A new species of *Osteocephalus* from Ecuador and a redescription of *O. leprieurii* (Duméril & Bibron, 1841) (Anura: Hylidae)

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**Abstract.** The South American spiny-backed treefrog, *Osteocephalus leprieurii*, as previously understood, is a composite of several species. We redescribe it morphologically on the basis of specimens from French Guiana and add other data on the biology of the species. We describe *O. mutabor* n. sp., previously confused with *O. leprieurii*, from the Amazon Basin of Ecuador. The two species differ in coloration, vocalizations and ontogenetic colour change. *Osteocephalus leprieurii* is remarkable for bearing nuptial excrescences not only on the thumb, but also under the fingers and on the chin. The vocal sac is semicircular expanding posterolaterally. *Osteocephalus mutabor* n. sp. is characterized by numerous dark transversal bars on the dorsum and a semicircular vocal sac. The amount of keratinized tips on the dorsal granules in males of both species is dependent on sexual activity.

**Resumen.** Bajo el nombre de la rana arborícola de espalda espinosa *Osteocephalus leprieurii*, de Sur America, como se ha entendido anteriormente, se confundieron diferentes especies. Se describe de nuevo la especie morfológicamente en base a especímenes de la Guayana Francesa y se añaden otros datos sobre su biología. Describimos *O. mutabor* n. sp. de la Cuenca Amazónica Ecuatoriana. Ambas especies se diferencian en coloración, vocalizaciones y cambio ontogenético de color. *Osteocephalus leprieurii* se caracteriza por poseer excrecencias nupciales no solo en el pulgar, sino también bajo los dedos y la barbilla. El saco vocal es semicircular con expansión posterolateral. *Osteocephalus mutabor* n. sp. se caracteriza por tener rayas oscuras transversales en el dorso y un saco vocal semicircular. La cantidad de puntas queratinizadas en los gránulos dorsales de los machos de ambas especies depende de la actividad sexual.

**Introduction**

The spiny-backed treefrogs of the genus *Osteocephalus* are widely distributed in Amazonia, the Guiana Shield, and southeastern South America. Trueb and Duellman’s (1971) review included five species, Duellman (1974) placed a sixth species from the Atlantic Forest of southern Brazil and Argentina in the genus. Seven more species were described by Mar-
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tins and Cardoso (1987), Henle (1981) (as Hyla), Jungfer and Schiesari (1995), Gorzula and Señaris (1996), Ron and Pramuk (1999), and Jungfer et al. (2000). Two species resurrected by Duellman and Mendelson (1995) brought the total to 15 species. Several more species are being described presently; we consider here one new species from Bolivia (Smith et al., in press) and a species from Peru described, but not named, by Duellman and Mendelson (1995). Still, the genus is far from being understood. Numerous specimens in collections of Amazonian frogs are difficult to assign to the recognized taxa, and characters of recently described species differing from those of the original five species have outdated the generic definition of Trueb and Duellman (1971) (see discussion below).

Osteocephalus leprieurii is among the species with a particularly wide geographical range. It was described from Cayenne, French Guiana (Duméril and Bibron, 1841) and subsequently reported from throughout the Amazon Basin southward to Bolivia (Duellman, 1993). Cochran and Goin (1970) compared Colombian material with the types of Hyla leprieurii Duméril and Bibron, 1841, Osteocephalus planiceps Cope, 1874, and Hyla vilarsi Melin, 1941, and stated they were synonymous. They confused at least two species, because O. planiceps is a valid western Amazonian species (Duellman and Mendelson, 1995). Trueb and Duellman (1971) examined O. leprieurii from the Guianas, western Amazonian Brazil, Peru, and Ecuador, namely from Santa Cecilia, Provincia Sucumbíos, Ecuador, and based their description of the ontogeny, osteology and morphology on specimens from the latter site. The ontogenetic change that these frogs undergo is dramatically different from specimens from near the type locality in French Guiana. Likewise, the calls and some morphological characters distinguish the frogs from French Guiana from those in western Amazonia. We describe the latter as a new species, O. mutabor, below.

Rodríguez and Duellman (1994) included O. leprieurii in their field guide of frogs of the Iquitos region, Peru, but their photo is a female specimen from Santa Cecilia, Ecuador, of O. mutabor n. sp. Duellman and Thomas (1996) reported on O. leprieurii from Balta, Departamento Ucayali, Peru. We have not seen these specimens and cannot assign them to a species. However, the mere mention of their having yellow venters in life excludes their being conspecific with the frog called O. leprieurii by Trueb and Duellman (1971), Duellman (1978), Rodríguez and Duellman (1994), and Duellman and Mendelson (1995). The descriptions of those authors all refer to O. mutabor, described herein, a frog that never has a yellow venter.

Osteocephalus leprieurii was included in the checklist of Bolivian anurans by De la Riva (1990) and analyses of calls were published by De la Riva et al. (1995). Smith et al. (in press) demonstrated that the Bolivian frog represented a new species that is presently being described. Smith et al. (in press) compared their new species with O. leprieurii, a species they consider conspecific with O. yasuni, and synonymised O. ayarzaguenai Gorzula and Señaris, 1996, with O. leprieurii. The description and photo published by Gorzula and Señaris (1996, 1998) agrees well with the frogs from French Guiana described here, and we concur with Smith et al. (in press) that O. ayarzaguenai is a junior synonym.
of O. leprieurii. A second specimen of O. ayarzaguenai reported on by Barrio and Fuentes (2000) from Mrakapiwei (spelled Makrapiwei by them) in the extreme south of Venezuela is also a female O. leprieurii of 51.8 mm SVL. It was kept alive for several months by the senior author.

Acquisition of fresh material and observations on live frogs, especially vocalizations and ontogenetic colour change, made us aware that O. leprieurii as presently known is a composite of more than one species with smaller ranges. The purpose of this paper is to redescribe and define O. leprieurii and to describe one new species that has previously been confused with it. Distinction of it from O. leprieurii, a frog with some morphologically variable characters, is warranted by the different vocalizations and juvenile colour patterns. We are aware that we do not resolve the taxonomic status of all populations previously assigned to O. leprieurii, a frog that can be mistaken for O. yasuni Ron and Pramuk, 1999, O. sp. (Smith et al., in press), or the species described herein. But the data presented will be helpful to clarify the status of some of the frogs previously assigned to O. leprieurii in other parts of the Guianas and Amazonia. While working with these frogs we have become aware that the morphology of preserved specimens of Osteocephalus alone is an insufficient tool to gain insight into the taxonomy of the genus.

