

The last one: A new species of *Osteocephalus* (Anura: Hylidae) from Colombia, with comments on the morphological and behavioral diversity within the genus

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Abstract

A new species of *Osteocephalus* (Anura: Hylidae) from Colombia, with comments on the morphological and behavioral diversity within the genus. A striking, undescribed species of *Osteocephalus* from the Amazonian slopes of the Andes in Departamento de Putumayo in southern Colombia is a member of the *Osteocephalus buckleyi* Group. Aside from minor morphological characters, the new species differs from all other members of the group by having a golden yellow iris with a median horizontal black stripe. The diversity in morphological and reproductive behavior reveals various features that are phylogenetically significant, but several species remain to be described.

Keywords: Comparative osteology, iris color, new species, oviposition sites, vocal sac structure.

Resumen

Una nueva especie de *Osteocephalus* (Anura: Hylidae) de Colombia, con comentarios sobre la diversidad morfológica y conductual dentro del género. Una llamativa especie no descrita de *Osteocephalus* de las laderas amazónicas de los Andes en Departamento de Putumayo en el sur de Colombia es miembro del Grupo *Osteocephalus buckleyi*. Además de los caracteres morfológicos menores, la nueva especie difiere de todos los demás miembros del grupo por tener un iris amarillo dorado con una franja negra horizontal mediana. La diversidad en morfología y comportamiento reproductivo revela varias características que son filogenéticamente significativas, pero quedan por describir varias especies.

Palabras clave: color del iris, sitios de oviposición, estructura del saco vocal, nuevas especies, osteología comparativa.

Resumo

Uma nova espécie de *Osteocephalus* (Anura: Hylidae) da Colômbia, com comentários sobre a diversidade morfológica e de comportamentos dentro do gênero. Uma espécie notável e não-descrita de *Osteocephalus* das encostas amazônicas dos Andes, no Departamento de Putumayo, no

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sul da Colômbia, é membro do grupo *Osteocephalus buckleyi*. Além de caracteres morfológicos menores, a nova espécie difere de todos os outros membros do grupo por apresentar íris amarela dourada com uma faixa preta horizontal mediana. A diversidade no comportamento morfológico e reprodutivo revela várias características filogeneticamente significativas, mas várias espécies ainda precisam ser descritas.

Palavras-chave: cor da íris, estrutura do saco vocal, locais de ovipostura, novas espécies, osteologia comparada.

Introduction

The Neotropics has the most diverse anuran fauna in the world (Duellman 1990). Two families are especially diverse—Hylidae currently with 721 species and Strabomantidae with 715 species (compiled from Frost 2019). New species continue to be discovered almost weekly, especially on the humid slopes of the Andes in northwestern South America, the haunt of the strabomantid genus *Pristimantis* with 526 species. These are followed by the Dendrobatoidea (321 species) and Centrolenidae (160 species). Although not as conspicuous as they were in southern Mexico and Central America before the disappearance of many species, hylids are represented by *Hyloscirtus* (38 species). Three other large genera of hylids occur in the Amazon and have species that range into the Andes; these are *Boana* (91 species), *Dendropsophus* (107 species) and *Osteocephalus* (24 species) (numbers of species from AmphibiaWeb 2019).

Throughout the latter half of the 20th century, *Osteocephalus* was nearly ignored. Trueb and Duellman's (1970) study on *O. verruciger* was an exception; this was followed by a review of the genus (Trueb and Duellman 1971), in which the authors placed many names in the synonymy of *O. buckleyi*. With the exception of the discovery of *O. subtilis* by Martins and Cardoso (1987), the genus drew little attention until the discovery of a canopy-dwelling species, *O. oophagus*, in which tadpoles in bromeliads feed on anuran eggs (Jungfer and Schiesari 1995). A series of publications based on molecular, as

well as morphological, data followed revealing the existence of numerous species in the upper Amazon Basin and Amazonian slopes of the Andes (Ron and Pramuk 1999, Jungfer and Lehr 2001, Jungfer and Hödl 2002, Jungfer *et al.* 2000, 2016, Ron *et al.* 2012). Extensive molecular analyses were provided by Jungfer and colleagues (2013, 2016) and by Ron *et al.* (2010). These analyses resulted in some well-supported clades within the genus. One clade contains stream-breeding species (*O. buckleyi*, *cabrerai*, *camufatus*, *cannatellai*, *carri*, *duellmani*, *festae*, *helenae*, *mimeticus*, *mutabor*, and *verruciger*) plus the one described herein. Another clade consists of species that breed in phytotelmas and have oophagus tadpoles (*O. castanelcola*, *deridens*, *fuscifacies*, *leoniae*, and *planiceps*). Most of these species deposit eggs in tree holes or bromeliads, but *O. castanelcola* deposits eggs in open Brazil-nut capsules (*Bertholletia excelsa*) on the ground (Moravec *et al.* 2009). With the exception of *O. oophagus*, which is nested within *O. taurinus*, two basally diverging lineages within *Osteocephalus* (*O. alboguttatus* and *O. taurinus*) deposit eggs in ponds (Jungfer *et al.* 2013).

Within the stream-breeding clade of *Osteocephalus*, the new species shares many characters with *O. verruciger*, which inhabits the Amazonian slopes of the Cordillera Oriental at elevations of 339–2100 m from Provincia Sucumbíos southward to the Cordillera Kampankis in northern Peru (Ron *et al.* 2012). Farther south in the Cordillera Oriental at elevations of 1342–2200 m a.s.l. another species, *Osteocephalus festae*, replaces *O. verruciger* at

elevations of 1342–2200 m a.s.l. in southern Ecuador southward to Departamento San Martín, Peru (Ron *et al.* 2010). Thus, there seem to be three allopatric species in a north–south range in the Andean cloud forests from southern Colombia to northern Peru.

An extensive trip (May 1974–August 1975) along the length of the Andes included important collections made in paramos and cloud forests in Colombia, Ecuador, and Peru. We (John Simmons, Linda Trueb, and Dana Duellman) searched for roads down from the paramos into cloud forest. Such roads commonly were steep and treacherous; wide places for parking the camper, especially at streams, were few in number. As we worked our way southward in Colombia, we went eastward from Pasto through the Valle de Sibundoy and over a pass at 2810 m and descended into cloud forest. John Simmons wrote in his journal: “we toiled on down the road on the 29th as far as Umbria only to find the jungle had been replaced by cattle pasture.” He went on to write that cattle grazed languidly among the rotting corpses of fallen trees and that we passed dirty gray shacks, weed-choked fences, and tired sad-eyed people trudging the roadsides with their heavy loads of yucca and platanos. Thus, in late September 1974, partially disturbed cloud forest existed between 1350 and 2810 m a.s.l.; most likely none exists there now.

At a small stream 10.3 km northwest of the small village, El Pepino, at an elevation of 1440 m a.s.l., we camped for three nights and collected many frogs of 17 species. This collection contained 19 specimens of a previously unknown *Osteocephalus*, which remains undescribed nearly five decades later. The first frogs that I ever described were *Eleutherodactylus* (then *Syrrophus*) *modestus* and *E. teretistes* (Duellman 1958). Going through Frost (2019), I was astonished to find that I am responsible for the names and descriptions of 240 species of frogs from the Neotropics; many of these were described with collaborators. Following is what is intended to be the last species that I will describe.

Materials and Methods

Frogs were euthanized in a weak solution of Chloretone, fixed in 5% formalin, and stored in 70% ethanol. Measurements and morphological characters follow Duellman (1970). The webbing formula was determined in the manner of Myers and Duellman (1982), and terminology of cranial elements follows Trueb (1973). Sex was determined by skin texture on the dorsum. Snout–vent length is abbreviated SVL, and interorbital distance as IOD. Abbreviations for institutions are: IAvH = Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia; ICN = Instituto de Ciencias Naturales, Museo de Historia Natural, Bogotá, Colombia; KU = Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA; QCAZ = Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Results

Osteocephalus omega sp. nov.

(Figures 1–8)

Holotype.—KU 169592, an adult male from 10.3 km (by road) northwest of El Pepino (1°4'56.8" N, 76°36'16.5" W), 1440 m, Departamento Putumayo, Colombia, one of a series collected by W. E. Duellman, L. Trueb, and J. E. Simmons on 27 September 1974.

