



A new species of spiny-backed treefrog (*Osteocephalus*) from Central Amazonian Brazil (Amphibia: Anura: Hylidae)

KARL-HEINZ JUNGFER¹, VANESSA K. VERDADE², JULIÁN FAIVOVICH^{3,4} & MIGUEL T. RODRIGUES⁵

¹*Institute of Integrated Sciences, Department of Biology, University of Koblenz–Landau, Universitätsstr. 1, 56070 Koblenz, Germany. E-Mail: khjungfer@aol.com*

²*Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Av. dos Estados, 5001, CEP 09210-971, Santo André, São Paulo, Brazil. E-mail: vanessa.verdade@ufabc.edu.br*

³*División Herpetología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”-CONICET, Angel Gallardo 470, 1405 Buenos Aires, Argentina. E-mail: julian@macn.gov.ar*

⁴*Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina*

⁵*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, CEP 05508-090, São Paulo, Brazil. E-mail: mturodri@usp.br*

Abstract

A new species of treefrog of the genus *Osteocephalus* is described from the Rio Abacaxis, a southern tributary of the Amazonas in the state of Amazonas, Brazil. This member of the *O. buckleyi* group is characterized by green dorsal colouration with irregular blotches of various shades of brown, light venter with tan spots and bold dark markings on the posterior surfaces of the thighs. It can be distinguished from its closest relative, *O. helenae* from the same general area, by the lack of an axillary membrane, a few indistinct tubercles on the proximal segment of Finger IV and single ulnar tubercles.

Key words: Amphibia, Anura, Hylidae; Amazonia, Brazil, *Osteocephalus camufatus* sp. nov.

Introduction

Spiny-backed treefrogs of the genus *Osteocephalus* are widespread in the Amazonian and Guianan regions of South America. A molecular phylogenetic study (Jungfer *et al.* 2013) defined five species groups and revealed that the number of species in the genus is largely underestimated and numerous species still await formal description. One of those is a member of the *Osteocephalus buckleyi* species group from Central Amazonia in Brazil distinguishable from their close relatives by molecular and morphological characters and referred to as Confirmed Candidate Species (following the terminology of Vieites *et al.* 2009) in that paper. Frogs of the *Osteocephalus buckleyi* group are stream-breeding, most of them occurring along the eastern Andean edge at elevations between 600 and 2300 m, namely *O. carri* (Cochran & Goin, 1970), *O. duellmani* Jungfer, 2011, *O. festae* (Peracca, 1904), *O. mimeticus* (Melin, 1941), *O. mutabor* Jungfer & Hödl, 2002, and *O. verruciger* (Werner, 1901). Several species also inhabit the lowlands eastward to the mouth of the Amazonas. These have been problematic from a taxonomic point of view. They were considered one single species, *O. buckleyi* (Boulenger, 1882), by Trueb & Duellman (1971), but several ones, also including an upland species (Lynch 2006), were later removed from its synonymy (Duellman & Mendelson 1995, Jungfer 2010, Jungfer *et al.* 2013) or described as new (Ron *et al.* 2012). These frogs from elevations mostly below 600 m currently comprise four species: *Osteocephalus buckleyi* from the western Amazon Basin in eastern Ecuador and northern to central Peru (Ron *et al.* 2012, Jungfer *et al.* 2013), *O. cabrerai* (Cochran & Goin, 1970) from southeastern Colombia (Cochran & Goin 1970; Lynch 2002), northeastern Peru (Jungfer 2010; Ron *et al.* 2012) and northeastern Ecuador (Ron *et al.* 2011), *O. cannatellai* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012 from lowlands, but also up to 1290 m asl. of the western Amazon Basin in northern Colombia, eastern Ecuador and northern Peru (Ron *et al.* 2012, Jungfer *et al.* 2013), and *O. helenae* (Ruthven, 1919) inhabiting a vast range from Santa Cruz, Bolivia, to the coastal Guianas (Jungfer *et al.* 2013).

Among these lowland species there are frogs that are partly or predominantly green dorsally and laterally (with individual variation), have posterior surfaces of the thighs light with dark spots or bars in preservative (though sometimes uniform bluish or brownish in life) and are tuberculate on the head, especially on the canthus rostralis and on the upper eyelids (Gorzula & Señaris “1988”, Duellman & Mendelson 1995, Lescure & Marty 2000, Lynch 2002, Lima *et al.* 2006, Kok & Kalamandeen 2008, Jungfer 2010, Ron *et al.* 2012). As these three characters are absent both in the aforementioned upland members of the *O. buckleyi* group (Trueb & Duellman 1970, 1971, Jungfer & Hödl 2002, Jungfer 2010, 2011, Ron *et al.* 2010) and all species of other groups (i.e. the *O. alboguttatus*, *O. leprieurii*, *O. planiceps* and *O. taurinus* groups) (e.g. Trueb & Duellman 1971, Duellman 1978, Duellman & Mendelson 1995, Jungfer *et al.* 2000, Jungfer & Hödl 2002), the lowland species can be distinguished relatively easily from the rest of their congeners. But they are not so easily distinguishable morphologically from one another (e.g. Ron *et al.* 2011). This also holds true for a new lowland species which has previously been identified on a molecular basis (Jungfer *et al.* 2013) using tissues from specimens obtained along the Rio Abacaxis, a southern tributary of the Amazonas in Amazonas, Brazil. Herein we proceed to its formal description.

Materials and methods

Measurements taken follow Duellman (2001), except that foot length is the distance from the bent tibiotarsal articulation to the tip of the fourth toe. Snout length is calculated as the distance between eye and naris proportional to head length (EN/HL). Terminology of skin texture is as described by Duellman & Lehr (2009) for terraranan frogs. Webbing formula is that of Savage & Heyer (1967), as modified by Myers & Duellman (1982). Enumeration of diagnostic characters follows Jungfer (2010). For ease of comparison unknown characters are also stated. Abbreviations are as follows: ED: eye diameter; EN: distance from eye to naris; FD: diameter of finger disc on third finger; FL: foot length; HL: head length; HW: head width; IN: internarial distance; SVL: snout-vent length; TD: tympanum diameter; TE: distance between tympanum and eye; TL: tibia length. Measurements (all in mm) were made using digital callipers or the ocular micrometer of a dissecting microscope if less than 5 mm. Museum abbreviations follow Frost (2015). The numerical code used for the new species by Jungfer *et al.* (2013) refers to “Ca” for candidate species, and the Genbank accession number of one of the sequences obtained from the holotype, using the system established by Padial *et al.* (2010).