Materials and methods

In order not to confound morphologically similar species not recognized yet, we redescribe O. leprieurii on the basis of preserved and live material from close to the type locality, “Cayenne” (Duméril and Bibron, 1841), and compare it with the holotype. We assume that by “Cayenne” the town was meant, and not the much larger district (arrondissement) by the same name. We used 27 preserved and live specimens from Arataï Biological Field Station (4°00’N / 52°34’W), 50 m a.s.l., Réserve Naturelle de Nouragues, French Guiana, 120 km airline SSW of Cayenne. Observations on the reproductive biology were made there and in the laboratory. Juvenile frogs of both species were obtained from adults that laid eggs in the laboratory. Those of O. leprieurii were from Arataï and those of the new species from the type locality.

Frogs were measured following Duellman (1970), except for head length (Heyer et al., 1990). Webbing formula is that of Savage and Heyer (1967), as modified by Myers and Duellman (1982). Abbreviations are as follows: ED: eye diameter; EN: distance from eye to nares; FD: diameter of finger disc on third finger; FL: foot length; HL: head length; HW: head width; IN: internarimal distance; SVL: snout-to-vent length; TD: tympanum diameter; TE: distance between tympanum and eye; TL: tibia length. Museum abbreviations are as follows: EPN: Escuela Politécnica Nacional, Herpetología, Quito; GNM: Göteborg Natural History Museum; MBUCV: Museo de Biología, Universidad Central de Venezuela, Caracas; MHNG: Muséum d’Histoire naturelle, Genève; MNHN: Muséum national d’Histoire naturelle, Paris; SMF: Senckenberg-Museum, Frankfurt am Main; SMNS: Staatliches Museum für Naturkunde, Stuttgart; and ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Calls of the new species were recorded with a Sony WM D6C tape recorder and a Sennheiser ME 66 directional microphone in an aquarium. Although because of the confinement (90 l of air volume) between glass walls, pulses in the calls of aquarium-recorded frogs are less easily readable in spectrograms — pulses are less clearly demarcated and notes get a tail because of echo effects — the recordings suit the purpose of defining the species. The calls of O. leprieurii were recorded by B. Gottsberger using a Sony WM D6C tape recorder and an AKG D 190 E microphone. Captive specimens were recorded in an aquarium (same size and equipment as above). Sounds were analyzed using Canary 1.2 software (Cornell University) on a Macintosh computer. Spectrograms were produced at a sample rate of 22 kHz and FFT (fast Fourier transform) size of 256 points.
**Osteocephalus leprieurii** (Duméril and Bibron, 1841) (figs 1A, C, 2, 3)

*Hyla leprieurii* Duméril and Bibron, 1841  
*Hyla leprieurii britti* Melin, 1941  
*Osteocephalus leprieurii* — Cochran and Goin, 1970 (part)  
*Osteocephalus leprieurii* — Trueb and Duellman, 1971 (part)  
*Osteocephalus leprieurii* — Lescure, 1976  
*Osteocephalus ayarzaguenai* — Barrio and Fuentes, 2000  
*Osteocephalus leprieurii* — Lescure and Marty, 2000  
*Osteocephalus leprieurii* — Smith, Reichle and Harvey, in press (part)

**Description of holotype.** MNHN 4629, a female of 47.2 mm snout-vent length (SVL). The specimen is a little soft and bluish grey in colour. No markings are visible except for a few indistinct suffusions on the back and hind legs. The snout is rounded in dorsal and lateral aspect. The canthus rostralis is distinct and angular, curved inwardly. The loreal region is concave. The dorsal surface of the head is smooth and slightly concave in the interorbital area. The nostrils open posterolaterally. The tympanum is horizontally elliptical, about 1.25 times wider than high and about half the diameter of the eye. A strong supratympanic fold extends from the posterior midlevel of the eye to an area well above (i.e. at tympanum width distance) the anterior level of the arm insertion.

The dentigerous processes of the vomers are angular, interrupted medially. The anterior line of vomerine teeth is in line with the posterior 1/4 of the elliptical and oblique choanae. The posterior edge is behind the posterior end of the choanae. There are 10 vomerine teeth on the left and 12 on the right.

The dorsum is smooth. Laterally, the skin is shagreen on the anterior half of the body between the limb insertions and otherwise smooth. An axillary membrane is absent. The throat and chest are weakly granular; the belly, proximal 2/3 of the ventral surfaces of the thighs, and cloacal area are granular. Other parts of the limbs are smooth. The cloacal opening is situated at the upper level of the thighs.

The thumb bears a large elliptical thenar tubercle. A subpalmar tubercle is small and ovoid. The subarticular tubercles are simple, except for the distal one on Finger IV, which is bifid. The relative length of the adpressed fingers is III>IV>II>I. The webbing formula is I basal II 1 3/4 — 3 III 2 3/4 — 2 1/2 IV.

On the foot there is a large elliptical inner metatarsal and a small flat outer one. The subarticular tubercles are single and conical. The proximal segments of all toes bear small rounded supernumerary tubercles; there is one each on Toe I and II, 3 in a line on Toes III and IV, and 2 on Toe V. The relative length of the adpressed toes is IV>V>III>II>I. The webbing formula is I 1 — 2⁺ II 1 — 2 1/2 III 1⁺ — 2 2/3 IV 2 1/2 — 1 V. The bones are white.
Systematics of *Osteocephalus*

**Figure 1.** A. Adult male *Osteocephalus leprieurii*, 46 mm SVL, from Arataí, French Guiana. B. Adult male *O. mutabor*, 51 mm, from the type locality. C. Freshly metamorphosed juvenile of *O. leprieurii*, 16 mm SVL, from Arataí, French Guiana. D. Freshly metamorphosed juvenile of *O. mutabor*, 17 mm SVL, from the type locality.
Figure 2. Adult male *O. leprieurii*, 46 mm SVL, from Arataí, French Guiana. A. Ventral aspect. B. Head.
Systematics of *Osteocephalus*

Additional material from Arataï, French Guiana. Females from Arataï, French Guiana, 120 km airline SSW of the type locality, agree morphologically with the holotype in almost all respects, with the exception of some features of the head. The snout is rounded (as in the holotype) to bluntly rounded dorsally in SMNS 9276. The canthus rostralis is pronounced in all specimens, but distinctly (as in the holotype) to weakly curved inwardly, and almost straight in SMNS 9276. The vomerine patches are separated (as in the holotype) or in contact with each other and angular (as in the holotype) to rounded, as in SMNS 9272. Males exhibit the same variation. SMNS 9274 and 9275 additionally have shorter, less elongated choanae. There is some variation in the amount of webbing. Formula of the hand is I basal II 1 3/4 — 3 III (2 1/2 — 2 3/4) — (2 1/4 — 2 1/2) IV. Webbing formula of the foot is I (1 — 1+) — (2 + — 2 1/2) II 1 — (2 1/2 — 2 3/4) III (1 — 1+) — (2 1/2 — 3) IV (2 1/3 — 2 3/4) — 1 V (fig. 4).