Paratypes.—All collected at the type locality by Duellman, Trueb, and Simmons on 27–29 September 1974: KU 169589–91, 169593–95, and 169600–01, adult males; KU 169599, subadult male; KU 169587 and 169597–98, adult females; KU 169603, subadult female; KU 169596 and 169604–07, juveniles.

Referred specimen.—IAvH 3544, an adult male with same data as paratypes. This specimen was sent to the Colombian institution in 1974 and was not examined subsequently; consequently, it is not designated as a paratype.

Comparisons with other species.—Most species in the *Osteocephalus buckleyi* Group have areolate skin on the flanks, but it is smooth in *O. mutabor*. Among the species of *Osteocephalus* inhabiting the upper Amazon Basin and adjacent slopes of the Cordillera Oriental of the Andes, *O. omega* is most like *O. festae* and *O. verruciger*; males of those three species have keratinized spiny tubercles on the dorsal surfaces of the head, body, and limbs (fewer tubercles in *O. festae*), but lack prominent tubercles on the outer edge of the tarsus. The iris is brown in *O. festae* and *O. verruciger*, in contrast to yellow in *O. omega*.

Osteocephalus buckleyi, *O. cabrerai*, and *O. cannatellai* differ from *O. omega* by having a bronze iris with irregular black reticulations and prominent tubercles of the outer edge of the tarsus, whereas *O. cabrerai* also has a row of tubercles on the lower jaw and a dermal fringe on the outer edge of Finger IV. All of the foregoing species and presumably *O. camufatus*, *carri*, *duellmani*, and *mimeticus* are stream breeders. The remaining species in the upper Amazon Basin deposit their eggs in bromeliads (*O. deridens* and *O. oophagus*) or are known, or presumed, to deposit eggs as a surface film in ponds (*O. alboguttatus*, *heyeri*, *fuscifacies*, *mutabor*, *planiceps*, *taurinus*, *vilersi*, and *yasuni*).

Description of holotype.—This species is placed in the genus *Osteocephalus* because adult males have spines on the dorsum of the head and body. Adult male, 52.8 mm SVL; head as wide as body, slightly longer than wide; top of head flat; snout truncate in dorsal view, broadly rounded in profile; canthus rostralis rounded, not elevated, straight; nostrils dorsolaterally protuberant; internarial area depressed; loreal region moderately concave; lips thick, rounded, barely flared; supratympanic fold moderately heavy, obscuring upper edge of tympanum; tympanic annulus and membrane distinct, separated from eye by distance slightly less than diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately robust; ulnar tubercles minute; transverse dermal fold on wrist absent; fingers moderately long with discs equal to about two-thirds diameter of tympanum; subarticular tubercles large, subconical; supernumerary tubercles absent; palmar tubercle not evident; pollical tubercle elongate; prepollex enlarged, bearing large, spiny nuptial excrescence; webbing absent between Fingers I and II, basal between Fingers II and III and between III and IV (Figure 1A). Hind limbs moderately long and slender; heels of adpressed limbs overlap by about one-fourth length of shank; no transverse dermal fold on heel; inner tarsal fold absent; inner metatarsal tubercle elongately ovoid, not visible from above; outer metatarsal tubercle absent; toes moderately long, slender, bearing discs slightly smaller than those on fingers; subarticular tubercles moderately large, subconical; supernumerary tubercles indistinct; toes about three-fourths webbed (Figure 1B); webbing formula $I1-2III1-2IV2-1V$.

Skin on dorsal surfaces of head, body, shanks, and dorsal surfaces and outer edges of tarsi bedecked with conical tubercles with keratinized tips; skin on anterior half of flank areolate, on posterior half smooth; skin on throat, belly, and posteroventral surfaces of thighs granular; other ventral surfaces smooth; thoracic fold absent. Cloacal opening directed posteriorly near upper level of thighs; cloacal flap short. Lateral ends of dentigerous processes of vomers slightly curved posterolaterally and located slightly behind large, round choanae; total vomerine teeth 19. Tongue cordiform, shallowly notched posteriorly, barely free behind; vocal slits short, along medial posterior margins of jaws; vocal sacs paired, connected by transverse tube.

Coloration in preservative: All dorsal and lateral surfaces head, body, and limbs dull dark brown; dorsal surfaces of hands and feet dull tan; all ventral surfaces tan with some small dark brown flecks on throat and chest; pale labial stripe and suborbital spot absent (Figure 2).

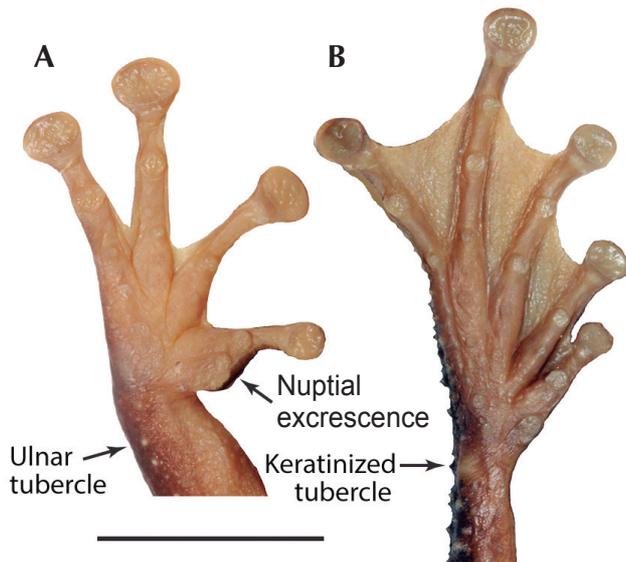


Figure 1. Palmar view of hand (A) and plantar view of foot (B) of the holotype of *Osteocephalus omega*, KU 169592. Line = 5 mm.

Coloration in life: Dorsal surfaces pale brown, slightly darker on head; tympanum brown; flanks, ventral surfaces, posterior margin of eyelid, and side of head from below eye to tympanum pale cream; webbing on foot reddish brown; posterior surfaces of thighs purplish brown; throat, chest, and anterior part of belly cream with black flecks; other ventral surfaces pinkish brown; bones white; iris golden yellow with median horizontal black to dark reddish brown stripe (Figure 3A).

Measurements (mm): SVL 52.8, tibia length 30.3, foot length 25.2, head width 18.1, head length 21.6, IOD 6.0, eyelid width 5.5, diameter of eye 6.2, tympanum diameter 4.7.

