Taxonomy and Systematics of Spiny-Backed Treefrogs, Genus *Osteocephalus* (Amphibia: Anura: Hylidae)

Dissertation

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Taxonomy and Systematics of Spiny-Backed Treefrogs, Genus *Osteocephalus* (Amphibia: Anura: Hylidae)

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Disclaimer

New taxon names and nomenclatural changes referred to this dissertation are disclaimed and unavailable for nomenclatural purposes according to ICZN Art. 8.3.

Contents

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Numerous of the data presented here have been accumulated during many years and would probably never have been published by me due to other professional work that needed to be done in first place. It was Ulrich Sinsch's idea to present them as a dissertation. By this the work on *Osteocephalus* became a target-oriented project rather than an accumulation of occasional publications (if at all), and Ulrich's mild pressure now and then made sure that it was finished in (more or less) due time. I have to thank him for his advice and persistency. My sincere thanks to Wolfgang Böhme (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn) and Stefan Lötters (Universität Trier) to act as co-referees. I am also greatly indebted to my family for their patience in the course of this time.

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1. GENERAL INTRODUCTION

Once established to accommodate one very large species of treefrog, the concept of *Osteocephalus* as a genus and its composition has seen dramatic changes during the last few years. Drastic reduction of species through synonymization, the discovery of new species and new, unusual reproductive modes and habitats, transfer to other genera together with taxonomically confusing ontogenetic changes and sexual dimorphism among individuals have made the group a true conundrum far from any natural phylogenetic system, which led J.D. Lynch (2002: 289), renown specialist of large and complex groups, to comment that *Osteocephalus* "…must represent some sort of biological illusion…". This work is a contribution to make *Osteocephalus* a biological reality by clarifying the taxonomy of numerous doubtful species, the morphological and reproductive diversity and its adaptive significance as well as the phylogenetic relationships within the genus and among its sister groups.

1.1. Introduction to the spiny-backed treefrogs (*Osteocephalus*)

Osteocephalus is a treefrog genus in the family Hylidae, subfamily Hylinae, tribe Lophyohylini (Faivovich *et al.* 2005). With 23 currently recognized species in five species groups (this work; see Chapter 3.3 and Table 4.2 on pp. 223-224), these frogs represent an important component of the amphibian fauna of pan-Amazonia (roughly the Amazon Basin and the Guiana Shield with its surrounding lowlands) and are distributed from coastal Venezuela (Delta Amacuro) and the Guianas throughout Amazonia to central Bolivia and central Brazil (Mato Grosso) and from the eastern Andean slopes from Colombia to Bolivia to north-eastern Brazil (Piauí). They range from sea level to 2200 m on the eastern flanks of the Andes (Trueb & Duellman 1971; Jungfer 2010, 2011; La Marca *et al.* 2010a,b; Ron *et al.* 2010).

Species inhabit humid primary or old secondary terra firme lowland and premontane forests, but are sometimes also present at the edge of human-modified regions. Few species have entered drier areas in the south-east along gallery forests (Trueb & Duellman 1971; Duellman 1978; Lynch 2006; La Marca *et al.* 2010b; Valdujo *et al.*

Fig. 1.1. Distribution of frogs of the genus *Osteocephalus* in northern South America. Delimitation based on distributional data of IUCN Red List of Threatened Species (2014), considerably expanded by own data. Dots represent localities where specimens with molecular data were available from.

2012). All *Osteocephalus* are nocturnal and arboreal. During the day they can be found hidden under tree bark, in epiphytic bromeliads or beneath large leaves such as *Philodendron* (pers. obs.). Only two species, *O. planiceps* and *O. yasuni*, were occasionally found hidden in leaf litter on the ground (Deichmann & Williamson 2007). At night they are encountered on bushes and trees at various heights (Duellman 1978; pers. obs.), very often on vertical trunks in a typical position oriented sideways (Fig. 1.2), running (rather than hopping) quickly upwards when disturbed. Only one out of hundreds of encounters were made of a female *O. deridens* foraging on the ground (pers. obs.).

Sizes in the different species range from 31.0 to 109.8 mm in snout-vent length (SVL) (Lynch 2002; this work, see Chapter 3.3.). Males of most species exhibit tuberculate

Fig. 1.2. Female *Osteocephalus planiceps* on a vertical log in a typical position (Estación Biológica Quebrada Blanco, Loreto, Peru).

or even spiny dorsal skin (hence the vernacular name), while backs in females are more or less smooth. A possible adaptive significance of this sexual dimorphism is given in Chapter 1.3.2. Apart from the tuberculate skin in males, some frogs in the genus may be readily recognized in the field by a golden iris interspersed with fine radiating dark lines or by the well ossified skull on which two dorsal lateral flanges (bony frontoparietal ridges) can be seen externally (Fig. 1.4. on p. 10). However, none of these characters pertains to all species in the genus. Of 20 characters used by Trueb & Duellman (1971) to define the genus, at least eight do not hold true any longer as a consequence of the discovery and description or more species exhibiting a wider range of adaptations. At present, apart from some molecular synapomorphies, the only phenetic synapomorphies of the genus are the red iris colour and light markings on the limbs of recently metamorphosed individuals. These characters are lost during later ontogeny (this work, see Chapter 3.3 and also Figs.1.4. on p. 10 and S1 on p. 154).

Most species deposit their eggs (Fig. S10 on p. 218) in stagnant water such as puddles or pools. Eggs are laid as a single-layer surface film, most likely an adaptation to relatively warm water low in oxygen contents (Wells 2007). Phytotelm-breeding species, both in the *O. planiceps* and the *O. taurinus* group (pers. obs.), have both retained this clutch type. But eggs laid by representatives of the stream-breeding *O. buckleyi* group, e.g. *O. buckleyi*, *O. mimeticus* and *O. verruciger*, also have surface-film clutches (pers. obs.), although this does not appear to be an advantage in the well aerated lotic water and indicates that stream-breeding is a derived character in *Osteocephalus* (this work; see Chapter 3.3).

Amplexus is axillary in hylids (Duellman & Trueb 1986). This also includes *Osteocephalus*. Only a few species in one phytotelm-breeding clade have a derived position termed gular amplexus (this work, see Chapter 3.3. and Fig. S11 on p. 219).

Vocal sacs in male *Osteocephalus* are situated laterally and are bilobed with a subgular expansion. A notable adaptive modification to the narrow confines of their calling sites occurs in both groups of phytotelm-breeding species that exhibit single, subgular vocal sacs (this work, see Chapter 3.3. and Fig. S9 on p. 217)

Depending on the egg-deposition site, larvae are either lentic or, in the *O. buckleyi* group, lotic. In accordance with all generalized Lophyohylini tadpoles, *Osteocephalus* larvae usually have two or more anterior and four or more posterior labial tooth rows (Trueb & Duellman 1970; Henle 1981; Hero 1990; Ron *et al.* 2010; Menin *et al.* 2011) and are omnivorous (pers. obs.). Only those species living in phytotelmata and

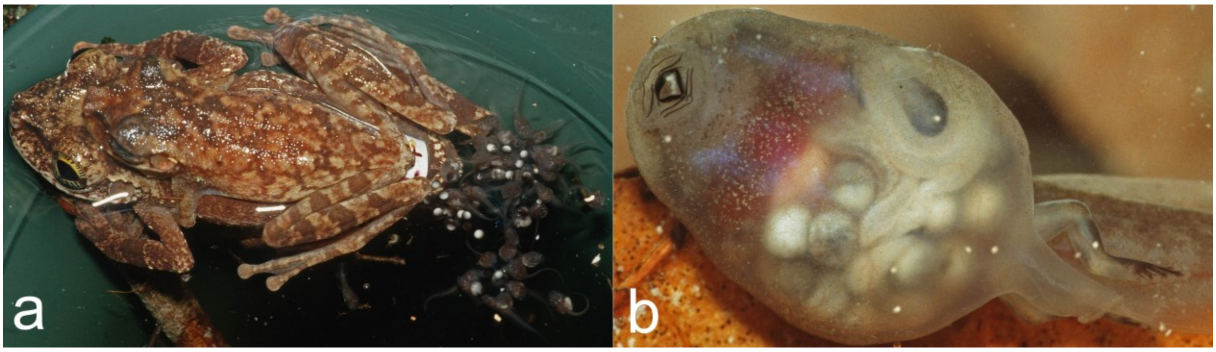

Fig. 1.3. Oophagy in *Osteocephalus*. a. Pair of *O. oophagus* feeding young larvae on fertilized eggs. b. Ventral view of a larva exhibiting reduced labial tooth rows and freshly eaten eggs (Reserva Adolpho Ducke, Amazonas, Brazil).

feeding on conspecific eggs have labial tooth rows reduced to three posterior and two anterior rows (Jungfer & Schiesari 1995; Schiesari *et al.* 1996; Jungfer *et al.* 2000; Fig. 1.3). Tadpoles in other groups with oophagous habits (e.g. the dendrobatid genus *Oophaga* or *Osteopilus* of Lophyohylini) exhibit similar reductions (Lannoo *et al.* 1987, Lötters *et al.* 2007).