Sexual dimorphism, like in most other species of *Osteocephalus*, is considerable. The largest preserved female is 54.5 mm in SVL (but one of our live specimens is about 61 mm). The dorsal surfaces are smooth. A few indistinct tubercles are visible under magnification on the eyelids, posterior to them, and on the supratympanic fold. The largest male is 45.7 mm. Depending on breeding condition, the presence of granules and spines is more or less pronounced. This has been especially noted in males that we have kept alive for more than two breeding seasons. Breeding males have numerous spines bearing keratinized tips on all dorsal surfaces except the forelimbs. A few spines are present in the loreal region and on the outer edge of Toe V. The thumb bears a large dark tan nuptial pad that extends...
dorsally and laterally from proximally of the disc to the base of the thumb. There are also keratinous excrescences ventrally between the disc and the subarticular tubercle and on the ventral surfaces of the other fingers (fig. 4). The spicules are patchy and less closely set and thus, lighter, but should not be mistaken for pigmentation. Spicules also border the gular area along the lower jaw.

Males that are not in breeding condition lack excrescences on the lower jaw, the thumb and on the other fingers. The dorsal spines are less pronounced and lack the keratinized tips. A small, non-breeding male of 41.1 mm (SMNS 9275) is identifiable sexually by the number of dorsal tubercles, which are non-pungent. Vocal slits open lateral to, and slightly posterior to the midlevel of the tongue. Weakly deflated vocal sacs extend on each side ventrolaterally from the throat at anterior tympanum edge level to the area above the arm insertion (fig. 2B).

In life, adults of both sexes are pale tan, reddish tan to dark tan dorsally and the flanks. There is a narrow darker tan interorbital band in almost all specimens. Up to four narrow dark tan transverse lines are present on the dorsum; they do not extend continuously, but
rather irregularly fragmented towards the dorsal edges laterally. In some individuals they are altogether lacking. Most specimens bear irregular spots, flecks, or lines on the dorsum. The loreal region, tympanum, and lateral area anterior to the arm insertion are dark tan. There is a creamy white to creamy tan subocular spot that extends as a faint line anteriorly to the tip of the snout in some specimens. A broad tan horizontal stripe is present in the iris. Otherwise, the iris is golden with irregular black vermiculation. The ground colour of the extremities is tan. Dark tan continuous or fragmented transverse bands are present on the lower arm, outer finger, leg, and outer toe. The webbing on the hands is tan, that of the feet tan to red. The posterior surfaces of the thighs are yellowish tan or yellowish red to brick red. The ventral surfaces are creamy white to yellowish white in females and pale yellow in males. The ventral abdominal vein is not visible through the skin (fig. 2A).

Breeding males are altogether lighter in coloration. They are ochre to dark yellow dorsally and bright yellow ventrally. The bones are white (green in juveniles and subadults).

Preserved specimens principally look the same. However, the dark tan dorsal markings fade, as well as the yellow coloration of the venter becomes pale yellow and the red webbing changes into tan. Measurements and proportions of adults from Arataï and the holotype are given in tables 1 and 2.

**Taxonomic status of Hyla leprieurii britti Melin, 1941.** Trueb and Duellman (1971) considered *Hyla leprieurii britti* Melin, 1941, to be a junior synonym of *O. leprieurii*. The holotype (GNM 489) from the Rio Uaupés, north of Rio Japú, Amazonas, Brazil, differs in some respects from the type of *O. leprieurii* and specimens from Arataï: It is a male having an SVL of 48.2 mm, which is larger than the female holotype and males from Arataï (up to 45.7 mm). It has a straight (instead of curved to almost straight) canthus rostralis. The anterior edges of the vomers are in line with the posterior 2/3 (instead of 1/4 to 1/3) of the choanae, which are oblique and bean-shaped (instead of elliptical). The eye diameter of 5.5 mm is relatively wide. Thus TD/ED is 0.618, which is relatively smaller than that of specimens from Arataï and the holotype (table 2). Proportions otherwise do not differ from the type or Arataï specimens. The webbing is within the range of the specimens from French Guiana, except that there is slightly less webbing on the outer edge of Toe III (1 1/3). The distal subarticular tubercle on Finger IV is bifid. Nuptial excrescences under the fingers and on the thumb are like those of males from Arataï. Except for a few bars on the limbs, darker coloration is absent or faded. The description given by Melin (1941) agrees with specimens from Arataï. Considering the variation even within the population from Arataï and in the absence of other biological data of frogs from northwestern Brazil, we agree with Trueb and Duellman (1971) that the taxon is a synonym of *Osteocephalus leprieurii*.

**Diagnosis and comparisons.** A medium-sized species of the genus with females reaching 61 mm and males 48.1 mm SVL. Strong sexual dimorphism: Dorsum of females smooth, with tubercles bearing spines in males. Other nuptial excrescences on the thumb, under the fingers and on the lower jaw. Skin on flanks smooth. Webbing on hand reaching to
Table 1. Measurements (ranges and means ± s; in mm) of two species of *Osteocephalus*: Holotype of *O. leprieurii* (MNHN 4629), adult *O. leprieurii* from Arataï (French Guiana) (2 females, 3 males), and adult type specimens of *O. mutabor* from three localities: San Pablo de Kantesiya (Sucumbíos, Ecuador) (2 females, 3 males), and Arutam (Pastaza, Ecuador) (1 female, 1 male). Abbreviations are as follows: SVL: snout-to-vent length; HL: head length; HW: head width; TL: tibia length; FL: foot length; ED: eye diameter; TD: tympanum diameter; FD: diameter of finger disc on third finger; EN: distance from eye to naris; IN: interminal distance; TE: distance between tympanum and eye.

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<th>Character</th>
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<th><em>O. leprieurii</em> holotype</th>
<th><em>O. leprieurii</em> Arataï</th>
<th><em>O. leprieurii</em> San Pablo</th>
<th><em>O. mutabor</em> Sumaco</th>
<th><em>O. mutabor</em> Arutam</th>
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<td></td>
<td></td>
<td>4.23 ± 0.38</td>
<td>4.00 ± 0.55</td>
<td>3.9-4.5</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>4.0 ± 0.21</td>
<td>4.32 ± 0.29</td>
<td>3.6-4.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>IN</td>
<td>f</td>
<td>3.5</td>
<td>3.0-3.7</td>
<td>4.05 ± 0.21</td>
<td>5.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>3.35 ± 0.50</td>
<td>3.9-4.2</td>
<td>4.50 ± 0.85</td>
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<tr>
<td></td>
<td></td>
<td>3.3</td>
<td>3.6-5.3</td>
<td>2.7-4.7</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>3.30 ± 0.00</td>
<td>3.3-0.37</td>
<td>3.0-3.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TE</td>
<td>f</td>
<td>2.0</td>
<td>1.9-2.5</td>
<td>3.24 ± 0.27 (n = 5)</td>
<td>4.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>2.20 ± 0.42</td>
<td>2.3-2.7</td>
<td>3.24 ± 0.27 (n = 5)</td>
<td>2.9-3.2</td>
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<tr>
<td></td>
<td></td>
<td>1.3-1.9</td>
<td>3.06 ± 0.15</td>
<td>1.6-2.2</td>
<td>2.0-2.7</td>
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</tr>
<tr>
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<td>1.67 ± 0.32</td>
<td>2.20 ± 0.24</td>
<td>1.83 ± 0.26</td>
<td>2.5</td>
<td></td>
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</tbody>
</table>
Systematics of *Osteocephalus*