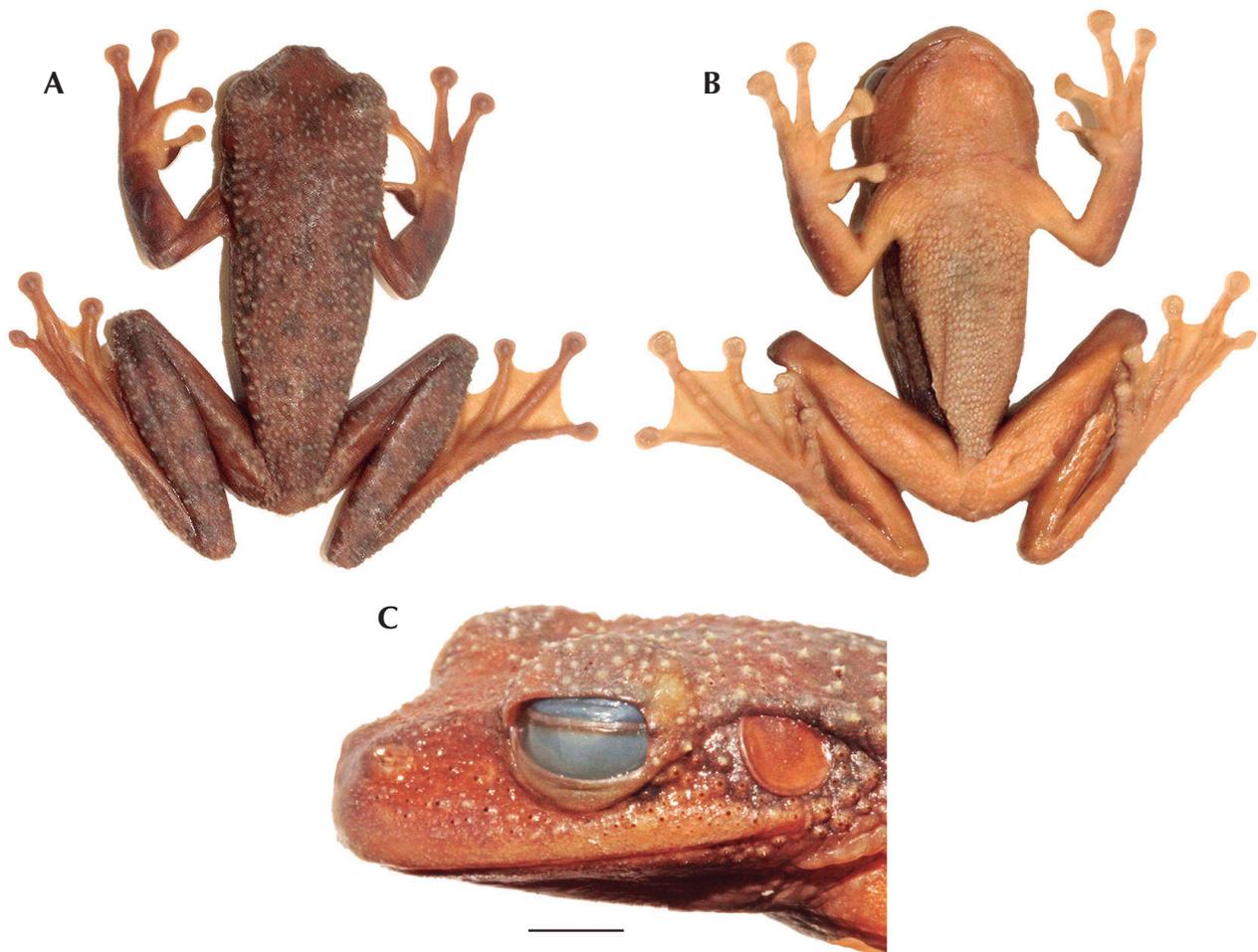


Figure 2. Dorsal, and ventral, and lateral views (head) of the holotype of *Osteocephalus omega*, KU 169592, having a SVL of 52.8 mm. Line = 5 mm and applies only to the lateral view of the head.

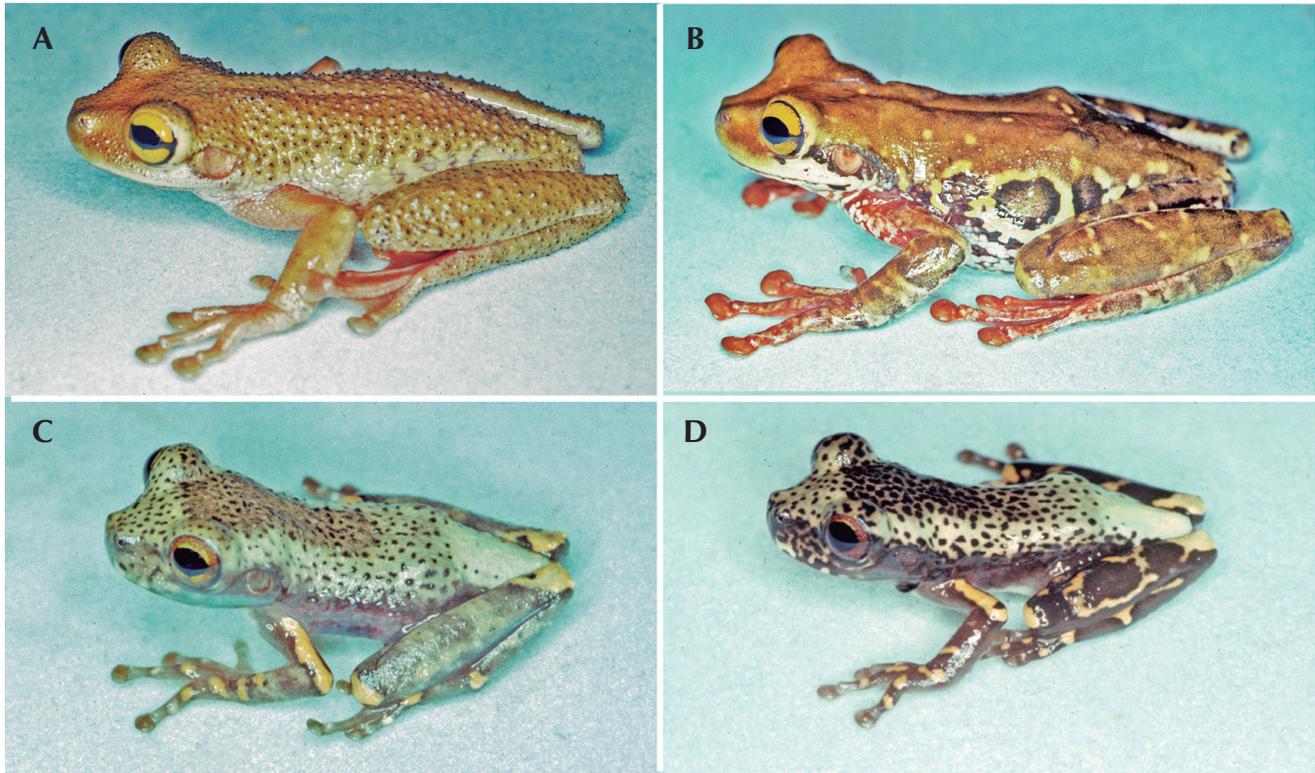


Figure 3. Living individuals of *Osteocephalus omega*. (A) Adult male holotype, KU 169592, SVL 52.8 mm; (B) Adult female, KU 169587; SVL 65.2 mm; (C) Juvenile, KU 169596, SVL 26.7 mm; (D) Metamorph, KU 169586, SVL 22.2 mm.

Variation.—Structurally, all adults are alike with the exception of minor differences in toe webbing. Coloration in preserved specimens reveals no significant differences in dorsal coloration, but the coloration of the flanks in females is evident in preserved specimens (Figure 4 A–C). Brown mottling is present on the throat and chest in females and males (Figure 4D, F). However, in some males the mottling is darker and covers the throat, chest, belly, and ventral surfaces of the thighs (Figure 4E).

As in other species of *Osteocephalus*, there is a dramatic ontogenetic change in coloration (Figure 3C, D). Color notes on a juvenile (KU 169586) are: Mid-dorsum of body brown. Snout and dorsolateral and posterior part of body cream with black flecks. Side of head, flanks, and dorsal surfaces of limbs dark brown with creamy white bars on lips and orange bars on limbs. Webbing and posterior thighs grayish tan. Throat and belly

white; other ventral surfaces bluish gray. Buccal cavity blue. Tongue pink. Iris carmen.

Variation in size in nine adult males is followed by that of three adult females (range, mean, one standard deviation in millimeters): SVL 28.4–53.8 ($= 51.5 \pm 2.71$), 62.7–69.4 (65.8 ± 2.98); tibia length 27.1–30.9 (28.6 ± 1.89), 35.5–39.7 (36.9 ± 1.45); foot length 22.7–25.3 (24.1 ± 1.12), 28.3–33.1 (30.5 ± 0.98); head width 16.5–18.4 (17.7 ± 1.79), 21.2–22.3 (21.9 ± 0.67); head length 17.9–22.3 (19.8 ± 2.46), 21.3–21.7 (21.5 ± 0.40); IOD 6.0–6.8 (6.5 ± 0.41), 9.09.6 (9.3 ± 0.61); eyelid width 5.0–6.5 (5.6 ± 0.89), 6.2–7.2 (6.8 ± 0.96); eye diameter 6.0–9.0 (7.17 ± 1.04), 6.6–7.0 (6.8 ± 0.84); tympanum diameter 4.5–6.1 (5.24 ± 7.21), 5.7–6.2 (6.01 ± 0.54). A subadult male has a SVL of 30.4 mm, and a subadult female, 41.3 mm. Five juveniles have SVLs of 26.7–36.7 mm ($29.5 \text{ mm} \pm 3.21$).

