skulls of *O. planiceps* and *O. yasuni* are shown in Fig. 5. Comparatively, the specimen of *Osteocephalus yasuni* has greater exostosis of the nasals, sphenethmoid, and frontoparietals than does *O. planiceps*. Dorsally, the sphenethmoid of *O. planiceps* is more exposed than that of *O. yasuni*. The frontoparietals of *O. planiceps* are narrowly separated anteromedially from the sphenethmoid; the frontoparietals and sphenethmoid of *O. yasuni* are joined anteromedially. The nasals of *O. yasuni* converge anteromedially whereas those of *O. planiceps* are separated narrowly. The vomers of *O. planiceps* are joined medially, whereas those of *O. yasuni* are separated. The dentigerous processes of *O. planiceps* are proportionately wider than those of *O. yasuni*. Additionally, the parasphenoid of *O. planiceps* has a long cultiform process that extends anterior to the level of the orbitonasal foramen. In contrast, the cultiform process of *O. yasuni* is broader and shorter that that

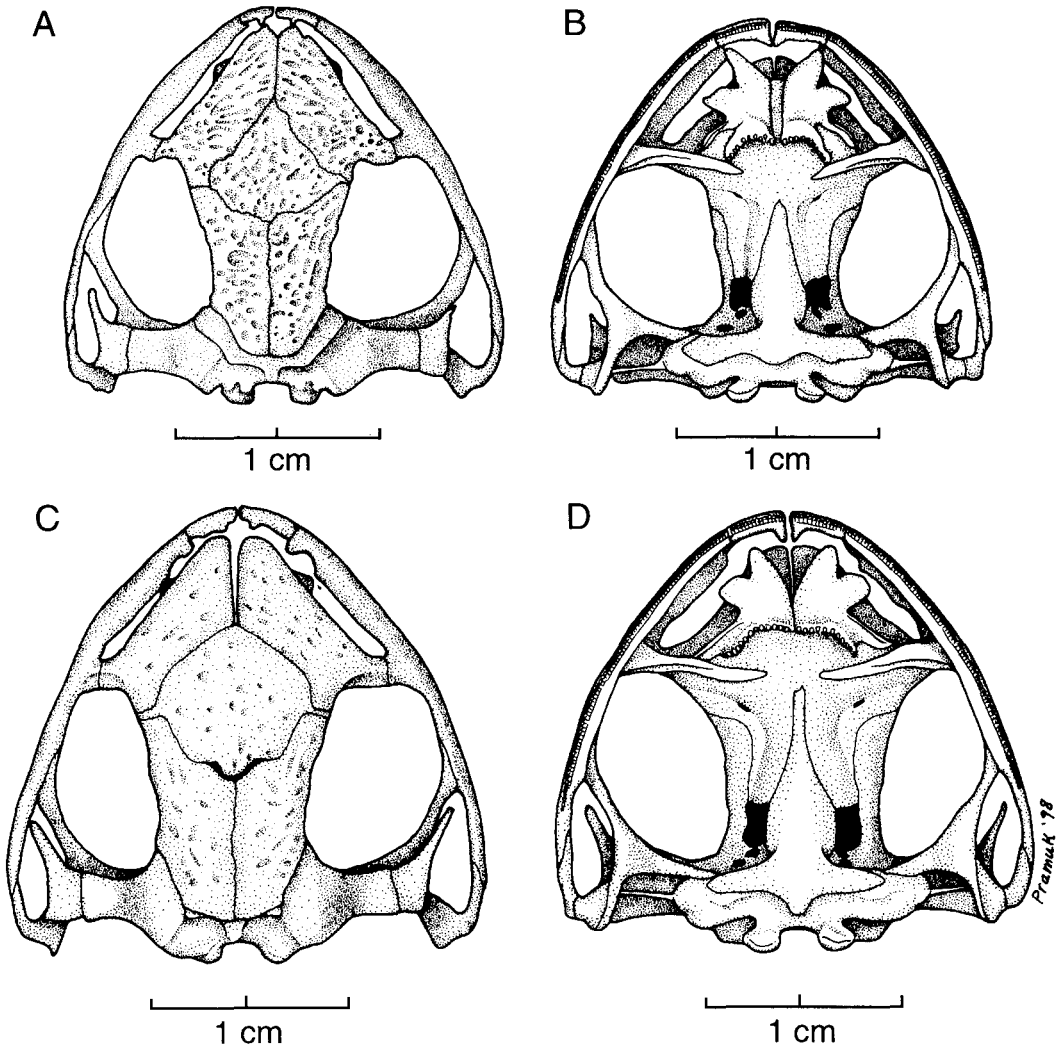

FIG. 5.—Skulls of *Osteocephalus yasuni* (QCAZ 11331, adult female, SVL = 61.9 mm; A = dorsal; B = ventral) and *O. planiceps* (QCAZ 5140, adult female, SVL = 69.9 mm; C = dorsal; D = ventral).

of *O. planiceps* and terminates at the level of the orbitonasal foramen. Many of the aforementioned differences in cranial morphology between *O. yasuni* and *O. planiceps* are the result of the greater overall ossification of the skull of *O. yasuni*.

Reproductive biology.—The eggs and tadpoles of *Osteocephalus yasuni* are unknown. Of 11 adult females examined, two collected in January and one in July had large pigmented eggs—(QCAZ 11321, average diameter of 30 randomly chosen eggs = 1.0 mm, 1720 eggs; QCAZ 8143, average diameter of 30 randomly chosen eggs = 0.9 mm, 2193 eggs; QCAZ 8144, average diameter of 30 randomly chosen eggs = 0.9 mm, 2778 