**Table 2.** Proportions (means ± s) of two species of *Osteocephalus*: Holotype of *O. leprieurii* (MNHNP 4629), adult *O. leprieurii* from Arataï (French Guiana) (2 females, 3 males), and adult type specimens of *O. mutabor* from three localities: San Pablo de Kantesiya (Sucumbíos, Ecuador) (2 females, 12 males), south slope of Volcán Sumaco (Napo, Ecuador) (3 females, 6 males), and Arutam (Pastaza, Ecuador) (1 female, 1 male). For abbreviations see table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>sex</th>
<th><em>O. leprieurii</em></th>
<th><em>O. leprieurii</em></th>
<th><em>O. mutabor</em></th>
<th><em>O. mutabor</em></th>
<th><em>O. mutabor</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>holotype</td>
<td>Arataï</td>
<td>San Pablo</td>
<td>Sumaco</td>
<td>Arutam</td>
</tr>
<tr>
<td>HL/SVL</td>
<td>f</td>
<td>0.333</td>
<td>0.345 ± 0.005</td>
<td>0.354 ± 0.001</td>
<td>0.353 ± 0.017</td>
<td>0.329</td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>0.344 ± 0.008</td>
<td>0.356 ± 0.009</td>
<td>0.366 ± 0.015</td>
<td>0.342</td>
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</tr>
<tr>
<td>HW/SVL</td>
<td>f</td>
<td>0.326</td>
<td>0.335 ± 0.004</td>
<td>0.341 ± 0.009</td>
<td>0.359 ± 0.011</td>
<td>0.338</td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>0.342 ± 0.020</td>
<td>0.346 ± 0.010</td>
<td>0.360 ± 0.010</td>
<td>0.344</td>
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<tr>
<td>TL/SVL</td>
<td>f</td>
<td>0.589</td>
<td>0.587 ± 0.012</td>
<td>0.539 ± 0.040</td>
<td>0.559 ± 0.043</td>
<td>0.567</td>
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<td></td>
<td>m</td>
<td>0.584 ± 0.046</td>
<td>0.549 ± 0.016</td>
<td>0.537 ± 0.031</td>
<td>0.519</td>
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<tr>
<td>FL/SVL</td>
<td>f</td>
<td>0.710</td>
<td>0.720 ± 0.022</td>
<td>0.655 ± 0.037</td>
<td>0.718 ± 0.055</td>
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<td>m</td>
<td>0.729 ± 0.039</td>
<td>0.674 ± 0.019</td>
<td>0.679 ± 0.029</td>
<td>0.670</td>
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<tr>
<td>TD/ED</td>
<td>f</td>
<td>0.723</td>
<td>0.742 ± 0.072</td>
<td>0.780 ± 0.036</td>
<td>0.682 ± 0.043</td>
<td>0.753</td>
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<tr>
<td></td>
<td>m</td>
<td>0.704 ± 0.022</td>
<td>0.698 ± 0.070</td>
<td>0.699 ± 0.058</td>
<td>0.741</td>
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<tr>
<td>TD/FD</td>
<td>f</td>
<td>1.308</td>
<td>1.132 ± 0.078</td>
<td>1.522 ± 0.203</td>
<td>1.195 ± 0.141</td>
<td>1.289</td>
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<tr>
<td></td>
<td>m</td>
<td>1.353 ± 0.272</td>
<td>1.586 ± 0.123</td>
<td>1.479 ± 0.180</td>
<td>1.720</td>
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<tr>
<td>IN/HW</td>
<td>f</td>
<td>0.227</td>
<td>0.186 ± 0.029</td>
<td>0.211 ± 0.004</td>
<td>0.215 ± 0.021</td>
<td>0.199</td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>0.222 ± 0.005</td>
<td>0.218 ± 0.039</td>
<td>0.169 ± 0.083(n = 5)</td>
<td>0.179</td>
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<tr>
<td>EN/HL</td>
<td>f</td>
<td>0.268</td>
<td>0.272 ± 0.002</td>
<td>0.280 ± 0.005</td>
<td>0.286 ± 0.008</td>
<td>0.313</td>
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<tr>
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<td>m</td>
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<td>0.260 ± 0.032</td>
<td>0.262 ± 0.010</td>
<td>0.314</td>
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<tr>
<td>EN/SVL</td>
<td>f</td>
<td>0.089</td>
<td>0.094 ± 0.002</td>
<td>0.099 ± 0.002</td>
<td>0.101 ± 0.008</td>
<td>0.103</td>
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<tr>
<td></td>
<td>m</td>
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<td>0.093 ± 0.011</td>
<td>0.096 ± 0.004</td>
<td>0.107</td>
<td></td>
</tr>
<tr>
<td>HL/HW</td>
<td>f</td>
<td>1.019</td>
<td>1.030 ± 0.027</td>
<td>1.038 ± 0.023</td>
<td>0.984 ± 0.024</td>
<td>0.973</td>
</tr>
<tr>
<td></td>
<td>m</td>
<td>1.007 ± 0.035</td>
<td>1.029 ± 0.017</td>
<td>1.016 ± 0.034</td>
<td>0.994</td>
<td></td>
</tr>
</tbody>
</table>

antepenultimate subarticular tubercle on inner edge of third finger. Dorsal colour shades of tan to ochre. Usually a thin transversal interorbital line. Dorsum with or without a few irregular darker tan markings, including transversal lines. Venter creamy white to bright lemon without markings. A broad light subocular spot, sometimes expanded into a fine light supralabial line. Flanks tan without markings. Bones white in adults. Dentigerous processes of vomers angular to rounded. Dorsal roofing bones of the skull not exostosed. Juveniles with reddish eyes, light upper arms, light knee and heel caps and green bones.