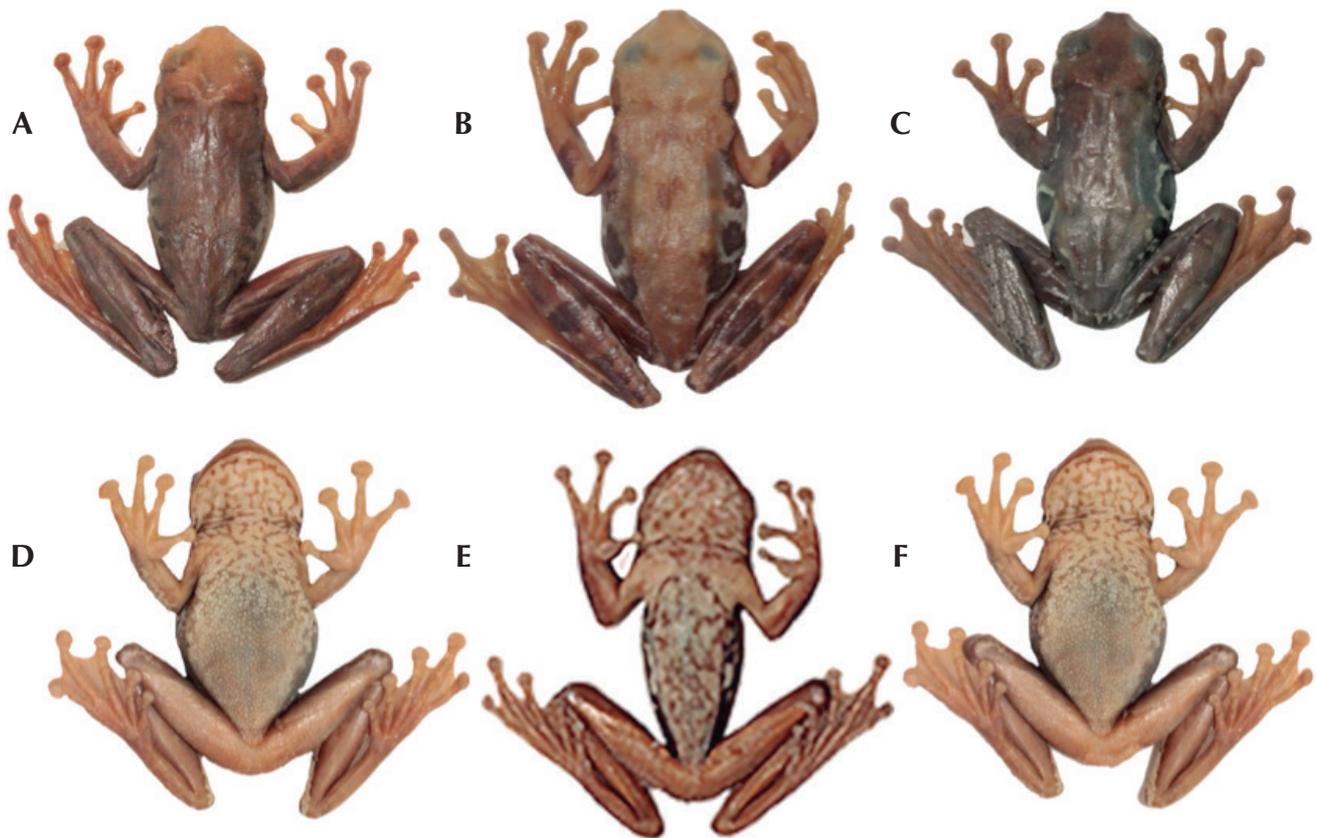


Figure 4. Variation in dorsal and ventral color patterns in preserved adult *Osteocephalus omega*. (A) KU 169598, female, SVL 69.4 mm; (B) KU 169597, female, 62.7 mm; (C) KU 169587, female, SVL 65.1 mm; (D) KU 169587, female, SVL 65.2 mm; (E) KU 169595, male, SVL 49.5 mm; (F) KU 169591, male, SVL 53.0 mm. Not pictured to scale.

Etymology.—The specific name is the last letter in the Greek alphabet and relates to this being intended to be my last description of a new species of frog.

Osteology.—Relatively little is known about the osteological diversity of *Osteocephalus*. The cranial structure of a few species has been described (viz., *O. taurinus*, Trueb 1970; *O. mutabor*, Trueb and Duellman 1971; *O. yasuni* and *O. planiceps*, Ron and Pramuk 1999) and there is some information on the axial skeletons of *O. buckleyi* and *O. mutabor* (as *O. leprieurii*) (Trueb and Duellman 1971). Examination of micro-CT scans of specimens of *O. verruciger* and *O. omega* (Figure 6) enable descriptions of these two taxa in reasonable detail and

comparisons of them with what is known of their congeners from the literature.

Cranial Osteology: All six taxa have broad, flat crania that are well ossified. The jaws are long and terminate in the region of the occipital condyles—some slightly anterior (*O. yasuni*, *planiceps*, *mutabor*), and some posterior to (*O. verruciger*), or at the level of, the condyles (*O. taurinus*, *omega*). The shape of the cranial rostrum varies. It is long and slightly acuminate (*O. yasuni*, *planiceps*) or broadly rounded (*O. taurinus*, *verruciger*, *mutabor*, *omega*). The skull table is hyperossified in each of the species. This is most marked in *O. taurinus*, in which the cranial skin is co-ossified with the underlying cranial elements. The surface of the skull table is

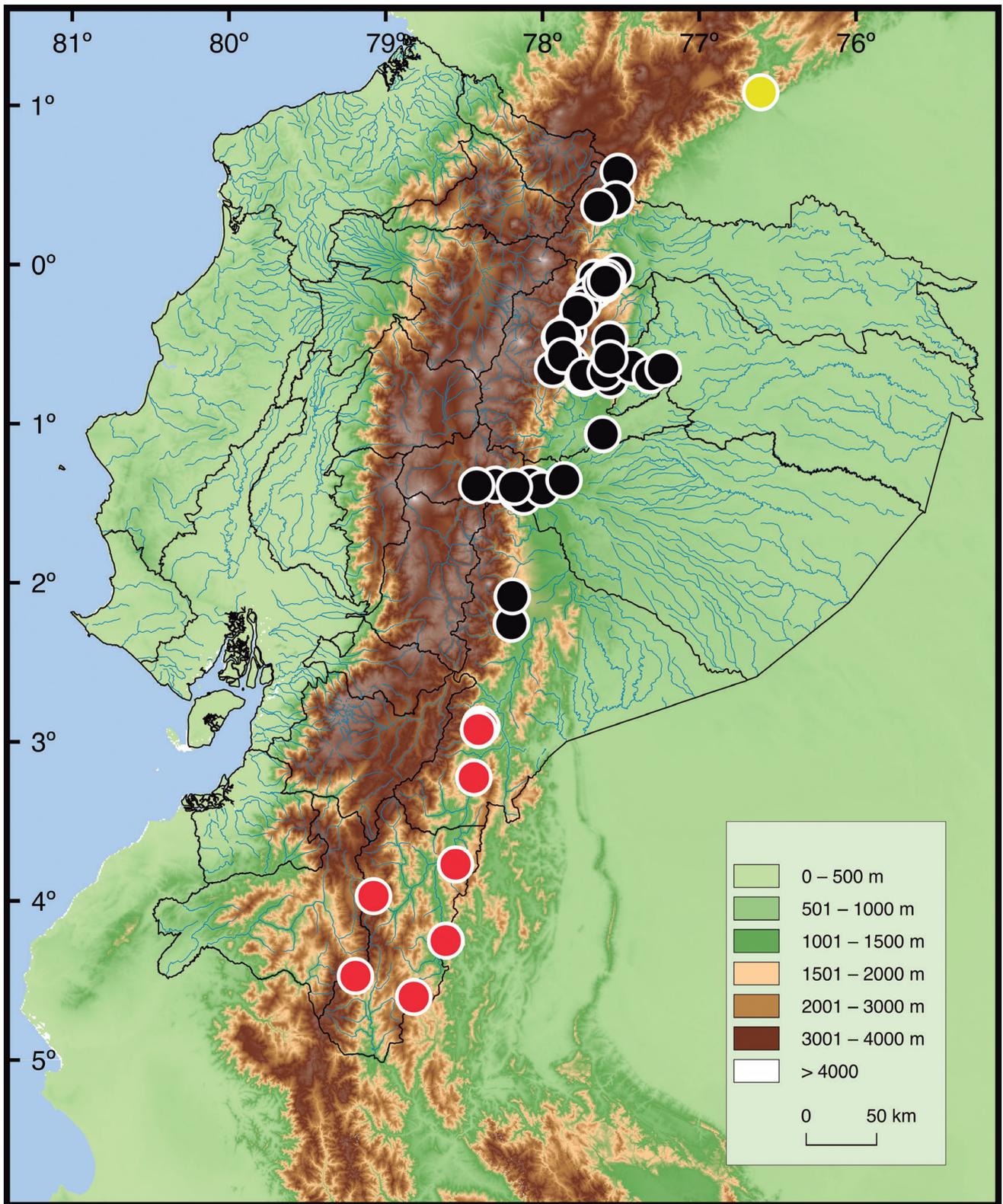


Figure 5. Localities of known occurrence of three species of *Osteocephalus* in Colombia and Ecuador. Red = *O. festae*; yellow = *O. omega*; black = *O. verruciger*.