Within at least two groups of *Osteocephalus*, both of them phytotelm-breeders, parental care evolved independently. *Osteocephalus oophagus* (*O. taurinus* group) usually utilizes water-filled leaf axils to deposit eggs. Subsequently, the pair (although not necessarily the parent father) returns at intervals of 5-7 days and deposits fertilized eggs that are eaten by their earlier-born siblings (Fig. 1.3). Tadpoles that do not receive nutritive eggs for most of their larval period fail to metamorphose and die (Jungfer & Weygoldt 1999).

Tadpoles of at least two species in the *O. planiceps* group, *O. castaneicola* and *O. deridens*, also receive nutritive eggs. (Jungfer *et al.* 2000; this work, see Chapter 3.1.1). While there are no data on *O. castaneicola*, in *O. deridens* the mother returns with a clasping male (i.e. the eggs get fertilized). A third species of the group, *O. leoniae*, appears to be more advanced as the female parent at least in some instances returns without a male, feeding the larvae on unfertilized and hence exclusively nutritive eggs (this work, see Chapter 3.3).

1.2. Historical background

There have been taxonomic problems both on generic and specific level ever since the name *Osteocephalus* was coined. Fitzinger (1843) was the first to use the generic name in combination with the specific epithet *taurinus*. But since he neither designated nor illustrated any specimens, both names have to be considered *nomina nuda*, although it is fairly obvious that he indeed had the frog now known under that name in his hands, for they refer very well to two characters that were considered diagnostic for the genus for many years (Trueb & Duellman 1970, 1971), i.e. the strongly exostosed cranium (*Osteocephalus*: Greek: “bone head”) and in several species two raised lateral frontoparietal flanges visible externally as longitudinal crests and maybe reminiscent of a bull’s robust head or horns (*taurinus*: Greek: “of bulls”). By describing *Osteocephalus taurinus*, Fitzinger’s predecessor at the Vienna Natural History Museum, Steindachner (1862), became the author of both the generic and the specific name. By naming *O. flavolineatus* in the same paper, he also produced the first junior synonym, because he considered a specimen of *O. taurinus* with a light median stripe (such as the male in Fig. 1.4. on p. 10) as a species of its own. In the years to follow, only few more species were included in the genus (Cope 1874, Goin 1961, Trueb 1970), until Trueb & Duellman (1971) thoroughly revised and defined the genus on the basis of 18 characters. They considered only five species valid and placed no less than 10 taxa in the synonymy of those five ones.

Subsequently, there were numerous descriptions, redescriptions and rearrangements to and from *Osteocephalus* (Duellman 1974; Henle 1981, 1992; Martins & Cardoso 1987; Duellman & Mendelson 1995; Jungfer & Schiesari 1995; Ron & Pramuk 1999; Jungfer *et al.* 2000; Jungfer & Lehr 2001; Smith & Noonan 2001; Jungfer & Hödl 2002; Lynch 2002, 2006; Faivovich *et al.* 2005; MacCulloch & Lathrop 2005; Wiens *et al.* 2006; Moravec *et al.* 2009; Jungfer 2010, 2011). Especially the description and placement with *Osteocephalus* of small species (i.e. with little or no cranial exostoses) and with phytotelmata as (suspected) breeding sites (Jungfer & Schiesari 1995; Jungfer *et al.* 2000; Jungfer & Lehr 2001; Lynch 2002; Moravec *et al.* 2009) resulted in Trueb & Duellman’s (1971) definition of the genus becoming more and more obsolete. No less than eight of the 18 characters used to define the genus were absent in those species. Moreover, several species from the highlands of the Guiana Shield had been transferred to the new genus *Tepuihyla* (Ayarzagüena *et al.* 1993). Additionally, the only species occurring outside pan-Amazonia, *O. langsdorffii*, was shown to be unrelated and placed in the new genus *Itapotihyla* (Faivovich *et al.* 2005) on the basis of molecular data. However, phylogenetic analyses of various authors (Faivovich *et al.* 2005; Wiens *et al.* 2006; Moen & Wiens 2009; Moravec *et al.* 2009; Ron *et al.* 2010, 2012; Pyron & Wiens 2011) provided increasingly stringent arguments for the monophyly of the remaining species of *Osteocephalus*, although relationships within the genus were still unsatisfactorily resolved, because few species were involved in the studies. Consequently, numerous taxonomic and systematic problems have still remained unresolved.

1.3. Alpha-taxonomic problems

For several reasons, *Osteocephalus* species are difficult to identify using external morphology alone. Molecular methods such as barcoding (e.g. Fouquet *et al.* 2007a; 2007b) have proven mighty tools for the identification of species. On the other hand, however, when wrongly identified samples are used in molecular studies, phylogenies easily become flawed. The following examples have become evident in the course of these studies and are only meant to illustrate that fact. Of two samples of “*O. oophagus*” taken from GenBank, both from French Guiana, Moravec *et al*. (2009) found one to cluster with *O. taurinus* and the other with species now in the *O. buckleyi* group. It is obvious that the latter 12+16S mitochondrial rRNA data refer to a wrongly identified specimen. Likewise, Fouquet *et al.* (2007a) found that 16S mitochondrial rRNA data of “*O. cabrerai*” and “*O. taurinus*” suggested that the two species were nested within *O. leprieurii*. Since they are easily distinguishable from *O. leprieurii*, multiple misidentifications appear to be plausible reasons for these results. Jungfer *et al.* (2013, see Chapter 3.3) used 12+16S sequence data of two frogs listed as “*O. taurinus*” from GenBank (JQ868514 and JQ868515), purportedly from “Brazil: Rio Branco, Acre” (originally used by Salerno *et al.* 2012 as *O.* cf. *taurinus*), that clustered with *O. oophagus* from the type locality in the phylogenetic analysis. *Osteocephalus oophagus* does not occur in the Rio Branco (capital of Acre State, Brazil) area (pers. obs.). It turned out that not only the identification, but also the locality (according to the USNM Division of Amphibians & Reptiles Collections Catalog) had been erroneous. The frogs were from the mouth of Rio Branco, a tributary of Rio Negro in Estado Roraima, Brazil, close to the type locality of *O. oophagus*.

What are the causes of the frequent misidentifications?

1.3.1. Juvenile colourations

All species for which data are available undergo a dramatic ontogenetic change. Recently metamorphosed *Osteocephalus* are different from adults (Figs. 1.4 on p. 10 and S1 on p. 154). Of 13 species of *Osteocephalus* which are known as juveniles, 12 share a white elbow and white distal part of the upper arm, a small white knee spot and a large white heel spot. These markings are absent in one species as a juvenile (*O. mutabor*) and in all adults. Of the 13 species, 11 exhibit a red iris. Only two have a reddish golden or black iris (*O. buckleyi*, *O. verruciger*). No adult *Osteocephalus* has a red iris. Only one species until recently in the genus, “*O.*” *pearsoni*, exhibits no ontogenetic colour change. This is one of the reasons why it was removed from the genus and placed in *Dryaderces* nov. gen. (this work, see Chapter 3.3). The juvenile colouration and ontogenetic change described is supposed to be a synapomorphy of the genus that is not present in other genera of the Lophyohylini (this work, see Chapter 3.3). Differences between different ages have led to multiple descriptions of several species of *Osteocephalus*, the juveniles usually referred to as *Hyla* (this work, see Chapter 3.2 and Chapter 3.3).

1.3.2. Sexual dimorphism in adults

In many species of *Osteocephalus* the skin structure of adult males is quite different from that of females. Males exhibit numerous tubercles dorsally on body and head, often extending anteriorly to the loreal region. In most cases, the tubercles bear spinous keratinized tips. The dorsal skin of females usually is smooth or granulate.

Apart from nuptial pads on the thumbs, males in some species of the *O. leprieurii* species group also develop keratinized excrescences in the shape of spicules ventrally along the lower jaw and the fingers. Breeding males in that group are usually brownish to greyish. They become bright yellow ventrally and brownish yellow above, whereas females do not differ from the usual colouration during breeding.

I am not completely certain if differences in skin texture of males and females have led to multiple descriptions of the same species. But this may have been the case in *Hyla orcesi* Funkhouser, 1956 and *Hyla riopastazae* Andersson, 1945. Both are synonyms of *O. verruciger* (Werner, 1901). While the syntypes of the latter are based on a subadult male (spiny back) and an adult female (smooth back) (Werner 1901), the holotype of *H. orcesi* is an adult male (spiny back) and that of *H. riopastazae* is an adult female (smooth back) according to Trueb & Duellman (1970). Differences in skin texture may have led at least Funkhouser (1956) to assume that her species was different from that of Andersson (1945). Both had apparently been unaware of Werner's (1901) description.

Jungfer & Hödl (2001) speculated on the adaptive significance of the dorsal skin texture differences of males and females. They stated that species with sexual dimorphism of that kind usually spawned in large choruses and often were explosive breeders with males outnumbering females by far. They argued that the spiny backs of males might have a function in quick sex recognition during an attempted amplexus. In fact, males breeding in phytotelmata scattered in the forest and not congregating, such as *O. oophagus* and frogs of the *O. planiceps* group, lack that kind of sexual dimorphism (with one exception: in *O. planiceps* there are sexually active males with and without spiny backs). Members of the *O. alboguttatus* group, in which neither reproductive mode nor any tadpole is known, also lack the dimorphic dorsal skin. This, and the fact that tadpoles of the group have never been found, might be an indication of an arboreal breeding site. Several species in the *O. buckleyi* species group call from scattered sites in vegetation along streams, where encounters between male conspecifics are likely to be rare. In some of them, such as *O. cabrerai*, sexual skin dimorphism is also weakly developed, while it is present in others (e.g. *O. verruciger*).