Results

Osteocephalus camufatus sp. nov.

(Figs. 1–4)

Osteocephalus buckleyi [Ca1_MTR12779_2748]—Jungfer *et al.* 2013

Holotype: MZUSP 142389 (field number MTR 12779), an adult male of 39.5 mm SVL with well-developed nuptial pads from Brazil: Amazonas: Igarapé-açu (04°20'40"S 58°38'06"W), right bank of Rio Abacaxis, 30 m asl., collected by Miguel T. Rodrigues, Sergio Marques de Souza, José Cassimiro and José Mário Guellere, on 9 January 2007 (Figs. 1–4).

Paratype: MZUSP 157020 (field number MTR 13147), an adult male with well-developed nuptial pads from Brazil: Amazonas: Areal, left bank of Rio Abacaxis (04°35'49"S 58°13'14"W), 39 m asl., collected by Miguel T. Rodrigues, Sergio Marques de Souza, José Cassimiro and José Mário Guellere, on 20 January 2007.

Diagnosis and comparisons. *Osteocephalus camufatus* may be diagnosed as (1) a small to medium sized species (as defined by Jungfer 2010: 29) in males (females unknown); (2) skin on dorsum of males shagreen with a few irregular small tubercles, only some bearing keratinized tips; (3) skin on flanks coarsely areolate between limb insertions; (4) rounded, tuberculate canthus rostralis curved inward; (5) frontoparietal ridges not visible externally; (6) dentigerous processes of vomers angular; (7) thick tuberculate supratympanic fold from the posterior edge of the orbit sloping in an arch towards the arm insertion, not reaching below tympanum posteroventrally; (8) webbing on inner edge of third finger extending slightly beyond penultimate subarticular tubercle; (9) distal subarticular

tubercle on Finger IV bifid; (10) dorsum boldly blotched irregularly; (11) throat, chest and venter creamy tan to creamy white with numerous irregular tan spots; (12) supralabial area with irregular light and dark markings; (13) flanks light with irregular dark markings; (14) vocal sacs paired, protruding ventral to angles of jaws; (15) juvenile colouration unknown; (16) tadpole habitat (most likely in pools along streams) and labial tooth row formula unknown; (17) colour of tibiofibular bones white in preservative.

O. camufatus is a member of the *O. buckleyi* species group as revealed by molecular data. A phylogenetic analysis using both maximum parsimony (MP) and likelihood (ML) inference resulted in trees that showed that *O. camufatus* was basal to a large and well-supported clade containing frogs from large areas of Amazonia and Guiana. The oldest available name for this clade is *O. helenae* (Jungfer *et al.* 2013). Uncorrected *p* distances of the mitochondrial 16S gene between *O. camufatus* and *O. helenae* from various localities were 1.3–2.6, while genetic divergences within *O. helenae*, whose subclade relationships are not yet sufficiently resolved, were 0.0–2.2 (Jungfer *et al.* 2013: Appendix S4d).

The new species shares with several other species of the group the following character states: 1) greenish ground colour, 2) strongly tuberculate canthus rostralis and upper eyelids and 3) posterior surfaces of thighs light with large dark brown spots in preservative. These three characters distinguish it from all frogs in the *O. alboguttatus*, *O. leprieurii*, *O. planiceps* and *O. taurinus* groups (Jungfer *et al.* 2013) in which the ground colours are shades of tan or brown, the canthus rostralis is smooth to granulate and the posterior thigh surfaces are uniform. From other species in the *O. buckleyi* group it differs as follows (characters of *O. camufatus* in parentheses): Six upland species from the eastern Andean slopes between 600 and 2300 m differ as follows: in *Osteocephalus carri*, a predominantly brown species (bold blotches of green and brown), the canthus rostralis and upper eyelids are smooth (strongly tuberculate) and the iris is black with golden spots in life (light); *O. duellmani* is a tan species with or without dark brown blotches (bold blotches of green and brown), with the posterior surfaces of the thighs uniform tan (marbled) and the canthus and upper eyelid bearing a few low tubercles (strongly tuberculate); *O. festae* exhibits brown ground colour (bold blotches of green and brown), a dark brown iris in life (light, Fig. 4) and uniform tan posterior thigh surfaces (marbled). Males of *Osteocephalus mimeticus*, *O. mutabor* (the latter also occurring as low as 150 m asl.) and *O. verruciger* have a brown ground color lacking green (blotches in shades of green and brown), uniform posterior thigh surfaces (marbled dark brown), and heavily tuberculate dorsa with numerous spinous tubercles bearing keratinized tips during breeding (a few irregular small tubercles, few of them with keratinization). Species of the *O. buckleyi* group from the lowlands (< 600 m asl.), that in some cases share the greenish ground colour of *O. camufatus*, differ as follows: *Osteocephalus buckleyi* has low tubercles or is smooth on the upper eyelid (strongly tuberculate), and has low or lacks tarsal tubercles (prominent). Breeding males of *O. buckleyi* exhibit dorsal tubercles, many with keratinized tips (few keratinized tips). *Osteocephalus cabrerai* has a row of tubercles on the lower jaw (absent) and an irregular, deep fringe on the outer edge of Finger IV (low tubercles on proximal segment of Finger IV). *Osteocephalus cannatellai* from lowlands, but also up to 1290 m asl. (Ron *et al.* 2012), appears to be larger (38.5–57.2 mm SVL in males, mean, 46.8 mm, Ron *et al.* 2012) (to 40.4 mm, but note that the sample size is *n*=2), and differs by a longer supratympanic fold that reaches the arm insertion (not reaching lower level of tympanum); axillary membrane present (absent); usually a dark venter varying from light grey to brown with or without dark markings (Ron *et al.* 2012) (yellowish white with small irregular brown spots). *Osteocephalus helenae* (Ruthven) is a variable frog throughout its range. Specimens from localities closest to the two sites known for *O. camufatus*, from about 230 km northwest of the type locality, near Manaus and other sites just north and south of the Amazonas in Amazonas, Brazil, exhibit an axillary membrane (absent), a scalloped fringe on the outer edge of Finger IV continued to the ulna (low, indistinct tubercles on proximal segment of Finger IV and single tubercles on ulna), and more webbing on the hand, reaching beyond the distal subarticular tubercle on Finger IV (to distal subarticular tubercle, Fig. 4a). Specimens from near Rio Branco, Acre, Brazil, roughly 1100 km WSW of the type locality of *O. camufatus*, have posterior thigh surfaces brown, finely mottled with cream (bold dark brown markings on light ground) and lack tubercles on the eyelids (present).