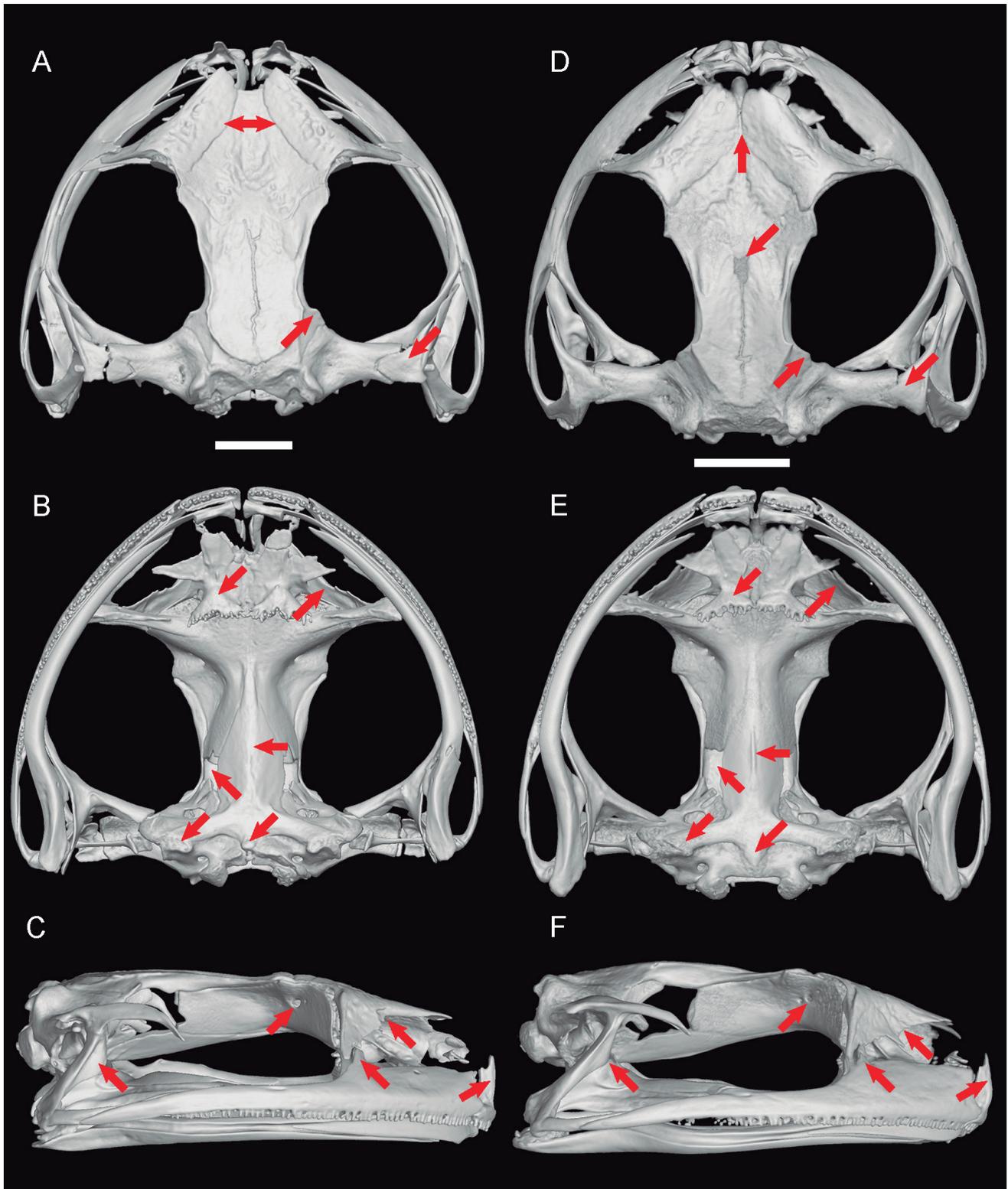


Figure 6. Comparative cranial osteology of *Osteocephalus omega* (A–C), KU 169598, female, 65.2 mm SVL, and *O. verruciger* (D–F), KU 164416, female, 63.2 mm SVL. Red arrows point to features noted in the text. White bars = 5 mm.

heavily exostosed in a pattern of pits and ridges; the frontoparietals have a complete medial articulation and a well-developed supraorbital flange. The width of the frontoparietals at the level of the epiotic eminence is the same as that at the anterior part of the orbit. Because a prominent supraorbital flange is absent in the other taxa, the width of the frontoparietals posteriorly is significantly less than that at the anterior part of the orbit. The skull table is sculptured in all except *O. mutabor*; the pattern in *O. yasuni* is an irregular pit-and-ridge, whereas that of *O. planiceps* consists of irregularly distributed pits. In *O. verruciger* and *O. omega*, the dermal sculpturing is markedly coarser and poorly defined in contrast to that of the other taxa. In each of these species, the sphenethmoid is broadly exposed dorsally and exostosed like the rest of the skull table. The frontoparietals completely articulate with one another medially (*O. taurinus*, *yasuni*), are narrowly separated (*O. omega*, *verruciger*), or more broadly separated in *O. mutabor*. If the anteromedial margins of the frontoparietals diverge from one another posterior to the sphenethmoid, then a portion of the frontoparietal fenestra is exposed (*O. verruciger*, *mutabor*). The nasals are extraordinarily large in *Osteocephalus*. They cover the entire olfactory capsule and articulate with one another medially (*O. yasuni*, *planiceps*, *mutabor*, *taurinus*), are narrowly separated medially (*O. verruciger*), or broadly separated (*O. omega*). The nasals usually cover the dorsolateral nasal capsule except in *O. omega*, in which most of the lateral part of the olfactory capsule is exposed.

In ventral aspect, it is obvious that each of these *Osteocephalus* has an exceptionally well ossified neurocranium. The posterior border of the bony sphenethmoid lies adjacent to (*O. verruciger*, *yasuni*, *planiceps*, *taurinus*), or forms the anterior margin of the optic fenestra (*O. omega*). The lateral walls of the neurocranium are approximately parallel (*O. taurinus*, *verruciger*, *yasuni*) or curved, imparting an hourglass shape (*O. planiceps*, *mutabor*, *omega*).

The neopalatines are broadly separated from one another medially; the medial tips of the bones lie approximately in line with the orbitonasal foramina posteriorly except in *O. planiceps*, in which the tips of the bones are more narrowly separated and terminate medial to the foramina. The vomers and dentigerous processes are large; each right process tends to be configured in a Γ shape and lies posteromedial to the internal choana. The lateral alae of the parasphenoid are posterolaterally oriented (*O. verruciger*, *omega*, *taurinus*, *mutabor*), but perpendicular to the long axis in *O. yasuni* and *O. planiceps*. The posteromedial process of the parasphenoid is acuminate (*O. verruciger*, *taurinus*, *mutabor*), with ventrally projecting knob (*O. omega*), or subacuminate (*O. yasuni*, *planiceps*). The cultriform process of the parasphenoid is lanceolate. The terminus of the process is long and narrow (*O. planiceps*, *verruciger*) or short and narrow (*O. omega*, *mutabor*, *yasuni*) with curved margins in the area of the optic fenestra; the sides of the process tend to be straight and converge to a point in *O. taurinus*. The venter of the cultriform process is unornamented (*O. yasuni*, *planiceps*, *mutabor*) and bears a well-defined longitudinal ridge (*O. verruciger*) or a knobby thickening (*omega*, *taurinus*).