eggs). One female collected in February and one in May had mixed pigmented and unpigmented eggs (QCAZ 5139, average diameter of 30 randomly chosen eggs = 0.48 mm; QCAZ 8909, average diameter of 30 randomly chosen eggs = 0.3 mm, 871 eggs). The remaining females had either undeveloped and unpigmented small eggs or empty ovi-

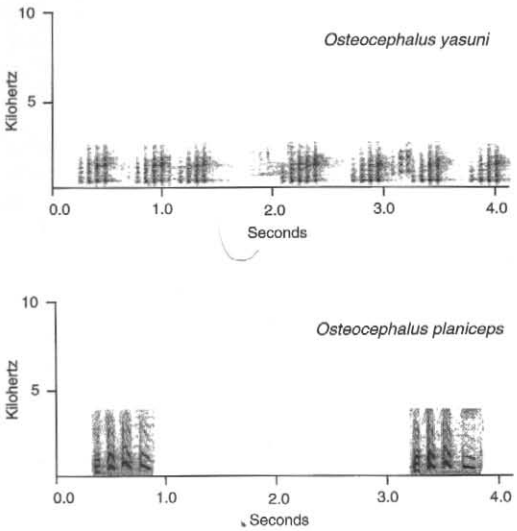

FIG. 6.—Spectrograms of the calls of *Osteocephalus yasuni* and *O. planiceps*. Sampling frequency 44.1 KHz.

ducts, and were collected in July and May. The external structure of the vocal sac of *O. yasuni* forms an everted pouch (width about two-thirds tympanum diameter), which dangles loosely beneath the supratympanic fold.

Reproductive behavior is based on Morley Reed's field notes (3 February 1995 and 11 May 1996). A chorus of several males was found on the night of 3 February 1995 in an area of flooded forest adjacent to the Río Tiputini (Provincia del Napo: Northern Production Facilities–Tivacuno Road, bridge over Río Tiputini). Another chorus was found at 2230 h on 11 May 1996 in flooded forest, along a small tributary of the Río Yasuní Drainage (Provincia del Napo: Pompeya–Iro Road 101 km from Pompeya). The creek was flooded to a depth of 50 cm. About six males were calling at distances of about 10–20 m from each other.

Call.—One male (QCAZ 11333, call QCAZ (S) 11333; SVL = 47.26 mm), part of a chorus, was recorded at 2230 h on 11 May 1996 while calling from the water surface next to a tangle of branches. The call is a repetitive sequence of four to five "chucks" (Fig. 6) and has the following parameters: (1) average duration of each call = 278.3 ms (range 250–332 ms, n = 7); (2) note repetition rate = 15.05 notes/s (range 13.84–16.0 notes/s); (3) average interval between notes = 45.1 ms (range 39–48 ms, n = 24); (4) dominant frequency of the call = 1.54 KHz; (5) call rate = 80 calls/min.