Fig. 1.4. Sexual dimorphism and ontogenetic change in *Osteocephalus taurinus* (Reserva Adolpho Ducke near Manaus, Amazonas, Brazil). Top left: male, 78 mm; right: female, 104 mm; insert: recently metamorphosed juvenile, 13 mm.

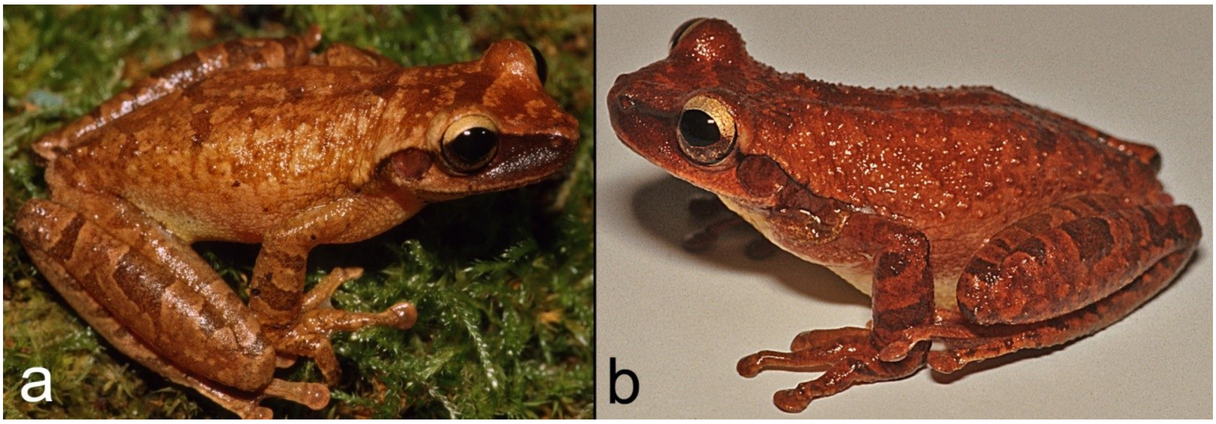

Fig. 1.5. Dorsal tuberculation in the same male individual of *Osteocephalus* aff. *leprieurii* (*O. leprieurii* Ca2) from Los Fierros, Santa Cruz, Bolivia a) outside and b) during the reproductive season (captive specimen).

1.3.3. Impact of breeding condition on the morphology of adult males

Trueb & Duellman (1971) described the various degrees of tuberculation with or without keratinization of the tips in the (then) five species of *Osteocephalus* and used them as distinguishing characters. As diagnostic characters they must, however, be considered with caution. Observations over longer periods of time indicate that not only keratinization of nuptial pads, but also of dorsal tubercles and (in *O. leprieurii*) the presence of keratinized spicules under fingers and lower jaw (Jungfer & Hödl 2002) is dependent on reproductive condition. Keratinization may be reduced or absent in males outside the breeding season making comparisons of these characters difficult (Fig. 1.5).

1.4. Problems with generic allocations

The growing number of species in the genus after Trueb & Duellman's (1971) revision resulted in a growing uneasiness of where to place some species. Ayarzagüena *et al.* (1993) transferred six species from highlands of the Venezuelan Guiana Shield formerly described as *Osteocephalus* to the new genus *Tepuihyla*. Although they used a combination of characters to define the genus, no phenotypic synapomorphy of the species of *Tepuihyla* is known, though they form a geographical unit. Subsequently, however, similar frogs described from the same general area were either placed with *Osteocephalus* (Smith & Noonan 2001; MacCulloch & Lathrop 2005) or *Tepuihyla* (Duellman & Yoshpa 1996; Mijares-Urrutia *et al.* 1999). Not surprisingly, Salerno *et al.* (2012), using molecular data, demonstrated that *Tepuihyla* was paraphyletic with respect to *Osteocephalus.* Molecular data were also used to demonstrate that *O. langsdorffii* from southern Brazil (i.e. outside the range of any other *Osteocephalus*) had to be transferred to a new genus, *Itapotihyla* (Faivovich *et al.* 2005).

This study used molecular data, partly supported by morphological characters, to resolve the generic status of most of the species previously referred to as *Osteocephalus* or *Tepuihyla*.

1.5. Widespread *vs*. cryptic species

Whereas most species of *Osteocephalus* have restricted distributions within pan-Amazonia, there are four species reported to occupy the larger part of that area, namely *O. buckleyi*, *O. leprieurii*, *O. planiceps* and *O. taurinus*. This is surprising insofar as recent studies on amphibians, mostly based on molecular data (Wynn & Heyer 2001; Heyer 2005; Ron *et al*. 2006; Elmer *et al*. 2007; Fouquet *et al*. 2007a,b; Brown & Twomey 2009; Padial & De la Riva 2009; Brown *et al*. 2011; Castroviejo-Fisher *et al*. 2011; Heyer & de Sá 2011; Jansen *et al*. 2011; Fouquet *et al*. 2012; Funk et al. 2012; Padial *et al*. 2012; Ron *et al*. 2012; Caminer & Ron 2014), have demonstrated that widespread “species” consisted of complexes of closely related species. Similar results were gained in other organisms, such as birds (Milá *et al.* 2012) or reptiles (Bergmann & Russell 2007).

Within *Osteocephalus* it had long been suspected that *O.* “*leprieurii*” from the species’ southern range in Bolivia (Fig. 1.5 on p. 11) were specifically distinct from northern populations (type locality: Cayenne, French Guiana) (Jungfer & Lehr 2001; Jungfer & Hödl 2002; Moravec *et al*. 2009). But no taxonomic action has been taken. This study corroborates this view and reveals that yet another undescribed species hides under that taxon name. *Osteocephalus buckleyi* has recently been investigated by Ron *et al*. (2012) in the western range (Ecuador, Peru) of the species. They described three species formerly considered to represent *O. buckleyi*. Although two of them have to be rejected here for different reasons, several more species were detected in the present study. One of them is described in a forthcoming publication (Chapter 3.1.3).

The range of *O. taurinus* is a huge area, covering almost the entire pan-Amazonian lowlands. Enormous size differences exist. Breeding specimens from the Manaus area measure 82 mm SVL in males and 104 mm in females, while those from some 250 km further to the south-west are only slightly larger than half of those sizes of Manaus specimens. Tackling that problem morphologically is difficult, because there is also a lot of intrapopulational variation, not only in size. Additionally, some populations have poorly been sampled and other biological data, such as calls, tadpoles or observations on breeding sites, are next to missing. However, it was recognized already in an early phase of this study, that *O. taurinus* is in fact a complex of several species. In the molecular analysis, a small species from central Amazonia, *O. oophagus*, was found to be nested within several populations of *O. taurinus*, a fact that rendered the latter paraphyletic. *Osteocephalus oophagus* has numerous morphological, bioacoustical (Fig. 1.6 on p. 14) and other behavioural characters that distinguish it from *O. taurinus sensu lato*. More data on O. "*taurinus*" will likely yield convincing data to distinguish between cryptic species currently only characterized by molecular data.

A fourth species with a considerable range, *O. planiceps* from western Amazonia in Colombia through to Peru, exhibits some variation in morphology and call structure. So far only one isolated population from the foot of Cerro de la Neblina in the extreme south of Venezuela can be considered as distinct both for molecular and morphological reasons and as yet undescribed.