Several obvious differences in the skulls of *Osteocephalus verruciger* and *O. omega* are evident in lateral view. The vault of the braincase is convex in *O. verruciger*, whereas it is flat in *O. omega*. The frontoparietal bears a narrow, but distinct lateral ridge in *O. omega*, whereas the margin of the bone is smooth in *O. verruciger*. Owing to the difference in the lengths of the maxillae, the angle formed by the ventral ramus of the squamosal and the maxilla is less acute in *O. omega* than in *O. verruciger*. In addition, there is an indistinct flange extending along the upper half of the shaft of the ramus in *verruciger*, whereas the flange is conspicuous in *O. omega*, being broader and larger and extending over three-quarters of the shaft. The head of the squamosal (i.e., the otic and zygomatic rami) is dorsoventrally flattened in *O. verruciger*, in

contrast to that of *O. omega*, which has a broad, lateral exposure. The differential dorsolateral development of the nasal (extensive in *O. verruciger* versus minimal in *O. omega*) is evident, along with the configurations of the pars facialis of the maxillae. In *O. verruciger*, the preorbital process is indistinct, whereas in *O. omega* it is obvious; in addition, the pars facialis of *O. omega* has a greater medial deflection than in *O. verruciger*. The alary process of the premaxilla has a flat leading edge in *O. omega*, but in *O. verruciger*, its profile is anteriorly convex; hence, one would expect the snout to be curved in *O. verruciger* versus truncate in lateral profile in *O. omega*.

Axial Osteology: Much less is known about postcranial osteology than cranial in *Osteocephalus*. Trueb and Duellman (1971) provided ventral views of the vertebral columns of *O. mutabor* and *O. buckleyi* along with brief comparisons with *O. taurinus* and *O. verruciger*. Likewise, there are cursory descriptions of the pectoral and pelvic girdles.

The axial column of *Osteocephalus* consists of eight procoelous presacral vertebrae, the sacrum, and a bicondylar urostyle. Although similar, the presacral vertebrae of *O. verruciger* and *O. omega* can be distinguished from one another. The transverse processes of Presacral II are exceedingly short (~25% length of transverse processes of Presacral III) and scoop-shaped in *O. omega*, whereas in *O. verruciger*, the processes are flat and more than half the length of those of Presacral III. *Osteocephalus mutabor* resembles *O. verruciger*. All three taxa are distinguished from *O. buckleyi*, which has exceedingly short transverse processes on Presacral Vertebrae V–VIII.

Remarks.—Sixteen other species of frogs were collected at the type locality. Three of these (*Dendropsophus bifurcus*, *Pristimantis lanthanites*, *Scinax ruber*) are common species in the Amazon Basin but ascend the Andean slopes wherever proper habitat exists; this usually is the result of human disturbance. *Pristimantis*

w-nigrum primarily inhabits elevations up to 3300 m in the Andes of Colombia, Ecuador, and Peru, but it descends on both Amazonian and Pacific slopes to elevations as low as 800 m. The other 12 species mostly are restricted to cloud forests at elevations of 740–2350 m; these include three centrolenids (*Centrolene bacata*, *Nymphargus megacheirus*, *N. siren*), two hemiphractids (*Gastrotheca andaquiensis*, *Hemiphractus bubalus*), two hylids (*Hyloscirtus phyllognathus*, *H. torrenticola*), one leptodactylid (*Leptodactylus wagneri*), and four strabomantids (*Niceforonia dolops*, *Pristimantis incomptus*, *P. petersi*, *Strabomantis cornutus*). These cloud forest inhabitants also are known from cloud forests at several localities in adjacent provincias, Sucumbíos and Napo, Ecuador.

Discussion

Subsequent to Trueb and Duellman's (1971) review of the genus, relatively little information was published on *Osteocephalus* until Jungfer and Schiesari (1995) described *Osteocephalus oophagus*, the first member of the genus known to breed in phytotelmata and to have the tadpoles nourished by subsequent egg depositions. Breeding in phytotelmata and production of nutrient eggs have been discovered in numerous canopy-dwelling hylids—*Anotheca* (Jungfer 1996), *Ecnomiohyla* and *Nyctimantis* (Jungfer pers. com.), the *Osteocephalus planiceps* Group (Jungfer *et al.* 2013), *Aparasphenodon arapapa* (Lourenço-de-Moraes *et al.* 2013), *Osteopilus brunneus* (Thompson 1996), and some species of *Trachycephalus* (Schliesari *et al.* 2003).

Osteocephalus is unique among hylid genera in exhibiting variation in vocal sac structure, iris color, and reproductive behavior within the genus. The most inclusive phylogenetic analysis of genetic data was published by Jungfer *et al.* (2013). In their tree (their Figure 4), 10 *O. verruciger* from Ecuador form a clade that is sister to a clade containing two *O. "verruciger"* and one *O. carri* from southeastern Colombia, one of the topologies available (Figure 7). In

most phylogenetic analyses based on molecular data (e.g., Ron et al. 2012, Jungfer *et al.* 2016), a clade containing *O. taurinus* with paired lateral vocal sacs and *O. oophagus* with a single subgular vocal sac is sister to all other *Osteocephalus*.

Three types of vocal sacs are present in *Osteocephalus* (Figure 8). A single median subgular vocal sac is present in members of the basal *O. alboguttatus* Group, males of which lack spiny texture on the dorsum, and in the *O. planiceps* Group, which contains five species that breed in phytotelmata. In these frogs, air passes from the lungs through paired vocal slits in the floor of the mouth directly into the subgular vocal sac formed by the thin *m. intermandibularis*. The paired confluent subgular vocal sacs characteristic of the *O. buckleyi* Group are formed by a transverse subgular tube composed of a somewhat thickened *m. intermandibularis*, which, lateral to the margins of the lower jaw, expands into a pair of inflatable vocal sacs. Air passes from the lungs through paired vocal slits in the floor of the mouth into the transverse subgular tube and then into the lateral vocal sacs (pers. obs.). Jungfer *et al.* (2013) denoted this type of vocal sac as being paired, situated laterally, with a subgular expansion. This term implies that the air flows from the vocal sacs into the subgular tube when the reverse is true. The paired lateral vocal sacs in *O. taurinus* are like those in *Trachycephalus typhonius* described by Duellman (1956) as *Phrynohyas spilomma*. In *O. taurinus*, vocal sacs are formed by posterolateral extensions of the *m. intermandibularis*. This muscle forms a tube along the inner margin of the jaw and extends posteriorly behind the angle of the jaw, where it expands into a pocket with many folds, the vocal sac.

The type of vocal sac is correlated with breeding sites. The paired lateral vocal sacs are present in species that call while floating on the surface of lentic water. The inflated vocal sacs about triple the width of the head, thereby necessitating a rather large site in which to vocalize. The large paired lateral vocal sacs are neither suitable for confined spaces such as tree holes or bromeliads (Figure 9)

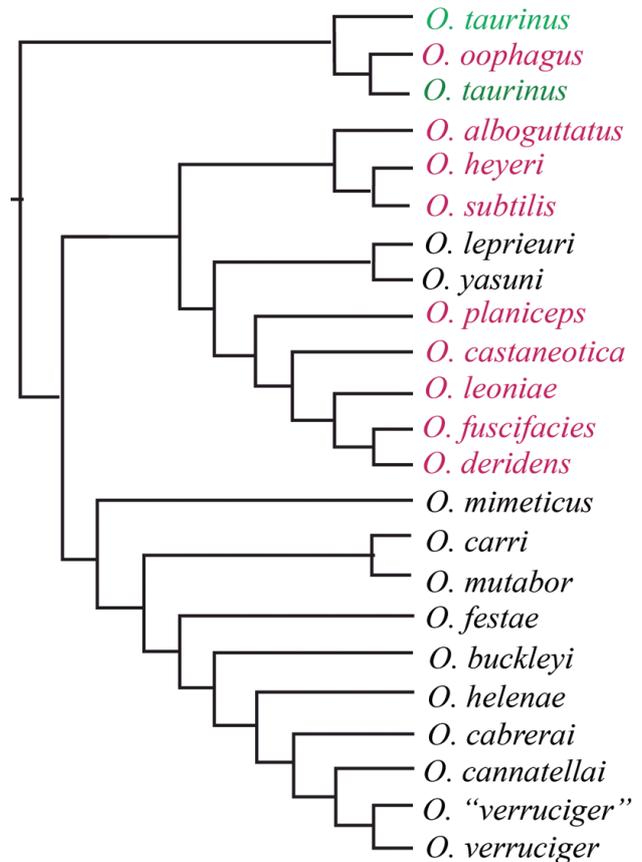


Figure 7. Simplified topology of phylogenetic tree inferred from parsimony analysis of molecular data by Jungfer *et al.* (2013). This shows that *Osteocephalus taurinus* is paraphyletic with respect to *O. oophagus*: (A) populations in the eastern Guiana Shield; (B) populations in the upper Amazon Basin. Their clade of samples of two *O. "verruciger"* from Colombia represents an undescribed species. Colors denote vocal sac structure: red = single, subgular; black = paired confluent subgular; green = paired, lateral.

nor for lotic water in which currents would displace calling frogs. Comparatively small lateral vocal sacs can be viewed as an adaptation to lotic water, where males call from secluded sites or while on rocks in streams. A single median subgular vocal sac is the most useful in confined spaces (Jungfer *et al.* 2013).