Frogs in the closely related genus *Dryaderces* are similar in general appearance to some frogs of the *O. buckleyi* group, but can be distinguished as follows: They differ in exhibiting bold dark ventral reticulation (dark spotting) and uniform dark iris (light iris) in *D. pearsoni* (Gaige), a longer snout of EN/HL 0.27–0.33 (shorter, EN/HL 0.25), non-tuberculate canthus rostralis (tuberculate) and light, uniform venter (venter with small dark spots) in *Dryaderces* sp. (*Dryaderces pearsoni* [Ca1_MTR13158_2768] of Jungfer *et al.* 2013) (KHJ, unpublished data). The inspection of a fresh specimen of “*Osteocephalus*” *inframaculatus* (Boulenger), a species until recently only

known from the holotype and tentatively placed with the *O. buckleyi* group by Jungfer (2010), was placed in *Dryaderces* by Hoogmoed (2013). It is easily distinguishable from *O. camufatus* by its bold dark markings on throat and chest and has a longer snout with EN/HL 0.33 (0.25) and larger tympanum with TD/HL 0.26 (0.22–0.23).

Description of holotype. Snout short (EN/HL 0.245) and blunt, head as long as wide. Nostrils raised, opening laterally. Snout truncate in dorsal and lateral outline. Canthus rostralis well-developed, rounded, describing an inwardly curved line, bearing large tubercles. Skin of head coarsely shagreen, orbits with a few additional small tubercles, some bearing small keratinized tips. A few more scattered keratinized tips on some tubercles of the head and anterior part of the body. No frontoparietal crests evident externally. Loreal region strongly concave bearing low tubercles. Lips flared below the eye. Choanae oblique, elliptical, though slightly angular. Dentigerous processes of vomers short, considerably shorter than choanae width, angular, not in contact with each other, bearing 4 teeth on the left and 3 on the right. The anterior edges of the dentigerous processes are in line with the posterior third of the choanae, their posterior edges well behind the posterior margins of the choanae. Tongue elliptical, slightly wider (by 6%) than long. The vocal sacs are paired, subgular and protrude ventral to the jaw articulation. A thick glandular supratympanic fold from the posterior part of the orbit medially, covering tympanic annulus dorsally from “11” (when tympanum is thought to be a clock face) to “3”, then sloping in a curve towards the arm insertion, reaching no further than the lower one third level of the tympanum. The latter is conspicuous, rounded (barely wider than high), with about 66% the diameter of the eye. Skin on dorsum coarsely shagreen with a few low, irregularly spaced tubercles. Transversal furrows on the shoulders are absent. Skin smooth between eye and tympanum and areolate posterior to the tympanum above the arm insertion, very coarsely areolate laterally between the limb insertions. Throat and belly areolate. Cloacal opening situated at about half the level of thighs, surrounded by large, irregular warts (except on the cloacal flap, which is smooth). Skin on arms shagreen with a few faint tubercles dorsally, hidden surfaces finely shagreen. A row of low ulnar tubercles also encompasses the proximal segment of Finger IV. Axillary membrane absent. Dorsal surfaces of hind legs shagreen, posterior surfaces of thighs and ventral parts of shank smooth, proximal three fourths of thigh coarsely areolate ventrally. A row of low outer tarsal tubercles from the heel to the proximal subarticular tubercle of Toe V. On the heel, three and four low tubercles, respectively, directed dorsally and laterally. Finger and toe discs elliptical and wider than long. Diameter of disc on Finger III is 74% of tympanum diameter. Relative finger length is $I < II < IV < III$. On the thumb dark brown nuptial excrescences on the posterolateral side from its base to the level of the distal end of the subarticular tubercle. A large elliptical thenar tubercle. Two rounded palmar tubercles. Proximal segments of Fingers II–IV tuberculate, two supernumerary tubercles each on Finger II and Finger IV. Subarticular tubercles conical except the distal ones on Finger III and Finger IV, which are bifid. Webbing formula is **I basal II 1 ½—2 ¾ III 2 ⅓—2 IV**.

On the foot a large elliptical inner metatarsal tubercle and a small rounded plantar tubercle. A larger rounded conical outer metatarsal tubercle in line with the row of tarsal tubercles. The latter form a shallow fringe on the distal part of the proximal toe segment that is continued to the toe disc. A few indistinct supernumerary tubercles on the proximal segments of Toes III–V. Subarticular tubercles single and conical. Relative lengths of appressed toes $I < II < III \leq IV < V$. Webbing formula: **I 1—2 II 1—2 III 1—1⁺ IV 1⁺—1 V**.

Measurements and proportions. SVL 39.5; HL 14.3; HW 14.3; TL 22.2; FL 26.8; ED 4.7; TD 3.1; FD 2.3; EN 3.5; IN 3.4; TE 2.0. HL/SVL 0.36; HW/SVL 0.36; TL/SVL 0.56; FL/SVL 0.68; TD/ED 0.66; TD/FD 1.35; EN/HL 0.25; EN/SVL 0.09; HL/HW 1.00; TE/TD 0.65; TD/HL 0.22.