Osteocephalus yasuni and *O. planiceps* have different calls (Fig. 6). In *O. planiceps*, the call is a succession of 2–4 "quacks" with the following parameters: (1) average duration of each call = 429 ms (range 260–590 ms, n = 2); (2) note repetition rate = 7.06 notes/s (range 5.63–8.77 notes/s); (3) average interval between notes = 75.06 ms (range 66–100 ms, n = 6); (4) dominant frequency of the call = 640 KHz; (5) call rate = 18 calls/min. The call of *O. planiceps* was recorded by Lynn Haugen in Peru, Departamento Loreto, ACEER, on 21 May 1996 between 2300 and 2400 h. The male (SVL = 55 mm) was calling from a bromeliad. *Osteocephalus yasuni* and *O. planiceps* are sympatric and syntopic in Yasuní and Iquitos, and the differences in their vocalizations might help to segregate them reproductively. The scant data available also suggest that both species have different calling sites with *O. yasuni* calling from the surface of streams and *O. planiceps* calling from bromeliads (Morley Reed and Lynn Haugen field notes).

Distribution and ecology.—*Osteocephalus yasuni* has been found in the upper Amazon Basin in Ecuador within a latitudinal range encompassed by the Río Napo to the north and the Río Yasuní to the south. Also, it occurs at two localities near Iquitos, Departamento Loreto, in northern Peru (Fig. 7). All localities are in the Wet Tropical Forest vegetation formation (Holdridge, 1964) with an elevational range of 180–250 m (Appendix I).

The Yasuní Scientific Research Station of Universidad Católica del Ecuador is on the bank of the Río Tiputini at an elevation of 230 m, Provincia del Napo, in eastern Ecuador. The vegetation of the area is primarily varzea (flooded forest), seasonally flooded forest, and terra firme forest. Eighty-four species of anurans are known to occur in the area of the Yasuní Research

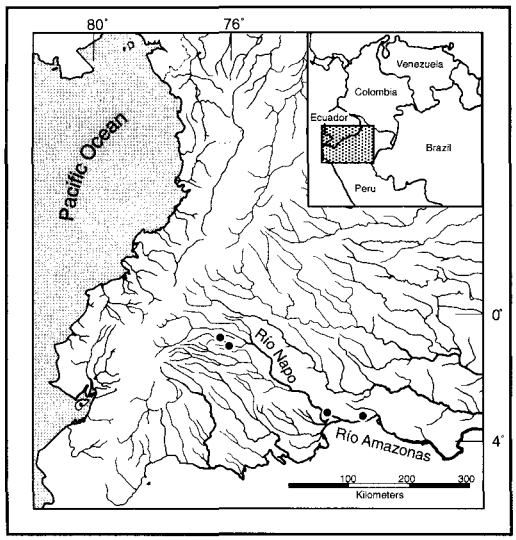

FIG. 7.—A generalized map showing the known distribution of *Osteocephalus yasuni*.

Station (Ron, 1998). *Osteocephalus planiceps, O. taurinus, O. buckleyi, O. cabrerai,* and an undescribed species of *Osteocephalus* that breeds in bromeliads are sympatric with *O. yasuni*. Although both *O. yasuni* and *O. planiceps* occur in terra firme forest, seasonally flooded forest, and in open areas, their distribution differs in each habitat. The composition of *O. yasuni* in terra firme, flooded forest, and open areas is 50%, 25%, and 25%, respectively (n = 12), whereas that of *O. planiceps* in the same habitat types is 60%, 8%, and 32%, respectively (n = 25).

The species is nocturnal. Of 12 specimens from the type locality, six were in primary terra firme forest, three in seasonally flooded forest 3–4 m from small streams, and three in open areas at the edge of a road. Ten were on vegetation at heights of 30–300 cm ($\bar{x}$ = 144 cm). One adult male was inactive on a tree trunk 160 cm above the ground by day, and a juvenile was inactive on vegetation at the edge of the Río Tiputini by day.

Stomach contents of 10 females and six males were examined. All stomachs contained one or no prey items; two had unidentifiable contents and eight were empty. Of the stomachs containing prey items, four contained one orthopteran each, one contained an arachnid (Araneae), and one a lepidopteran larva.