A variety of colors and patterns are displayed by the irises of *Osteocephalus*. In addition to the 16 species shown in Figure 10, the irises *O. castaneicola* and *O. oophagus* resemble those of

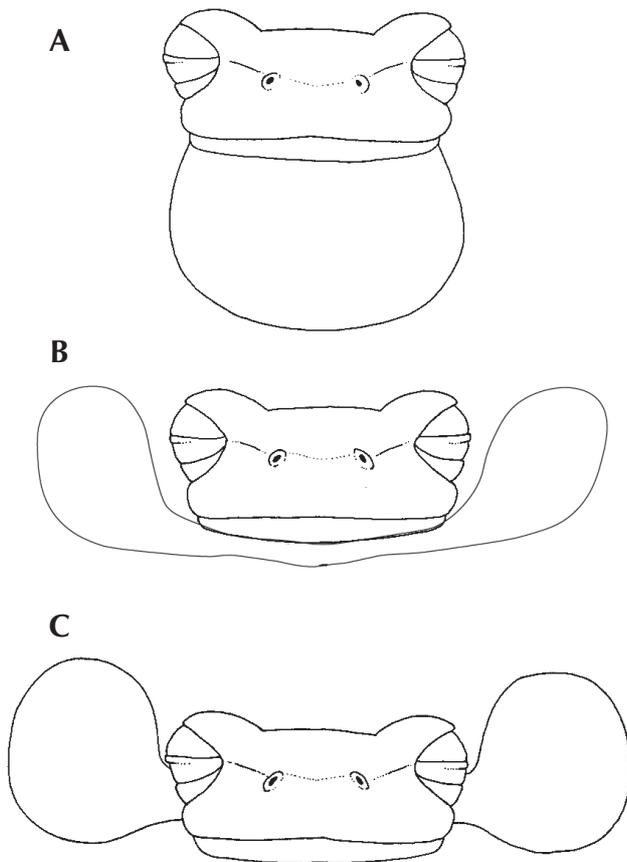


Figure 8. Vocal sac structure in *Osteocephalus*. (A) Single, subgular; (B) Paired, confluent subgular; (C) Paired, lateral.

O. taurinus by being cream with radiating black lines (Moravec *et al.* 2009, and Jungfer and Schiesari 1995, respectively). The irises are pale yellow to dull cream or creamy tan with black reticulations in *O. leoniae* (Jungfer and Lehr 2001), *O. helenae* (Kok 2019), and *O. leprieurii* (CalPhotos 2019), respectively. Characteristically, a median horizontal dark brown or black stripe is present (not evident in *O. cannatellai*, *O. mimeticus*, and *O. subtilis*). Radiating black lines are restricted to species in the lowlands (e.g., *O. castaneicola*, *oophagus* and *taurinus*), whereas uniform yellow, cream, or brown irises occur in stream-breeding species in the Andes (e.g., *O. carri*, *festae*, *omega*, and *verruciger*). Inasmuch as anurans have excellent night vision and color

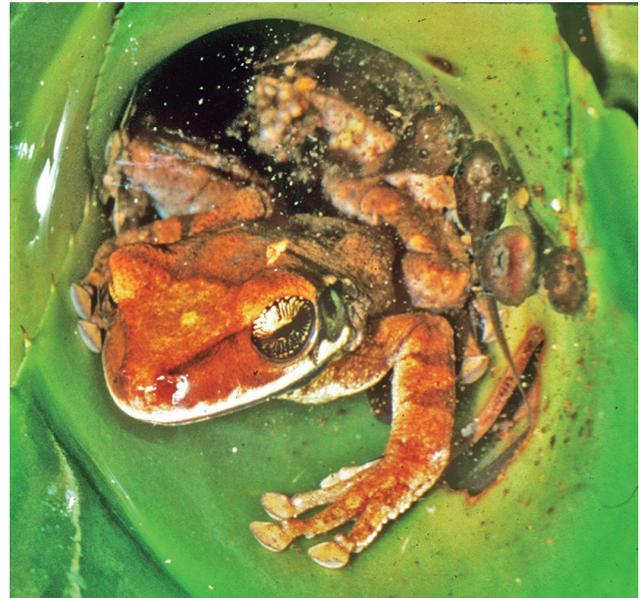


Figure 9. Male and tadpoles of *Osteocephalus deridens* in bromeliad at the Amazon Conservatory for Tropical Studies, Departamento Loreto, Peru. Photo courtesy of Julian C. Lee.

recognition (Ewart and Schwippert 2006), the coloration of the iris may be an important factor in species recognition.

The center of *Osteocephalus* diversity is in Amazonian Ecuador, where at the Estación Biodiversidad Tiputini (elevation 190–270 m a.s.l.), Provincia Orellana, eight species of *Osteocephalus* have been recorded. These species use several breeding sites. *Osteocephalus taurinus* and *O. yasuni* breed in lentic ponds; *O. buckleyi*, *cabrerai*, and *mutabor* are stream breeders, whereas *O. deridens*, *fuscifacies*, and *planiceps* breed in phytotelmata.

The stream-breeding *Osteocephalus* inhabiting the eastern face of the Andes in Colombia are poorly known. Frogs of apparently two species (Figure 11 A and C) have been tentatively identified as *O. carri*. Frogs of two other species have been referred to *O. verruciger* (Figure 11 D and E); these frogs have cream or orange irises with median horizontal brown streaks, thereby resembling *O. omega* (compare with Figure 3 A and B), but differing from that species in the color pattern of the flanks. Also, they differ in

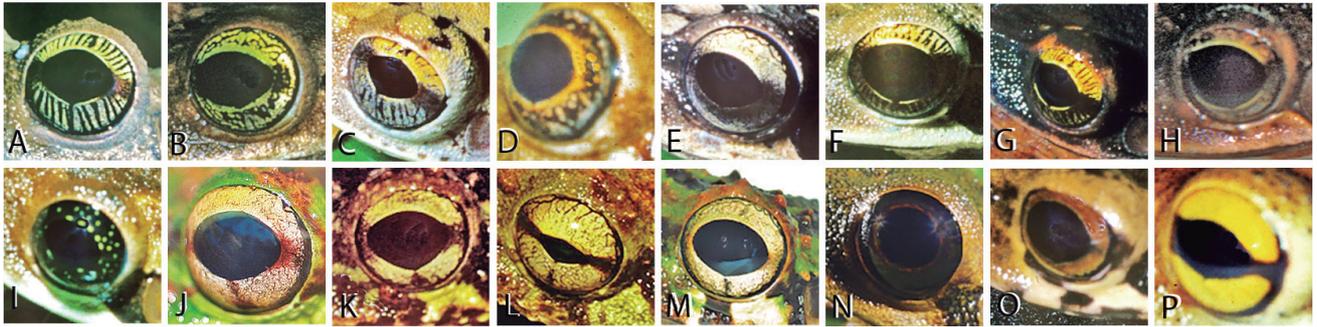


Figure 10. Coloration of irises of 16 species of *Osteocephalus*. (A) *O. taurinus*, KU 220227; (B) *O. alboguttatus*, KU 111729; (C) *O. heyeri*, KU 220285; (D) *O. subtilis*, no number, A. Cardoso; (E) *O. yasuni*, KU 220894; (F) *O. planiceps*, KU 221936; (G) *O. fuscifacies*, KU 221943; (H) *O. mutabor*, KU 125962; (I) *O. mimeticus*, KU 212190; (J) *O. camufatus*, (Jungfer *et al.* 2016); (K) *O. buckleyi*, KU 123171; (L) *O. cabrerai*, (Jungfer *et al.* 2016); (M) *O. cannatellai* (Ron *et al.* 2012); (N) *O. festae* (Ron *et al.* 2010); (O) *O. verruciger*, KU 143545; (P) *O. omega*, KU 169587. Unless noted otherwise, photographs are by the author.

the coloration of the flanks and iris from *O. verruciger* from Ecuador (Figure 11, B and E). Obviously, the systematics of these Colombian populations are in dire need of thorough studies.