The golden iris with irregular black vermiculation distinguishes *O. leprieurii* from species with golden irises with radiating dark lines: *O. deridens*, *O. elkejungingerae*, *O. fuscifacies*, *O. oophagus*, *O. planiceps*, *O. sp.* (Duellman and Mendelson, 1995), *O. taurinus*, and *O. verruciger*. The irises of *O. pearsoni* and *O. subtilis* are dark (deep coppery tan to black). The iris is reticulate, but the tarsus is tuberculate to fringed in *O. buckleyi*, *O. cabrerai* and *O. langsdorffii* (smooth in *O. leprieurii*). The iris is reticulate in *O. sp.* (Smith et al., in press), which also has a yellow venter, but this species lacks sexual size dimorphism and possesses a bicoloured iris. *Osteocephalus mutabor*, which also has a reticulate iris, is differentiated below. *Osteocephalus leprieurii* most closely resembles *O. yasuni*. The latter species has fewer dorsal spines in males.
and was reported to lack subdigital nuptial excrescences (Ron and Pramuk, 1999). Both characters, however, may depend on the breeding condition of the specimens at the time of preservation. *Osteocephalus yasuni* lacks the transverse markings on the dorsum, but is otherwise difficult to distinguish morphologically. The advertisement calls of both species are different (Ron and Pramuk, 1999; personal data, K.H.J.), as well as their behaviour. Live *O. yasuni* are much less fugitive and secretive than *O. leprieurii* (personal observation, K.H.J).

**Vocal sacs and vocalizations.** Calling *Osteocephalus leprieurii* have a moderately distensible subgular and paired vocal sacs distensible ventrolaterally to laterally. They extend posteriorly slightly beyond the area above the upper arm insertion. In preserved breeding males the wrinkled skin of the lateral vocal sacs usually is visible, while the gular area always is smooth.

A male of *O. leprieurii* was recorded at Aratai by B. Gottsberger on 4 March 1998 at 10 h at an air temperature of 23°C in a chorus that had its peak during the night. With fewer males involved in calling activity, individuals could be sorted out. The frog was calling about 40 cm from the microphone.

Vocalizations in a chorus are complex and consist of at least two different types of notes (fig. 5). Type 1 is a pulsed note consisting of three pulses. Each of the notes is frequency modulated and has numerous harmonics, the second or third harmonic is dominant. The fundamental frequency is 0.680-1.036 kHz and the dominant frequency 1.036-1.740 kHz. Nine notes have durations of 99-127 ms (\(\bar{x} = 114.3\) ms). Pulse lengths are 14-36 ms (\(\bar{x} = 23.1; n = 27\)) with pulse intervals of 10-31 ms (\(\bar{x} = 24.6; n = 18\)). Type 1 notes are followed by Type 2 notes or repeated once or twice. Type 2 is a single note emitted 1-3 times consecutively. It is greatly frequency modulated and has a fundamental frequency of about 0.75 to 1.3 kHz. It is low in the beginning, rises in the central section of the note, and drops again toward the end. The dominant frequency, between 1.5 and 2.9 kHz, is found in the third to sixth harmonic and changes in the same way. Note length is 61.8-77.9 ms (\(\bar{x} = 67.5; n = 4\)). Sometimes notes about 2.5 times as long (156.8 and 163.6 ms; \(n = 2\)) are produced. These may correspond to those of Type 2. They have less energy, but look like Type 2 notes in the first two fifths, while the final segment is not, or little, frequency modulated.

A male that was kept in the laboratory and placed singly into an aquarium produced only Type 1 notes that consisted of 5-6 pulses. When other male individuals were added, both types of calls were emitted. This indicates that social context greatly influences the vocal behaviour of *O. leprieurii*.

**Reproductive behaviour.** *Osteocephalus leprieurii* is an explosive breeder. At Aratai individuals congregated and spawned in large numbers on nights preceded by heavy rains. Gottsberger (1999) recorded four explosive breedings during the shorter one of two annual rainy seasons between mid-December 1997 and early March 1998. Males sometimes called one or two nights before or after these nights, but ceased in between. Spawning occurred
Figure 5. Vocalizations of a male *O. leprieurii* recorded at Arataí, French Guiana (23°C air temperature). The first two notes (between 0 and 0.3 s) are of Type 2, as may be the third (between 0.4 and 0.6 s). The last two notes (between 0.8 and 1.0 and between 1.1 and 1.3 s) are of Type 1.

during the later half of the night and continued until noon the following day. Eggs are laid into seasonally flooded pools.

Captive females were able to lay eggs twice within six months, but because they did not have more than two opportunities, the actual potential to spawn may be higher. Eggs float as a single layer film on the surface of the water. They are 1.53-1.63 mm (\(\bar{x} = 1.59\) mm; \(n = 10\)) in diameter and have a dark grey animal and a white vegetal pole. One clutch contained 2882 eggs.

*Ontogenetic colour change.* Newly metamorphosed juveniles are 12-14 mm in SVL. In life they are pale grey to pale tan dorsally. A few ill-defined darker tan flecks are present on the dorsum, thigh, and tibia. A white supralabial stripe, often expanded below the eye, extends along the whole upper jaw. The iris is yellow during the first three or four days, then changes to pale orange or pale red. The upper arm and elbow are creamy white, and the knee and heel are creamy white to pale grey; the fingers and feet are orange to pale red. Other dorsal surfaces of the extremities are grey to greyish tan. The throat and abdomen are white, and the ventral surfaces of legs and arms are pale grey and somewhat translucent. The bones are green (fig. 1C). During the next few weeks colours do not change much. In specimens of 20 mm SVL, the reddish coloration of eyes, fingers and feet becomes more intense. Dorsally, the tan coloration becomes darker on the anterior two thirds of the body, whereas the posterior part of the body and legs are greyish tan. Specimens longer than
23 mm SVL lack creamy white colour on elbows and distal third of upper arm. The iris is golden with a red hue toward the pupil, veined by black reticulation. Frogs of 28 mm SVL still have red or reddish fingers and toe discs, but otherwise look like adults. At 32 mm SVL, fingers and toe discs are pale tan. Bones are green in all specimens up to that size. Sexes of subadult males and females of 37 mm are already distinguishable by their granular dorsa and yellow venters or smooth dorsa and white venters, respectively. The tibiofibulae in these specimens are still green. In frogs of 40 mm and larger, the bones are white.

Habitat and distribution. At Arataï, French Guiana, *O. leprieurii* is a common species in lowland rain forest at about 50 m a.s.l., where it occurs both in terra firme and seasonally flooded forest. Data accompanying preserved specimens indicate that the species is also a forest dweller in other parts of its range.

The exact range of *O. leprieurii* is unknown. It occurs on the Guiana Shield in French Guiana, Surinam, Guyana, Venezuela, and northern Brazil southward at least to the Rio Negro and Rio Uaupés. Literature records of the species from farther south might have been misidentified as *O. yasuni*, *O. mutabor* or *O. sp.* (Smith et al., in press). Specimens examined here are from elevations of 50-700 m a.s.l.; the holotype of *O. ayarzaguenai* was collected at 860 m a.s.l. (Gorzula and Señaris, “1996” [1997]).