TABLE 3.—Character loading, percentage of explained variance for principal components (PC) I–III. Analysis applied over eight morphometric variables; abbreviations as in legend to Table 1 plus FEL = femur length.

	Size-free morphology		
Variable	PC I	PC II	PC III
SVL	<0.001	0.008	0.999
HL	−0.354	0.471	−0.005
HW	−0.301	0.441	0.012
ED	−0.183	0.491	−0.027
TD	−0.256	−0.396	−0.014
FEL	−0.496	−0.008	−0.005
TL	−0.477	−0.270	0.006
FL	−0.496	−0.008	0.005
Eigenvalue	3.05	1.19	1.00
%	38.1	14.9	12.5

Morphometric comparisons.—Measurements of morphological characters for five species of *Osteocephalus* are shown in Table 1. In the PCA of size-free morphology for five species of *Osteocephalus,* the first three principal components account for 65% of the variation (Table 3). The highest loadings for PC1 are for femur, tibia, and foot lengths. This axis describes a gradient of variation in hind-limb length. PC2 describes a gradient based on eye diameter and head size. Most of the variation in body proportions among *O. leprieurii, O. planiceps, O. taurinus, O.* sp. (Balta), and *O. yasuni* is related to limb length and skull shape. The most polarized morphometric character is in *O. leprieurii,* which has significantly shorter legs than do the other species. *Osteocephalus leprieurii* and *O. taurinus* are the most distinctive species morphometrically.

Axes PC I versus PC II and PC I versus PCIII are plotted in Fig. 8. According with the PCA, *O. yasuni* differs morphometrically from *O. taurinus, O. leprieurii,* and *O.* sp. (Balta). It has a high overlap with *O. planiceps.*

Canonical scores for Axes 1 and 2 from the DFA are plotted in Fig. 9. According to the DFA, *Osteocephalus yasuni* has low morphometric overlap with *O. leprieurii, O. taurinus,* and *O.* sp. (Balta) whereas it

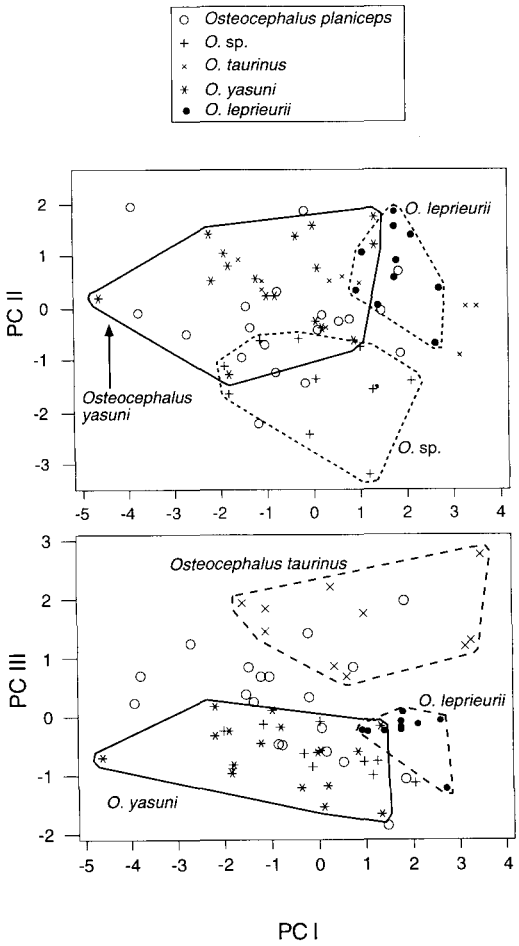

FIG. 8.—Scores from PCA on SVL and seven size-corrected morphological variables for 66 specimens of *Osteocephalus*.