Colour in preservative. The ground colour of head and dorsum is light (green in life) with numerous, more or less irregular blotches in tan and dark brown (various shades of brown in life). This pattern extends to the lateral sides of the head and body. One ill-defined dark brown mark somewhat more conspicuous than others has two arms between the eyes (including the orbits), two between the tympana and on midbody the posterior two arms diverging like the lower part of an X and are continued on the flanks. Two additional ill-defined dark brown marks posteriorly to the proximal part of the sacrum, continued to the flanks. Throat and belly with small irregular brown spots. Although there are light areas on the upper lip, there are no discrete labial marks distinguishable from the rest of the pattern. Tympanum tan. Arms dorsally and laterally with irregular dark brown crossbars, with irregular brown spotting ventrally. Legs dorsally with irregular dark brown crossbars, posterior surfaces of thigh and calf marbled dark brown. Ventral surfaces of thigh tan with lighter areolae, of femur tan peppered with darker markings. Webbing tan, slightly marbled. Subcloacal warts are in creamy white and different shades of tan.



FIGURE 1. a. Dorsal, b. ventral view of the preserved holotype of *O. camufatus* sp. nov.

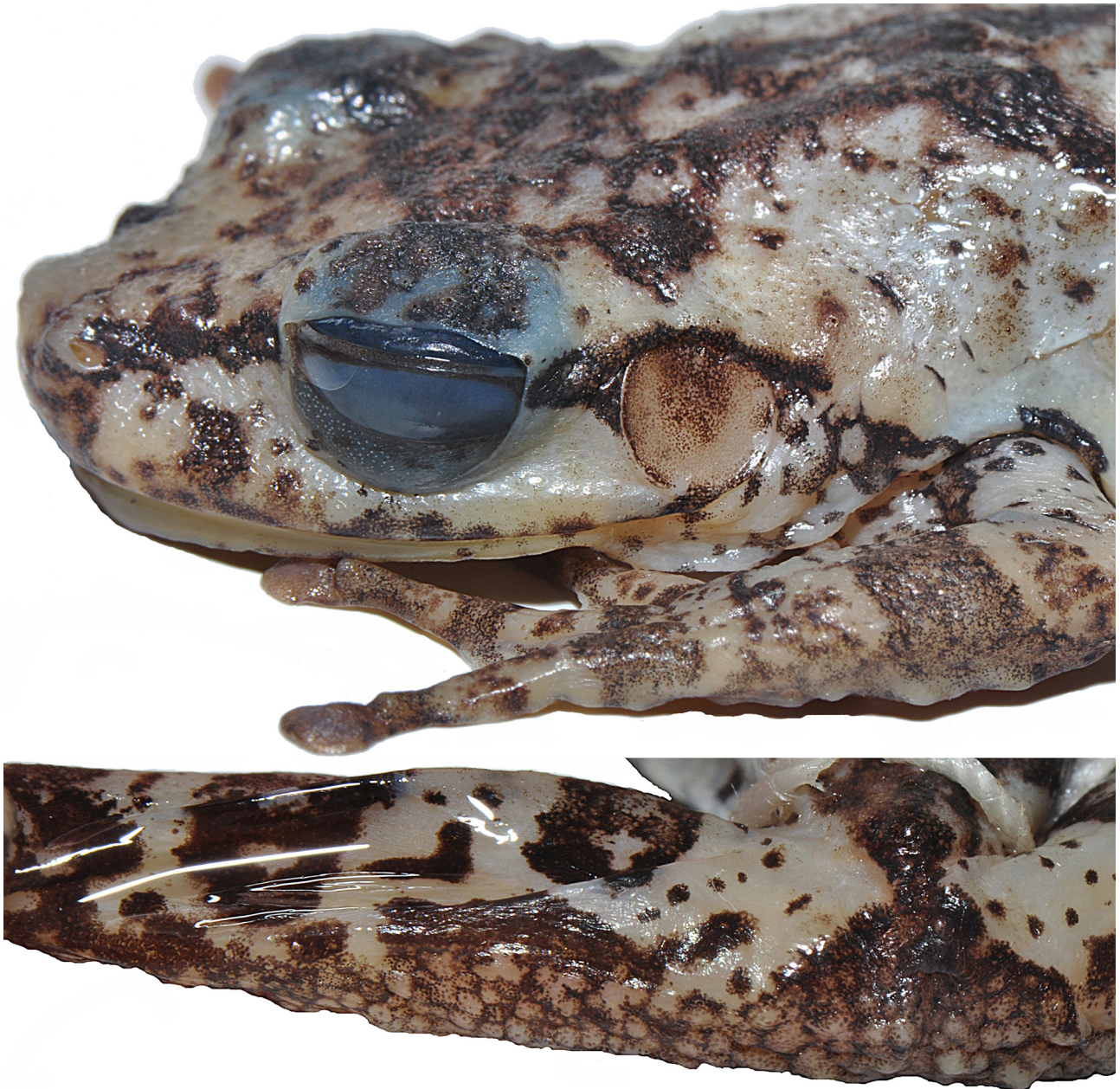


FIGURE 2. Lateral view of the head, circumcloacal area and posterior surface of thigh of the preserved holotype of *O. camufatus* sp. nov.

Colour in life. Colours were taken from photographs (Fig. 4). Dorsal surfaces covered by bold blotches of different shades of green and brown. A light mark posteroventral to the eye is light green, the posterior part of the upper lip dark brown, of the lower lip white. The tympanum is tan. The iris is light tan in its upper half and creamy white in its lower one, the latter bearing a diffuse dark brown median vertical streak. Upper and lower halves are separated by a weakly demarcated reddish brown horizontal streak and are both finely reticulated black. Some light blue coloration can be seen on the hidden surface of the thigh. Outer tarsal and heel as well as ulnar tubercles are tipped white.