### Osteocephalus mutabor n. sp. (figs 1B, D, 6-9, 11)

*Osteocephalus leprieurii* — Trueb and Duellman, 1971 (part)
*Osteocephalus leprieurii* — Duellman, 1978
*Osteocephalus leprieurii* — Duellman and Mendelson, 1995

**Holotype.** EPN H-6658, an adult male from Ecuador: Provincia Napo: South slope of Volcán Sumaco on Río Pucuno, 1000 m a.s.l., between Guamaní and Guagua Sumaco (0°42′24″S / 77°35′54″W), collected by K.-H. Jungfer and O. Piskurek on 22 August 1998.

**Paratypes.** Twenty-nine specimens, all from Ecuador: EPN H-6659 (female), same data as holotype; EPN H-5716-9 (males) from Provincia Sucumbíos: Cascales, between Comuna Duvuno and Chunchuloma, collected by A. Almendáriz; MHNG 2260.4-6, 2260.97, 2366.43, 2366.45, 2366.48 (all males), 2366.53 (subadult female), 2366.61-63, 2366.67 (all males), 2373.84 (female), 2373.86 (female), 2373.87, 2556.57 (both males), all partly dissected, from Provincia Sucumbíos: San Pablo de Kantesiya, collected by J.M. Touzet; EPN H-5695 (male), 5696 (female), 5697-9 (males) from Provincia Napo: Comuna Veinticuatro de Mayo, collected by A. Almendáriz; ZFMK 66237 (male) from Provincia Napo: Río Chaloyacu on Carretera Narupa — Coca, collected by R. Perez; SMF 79721 (female) and SMF 79722 (male) from Provincia Pastaza: vicinity of Arutam Biological Field Station, 1°47′22″S / 77°50′53″W, 780-790 m a.s.l., collected by G. Köhler and R. Seipp.
Diagnosis and comparisons. A medium sized species of the genus with females reaching 75.7 mm and males 50.3 mm SVL. Strong sexual dimorphism: dorsum of females smooth, with tubercles bearing spines in males. Breeding males with well developed nuptial pads on the thumb, but without additional excrescences on the fingers and the chin. Skin on flanks smooth. Webbing on hand hardly or just reaching proximal edge of antepenultimate subarticular tubercle on inner edge of third finger. Dorsal colour tan. Interorbital line present. Dorsum with numerous transverse lines or other markings. Venter creamy white, sometimes suffused with tan spots. A broad light subocular spot and a fine pale supralabial line around the snout. Flanks without markings. Bones green in juveniles and adults. Dentigerous processes of vomers angular. Dorsal roofing bones of the skull not exostosed. Juveniles with red eyes, broad creamy white interorbital bar and dorsolateral stripes, lacking pale elbows, knees, and heels.

The new species is easily distinguished from all other Osteocephalus by its bold dorsal transverse markings, usually 6-17 lines, sometimes modified to broken-up lines or complex vermiculation (fig. 8). Osteocephalus leprieurii occasionally has up to four short transversal lines on the dorsum, irregularly fragmented towards the dorsal edges laterally,
but it has a bifid distal subarticular tubercle on Finger IV (single in most *O. mutabor*) and nuptial excrescences in breeding males under the fingers and on the lower jaw (lacking). Some *O. sp.* (Smith et al., in press) have broad transversal bands on the dorsum. This species lacks sexual size dimorphism and possesses a bicoloured iris. Some *O. planiceps* have irregular transversal bands or lines on the backs. The latter species has a golden iris with straight radiating dark lines (golden with reticulate dark pattern) and the distal subarticular tubercle on Finger IV is bifid (single in most *O. mutabor*).

**Description of holotype.** An adult male of 48.3 mm SVL. Head slightly wider than body and slightly wider than long. Snout rounded in lateral and in dorsal view. Canthus rostralis distinct, rounded and curved inwardly. Head concave dorsally. Loreal region concave. Nostrils elevated, opening dorsolaterally. Dentigerous processes of vomers bearing six teeth on the left and eight on the right, in between choanae, angular; anterior edges reaching the midlevel of the choanae, posterior edges reaching beyond the choanae, which are relatively small, ovoid, oblique. Vocal slits open medial to the mandible articulation and the posterior level of the tongue.

A thick supratympanic fold extending from behind the eyes to above the tympanum and curves downward to the insertion of the arm. Tympanum conspicuous, rounded, slightly wider than high. Tympanum diameter about 75% of eye diameter. Dorsum strongly granular from posterior half of orbits to vent; about a third of the granules bearing small keratinized tips. Anterior part of the head with a few keratinized tips dorsally and on the snout, smooth laterally. Body slightly shagreen above arm insertion, smooth laterally.
Chest and belly granular. Throat smooth, with a thick transverse fold of the vocal sac. Cloacal opening situated at midlevel of thighs. Numerous rounded tubercles below the vent. Axillary membrane absent. Arms smooth. Thumb bearing large nuptial pad that extends from base of thumb laterally and dorsally almost to the proximal edge of the disk laterally. A large thenar tubercle on the thumb. Subarticular tubercles single, one on Finger I, two on Fingers II and III, and three on Finger IV. Relative length of adpressed fingers 3 > 4 > 2 > 1. Webbing formula I basal II 2⁻ — 3⁺ III 2 3/4 — 2 1/2 IV.

Legs slightly granular dorsally, especially on tibia. Proximal one third of thighs granular ventrally. Other surfaces smooth. Foot bearing a large elliptical inner metatarsal tubercle and a small flat rounded outer metatarsal tubercle. Subarticular tubercles single, one each on Toes I and II, two on Toes III and V, and four on Toe IV. Relative length of adpressed toes 4 > 3 > 5 > 2 > 1. Webbing formula I 1 1/2 — 2⁺ II 1+ −2 1/2 III 1 1/3 — 2 1/2 IV 2 1/2 — 1 V. Tarsal fold absent.

Measurements: SVL: 48.3 mm; HL: 17.8 mm; HW: 18.1 mm; TL: 25.9 mm; FL: 33.4 mm; ED: 6.1 mm; TD: 4.5 mm; FD: 3.0 mm; EN: 4.6 mm; IN: 3.7 mm; TE: 2.7 mm.
Figure 8. Colour pattern variation in preserved specimens of *O. mutabor* from San Pablo de Kantesiya, Provincia Sucumbíos, Ecuador (from left: MHNG 2366.53, 2260.4, 2366.45, 2260.97, 2366.6, 2366.63).

Figure 9. Fully distended semicircular vocal sac of a male *O. mutabor* calling in an aquarium.