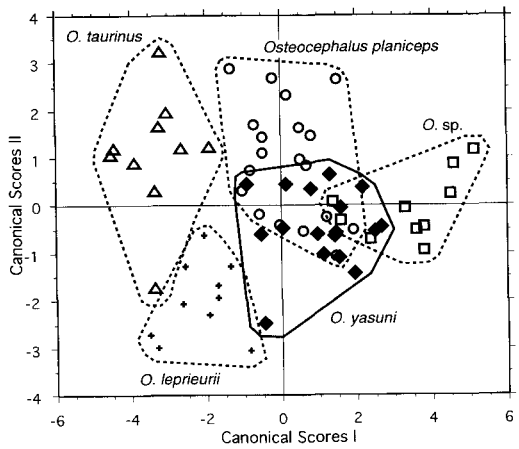

FIG. 9.—Axes 1 and 2 from canonical variates analysis based on SVL and seven size-corrected morphological variables for 66 specimens of *Osteocephalus*.

has high morphometric overlap with *O. planiceps*. These data indicate that the specimens belonging to *Osteocephalus* from Balta, Peru, form a distinctive group with respect to the other four species considered. This finding reinforces our suspicion that those specimens belong to a new and undescribed species. The coloration patterns of *Osteocephalus* sp. (Balta) and *O. yasuni* are quite similar. They share (1) dark interorbital line, (2) absence of dark blotches or spots on venter and flanks, (3) presence of narrow, pale labial stripe confluent with suborbital pale mark, and (4) similar dorsal and ventral pattern in preservative. However, the species are distinguished by differences in body shape and proportions (as defined in the multivariate analyses).

In the jackknifed classification procedure, 73% of the specimens were correctly classified under their own species. All individuals of *Osteocephalus leprieurii* were classified correctly. Of 10 *O. taurinus*, only one was misclassified as *O. leprieurii*. Of 10 *Osteocephalus* sp., two were misclassified as *O. yasuni* and one as *O. planiceps*. Of 17 *O. yasuni*, one was misclassified as *Osteocephalus* sp., four as *O. planiceps*, and one as *O. leprieurii*. Of 19 *O. planiceps*, seven were misclassified as *O. yasuni*, and one as *O. taurinus*.

DISCUSSION

Based on the presence of paired vocal sacs that inflate posterior to the jaw articulation, *Osteocephalus* has been considered to be related to the genera *Argenteohyla*, *Phrynohyas*, and *Trachycephalus* (Duellman, 1971; Trueb, 1970*a*,*b*; Trueb and Duellman, 1971). The generic placement of *O. yasuni* is based on the absence of diagnostic features that associate it with *Argenteohyla*, *Phrynohyas*, or *Trachycephalus*. *Osteocephalus yasuni* lacks ornamentation of the premaxillae (a synapomorphy for *Trachycephalus* (da Silva,

1998; Trueb, 1970*a*)), the thick and glandular dorsal skin of *Phrynohyas* (Duellman, 1971), and the well-developed metatarsal tubercles and vomerine teeth situated in transverse ridges of *Argenteohyla* (Trueb, 1970*b*). Furthermore, *Osteocephalus yasuni* shares the brown color pattern and sexually dimorphic skin texture of most species of *Osteocephalus* such as *O. taurinus* (the type species for the genus), *O. buckleyi, O. leprieurii, O. planiceps,* and the undescribed species from Balta.

Traditionally, the genus *Osteocephalus* has been diagnosed by two characters: (1) males with paired vocal sacs at the angle of the jaw and (2) roof of skull exostosed and/or co-ossified in most species (Goin, 1961; Trueb 1970*a*; Trueb and Duellman, 1971). The monophyly of the genus *Osteocephalus* (as currently defined) is not supported by any of those characters because they are shared with species belonging to other genera (e.g., *Phrynohyas, Argenteohyla, Trachycephalus)* and, therefore, presumably are synapomorphies of a clade larger than *Osteocephalus.* At present, there are no known synapomorphies to support the monophyly of the genus *Osteocephalus.*

A recent phylogenetic analysis of the subfamily Hylinae that includes four species of *Osteocephalus* demonstrates that the genus is paraphyletic and is part of a clade of casque-headed hylines (da Silva, 1998). Subsequent to the generic revision of Trueb and Duellman (1971), the number of recognized species within *Osteocephalus* has more than doubled, and there have been no detailed studies of the internal and external morphology of the group. Morphological examinations and phylogenetic analyses will be necessary to determine its taxonomic status and evolutionary relationships with other taxa of casque-headed frogs.

RESUMEN

Se describe una nueva especie de rana del género *Osteocephalus* del Parque Nacional Yasuní, Ecuador. Es una especie de tamaño mediano que se parece más a *O. planiceps* que a ninguna otra especie de ese género y de la cual se diferencia por ser más pequeña y carecer de puntos cafés en los flancos y líneas pálidas en los talones y alrededor de la cloaca. *Osteocephalus yasuni* se distingue de las otras especies de *Osteocephalus* por tener una coloración ventral amarilla.