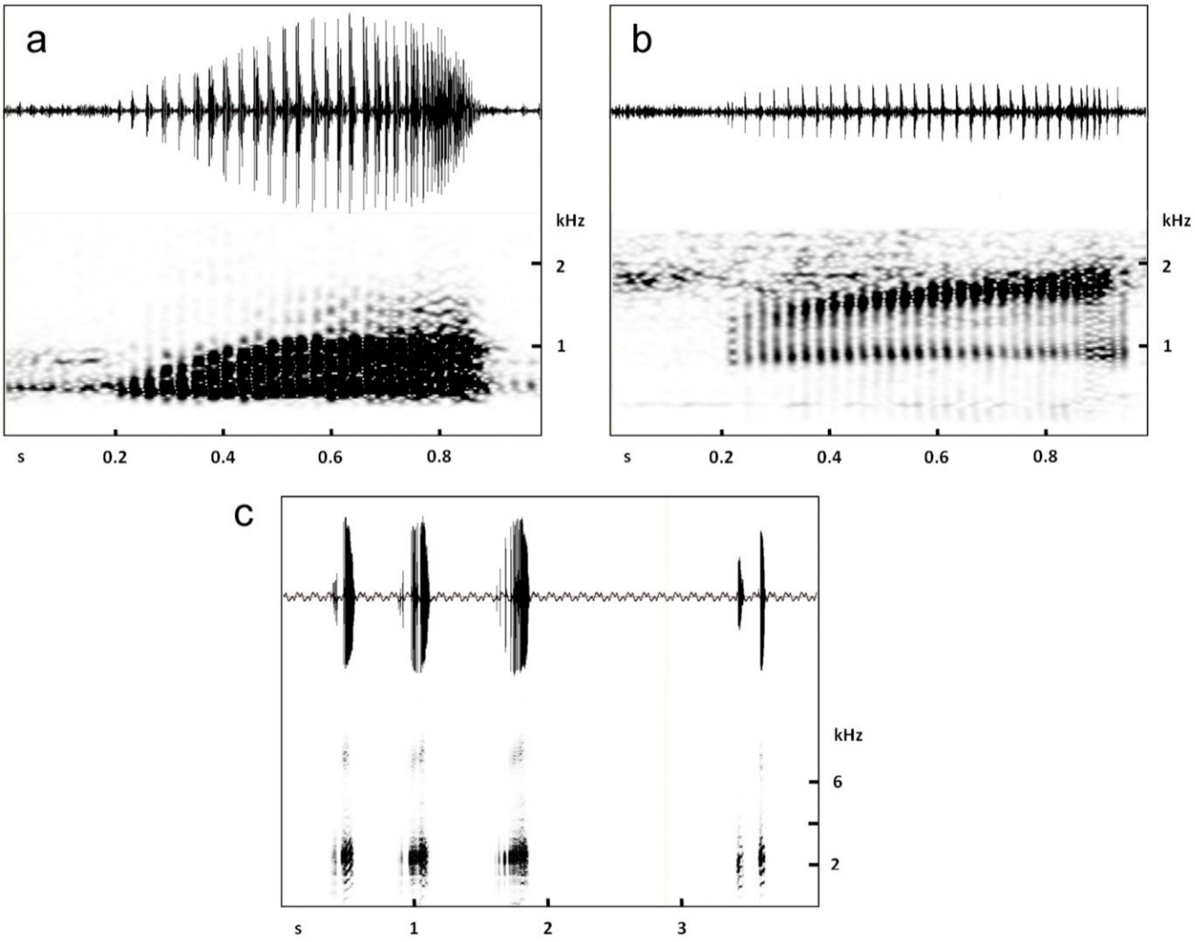

Fig. 1.6. Oscillograms (above) and sound spectrograms (below) of three advertisement calls of frogs in the *O. taurinus* species group. a. *O. taurinus* Ca5 (Candidate Species 5) from French Guiana (Marty & Gaucher 1999); b. *O. taurinus sensu stricto* (each *sensu* this work; see Chapter 3.3) from northern Bolivia (recording by S. Reichle); c. *O. oophagus* from the type locality in Amazonas, Brazil. While calls a and b are structurally similar in consisting of a long series of pulses, call c is broken up into three distinct notes (plus two additional notes most likely representing a territorial component). In our molecular analysis (Chapter 3.3), b (*O. taurinus sensu stricto*) and c (*O. oophagus*) are sister groups, while a (*O. taurinus* Ca5) is sister to (b+c). The huge bioacoustical differences between the closely related b (*O. taurinus sensu stricto*) and c (*O. oophagus*) indicate that the less related c represents a species of its own (otherwise rendering *O. taurinus* paraphyletic).

1.6. Objectives

The specific objectives of this research are to (1) provide an overview of the currently known species and their taxonomic identity; (2) resolve cases of synonymy; (3) reveal new taxa including cryptic species, especially among those that are currently believed to be wide-ranging species; (3) find out about relationships within *Osteocephalus*; (4) delimit the genus against closely related genera; (5) study the evolution of the genus with respect to reproductive adaptations and behaviour; (6) obtain a basic understanding of the current distribution patterns.

2. MATERIALS AND METHODS

Specific materials and methods are indicated in each of the articles of Chapter 3. Due to the huge distribution area of the genus, numerous loans of preserved specimens were necessary. This was not always possible for the sheer number or value of specimens and frogs had to be inspected at the respective institutions. Visits were made to the Instituto Nacional de Ciencias (ICN), Bogotá, Colombia, Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Bonn, Germany, Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde (MTD), Dresden, Germany, Muséum d'histoire naturelle (MHNG), Genève, Switzerland, Museum of Natural History, Kansas University (KU), Lawrence, USA, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru, Natural History Museum (BM), London, United Kingdom, Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil, Staatliches Museum für Naturkunde (SMNS), Stuttgart, Germany and Naturhistorisches Museum (NMW), Wien, Austria.

Observations of live specimens especially for this project were obtained during six short field trips (2-7 nights in the field per locality) to Peru (Amazonas: Santa María de Nieva, Pongo de Manseriche, Río Marañon; Loreto: Estación Biológica Quebrada Blanco, Alto Río Tamshiyacu, Río Ampiyacu, Río Sucusari, Río Yarapa; San Martín: Tarapoto). Specimens collected during these trips have been or will be deposited at MTD and MUSM.

Numerous observations, such as egg deposition, larvae, parental care, freshly metamorphosed specimens or vocalizations, could not always be made in the field. In those cases, larvae and frogs were collected, transferred to terraria of different dimensions and equipment and observed there, to be deposited at the mentioned institutions later.

Vocalizations were recorded in the field or in terraria or aquaria with a Sony WM-D6C recorder or a digital Zoom H2n Handy Recorder in combination with a Sennheiser ME 66 directional microphone. If necessary, recordings were digitized by converting a recording to a wav file (44.1 kHz, 24 bit, mono) with Magix Audio Cleaning Lab 16 deluxe. Calls were analyzed with Adobe Audition 1.0. Sound spectrograms were visualized displaying them through Fast Fourier Transformation (FFT) with Hanning windowing function at 1024 bands resolution (linear energy plot at 0.8%).

3. RESULTS

3.1. Descriptions of new species of *Osteocephalus*

3.1.1. *Osteocephalus castaneicola* Moravec, Aparicio, Guerrero-Reinhard, Calderón, Jungfer & Gvoždík, 2009

This part was published in *Zootaxa* as follows:

Moravec, J., J. Aparicio, M. Guerrero-Reinhard, G. Calderón, K.-H. Jungfer & V. Gvoždík (2009): **A new species of *Osteocephalus* (Anura: Hylidae) from Amazonian Bolivia: first evidence of tree frog breeding in fruit capsules of the Brazil nut tree**. *Zootaxa*, 2215: 37-54.

Own contribution: Parts of comparisons, distribution and discussion.

Abstract

A new species of *Osteocephalus* is described from lowland Amazonia of the Departamento Pando, northern Bolivia. The new species is most similar to *Osteocephalus planiceps* but differs by its smaller size (SVL 47.8–51.3 mm in males, 47.7–63.3 mm in females), absence of vocal slits, lack of sexual dimorphism in dorsal tubercles, single distal subarticular tubercle on the fourth finger, absence of dark spots on flanks, and by bicoloured iris with fine dark reticulate to radiate lines. The new species inhabits terra firme rainforest, breeds in water-filled fruit capsules of the Brazil nut tree and has oophagous tadpoles. Estimations of phylogenetic relationships within *Osteocephalus* based on mitochondrial DNA sequences show that the new species is closely related to *O. planiceps* and *O. deridens*.

Key words: Amphibia, Anura, Bolivia, Hylidae, Molecular Phylogeny, New Species, Oophagy, *Osteocephalus castaneicola*

Introduction

Hylid frogs of the genus *Osteocephalus* represent typical anuran forms adapted to arboreal mode of life in rainforests of South America. They are excellent climbers and many of them evolved different reproductive adaptations to decrease competition and predator pressure. In this respect, the most specialized species call from or breed in bromeliads or other phytotelmata and provide biparental care to oophagous tadpoles (Jungfer & Schiesari 1995, Jungfer & Weygoldt 1999, Jungfer *et al.* 2000, Jungfer & Lehr 2001, Jungfer & Hödl 2002). Currently, the genus *Osteocephalus* comprises 20 recognized species distributed in the Amazon basin, Guianas and upper drainages of Río Magdalena and Río Orinoco in Colombia and Venezuela (Frost 2009). Nevertheless, *Osteocephalus* alpha taxonomy is far from stable. Existence of several unnamed species is mentioned by Jungfer & Hödl (2002).

Currently, four species of *Osteocephalus* are known to be present in Bolivia: *O. buckleyi* Goin, *O. pearsoni* Gaige, *O. taurinus* Steindachner and an undescribed *Osteocephalus* sp. (A) (sensu Jungfer & Lehr 2001). The latter one was originally associated with the name *O. leprieurii* (Duméril & Bibron) and its formal description remains under process of publication since long ago (see De la Riva *et al.* 2000, Jungfer & Lehr 2001, Jungfer & Hödl 2002). Apart from this, recent field research in the Departamento Pando (the northernmost region of Bolivia, situated in the south-western Amazonian basin within the zone of tall evergreen lowland rainforest) revealed that at least two other taxa of *Osteocephalus* occur in Bolivian Amazonia. One, *Osteocephalus* sp. (B), is morphologically similar to *O. leprieurii* (see Moravec & Aparicio 2004). The second taxon, *Osteocephalus* sp. (C) represents a morphologically well differentiated, still unnamed species, which reproduces in abandoned water-filled fruit capsules of the Brazil nut tree. This contribution is aimed at the description of the latter.