Variation in the paratype. An adult male slightly larger than the holotype (40.4 mm SVL) with well-developed nuptial pads. The snout is bluntly rounded in dorsal aspect. The dentigerous processes bear five teeth on each side. Keratinized tips on tubercles are lacking entirely. Coloration is similar, but the large tan dorsal mark is less conspicuously outlined. The belly is spotted evenly. There is slightly more webbing on the hand with **I** basal **II** $1\frac{2}{3}$ — $2\frac{2}{3}$ **III** 2—2 **IV** and little variation on the foot: **I** 1^+ —2 **II** 1—2 **III** $1-1\frac{1}{3}$ **IV** $1\frac{1}{3}$ —1 **V**. There is also little variation in proportions.



FIGURE 3. a. Right hand and forearm and b. right foot of the preserved holotype of *O. camufatus* sp. nov. Not to scale.

Measurements and proportions. SVL 40.4; HL 15.0; HW 14.9; TL 21.2; FL 25.9; ED 5.0; TD 3.4; FD 2.1; EN 3.7; IN 3.3; TE 1.9. HL/SVL 0.37; HW/SVL 0.37; TL/SVL 0.53; FL/SVL 0.64; TD/ED 0.68; TD/FD 1.62; EN/HL 0.25; EN/SVL 0.09; HL/HW 1.01; TE/TD 0.56; TD/HL 0.23.

Distribution and habitat. The new species is so far only known from two sites about 54 km apart along the terra firme forests of the right bank of the Rio Abacaxis, a black water river south of the Amazonas that discharges into Paran do Arari, a white water channel delimiting the southern border of Ilha de Tupinambarana (Fig. 5). This

is a huge island (about 300 km long) extending between Nova Olinda do Norte on the lower Rio Madeira to Parintins on the Amazonas. Habitat at Igarapé-açu consisted of typical terra firme forest with higher trees reaching up to 40 m and a diameter at breast height of around 80–100 cm. The understory was particularly rich in low palm trees and the leaf litter was dense. The specimen was obtained close to a small stream perched on a tree about 1 m high. At Areal, a site further upstream (also referred to as Paca or Pacamiri locally) the local habitat consisted of an extensive white sand area (campinarana) with scattered vegetation near the margin of the river with abundant clumps of ground bromeliads, gradually replaced by denser areas covered by palm trees and then terra firme forest. The terra firme forest with large trees became more evident farther from the river margin, where the second specimen was obtained.

Etymology. The species name *camufatus* is the Latinized past participle of Italian *camuffare*, to disguise or mask, from which the word *camouflaged* is derived, in allusion to the shape-dissolving pattern of greens and browns of the new species.



FIGURE 4. Adult male holotype of *O. camufatus* n. sp. from Igarapé-açu, Rio Abacaxis, Estado Amazonas, Brazil. Enclosure: close-up of the eye.

Acknowledgements

We are grateful to to Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior (CAPES) for funding. For help in field we thank Sergio Marques de Souza, José Cassimiro and José Mário Guellere. JF thanks ANPCyT 2011–1895, 2013-404, Grants 2012/10000-5, and 2013/50741-7, São Paulo Research Foundation (FAPESP), and CONICET PIP 11220110100889. For access to comparative material we are grateful to Ana Almendáriz (EPN), Franco Andreone (MZUT), Rafe Brown, Linda Trueb and William E. Duellman (KU), Barry T. Clarke and Colin McCarthy (BMNH), Jesús Córdova and César Aguilar (MUSM), Raffael Ernst (MTD), Darrel R. Frost and David Kizirian (AMNH), Alexander Haas and Jakob Hallermann (ZMH), W. Ronald Heyer (USNM), Gunther Köhler (SMF), John D. Lynch (ICN), Göran Nilson (GNM), Ronald Nussbaum and Greg Schneider (UMMZ), Dennis Rödder and Wolfgang Böhme (ZFMK), Andreas Schlüter (SMNS), Andreas Schmitz (MHNG), Harold K. Voris (FMNH), Hussam Zaher, Carolina Castro-Mello and Alberto Barbosa de Carvalho (MZUSP). We also thank Albertina Lima for photos of additional material from Central Amazonia. Two anonymous reviewers made helpful comments.