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LITERATURE CITED

AYARZAGÜENA, J. 1992. Un nuevo género para las especies del "grupo *Osteocephalus rodriguezi*" (Anura: Hylidae). Memoria de la Sociedad de Ciencias Naturales La Salle 52:213–221.

AYARZAGÜENA, J., J. C. SEÑARIS, AND S. GORZULA. 1992. El grupo *Osteocephalus rodriguezi* de las tierras altas de la Guayana venezolana: descripción de cinco nuevas especies. Memoria de la Sociedad de Ciencias Naturales La Salle 52:113–142.

BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia. Ecaudata in the Collection of the British Museum, 2nd ed. British Museum, London, U.K.

COCHRAN, D. M., AND C. J. GOIN. 1970. Frogs of Colombia. United States National Museum Bulletin 281:1:655.

COPE, E. D. 1874. On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. Proceedings of the Academy of Natural Sciences of Philadelphia 25:120–137.

DA SILVA, H. R. 1998. Phylogenetic Relationships of the Family Hylidae with Emphasis on the Relationships within the Subfamily Hylinae (Amphibia: Anura). Ph.D. Dissertation, University of Kansas, Lawrence, Kansas, U.S.A.

DUELLMAN, W. E. 1970. Hylid frogs of Middle Amer-

ica. Monograph of the Museum of Natural History University of Kansas 1:1–753.

———. 1971. A taxonomic review of South American hylid frogs, genus *Phrynohyas*. Occasional Papers of the Museum of Natural History University of Kansas 4:1–21.

———. 1974. A reassessment of the taxonomic status of some Neotropical hylid frogs. Occasional Papers of the Museum of Natural History University of Kansas 27:1–27.

DUELLMAN, W. E., AND M. S. HOOGMOED. 1992. Some hylid frogs from the Guiana highlands, northeastern South America: new species, distributional records, and a generic reallocation. Occasional Papers of the Museum of Natural History University of Kansas 147:1–21.

DUELLMAN, W. E., AND J. R. MENDELSON III. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. University of Kansas Science Bulletin 55:329–376.

DUMÉRIL, A. M. C., AND G. BIBRON. 1841. Erpétologie générale ou historie naturelle compléte des reptiles, Vol. 8. Paris, France.

FROST, D. R. 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press and the Association of Systematics Collections, Lawrence, Kansas, U.S.A.

GAIGE, H. T. 1929. Three new tree-frogs from Panama and Bolivia. Occasional Papers of the Museum of Zoology University of Michigan 207:1–6.

GOIN, C. J. 1961. Synopsis of the genera of hylid frogs. Annals of the Carnegie Museum 36:5–18.

HAFFER, J. 1987. Biogeography of Neotropical birds. Pp. 104–150. *In* T. C. Whitemore and G. T. Prance (Eds.), Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford, U.K.

HENLE, K. 1981. *Hyla elkejungingerae*, ein neuer Hylidae aus dem peruanischen Regenwald (Amphibia: Salientia: Hylidae). Amphibia-Reptilia 2: 123–132.

HOLDRIDGE, L. R. 1964. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

JUNGFER, K., AND L. C. SCHIESARI. 1995. Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura, Hylidae), with oophagous tadpoles. Alytes 13:1–13.

LESCURE, J. 1982. Les amphibiens anoures de la foret Guyanaise (Region de Trois Sauts, Guayane Française). Memoires du Museum National d'Histoire Naturelle Serie A Zoologie 132:43–52.

LUTZ, B. 1973. Brazilian Species of *Hyla*. University of Texas Press, Austin, Texas, U.S.A.

MARTINS, M., AND A. J. CARDOSO. 1987. Novas espécies de hilídos do Estado do Acre (Amphibia: Anura). Revista Brasileira de Biologia 47:549–558.

MINITAB. 1995. Users Guide: Release 10.51 Xtra. Minitab Inc. State College, Pennsylvania, U.S.A.

PRANCE, G. T. 1979. Notes on the vegetation of the Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31:26–38.