Materials and methods

Collected specimens (for exact localities see type specimens, Appendix, and Fig. 3.1.4) were fixed and stored in 70 % ethanol. Measurements are given in millimetres (mm) and were taken to the nearest 0.1 mm using a dissecting microscope and electronic digital calipers. Notes on colour in life were taken from field notes and colour photographs. Webbing formulae follow the standards of Myers & Duellman (1982), whereas all other terminology is that of Duellman (1970). Measurement abbreviations used throughout the text are: EN, eye to nostril distance; ED, horizontal eye diameter; ELW, upper eyelid width; FL, foot length as the distance from the heel to the tip of the fourth toe; HL, head length as the straight line distance from the posterior edge of the jaw articulation to the tip of the snout; HW, greatest head width; IOD, interorbital distance; SVL, snout-vent length; TD, horizontal tympanum diameter; and TL, tibia length. Specimens morphologically examined are listed in the Appendix. Institutional acronyms used are those listed in Leviton *et al.* (1985) with the following additions and corrections: CBF, Colección Boliviana de Fauna, La Paz; NMP6V and NMP6d, National Museum Prague.

For purpose of genetic analyses, tissue samples from 13 specimens of five *Osteocephalus* species, including *O.* sp. (B) and *O.* sp. (C), were taken from preserved voucher specimens (Table 3.1.1). We targeted a 1943 bp fragment of mitochondrial DNA (mtDNA) comprising partial 12S rRNA (12S), complete transfer RNA-Valin (tRNA-Val) and partial 16S rRNA (16S) genes. Our own DNA sequences were compared to and evaluated together with sequences of comparable mtDNA fragments of nine *Osteocephalus* species (14 individuals) obtained from GenBank. Additional sequences from five individuals of four species of genera *Tepuihyla*, *Itapotihyla*, *Osteopilus* and *Acris* were also taken from GenkBank and used as outgroups (for their outgroup position see Faivovich *et al.* 2005, Wiens *et al.* 2006, Moen & Wiens 2009). For overview of all samples, their coverage, and GenBank accession numbers see Table 3.1.1. Total genomic DNA was extracted from tissue samples using a commercial kit following the manufacturer’s protocol. The whole portion of the targeted mtDNA was amplified using primers 12Sa [5'CTGGGATTAGATACCCCACTA-3 '; adapted from Kocher *et al .* (1989)] and 16SH1 [5'-CCGGTCTGAACTCAGATCACGT-3'; Palumbi *et al.* (1991)]. However, we were able to obtain only shorter separate fragments of the 12S (352 bp) and 16S (549 bp) genes in five samples due to low quality of their DNA using two pairs of primers: 12Sa / 12Sbs [12Sbs: 5'-TGAGGAGGGTGACGGGCGGT-3', adapted from Kocher *et al.* (1989)] and 16SL1 / 16SH1 [16SL1: 5'-CGCCTGTTTAACAAAAACAT-3', adapted from Palumbi *et al.* (1991)]. Amplification of all fragments involved an initial cycle of denaturation at 94 °C for 15 min, and 35 subsequent cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by a final extension step of 72 °C for 10 min. Sequencing was carried out using the 12Sa and 16SH1 primers and newly designed internal primers 16SLin (5'AGTACCGYAAGGGAAAG-3') and 16SinH (5'-TCTTCTTGTTACTAGTT-3') by Macrogen Inc. (Seoul, Korea, http://www.macrogen.com). The sequences obtained have been deposited in GenBank (FJ965291–FJ965308). Alignment was made by ClustalW (Thompson *et al.* 1994) as implemented in BioEdit 7.0 (Hall 1999) and checked by eye. The best-fit model of sequence evolution was selected using jModelTest 0.1.1 (Posada 2008) using maximum likelihood optimized trees calculated by the implemented PhyML algorithm (Guindon & Gascuel 2003). Both, the Akaike information criterion (AIC; Akaike, 1974) and the Bayesian information criterion (BIC; Schwarz 1978) selected the same best fit model: transitional model 2 with gamma rate variation among sites (TIM2+G; Posada 2003). Phylogenetic trees were built using maximum likelihood method (ML) by PhyML 3.0 (Guindon & Gascuel 2003), and for comparison by RAxML 7.0 (Stamatakis 2006), and using Bayesian analysis (BA) by MrBayes 3.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Parameters were set in PhyML as follows: base frequencies A = 0.35, C = 0.21, G = 0.18, T = 0.26, substitution rate matrix AC = AT = 5.31, AG = 10.77, CG = GT = 1.00, CT = 37.85 and gamma shape rate variation among sites $\alpha = 0.151$. BioNJ tree was used as an initial tree, the best of the nearest neighbour interchange (NNI), and the ‘new’ subtree pruning and regrafting algorithm (SPR; Hordijk & Gascuel 2005) of branch swapping was used as a tree topology search, with options to optimize the topology and branch lengths. Bootstrap values were computed based on 1000 resampled data sets (Felsenstein 1985). ML using RAxML was computed with the general time-reversible model with rate heterogeneity (GTR+G; Tavaré 1986), with parameters estimated during the run. The same was done in the case of BA. The BA was performed with two runs and four chains for each run for 6 x 106 generations, and sampling every 100th tree. The first 300 trees (burn-in value) were discarded, as log-likelihood scores of sampled trees plotted against the generation time showed that stationarity was fully achieved after the first 20,000 generations. A majority rule consensus tree was then produced from the remaining trees after discarding the burn-in trees, and the posterior probabilities (BPP) calculated as the frequency of samples recovering any particular clade (Huelsenbeck & Ronquist 2001). The BA was run four more times with random starting trees and the results were compared to check for local optima. Genetic uncorrected *p* distances were calculated in PAUP* (Swofford 2003).

Results

Both ML analyses, PhyML (Guindon & Gascuel 2003) and RAxML (Stamatakis 2006), resulted in most likely trees with the same topology with log likelihoods (ln*L*) = -7486.82 and -7489.98, respectively. Although, the bootstrap support of the relationships among main clades and most of species was very low. All independent BA runs resulted in essentially identical topologies and likelihood estimates. The majority rule consensus Bayesian tree (mean ln*L* = -7534.54; Fig. 3.1.1) had the same topology as both ML trees, when branches of the ML trees with the bootstrap support below 50% were collapsed. The estimation of phylogenetic relationships within the genus *Osteocephalus* shows that four main phylogenetic lineages can be distinguished within the studied species: (1) individual lineage formed by *O. alboguttatus* (Boulenger); (2) lineage comprising *O.* “*oophagus*” Jungfer & Schiesari from French Guiana and *O. taurinus* (support 1.00/94 = BPP/ML bootstrap), however, the latter is further structured forming a sublineage from Peru and Bolivia, while next samples from French Guiana and Venezuela form a polytomy within the whole clade (low support of their relationships); (3) clade of not very high statistical support (0.81/68) comprising three well supported sublineages: (i) *O. mutabor* Jungfer & Hödl, (ii) *O. buckleyi, O. cabrerai* (Cochran & Goin)*, O. verruciger* Werner and another sample of *O.* “*oophagus*” from French Guiana showing remarkably low mutual genetic differentiation (support 1.00/90), and (iii) Bolivian population of *Osteocephalus* sp. (B) clustering close to *O. leprieurii* from French Guiana (support 0.95/91); (4) clade (support 1.00/98) consisting of four sublineages represented by (i) *O. deridens* Jungfer, Ron, Seipp & Almendáriz, (ii) *O.* “*leprieurii*” from Venezuela, (iii) *O. planiceps* Cope, and (iv) the unnamed Bolivian *Osteocephalus* sp. (C). The representatives of the two known populations of *Osteocephalus* sp. (C) form a well supported (1.00/ 92) separate lineage within the fourth clade. *O. planiceps* seems to be the closest relative of *Osteocephalus* sp. (C), with 3.0 % of mean uncorrected *p*-distances in 16S rRNA (Table 3.1.2), which is concordant with suggested interspecific level in this molecular marker in frogs (Fouquet *et al.* 2007, Vieites *et al.* 2009). This fact also corresponds to the unique morphology and life history of this species and justifies us to describe it as a new species herein.

Osteocephalus castaneicola **sp. n.**

Figs. 3.1.2 (A–E), 3.1.3 (A–B)

Holotype. CBF 6051, adult male from the vicinity of the settlement of San Antonio de Filadelfia, 11°18’ S, 67°23’ W, ca. 200 m a.s.l., Provincia Manuripi, Departamento Pando, Bolivia, collected on 22 November 2007 by J. Moravec, M. Guerrero-Reinhard and G. Calderón.

Paratopotypes. NMP6V 73810/1–3, two adult males and an adult female, same locality and collecting data as holotype; CBF 6052, adult female, same locality and collecting data as holotype;

Paratypes. CBF 6053–6054, adult male and adult female from San Antonio del Matti, 11°30’S, 68°53’W, ca. 270 m a.s.l., Provincia Manuripi, Departamento Pando, Bolivia, collected on 27 November 2007 by J. Moravec, M. Guerrero-Reinhard and G. Calderón; NMP6V 73820, adult female, same locality and collecting data as CBF 6053–6054.