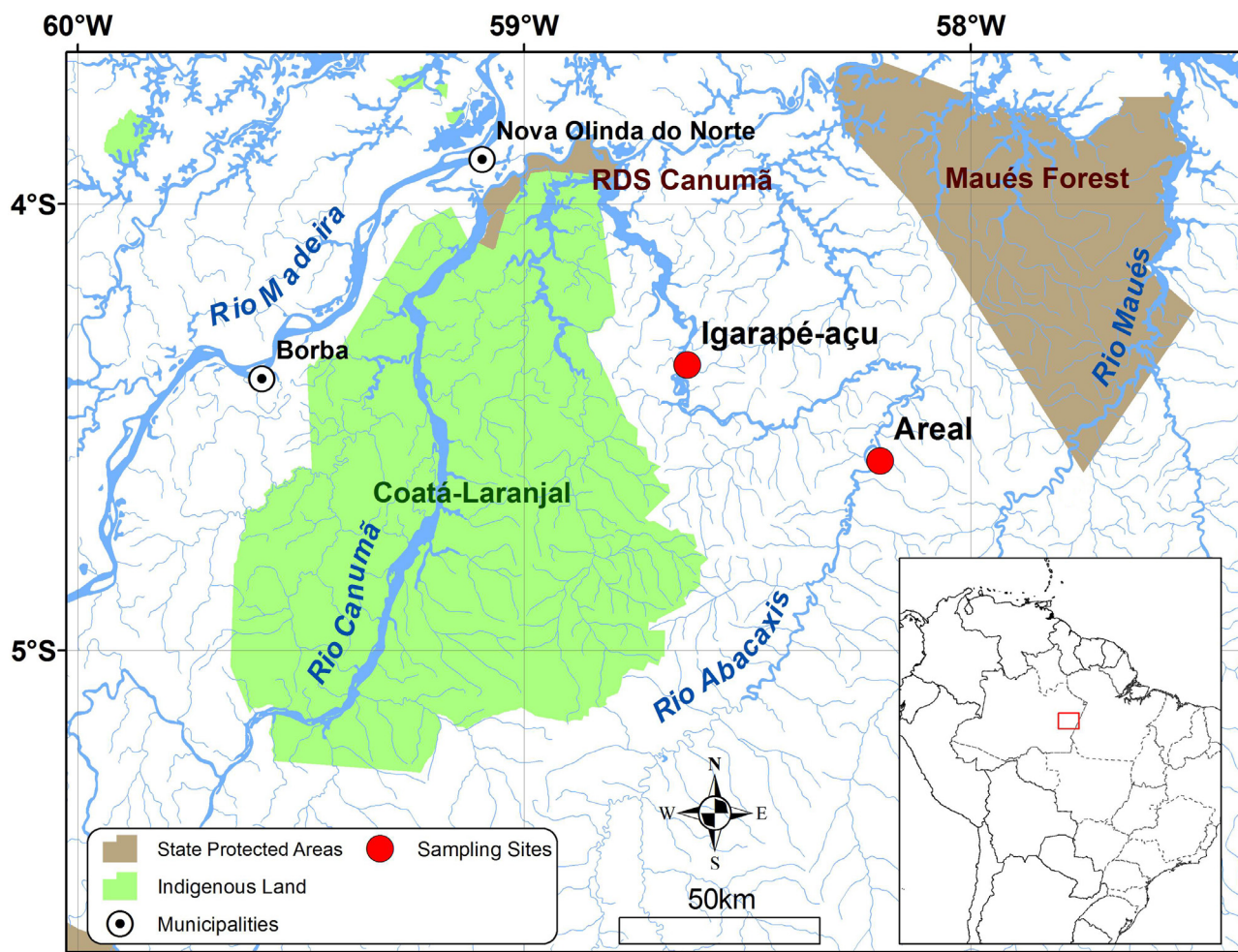


FIGURE 5. Map of the collecting sites of *Osteocephalus camufatus* sp. nov. (red dots) in Estado Amazonas, Brazil. The type locality is Igarapé-açu.

References

- Cochran, D. & Goin, C.J. (1970) Frogs of Colombia. *United States National Museum Bulletin*, 288, 1–655.
<http://dx.doi.org/10.5479/si.03629236.288.1>
- Duellman, W.E. (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication University of Kansas Museum of Natural History*, 65, 1–352.
- Duellman, W.E. (2001) *Hylid frogs of Middle America*. Society for the Study of Amphibians and Reptiles, Ithaca, 1159 pp. + 92 pls.
- Duellman, W.E. & Lehr, E. (2009) *Terrestrial-breeding frogs (Strabomantidae) in Peru*. Natur- und Tier-Verlag, Münster, 382 pp.
- Duellman, W.E. & Mendelson, J.R. (1995) Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. *University of Kansas Science Bulletin*, 55, 329–376.
<http://dx.doi.org/10.5962/bhl.part.779>
- Frost, D.R. (2015) Amphibian Species of the World 6.0, an Online Reference. Available from: <http://research.amnh.org/herpetology/amphibia/index.html> (accessed 30 November 2015)
- Gorzula, S. & Señaris, J.C. ("1998" [1999]) Contribution to the herpetofauna of the Venezuelan Guayana I. A data base. *Scientia Guianae*, 8, 1–270.
- Hoogmoed, M. (2013) Rediscovery of the rare tree frog *Hyla inframaculata* Boulenger, 1882 (Anura: Hylidae), in Amazonian Brazil with notes on variation and distribution, and its generic allocation. *Amphibia-Reptilia*, 34, 421–432.
<http://dx.doi.org/10.1163/15685381-00002907>
- Jungfer, K.-H. (2010) The taxonomic status of some spiny-backed treefrogs, genus *Osteocephalus* (Amphibia: Anura: Hylidae). *Zootaxa*, 2407, 28–50.

- Jungfer, K.-H., Faivovich, J., Padial, J.M., Castroviejo-Fisher, S., Lyra, M.M., Berneck, B.V.M., Iglesias, P.P., Kok, P.J.R., MacCulloch, R.D., Rodrigues, M.T., Verdade, V.K., Torres Gastello, C.P., Chaparro, J.C., Valdujo, P.H., Reichle, S., Moravec, J., Gvoždík, V., Gagliardi-Urrutia, G., Ernst, R., De la Riva, I., Means, D.B., Lima, A.P., Señaris, J.C., Wheeler, W.C. & Haddad, C.F.B. (2013) Systematics of spiny-backed treefrogs (Hylidae: *Osteocephalus*): an Amazonian puzzle. *Zoologica Scripta*, 42, 351–380 + online appendix. Available from: <http://onlinelibrary.wiley.com/doi/10.1111/zsc.12015/supinfo> (Accessed 19 May 2016)
- Jungfer, K.-H. & Hödl, W. (2002) A new species of *Osteocephalus* from Ecuador and a redescription of *O. lepreurii* (Duméril & Bibron, 1841) (Anura: Hylidae). *Amphibia-Reptilia*, 23, 21–46.
<http://dx.doi.org/10.1163/156853802320877609>
- Jungfer, K.-H., Ron, S., Seipp, R. & Almendáriz, A. (2000) Two new species of hylid frogs, genus *Osteocephalus*, from Amazonian Ecuador. *Amphibia-Reptilia*, 21, 327–340.
<http://dx.doi.org/10.1163/156853800507525>
- Kok, P.J.R. & Kalamandeen, M. (2008) Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana. *ABC Taxa*, 5, 1–278.
- Lescure, J. & Marty, C. (2000) Atlas des Amphibiens de Guyane. *Patrimoines Naturels*, 45, 1–388.
- Lima, A.P., Magnusson, W.E., Menin, M., Erdtmann, L.K., Rodrigues, D.J., Keller, K. & Hödl, W. (2006) *Guia de sapos da Reserva Adolpho Ducke, Amazônia Central. Guide to the frogs of Reserva Adolpho Ducke, Central Amazonia*. Attema Design Editorial, Manaus, 168 pp.
- Lynch, J.D. (2002) A new species of the genus *Osteocephalus* (Hylidae: Anura) from the western Amazon. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 26, 289–292.
- Lynch, J.D. (2006) The amphibian fauna in the Villavicencio region of eastern Colombia. *Caldasia*, 28, 135–155.
- Myers, C.W. & Duellman, W.E. (1982) A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates*, 2752, 1–32.
- Padial, J.M., Miralles, A., De la Riva, I. & Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7 (16), 1–14.
<http://dx.doi.org/10.1186/1742-9994-7-16>
- Ron, S.R., Toral, E., Venegas, P.J. & Barnes, C.W. (2010) Taxonomic revision and phylogenetic position of *Osteocephalus festae* (Anura, Hylidae) with description of its larva. *ZooKeys*, 70, 67–92.
<http://dx.doi.org/10.3897/zookeys.70.765>
- Ron, S.R., Toral, E., Ortiz, D. & Almendáriz, A. (2011) Amphibia, Hylidae, *Osteocephalus cabrerai* Cochran and Goin, 1970: First confirmed records from Ecuador with distribution map. *Check List*, 7, 323–325.
- Ron, S.R., Venegas, P.J., Toral, E., Read, M., Ortiz, D.A. & Manzano, A.L. (2012) Systematics of the *Osteocephalus buckleyi* species complex (Anura, Hylidae) from Ecuador and Peru. *ZooKeys*, 229, 1–52.
<http://dx.doi.org/10.3897/zookeys.229.3580>
- Savage, J.M. & Heyer, W.R. (1967) Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. *Beiträge zur Neotropischen Fauna*, 5, 111–131.
<http://dx.doi.org/10.1080/01650526709360400>
- Trueb, L. & Duellman, W.E. (1970) The systematic status and life history of *Hyla verrucigera* Werner. *Copeia*, 1970, 601–610.
<http://dx.doi.org/10.2307/1442303>
- Trueb, L. & Duellman, W.E. (1971) A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. *Occasional Papers of the Museum of Natural History, The University of Kansas*, 1, 1–48.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Science of the United States of America*, 106, 8267–8272.
<http://dx.doi.org/10.1073/pnas.0810821106>