Coloration. In alcohol all dorsal surfaces of the body are tan. A dark tan interorbital line is followed posteriorly by ten more transverse lines. Dark tan lines or bars are also present on the tibia and the lower arm. A large creamy white subocular spot extends to the tympanum and extends as a narrow supralabial stripe around the snout. The lower
jaw is bordered by a fine tan line. Other surfaces of the head are tan. The vent region is dark tan, bordered by a narrow white line above the vent. Subanal tubercles are light tan. Dorsolaterally the frog is tan. Ventrolaterally it is creamy white, same as all other ventral surfaces, except for the discs of the fingers (tan) and the soles of the feet (suffused with pale tan pigmentation). The posterior surfaces of the thighs are uniformly pale tan. The bones are green.

In life, colours were essentially the same. The iris was golden yellow with irregular black reticulation and a dark tan bar at midlevel. The posterior surfaces of the thighs were uniform tan. There were no yellow surfaces, neither at the time when the frog was preserved, nor some weeks before when it had been breeding.

**Variation.** *Osteocephalus mutabor* exhibits sexual dimorphism and intrapopulational and geographical variation. Measurements and proportions are given in tables 1 and 2.

All specimens have numerous transversal markings dorsally, consisting of 6-17 lines. In a few specimens the lines are fragmented or modified as complex vermiculation (fig. 8). In one third of the 15 specimens with undamaged venters there is a suffusion of tan spots ventrally on the belly and gular area. Three specimens in the type series have slightly oblong, instead of ovoid choanae. Most specimens have a single distal subarticular tubercle on Finger IV, but in four specimens there is a slightly bifid tubercle on one of both Fingers IV (while on the other finger it is single), and both specimens from Arutam have the tubercles on the right and left Fingers IV distinctly bifid. Variation in webbing on the
Figure 11. Intermediate colour pattern of a subadult female *O. mutabor*, 36 mm SVL from the type locality.

hand is I basal II (2−2) — (3 − 3 1/3) III (2 3/4 − 3) — (2 1/2 − 2 2/3) IV. Duellman and Trueb (1971: 14) provide a drawing of the hand of a male (as *O. leprieurii*) from Lago Agrio, Ecuador. On the foot, it is I (1 + 1/2) — (2 − 2 1/2) II (1 − 1 1/3) — (2 + 2 2/3) III (1 + 1 1/3) — (2 1/2 − 3) IV (2 1/2 − 3) — (1 − 1+) V.

Depending on sexual activity, males differ in dorsal granulation. In breeding males, most tubercles are tipped by keratinous spines, whereas non-breeding males lack nuptial pads and most of the spines. Males are smaller than females. Male paratypes from throughout the known range (Sucumbíos to Pastaza Provinces, Ecuador) are 35.6-50.3 mm in SVL ($\bar{x} = 44.1$ mm $\pm$ 0.31; $n = 23$), females are 52.7-75.7 mm ($\bar{x} = 60.5$ mm $\pm$ 8.91; $n = 6$). Females are smooth dorsally and lack keratinous spines.

Geographically, there is considerable variation in SVL. The smallest specimens are from the Río Aguarico drainage in northern Ecuador. Males from San Pablo de Kantesiya are 43.0 mm $\pm$ 2.63 ($n = 12$) in SVL, females are 56.5 mm $\pm$ 5.37 ($n = 2$) in SVL. Males from the south slope of Volcán Sumaco (upper Río Napo drainage) are 45.0 mm $\pm$ 3.55 ($n = 6$) in SVL, females are 58.1 mm $\pm$ 6.67 ($n = 3$). The largest specimens are from the southernmost locality from which frogs were available, Arutam in the Río Pastaza drainage. The single male is 50.3 mm, and the female is 75.7 mm in SVL. Apparently
there is a clinal increase in size from north to south. Data from approximately 200 km SE of Arutam, near Andoas, Departamento Loreto, Peru, confirm this in males (Duellman and Mendelson, 1995). Their largest male is 50.1 mm, whereas their largest female is 67.0 mm, smaller than the female from Arutam, but still slightly larger than the largest specimen from Volcán Sumaco.

Colours in life are like those described for the holotype. Through the skin of the posterior part of the venter the abdominal vein (fig. 6) and, in gravid females, the eggs are visible. The ventral abdominal vein usually fades in preserved specimens.

Vocal sacs and vocalizations. In calling males the single vocal sac is distended both ventrally and laterally, a state that can best be termed semicircular (fig. 9). Posteriorly, it extends to an area above the arm insertion.

Males were recorded at 22.2°C in an aquarium. The advertisement call of *O. mutabor* consists of a series of 9-19 notes ($\bar{x} = 12.5; n = 11$ calls) (fig. 10). Notes are pulsed, and there are 1-7 pulses per note ($\bar{x} = 4.0; n = 138$ notes). Usually, the notes of the first third of the call and the last note have less pulses than the other notes. Calls have lengths of 3.02-6.43 s ($\bar{x} = 4.41$ s; $n = 11$). Twenty-two notes randomly chosen from the central section of 11 calls have lengths of 0.12-0.28 s ($\bar{x} = 0.21$ s), and corresponding (following) internote intervals of 0.11-0.30 s ($\bar{x} = 0.17$ s). The fundamental frequency is between 0.51 and 0.72 kHz; the dominant frequency is between 0.86 and 1.30 kHz. Sometimes a short call is produced in between longer ones. It is made up of two notes, each consisting of two pulses. Structurally, it is not different from notes within the long call.

Reproductive behaviour. Our own field experience is too limited to give information on the breeding season of *O. mutabor*. Duellman (1978) assumed that it was a lengthy period of time, because juveniles were found from March to November. We observed spawning in the aquarium. Males called from twigs or the edge of water. Pairs spawned while sitting in shallow water. Females first flexed their backs slightly upward, then strongly downward, at the same time raising the cloaca above the water line. About 30-40 eggs were released as a small clump floating at the surface. Within about half an hour the eggs formed a single-layer surface film. Duellman (1978) obtained 15 gravid females in May with 480-1150 ($\bar{x} = 839$) mature ovarian eggs. We obtained two clutches with 821 and 1330 eggs.

Ontogenetic colour change. Trueb and Duellman (1971) described the ontogenetic change in colour pattern of preserved frogs of this species. Colour change in live specimens is even more drastic (fig. 1D, 11). Tadpoles at Stage 42 (Gosner, 1960) already have bright red eyes. Newly metamorphosed froglets are 16-17 mm in SVL. They are olive brown to tan dorsally and laterally. A broad interorbital bar is fused or not on the orbit with a broad dorsolateral stripe on each side, fused or not above the vent. Bar and stripes are creamy white to creamy yellow. The iris is bright red. A supralabial stripe and a subocular spot are absent. Limbs are yellowish green, somewhat translucent, and lack any light knee, elbow, or heel spots. Hands and fingers are coloured like the rest of the limbs. Ventral surfaces are
yellowish and translucent. Bones are green. Males of 30-35 mm and females of 30-40 mm are pale olive to pale tan with fading greenish cream dorsolateral stripes and interorbital bar. On the back and on the limbs, transverse dark tan stripes and bars are present. There is a creamy white subocular spot and the iris is coppery red. Sexes are distinguishable by the presence or absence of granules.