Diagnosis. A medium-sized species of *Osteocephalus* as revealed from mtDNA analyses, which can be distinguished by the following combination of characters: (1) medium size, SVL 47.8–51.3 mm in males, 47.7–63.3 mm in females; (2) snout rounded in dorsal view, rounded and slightly inclined posteroventrally in lateral view; (3) canthus rostralis distinct, angular, distinctly curved medially; loreal region concave; (4) low frontoparietal ridges well-marked in large individuals; (5) tympanum large, round to oval, about 62.5–76.5% of eye diameter, tympanic annulus distinct; supratympanic fold markedly developed; (6) vocal slits absent, vocal sac indistinct; (7) vomerine odontophores large, prominent, angular, narrowly separated or in contact medially, between oblique choanae, bearing 6–14 vomerine teeth each; (8) skin on dorsal surfaces with numerous minute tubercles; (9) low tarsal and ulnar tubercles present, slightly larger than dorsal tubercles; (10) axillary membrane absent; (11) basal webbing on hand [webbing formula II (2^{-}–2^{+})—(3^{-}–3^{+}) III (3^{-}–3)—($2^{2}/_{3}$–3^{-}) IV]; toes about three fourths webbed [webbing formula I (1–$1^{1}/_{4}$) — ($1^{2}/_{3}$–2^{-}) II (1–1^{+})—(2^{-}–2) III (1–1^{+})—($1^{2}/_{3}$–2) IV ($1^{2}/_{3}$–2^{-})—(1^{-}–1) V]; (12) single,

Table 3.1.1. *Osteocephalus* and outgroup species included in the molecular phylogenetic analyses.

Species	Code	Country	Locality	Museum Number	GenBank Accession Number			Note/Reference
					12S rRNA	tRNA-Val	16S rRNA	
O. alboguttatus		Ecuador	Sucumbios	KU 143119	DQ380347	-	-	Wiens *et al.* 2006
O. buckleyi		Ecuador	Napo: Jatun Sacha, 420 m	LAC 2216	DQ380378	-	EU034082	Wiens *et al.* 2006; Moen & Wiens 2009
O. cabrerai		Brazil	Acre, 5 km N Porto Walter, inland from Rio Jurua	JPC 13178; LSUMZ H-13720	AY843705	AY843705	AY843705	Faivovich *et al.* 2005
O. deridens	der1	Peru	Loreto: 40 km SW of Iquitos	NMP6V 71262/2	FJ965304	-	FJ965291	this study
O. leprieurii		French Guiana	Creek of Margot		-	-	EF376066	Salducci *et al.* 2005
O. 'leprieurii'		Venezuela	Amazonas: Neblina Base Camp on Río Mawarinuma (= Río Baria)	AMNH-A 1312546	AY549361	AY549361	AY549361	Faivovich *et al.* 2004
O. mutabor		Peru	Loreto: 1.5 km N Teniente López, elev. range 310–340 m	KU 221930	DQ380379	-	-	Wiens *et al.* 2006
O. 'oophagus'		French Guiana	Kaw Road, 04°42' N / 52°18' W	MNHN 2001.0828	AY843708	AY843708	AY843708	Faivovich *et al.* 2005
O. 'oophagus'		French Guiana	Mountain of Kaw		-	-	AF467267	Salducci *et al.* 2002
O. planiceps	pla1	Peru	Loreto: Puerto Almendras	NMP6V 71174/1	FJ965305	-	FJ965292	this study
O. planiceps	pla2	Peru	Loreto: Anguilla	NMP6V 71264/1	FJ965306	-	FJ965293	this study
O. planiceps	pla3	Peru	Loreto: Anguilla	NMP6V 71264/2	FJ965307	-	FJ965294	this study
O. planiceps		Peru	Loreto: San Jacinto: 175 m	KU 221933	DQ380380	-	-	Wiens *et al.* 2006
O. taurinus	tau1	Bolivia	Pando: Santa Crucito	CBF collections	FJ965296	FJ965296	FJ965296	this study
O. taurinus		French Guiana	Saül		-	-	EF376067	Salducci *et al.* 2005
O. taurinus		Peru	Loreto: Teniente López, 310 m	KU 221941	AY819380	-	AY819512	Wiens *et al.* 2005
O. taurinus		Peru	Madre de Dios: Cusco Amazónico	KU 205406; WED 55452	AY326041	AY326041	AY326041	Darst & Cannatella 2004

Table 3.1.1. (continued)

Species	Code	Country	Locality	Museum Number	GenBank Accession Number			Note/Reference
					12S rRNA	tRNA-Val	16S rRNA	
O. taurinus		Venezuela	Amazonas, Neblina Base Camp on Río Mawarinuma (= Río Baria), 140 m	AMNH-A 131245	-	-	'AY843709' **	Faivovich *et al.* 2005
O. verruciger		Ecuador	Napo: Río Azuela, 9.5 km W Reventador, 1630 m	KU 217751	DQ380381	-	-	Wiens *et al.* 2006
O. sp. (B)	spB1	Bolivia	Pando: Palmira	NMP6d 41/2009	FJ965297	FJ965297	FJ965297	this study
O. sp. (B)	spB2	Bolivia	Pando: Canadá	NMP6V 73105	FJ965298	FJ965298	FJ965298	this study
O. sp. (B)	spB3	Bolivia	Pando: Nacebe	NMP6V 72173/1	FJ965299	FJ965299	FJ965297	this study
O. sp. (B)	spB4	Bolivia	Pando: Nacebe	NMP6V 72173/3	FJ965308	-	FJ965295	this study
O. sp. (C) = *castaneicola*	spC1	Bolivia	Pando: San Antonio de Filadelfia	CBF 6051	FJ965300	FJ965300	FJ965300	**holotype**; this study
O. sp. (C) = *castaneicola*	spC2	Bolivia	Pando: San Antonio de Filadelfia	NMP6V 73810/3	FJ965301	FJ965301	FJ965301	this study
O. sp. (C) = *castaneicola*	spC3*	Bolivia	Pando: San Antonio de Filadelfia	NMP6d 28/2009	FJ965302	FJ965302	FJ965302	this study
O. sp. (C) = *castaneicola*	spC4	Bolivia	Pando: San Antonio del Matti	NMP6V 73820	FJ965303	FJ965303	FJ965303	this study
Tepuihyla edelcae		Venezuela	Estado Bolívar, Auyantepui (2015 m)	MNHNP 1998–311	AY843770	AY843770	AY843770	Faivovich *et al.* 2005
Osteopilus septentrionalis		Cuba	Guantánamo, Guantánamo bay	USNM 317830	AY843712	AY843712	AY843712	Faivovich *et al.* 2005
Itapotihyla langsdorffii		Argentina	Misiones, General Belgrano, 10 Km N Bernardo de Irigoyen, Salto Andresito	MACN 38643	AY843706	AY843706	AY843706	Faivovich *et al.* 2005
Itapotihyla langsdorffii		Brazil	São Paulo: Estaçao Ecologica de Jureia, N of Jureia	USNM 303287	AY819379	AY819379	AY819511	Wiens *et al.* 2005
Acris crepitans		USA	Alabama, De Kalb Co., Powerline access Rd., 1/10 mi W of Lookout Mt. Boys Camp Rd.	LSUMZ H-2164	AY843559	AY843559	AY843559	Faivovich *et al.* 2005

* tadpole from a water-filled fruit capsule of the Brazil nut tree

** AY843709 sequence is a chimera; the 12S rRNA part corresponds fully to AY843707 (*O. 'leprieurii'*; Faivovich *et al.* 2005), which is, moreover, the same sequence of the same individual as AY549361 (Faivovich *et al.* 2004); we used only the 16S rRNA part

TABLE 3.1.2. Uncorrected *p*-distances in percentage among *Osteocephalus* species and outgroup genera included in the phylogenetic analysis. Below diagonal are genetic distances based on the 352bp 12S rRNA fragment, above diagonal are distances based on the 380 bp 16S rRNA fragment, and on diagonal within species mean uncorrected *p*-distances, if applicable.