APPENDIX. Material examined of frogs of the *Osteocephalus buckleyi* species group.

- Osteocephalus buckleyi*: ECUADOR: Napo: Jatun Sacha: KU 217746, SMNS 13714-5. Orellana: Hacienda Primavera, 40 km S Coca: MHNG 2556.58; Yasuní (S 00°41'00"; W 76°24'00"): SMNS 13713. Pastaza: Canelos: BMNH 1947.2.13.40–1947.2.13.41, 1947.2.13.43, 1947.2.13.44 (lectotype), 1947.2.13.45. Sucumbios: San Pablo de Kantesiya: MHNG 2366.39–2366.40; Santa Cecilia: KU 105208–9, 150492–3, 152477, 175500; Shushufindi: MHNG 2560.61. PERU: Loreto: 28 km S Iquitos: MUSM KHJ-F 067.
- Osteocephalus cabrerai*: COLOMBIA: Amazonas: Caño Guacayá: USNM 152759 (holotype). Leticia, Río Pure: ICN 46691–701. PERU: Loreto: Quebrada Negra, Río Iauasiyacu: MUSM KHJ-082–3. Ucayali: 65 km ENE Pucallpa, SE slope Cerro Tahuayi: MUSM 649. Parque Nacional Sierra del Divisor (08°12'16.4"S; 73°52'58.3"W): MUSM 24411, 24413–4.
- Osteocephalus camufatus*: BRAZIL: Amazonas: Igarapé-açu, right bank of Rio Abacaxis, 30 m (04°20'40"S; 58°38'06"W): MZUSP 142389. Areal, left bank of Rio Abacaxis, 39 m (04°35'49"S; 58°13'14"W). MZUSP 157020.

- Osteocephalus carri*: COLOMBIA: Caquetá: Parque Nacional Cordillera Los Picachos, vereda Cristo Rey, 1500–1600 m: ICN

MC-9037-40, MC-9101-2, MC-9440-1, MC-944357, MC-9459, MC-9460-3, MC-9465-81, MC-9483-9, MC-9649-50, MC-9661, MC-9794. Parque Nacional Cordillera Los Picachos, vereda La Esperanza, 1380-1440 m: ICN MC-9802-5, MC-9845, MC-9871-2. *Huila*: Acevedo, Río Suaza, Río Aguas Claras, near San Adolfo, 1400 m: FMNH 69702 (holotype). *Meta*: Villavicencio, parte alta Caño Maizazo: ICN 26988.

Osteocephalus duellmani: ECUADOR: *Morona-Santiago*: Cordillera del Cóndor, Río Piuntza, 1910 m asl, about 3°25'S, 78°27'W: KU 147171 (paratype), 147172 (holotype).

Osteocephalus festae: ECUADOR: *Morona-Santiago*: Valle de Santiago (= lower Río Zamora): MZUT An. 208 (holotype). *Napo*: Archidona: MHNG 2560.60. Loreto, Ávila, subcentro Caimítoyacu: EPN 5577-8. *Sucumbios*: Cuyabeno, Campamento Concienti: EPN AA-5611, AA-5607.

PERU: *Cajamarca*: San Ignacio: El Sauce: MUSM 19224. *San Martín*: 1 km NW Venceremos, 1600 m: KU 217302. 14 km W Venceremos, 2000 m: KU 217303.

Osteocephalus helenae: BOLIVIA: *Santa Cruz*: Buena Vista: MZUSP 95529. BRAZIL: *Acre*: Catuaba (S10°04'00"; W63°37'00"): SMNS 14190-1, 17502, 17520. *Amapá*: Río Maracá, boca Igarapé Camaipí: MZUSP 99990-99999; Seringal Boa Fortuna: MZUSP 74253. *Amazonas*: Reserva Adolpho Ducke: MZUSP 59516, 74253, 75648, 84581; Reserva INPA-WWF (Río Preto): MZUSP 58055. *Rondônia*: Cachoeira de Nazaré, Río Machado: MZUSP 63805. UHE Samuel: MZUSP 76921. GUYANA: *Cuyuni-Mazaruni*: Kartabo: AMNH H-13492. *Demerara-Mahaica*: Marudi Creek: AMNH A-46233. *Essequibo*: Shudikar-wau: AMNH A-49252. *Essequibo Islands-West Demerara*: Dunoon: UMMZ 52681 (holotype). *Potaro-Siparuni*: Iwokrama Forest: MTD 48360-2; Magdalen's Creek, NW bank of Konawaruk River, ca. 40 km WSW Mabura Hill: AMNH A-166220-4, 166229. VENEZUELA: *Amazonas*: SW sector of Cerro Yapacana: AMNH-A 100598.