RIVERO, J. A. 1968. A new species of *Hyla* (Amphibia, Salientia) from the Venezuela Guayana. Breviora 307:1–5.

RON, S. 1998. Biogeographic Area Relationships of Lowland Neotropical Rainforests Based on Cladistic Analysis of Anurans. M.A. Thesis, University of Kansas, Lawrence, Kansas, U.S.A.

SAVAGE, J. M., AND W. R. HEYER. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beiträge zur Neotropischen Fauna 2:111–131.

STEINDACHNER, F. 1862. Überzwei noch unbeschriebene Batrachier. Archives of Zoological Anatomy and Fisiology 2:77–82.

TAYLOR, W. R., AND G. C. VANDYKE. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.

TRUEB, L. 1970*a*. The evolutionary relationships of casque-headed tree frogs with co-ossified skulls (family Hylidae). University of Kansas Publications Museum of Natural History 18:547–716.

———. 1970*b*. The generic status of *Hyla siemersi* Mertens. Herpetologica 20:254–267.

TRUEB, L., AND W. E. DUELLMAN. 1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occasional Papers of the Museum of Natural History University of Kansas 1:1–47.

WERNER, F. 1901. Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 50: 593–614.

ZIMMERMANN, B. L., AND M. T. RODRIGUES. 1990. Frogs, snakes and lizards of the INPA-WWF reserves near Manaus, Brazil. Pp. 426–454. *In* A. Gentry (Ed.), Four Neotropical Rainforests. Yale University Press, New Haven, Conneticut, U.S.A.

ZIMMERMANN, B. L, AND D. SIMBERLOFF. 1996. An historical interpretation of habitat use by frogs in a Central Amazonian forest. Journal of Biogeography 23:27–46.

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APPENDIX I

Material Examined

Osteocephalus buckleyi.—PERU: Loreto: Teniente López, KU 221926; Loreto: Mishana, Río Nanay, KU 174916, KU 192021.

Osteocephalus cabrerai.—ECUADOR: Napo: Yasuní Scientific Research Station Universidad San Francisco de Quito, QCAZ 10224, 10226; Río Yasuní, QCAZ 7358, 7360.

Osteocephalus langsdorffii.—BRAZIL: Rio de Janeiro: Vila do Abrão, Ilha Grande, Angra dos Reis, MNRJ 15678–9.

Osteocephalus planiceps.—ECUADOR: Napo: Parque Nacional Yasuní, QCAZ 5186, 8320; Pompeya–Iro Road 38 km Southeast from Pompeya, QCAZ 5134, 5140 (cleared and stained), 8090, 8095, 8132, 8176, 8197, 8249, 8265; Pompeya–Iro Road 105 km Southeast from Pompeya, QCAZ 5463, 8230, 8231, 8217, 8317; Northern Production Facilities–Tivacuno Road, 230 m, QCAZ 8145.

Osteocephalus—sp. PERU: Loreto: Río Curania, Balta, 300 m, KU 196955, 196960–62, 196973, 196977–79, 196986, 196990.

Osteocephalus taurinus.—ECUADOR: Sucumbíos: Santa Cecilia, 340 m, KU 155478, 105230–32. Napo: Parque Nacional Yasuní, Universidad Católica Scientific Research Station, 230 m, QCAZ 11289–90.

Osteocephalus verruciger.—ECUADOR: Napo: S slope Coordillera del Due, 1150 m, KU 123181, 123184–6; 2 km SWW Rió Reventador, 1490 m, QCAZ 164411.

Osteocephalus yasuni.—ECUADOR: Napo: Parque Nacional Yasuní, Universidad Católica Scientific Research Station, 230 m, QCAZ 9809, 10879, 11329, QCAZ 11331 (clear-and-stained), QCAZ 11332, 11334, 11336–37, KU 224636–7; Pompeya–Iro Road 38 km Southeast from Pompeya, 230 m, QCAZ 5139, 7939–40, 8459, 11330; Pompeya–Iro Road 100 km SE Pompeya, QCAZ 11333; Northern Production Facilities–Tivacuno Road, QCAZ 8143–44. PERU: Loreto: junction of Río Yanamono and Río Amazonas, 180 m, KU 222339; Quebrada Grande, junction of Río Sucusari and Río Napo, ACEER, 210 m, KU 222340.