	12S/16S rRNA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	*O. alboguttatus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	*O. buckleyi*	5.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	*O. cabrerai*	4.8	1.4	-	8.2	5.6	6.8	-	5.5	0.8	6.1	-	5.5	5.3	-	5.5	5.8	-	5.7	6.9	11.6	10.0	11.6	-	13.4
4	*O. deridens*	6.8	8.0	8.0	-	8.2	4.5	-	8.4	8.5	3.4	-	8.4	8.7	-	8.4	9.2	-	8.6	5.3	12.4	9.7	13.4	-	15.0
5	*O. leprieurii* F. Guiana	-	-	-	-	-	7.7	-	6.1	5.3	5.8	-	5.3	5.3	-	5.3	5.8	-	1.2	6.8	11.6	10.8	11.6	-	14.5
6	*O. "leprieurii"* Venezuela	5.4	3.7	4.5	5.7	-	-	-	7.9	6.6	2.4	-	7.9	7.6	-	7.9	8.7	-	7.8	4.4	10.5	9.5	12.1	-	14.7
7	*O. mutabor*	4.3	2.8	2.6	8.0	-	4.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	*O. "oophagus"* AY843708	5.1	4.5	4.8	8.2	-	4.8	4.0	-	5.3	7.1	-	2.1	1.6	-	2.1	2.6	-	6.7	7.6	10.8	10.0	11.8	-	14.7
9	*O. "oophagus"* AF467267	-	-	-	-	-	-	-	-	-	5.8	-	5.3	4.7	-	5.3	5.6	-	5.1	6.6	10.8	9.5	10.6	-	12.9
10	*O. planiceps* pla1-pla3	4.8	3.7	4.0	5.4	-	1.7	4.3	4.3	-	**0.0/0.0**	-	6.8	6.9	-	6.8	7.6	-	6.4	3.0	10.3	8.7	11.6	-	14.5
11	*O. planiceps* DQ380380	4.5	3.4	3.7	5.4	-	2.0	4.0	4.0	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	*O. taurinus* tau1	4.5	4.0	4.3	7.4	-	4.3	3.4	0.9	-	3.7	3.4	-	1.6	-	0.0	2.1	-	5.9	7.4	11.1	9.5	10.0	-	14.5
13	*O. taurinus* F. Guiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.6	1.1	-	5.7	7.4	10.8	9.2	10.8	-	14.2
14	*O. taurinus* Peru AY819380	4.5	4.5	4.8	7.4	-	4.8	4.0	1.4	-	4.3	4.0	0.6	-	-	-	-	-	-	-	-	-	-	-	-
15	*O. taurinus* Peru AY326041	4.3	4.3	4.5	7.1	-	4.5	3.7	1.1	-	4.0	3.7	0.3	-	0.3	-	2.1	-	5.9	7.4	11.1	9.5	10.0	-	14.5
16	*O. taurinus* Venezuela	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.4	8.2	11.8	9.7	11.3	-	14.7
17	*O. verruciger*	5.4	0.9	0.6	8.2	-	4.0	3.1	4.8	-	4.0	3.7	4.3	-	4.8	4.5	-	-	-	-	-	-	-	-	-
18	*O.* sp. (B) spB1-spB4	5.5	3.1	3.9	8.6	-	4.9	3.1	4.6	-	4.3	4.0	4.0	-	4.6	4.3	-	3.9	**0.4/0.5**	7.4	12.0	10.7	11.7	-	14.6
19	*O.* sp. (C) = *castaneicola* spC1-spC4	4.5	3.3	4.2	5.3	-	1.9	3.9	3.9	-	1.4	1.1	3.3	-	3.9	3.6	-	3.6	4.0	**0.2/0.6**	10.4	8.6	11.5	-	14.6
20	*Tepuihyla edelcae*	6.3	5.1	5.4	8.5	-	5.7	5.4	5.1	-	5.4	5.1	4.3	-	4.8	4.5	-	5.4	6.0	4.8	-	9.2	11.6	-	13.2
21	*Osteopilus septentrionalis*	4.8	4.8	4.5	8.0	-	5.7	4.8	4.3	-	5.1	4.8	3.7	-	4.3	4.0	-	5.1	5.5	4.8	5.1	-	11.1	-	12.4
22	*Itapotihyla langsdorffii* Argentina	8.0	6.0	6.0	10.2	-	8.0	6.8	6.8	-	7.4	7.1	6.5	-	7.1	6.8	-	6.3	6.6	7.0	5.7	6.0	-	-	12.6
23	*Itapotihyla langsdorffii* Brazil	8.0	6.0	6.0	10.0	-	7.7	6.8	6.8	-	7.1	6.8	6.5	-	7.1	6.8	-	6.3	6.6	6.8	5.7	6.0	0.6	-	-
24	*Acris crepitans*	9.1	8.8	8.8	11.6	-	9.1	9.7	9.9	-	8.8	8.8	9.4	-	9.9	9.7	-	9.1	9.7	9.0	9.1	8.2	10.2	9.9	-

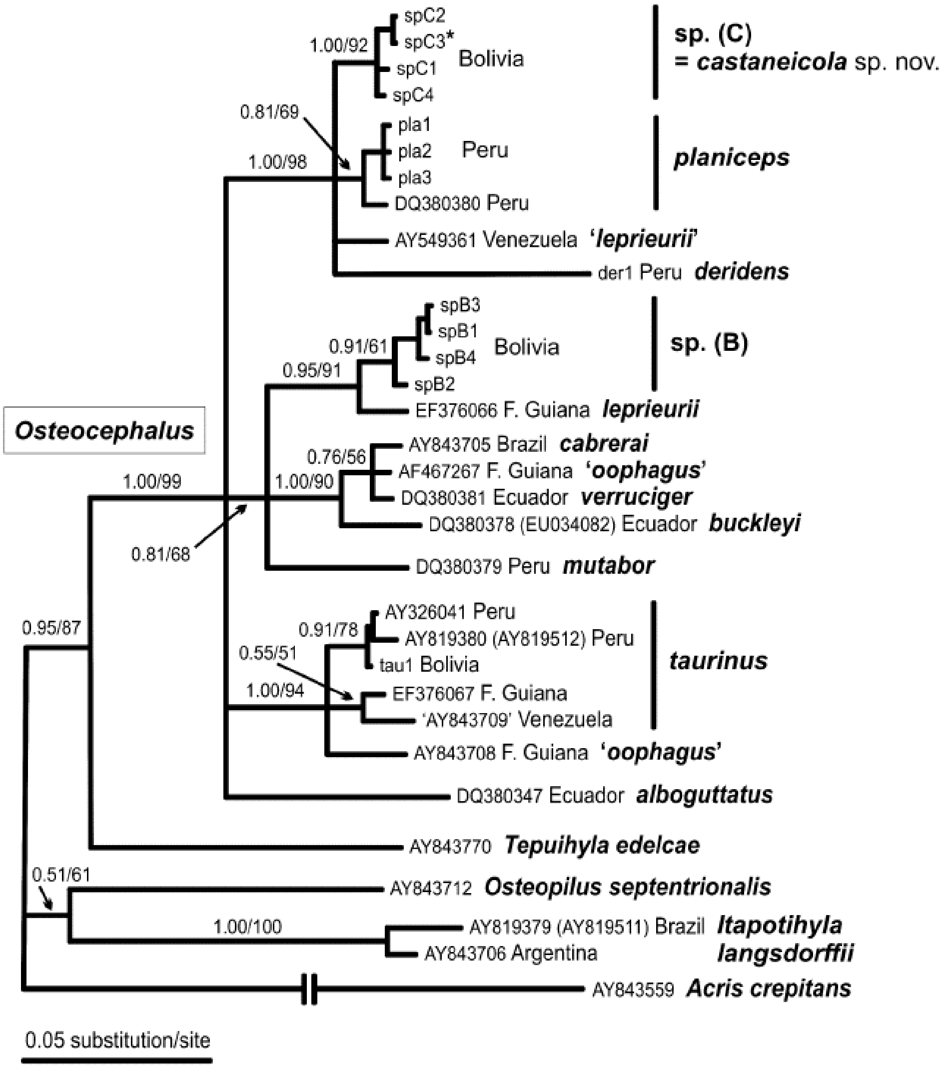

Figure 3.1.1. The majority rule consensus tree of the Bayesian phylogeny of the frog genus *Osteocephalus*, using mitochondrial 12S rRNA – tRNA-Val – 16S rRNA data. Nodal support, Bayesian posterior probabilities (BPP) and maximum likelihood (PhyML) bootstrap (1000 pseudoreplicates), are indicated. Collapsed branches were supported <50% bootstrap and < 0.50 BPP. The asterisk denotes the tadpole sample from a water-filled fruit capsule of the Brazil nut tree. *Osteocephalus* "*oophagus*" no. AF467267 may represent *O. cabrerai* according to Fouquet *et al.* (2007, Supporting Information).

round distal subarticular tubercle under the fourth finger; (13) dark keratinous excrescences restricted to prepollex; (14) in life, dorsum tan, pale brown to purple brown, with scarce narrow irregular dark brown markings; a narrow pale supralabial line expanding in a subocular spot; flanks pale, without markings; hidden surfaces of thighs light brown; throat and belly creamy white; a narrow dark line along the mandible; ventral surfaces of thighs fleshy pink; iris bicoloured with a dark horizontal stripe, golden above, bronze below, both parts with fine dark reticulate to radiate lines; tibiae green or white; (15) in life, newly metamorphosed juveniles light brown dorsally, with a dark interorbital spot, bright orange iris, and creamy white upper arms, knees and heels.