Osteocephalus mimeticus: PERU: *Ayacucho*: San José on Río Santa Rosa, 1005 m: KU 196994-5. Sivia, Río Apurimac, 760 m: FMNH 39853. *Cuzco*: Pozo Pagoreni, Comunidad Kiriguetti: MUSM 21872. Zona Reservada Nahua Kugapakori: MUSM 23179-80, 23188, 23207, 23218, 23226. *Huánuco*: Fundo Flor, Río Pachitea, 300 m: SMNS 6515. *San Martín*: W slope Abra Tangarana, 7 km NE San Juan de Pacaysapa, 1080 m: KU 212189-90. Cataratas Ahuashiyacu, 14 km NE Tarapoto, 730 m: KU 212191. Río Cainarache, 33 km NE Tarapoto on road to Yurimaguas: KU 209454-5. Río Cumbaza Valley, 9.4 km N Tarapoto, 390 m: KU 212182-5. Roque: GNM 469 (lectotype). Pongo de Shilcayo, ca. 4 km NNW Tarapoto, 470 m: KU 212196-9. 14 km ESE Shapaja, 360 m: KU 212193. 22.7 km NE Tarapoto, 810 m: KU 212200. 28 km NE Tarapoto, 600 m: KU 212201-3. 29 km NE Tarapoto, 550 m: KU 212181. Tocache, Río Huallaga: MUSM 10845. Venceremos, 89 km NW Rioja, 1650 m: KU 212186-7. *Pasco*: Pozuzo, 770 m: MUSM 20351. Puerto Bermudez: MUSM 17801. Santa Isabel: MUSM 17847-52, 18022, 18024. Yaupi, Río Paucartambo, 1600 m: KU 136312. *Ucayali*: Boquerón del Padre Abad: ZFMK 33352, 39614-5, 39748-50, 39752-3, 40152-3.

Osteocephalus mutabor: ECUADOR: *Napo*: South slope of Volcán Sumaco on Río Pucuno, 1000 m, between Guamaní and Guagua Sumaco (0° 42' 24" S; 77° 35' 54" W): EPN H-6658 (holotype), EPN H-6659 (paratype). Comuna Veinticuatro de Mayo: EPN H-5695-9 (paratypes). Río Chaloyacu on Carretera Narupa - Coca: ZFMK 66237 (paratype). San Pablo de Kantesiya: MHNG 2260.4-6, 2260.97, 2366.43, 2366.45, 2366.48, 2366.53, 2366.61-63, 2366.67, 2373.84, 2373.86-87, 2556.57 (paratypes). *Pastaza*: Canelos, 530 m: KU 120915. Locación Petrolera Garza 1, NE Montalvo, 300 m: KU 217747-9. Vicinity of Arutam Biological Field Station: SMF 79721-2 (paratypes). *Sucumbios*: Cascales: EPN-H5716-9 (paratypes). Limoncocha, 200 m: KU 99210-6. Santa Cecilia, 340 m: KU 105210-20, 109509-11, 111971, 122964-87, 123169, 150494-5, 152277.

PERU: *Loreto*: San Jacinto, 175-190 m: KU 221928. 1.5 km N Teniente Lopez, 310-340 m: KU 221929-32.

Osteocephalus verruciger: COLOMBIA: *Caquetá*: Municipio de Florencia: Escuela Tarquí, carretera Altamira-Florencia km 48-49: ICN 23648. Municipio de Florencia: 35.2 km. arriba de Florencia: ICN 23943. Municipio de Florencia: Vereda Tarquí 38.8-39.0 km: ICN 23944-5, ICN 23948, ICN 23952, ICN 23954. Municipio de Florencia: Vereda Tarquí 13.2 km arriba de Florencia: ICN 23946. Municipio de Florencia: 39.3 km arriba de Florencia: ICN 23947. *Huila*: Acevedo, Río Suaza, Río Aguas Claras near San Adolfo, 1400 m: FMNH 69709-10. Palestina: ICN 01542. *Putumayo*: 10.3 km W El Pepino, 1440 m: KU 169586-7, 169589-93, 169595-6, 169599, 169601-4, 169606-7. ECUADOR: *No specific locality*: ZMH-A946 (syntype). *Cotopaxi*: Las Pampas (in error): MHNG 2259.20, 2560.62, 2560.64-68. *Napo*: El Reventador: MHNG 2259.18, 2273.28, 2485.65-70, 2560.63. 2 km SSW Río Reventador, 1700 m: KU 164408, 164414, 164416-9, 164421, 164423-4, 164426. 3.2 km NNE Oritoyacu, 1910 m: KU 178839-44. Río Azuela, 1740 m: KU 143210-2, 143215-7, 143219-24, 164434, SMNS 14197. Río Azuela, 9.5 km W of Reventador, 1630 m: KU 217750-1. Río Salado, 1 km upstream from Río Coca, 1420 m: KU 164437, 164442, 178844, 178846-7. 0.7 km NE Río Salado bridge on Lago Agriro road, 1380 m: KU 190054. San Rafael: MHNG 2259.19, 2272.98-99. S slope Cordillera del Due, 1150 m: KU 123181, 123186. 11.1 km NE Santa Rosa, 1900 m: KU 19004953. 16.5 km NNE Santa Rosa, 1700 m: KU 143209. *Pastaza*: 9.5 km NW Mera, 1270 m: KU 178848. *Tungurahua*: 11 km E Río Negro, 1170 m: KU 146469-70.