Habitat and distribution. The type locality in the Cordillera Galeras is a steep slope bordering Río Pucuno on the road from Narupa (near Jondachi) to Coca, 0°42′24″S / 77°35′54″W (GPS reading), about 44 km (by road) from Narupa. Single frogs of both sexes were encountered on trees in primary forest there. A small breeding chorus of about 10 males was found at the edge of the forest in secondary vegetation (Hedychium coronarium, Zingiberaceae) along a shallow, slowly running roadside ditch. At a second site, at Selva Viva, Napo Province, Ecuador, about 600 m a.s.l., we observed a single male that had apparently been calling in the grassy vegetation at the edge of a temporary puddle in primary forest. Duellman (1978) reported the species from both primary and secondary forest near Santa Cecilia, Sucumbíos Province, Ecuador.

Osteocephalus mutabor is a frog of low to intermediate elevation on the western Andean foothills. The type locality at 1000 m a.s.l. seems to be near the upper level of its range. Trueb and Duellman (1971) mention a site at 1100 m that most likely refers to O. mutabor. The lowest site in Ecuador is San Pablo de Kantesiya on the Río Aguarico at approximately 250 m. We have seen specimens only from Sucumbíos, Napo and Pastaza Provinces in Amazonian Ecuador. The species may well range northward into Colombia. Duellman and Mendelson (1995) reported the species from two sites close to the Peruvian-Ecuadorian border near Andoas, Peru, at 185 and 333 m a.s.l. Because misidentifications with O. leprieurii-like frogs cannot be ruled out we do not include other literature records here.

Etymology. The specific name is the first person singular future of the Latin verb mutare (“I will change”), referring to the dramatic ontogenetic colour change that the juveniles of this species undergo.

Discussion

Trueb and Duellman (1971) used 20 characters to define Osteocephalus on the basis of five species. One of the characters (amount of webbing) was slightly altered by Duellman and Hoogmoed (1992) to accommodate O. rodriguezi (Rivero, 1968), a species later transferred to the genus Tepuihyla (Ayarzagüena et al., 1992). With more than three times the number of species some of the original characters do not hold true for the whole genus any more. These are listed below. The numbers refer to Trueb and Duellman’s (1971) numbers of characters. (1) Skull broader than long: slightly longer than broad in O. deridens (Jungfer et al., 2000), O. sp. (Smith et al., in press), and O. subtilis (Martins and Cardoso, 1987). (6) Vocal sacs paired, posterior, and when inflated protruding posteroventral or

Part of the differences that exist within the genus can be referred to the adaptive radiation of the various species with respect to their reproductive biology. It has been supposed that a single median subgular vocal sac is the ancestral state in frogs (Liu, 1935), a semicircular and the paired vocal sacs would be derived from the single subgular state. However, those *Osteocephalus* known to have the single subgular state (*O. deridens*, *O. fuscifacies*, *O. oophagus*, and *O. planiceps*) are specialized with respect to their calling or breeding site. At least *O. deridens* and *O. oophagus* breed in bromeliads, and *O. fuscifacies* and *O. planiceps* call from there. A relatively small subgular vocal sac may be an adaptation towards limited space in a narrow leaf axil and could therefore be derived within the genus. All species breeding in or calling from bromeliads, except *O. planiceps*, are small to medium-sized frogs. An example for a similar adaptation can be found in the related genus *Phrynohyas*, in which a small species breeding in treeholes has a subgular vocal sac instead of the paired ones of all other species that are more generalized in their reproductive biology (Jungfer and Gaucher, in prep.). Traditional pond-breeding species, such as *O. leprieurii* and *O. taurinus*, usually sit on vegetation or float in water while calling. Both of them have paired lateral vocal sacs (with an additional subgular vocal sac in *O. leprieurii*) that might have been derived from a character state similar to that of *O. mutabor*.

The differences in denticle rows among *Osteocephalus* tadpoles have been considered to be reductions in the case of *O. oophagus* (Jungfer and Schiesari, 1995). These tadpoles do not rasp, but eat conspecific eggs. Dentine row reductions in oophagous tadpoles are also known in dendrobatid frog larvae and other groups (Lannoo et al., 1987). High numbers of denticle rows, such as in the stream-breeding *O. buckleyi*, may be explained as an adaptation towards lotic water. The fact that the pond-breeding *O. taurinus* has the same number of denticle rows as *O. buckleyi* and that the latter lays eggs in single-layer surface films (personal observation, KHJ) indicates that stream-breeding is derived in *Osteocephalus*. Surface films are considered to be adaptations to warm, stagnant water low in oxygen contents to allow embryos to get oxygen directly from the surface of the water (Duellman and Trueb, 1986) and should be of little value in a stream.
The spiny backs of many male *Osteocephalus* may have a function in quick sex recognition during amplexus in choruses of explosive-breeding species in which males outnumber females by far, such as *O. leprieurii* (Gottsberger, 1999) or *O. taurinus* (Bokermann, 1964). Phytotelmata-breeding species, such as *O. oophagus*, are scattered throughout the forest and do not occur in large congregations (Jungfer and Weygoldt, 1999). Slower sex recognition by other means than skin texture may not be disadvantageous there. Apart from *O. oophagus*, smooth dorsa are present in the bromeliad-breeding or -calling *O. deridens*, *O. fuscifacies*, and *O. sp.* (Duellman and Mendelson, 1995), and the backs of male *O. planiceps* are granular rather than spinous.

Despite the differences among species, there are enough characters left to unite them. One that has not been included yet in the definition of the genus is the great ontogenetic change that all species undergo, in which juveniles are known. Species of *Osteocephalus* have, on the basis of juveniles, been described as *Hyla* (e.g. *H. elkejungingerae* Henle, 1981) or otherwise been misidentified (e.g. *O. leprieurii* as *Phrynohyas venulosa*, Lescure et al., 1996: fig. 16). Most juvenile *Osteocephalus* resemble each other so closely that they are difficult to distinguish. Almost all species for which descriptions are available, *O. deridens* (Jungfer et al., 2000), *O. elkejungingerae* (Henle, 1981), *O. leprieurii* (this study), *O. oophagus*, *O. taurinus* (Jungfer and Schiesari, 1995), have red eyes and white spots on heels, knees, and arms. Several species look the same, and some, such as *O. mutabor*, have at least the red eyes or white spots (personal observation, KHJ). Considering that ontogeny repeats part of the phylogeny of a species, the similar juvenile colorations of several species indicate that they are all closely allied.

As several more species await description and more data on morphology, reproduction, and ontogeny will be gathered with them, a redefinition of the genus at this time seems to be premature.

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Systematics of Osteocephalus


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