The status of *Osteocephalus oophagus* has been questioned by Motta *et al.* (2018), who noted low interspecific divergences in the 16S rRNA gene between *O. oophagus* and *O. taurinus*. Based on the result of only 1.2–3.0% genetic divergence they suggested that *O. oophagus* should be synonymized with *O. taurinus*. Their suggestion does not take into account basic morphological and behavioral differences—e.g., vocal sac structure, size, and oviposition sites (Figure 7).

In 2011 Ron included *Osteocephalus duellmani* in *Anfibios del Ecuador* (an online reference) based on Jungfer’s (2011) species description. Three specimens (QCAZ 65004–06 from Cerro Plateado, Provincia Zamora Chinchipe, were initially listed as “*O. duellmani*” but subsequently were identified as *O. festae* (Peracca), of which *O. duellmani* may be a junior synonym (Santiago Ron pers. com.). It is not included in the 2019 version of *Anfibios del Ecuador* (Ron *et al.* 2019).

Last, in recent years there have been two vernacular names used for members of the genus

Osteocephalus. Jungfer *et al.* (2013) coined the vernacular name Spiny-backed Treefrogs. That name is a valid descriptor of all members of the genus, except the basal *O. alboguttatus* Group, males of which lack spines on the dorsum. Santiago Ron has persisted in using the term casque-headed, which applies only to one species of *Osteocephalus* (*O. taurinus*), whereas it applies to several other genera of hyliid frogs—*Aparaspenodon*, *Corythomantis*, *Diaglena*, *Trachycephalus*, and *Tripurion* (Trueb 1970). I recommend the use of Spiny-backed Treefrog for *Osteocephalus*.

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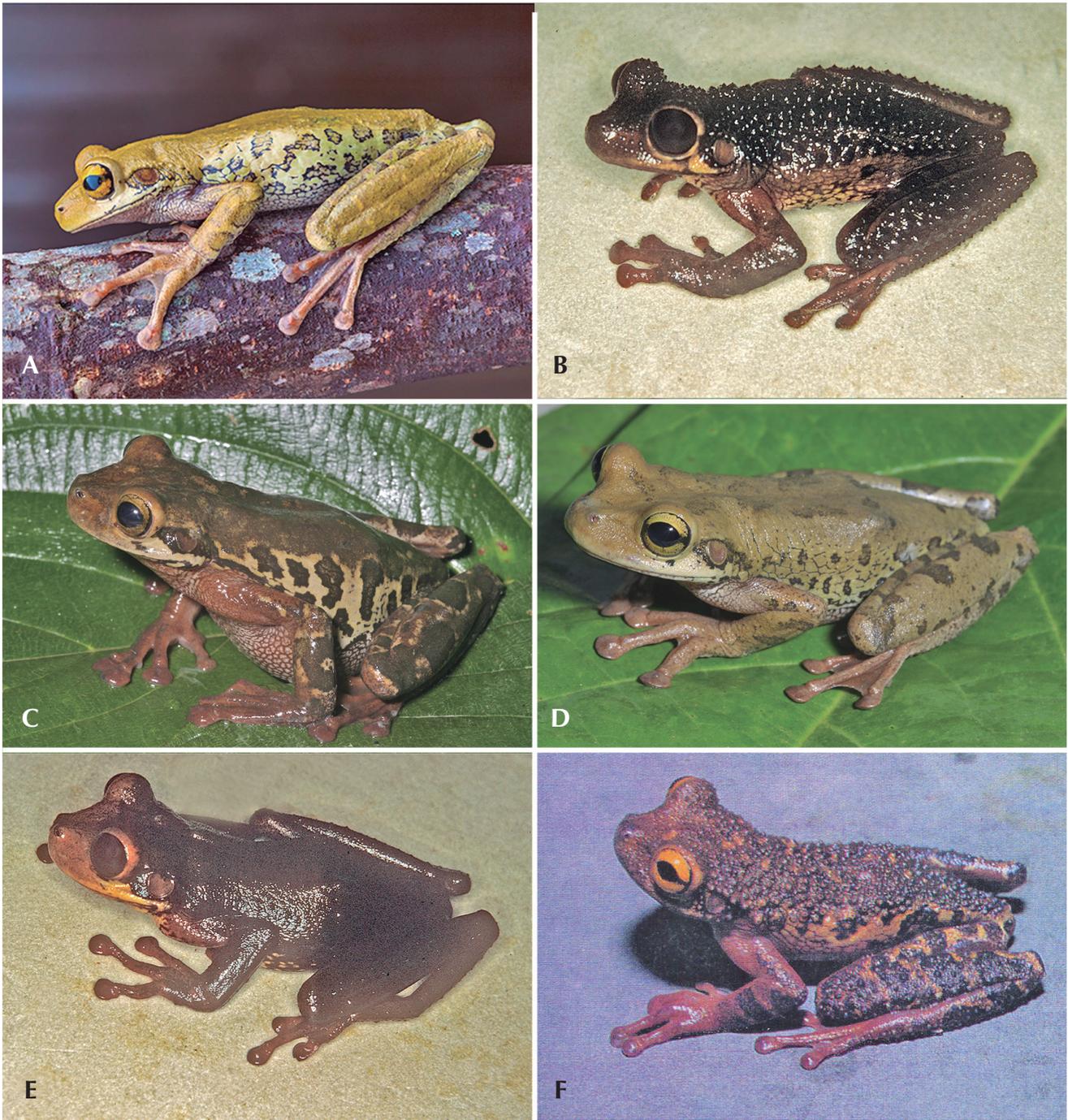


Figure 11. Examples of *Osteocephalus*. (A) *O. carri*, adult female, from near Acevedo, 2400 m, Departamento Huila, Colombia; courtesy of K.-H. Jungfer. (B) *O. verruciger*, KU 123177, adult male, 52.9 mm SVL, from the Cordillera del Dué, Provincia Napo, Ecuador; photo by author. (C) *O. carri*, TRG field number 1746 deposited in ICN, adult female, from Finca Los Lirios, Km 28 via Florencia-Suaza, Departamento Caquetá, Colombia; photo by Taran Grant. (D) *O. "verruciger,"* courtesy of K.-H. Jungfer. (E) *O. verruciger*, KU 123176, adult female, 65.8 mm SVL, from the Cordillera del Dué, Provincia Napo, Ecuador; photo by author. (F) *O. "verruciger,"* adult male, ICN 23942, 54.1 mm SVL, from Vereda La Portada, 35.2 km above Florencia, 1230 m, Departamento Caquetá, Colombia. (Ruíz *et al.* 1996).

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Appendix I. Comparative specimens examined.

Osteocephalus alboguttatus: ECUADOR: *Sucumbíos*: Santa Cecilia, KU 146958–88. *O. buckleyi*: ECUADOR: *Sucumbíos*: Lago Agrio, KU 126646; Puerto Libre, KU 123172; Santa Cecilia, KU 109506, 150492–93, 152477, 152808–09. 175500. PERU: *Loreto*: San Jacinto. KU 221927; 1.5 km N Teniente Lopez, KU 221926. *O. deridens*: PERU: *Loreto*: Río Napo at Río Mangua, KU 192021; Río Napo at Río Sucusari, KU 192021; *San Martín*: Río Cainarachi, 33 km NE Tarapoto on road to Yurimaguas, KU 209447–49. *O. duellmani*: ECUADOR: Morona Santiago: Río Piuntza, KU 147171–72. *O. fuscifascies*: PERU: *Loreto*: Teniente López, KU 221943. *O. leoniae*: PERU: *San Martín*: Río Cainarachi, KU 209447–53; 14 km ESE Shapaja, KU 212180. *O. mutabor*: ECUADOR: *Sucumbíos*: Limoncocha, KU 99210–16; Santa Cecilia, KU 105210–20. *O. taurinus*: ECUADOR: *Sucumbíos*: Santa Cecilia, KU 105230–32, 123174, 146468, 155478. *O. verruciger*: ECUADOR: *Napo*: 3.2 km NNE Ontoyacu, KU 178838–43; Río Azuela, KU 143210–17, 143219–24; 2 km SSW Río Reventador, KU 164405–18; south slope Cordillera del Dué, KU 123176–88. *O. yasuni*: Río Yasuni, 159 km upstream from Río Napo. KU 175196, 175198, 175205–06. PERU: *Loreto*: Explorama Lodge, KU 220894.