Comparisons. Morphologically, *O. castaneicola* can be distinguished from all other Amazonian species of *Osteocephalus* by absence of vocal slits and by the following combinations of characters: from *O. alboguttatus* by more extensive webbing and by colouration (*O. alboguttatus*: toes two thirds webbed, light brown dorsum with small blackish dots, flanks and upper surface of thighs with small round white spots, beneath whitish with dark reticulation) (Boulenger 1882, Duellman 1978); from *O. buckleyi* by absence of large tarsal tubercles, absence of patagium and by eye colouration (*O. buckleyi*: large tubercles along the tarsus, well developed patagium, light iris without conspicuous dark pattern) (Boulenger 1882, Cochran & Goin 1970; examined specimens listed in the Appendix); from *O. cabrerai* by absence of large dorsal, ulnar and tarsal tubercles, absence of patagium and by colouration (*O. cabrerai*: large wart-like tubercles on head and dorsum, large tubercles along the ulna and tarsus, small patagium, irregularly mottled dorsal pattern, light iris with very fine vermiculation) (Cochran & Goin 1970; examined specimens listed in the Appendix); from *O. carri* (Cochran & Goin) by colouration (*O. carri*: dense large irregular dark spots on the dorsum, black spots on flanks, fuscous throat and chest) (Cochran & Goin 1970); from *O. deridens* by larger size and by colouration (*O. deridens*: SVL up to 34.9 mm in males and 50.6 mm in females, dorsum light or dark tan with or without irregular darker or lighter markings, golden yellow iris with a dark horizontal stripe and regular dark radiation (Jungfer *et al.* 2000; examined specimens listed in the Appendix); from *O. elkejungingerae* (Henle) by skin texture and by colouration (*O. elkejungingerae*: conspicuous tubercles with keratinized tips in breeding males, dorsum with broad light dorsolateral stripes in juvenile and subadult specimens (Henle *et al.* 1983; Jungfer *et al.* 2000; examined specimens listed in the Appendix); from *O. fuscifacies* by larger size and by colouration (*O. fuscifacies*: SVL up to 45.6 mm in males and 53.2 in females, dorsum light or dark tan with or without irregular darker or lighter markings, light subocular spot absent, venter dark with creamy white granules or creamy white, golden iris with a dark horizontal stripe and regular dark radiation (Jungfer *et al.* 2000; examined specimens listed in the Appendix); from *O. heyeri* Lynch by larger size and by colouration (*O. heyeri*: SVL up to 36.1 mm in males and 47.7 mm in females, dorsum brown with darker markings and pale spots, flanks with pale spots, hidden surfaces of limbs dark brown with pale spots, iris dark) (Lynch 2002); from *O. leoniae* Jungfer & Lehr by larger size and by colouration (*O. leoniae*: SVL up to 42.0 mm in males and 53.2 mm in females, upper part of iris yellow without dark markings, unpigmented nuptial pads, bold dorsal pattern) (Jungfer & Lehr 2001, Chávez *et al.* 2008); from *O. leprieurii* by nuptial excrescences restricted to prepollex, skin texture and by colouration (*O. leprieurii*: prepollical and subdigital nuptial excrescences, numerous conspicuous tubercles with keratinized tips in breeding males, golden iris with dark vermiculation, white supralabial stripe in juveniles) (Jungfer & Hödl 2002); from *O. mutabor* by skin texture and by colouration (*O. mutabor*: numerous conspicuous tubercles with keratinized tips in breeding males, bold dark transverse markings, golden yellow iris with dark vermiculation, white dorsolateral stripes in juveniles) (Jungfer & Hödl 2002; examined specimens listed in the Appendix); from *O. oophagus* by head shape and by colouration (*O. oophagus*: truncate snout in dorsal view, white mottling or reticulation on posterior half of the flanks, golden iris with regular black radiation, orange spots on elbow, knee and heel in juveniles) (Jungfer & Schiesari 1995; examined specimens listed in the Appendix); from *O. pearsoni* by skin texture and by colouration (*O. pearsoni*: small nonspinous tubercles in males, black reticulation on the venter, dark iris) (Trueb & Duellman 1971, Jungfer & Schiesari 1995, Jungfer & Lehr 2001); from *O. planiceps* by smaller size, skin texture, keratinous excrescences restricted on prepollex and by colouration (*O. planiceps*: SVL up to 65.9 mm in males and 88.2 mm in females, numerous conspicuous tubercles with keratinized tips in breeding males, keratinous excrescences extending laterally to disc of thumb, dark spots on flanks, iris with regular black radiation) (Cope 1874, Duellman & Mendelson 1995, Jungfer & Lehr 2001, examined specimens listed in the Appendix); from *O.*

subtilis Martins & Cardoso by larger size and by colouration (*O. subtilis*: SVL up to 38.8 mm in males, dark iris) (Martins & Cardoso 1987); from *O. taurinus* by smaller size, less webbing on the hands and by colouration (*O. taurinus*: SVL up to 81.0 mm in males and 94.1 in females, fingers one-half webbed, dark spots on flanks, small brown flecks on the throat, chest and sides of the belly, greenish gold iris with regular black radiation) (Duellman 2005; examined specimens listed in the Appendix); from *O. verruciger* by skin texture and by colouration (*O. verruciger*: numerous conspicuous tubercles with keratinized tips in breeding males, uniform reddish brown iris) (Trueb & Duellman 1971, Jungfer *et al.* 2000, Jungfer & Hödl 2002); from *O. yasuni* by skin texture and by colouration (*O. yasuni*: numerous conspicuous tubercles with keratinized tips in breeding males, yellow venter in adults, iris with irregular dark reticulation, intense yellow-orange venter and webbing in juveniles) (Ron & Pramuk 1999, Jungfer *et al.* 2000, Jungfer & Hödl 2002, Cisneros-Heredia 2007). There are seven available names in the synonymy of four *Osteocephalus* species: *Hyla festae* Peracca, 1904 (type locality: Ecuador: “Valle de Santiago” (= lower Río Zamora) Province of Morona-Santiago) in the synonymy of *O. buckleyi*; *Hyla leprieurii britti* Melin, 1941 (type locality: Brazil: “Río Uaupés (north of the Río Japú”, Amazonas) and *Osteocephalus ayarzaguenai* Gorzula & Señaris, 1997 (type locality: Venezuela: “Campamento Airo, Valle del Río Karuay”, Estado Bolívar) in the synonymy of *O. leprieurii*; *Osteocephalus flavolineatus* Steindachner, 1862 (type locality: Brazil: “Cocuy” (= Cucuí), Amazonas) and *Hyla depressa* Andersson, 1945 (type locality: Ecuador: “Río Pastaza, Watershed”) in the synonymy of *O. taurinus*; and *Hyla riopastazae* Andersson, 1945 (type locality: Ecuador: “Baños, Río Pastaza, Provincia Tungurahua”) and *Hyla orcesi* Funkhouser, 1956 (type locality: Ecuador: “[Río] Pacayacu, a stream that flows into the Cotapino, drainage of the Suno, Río Napo region”) in the synonymy of *O. verruciger*. The new species differs from all of them by the following combination of characters: from *Hyla festae* by smaller size and by colouration (female holotype of *H. festae*: SVL 75.0 mm, large median longitudinal dark brown blotch on the dorsum, dark brown spots on flanks, throat and belly) (Trueb & Duellman 1971); from *Hyla leprieurii britti* by nuptial excrescences restricted to prepollex and by skin texture (male holotype of *H. l. britti*: prepollical and subdigital nuptial excrescences and tuberculate dorsum) (Trueb & Duellman 1971, Jungfer & Hödl 2002), from *Osteocephalus ayarzaguenai* by colouration (*O. ayarzaguenai*: golden iris with dark vermiculation) (Jungfer & Hödl 2002; examined specimen listed in the Appendix); from *Osteocephalus flavolineatus* by smaller size and colouration (female holotype of *O. flavolineatus*: SVL 81.8 mm, light middorsal stripe, spots on the flanks) (Cochran & Goin 1970, Trueb & Duellman 1971); from *Hyla depressa* by smaller size, skin texture, and by colouration (male holotype of *H. depressa*: SVL 68.9 mm, tuberculate dorsum, light middorsal stripe) (Cochran & Goin 1970, Trueb & Duellman 1971); from *Hyla riopastazae* by colouration (*H. riopastazae*: brown spots and mottling on throat, chest and belly) (Trueb & Duellman 1971); and from *Hyla orcesi* by skin texture and by colouration (*H. orcesi*: tuberculate dorsum, ventral surfaces dirty brown) (Cochran & Goin 1970, Trueb & Duellman 1971).

Description of the holotype. Adult male 51.3 mm SVL. Head narrower than body, slightly longer than wide; snout rounded in dorsal view, moderately protruding in lateral view; distance from nostril to eye shorter than diameter of eye; canthus rostralis distinct, angular, curved medially; loreal region concave; internarial area slightly depressed; nostrils moderately protuberant, directed laterally; interorbital area flat, IOD 112.2% of ELW; lateral margins of the frontoparietals barely visible through skin; eye large, strongly protuberant, its diameter about five times depth of lip below eye; tympanic membrane clearly evident, large, slightly wider than high, about two third of eye length, separated from eye by ca. 50% of its diameter; tympanic annulus distinct; supratympanic fold conspicuous, covering upper edge of tympanum, continuing above insertion of arm. Arm slender, axillary membrane absent; small low tubercles scattered along ventrolateral edge of forearm; relative length of fingers I<II<IV<III; fingers bearing large, oval discs, that of third finger about half of tympanum diameter; subarticular tubercles prominent, round, single; supernumerary tubercles present; palmar tubercle large, flat, disunited distally; prepollical tubercle large, flat, elliptical; prepollex enlarged; large dark keratinous nuptial excrescences covering inner surface of prepollex up to subarticular tubercle of thumb (Fig. 3.1.3); webbing rudimentary between fingers I and II; webbing formula of fingers II2^{-}—3^{-}III3^{-}—3^{-} IV. Legs moderately long, slender; heels overlapping when limbs flexed perpendicular to the axis of body; small raised tubercles on the outer edge of tibiotarsal articulation; small low tubercles scattered along the ventrolateral edge of foot; toes moderately long, bearing oval discs slightly smaller than those of fingers; relative length of toes I<II<V<III<IV; outer metatarsal tubercle distinct, small, round;

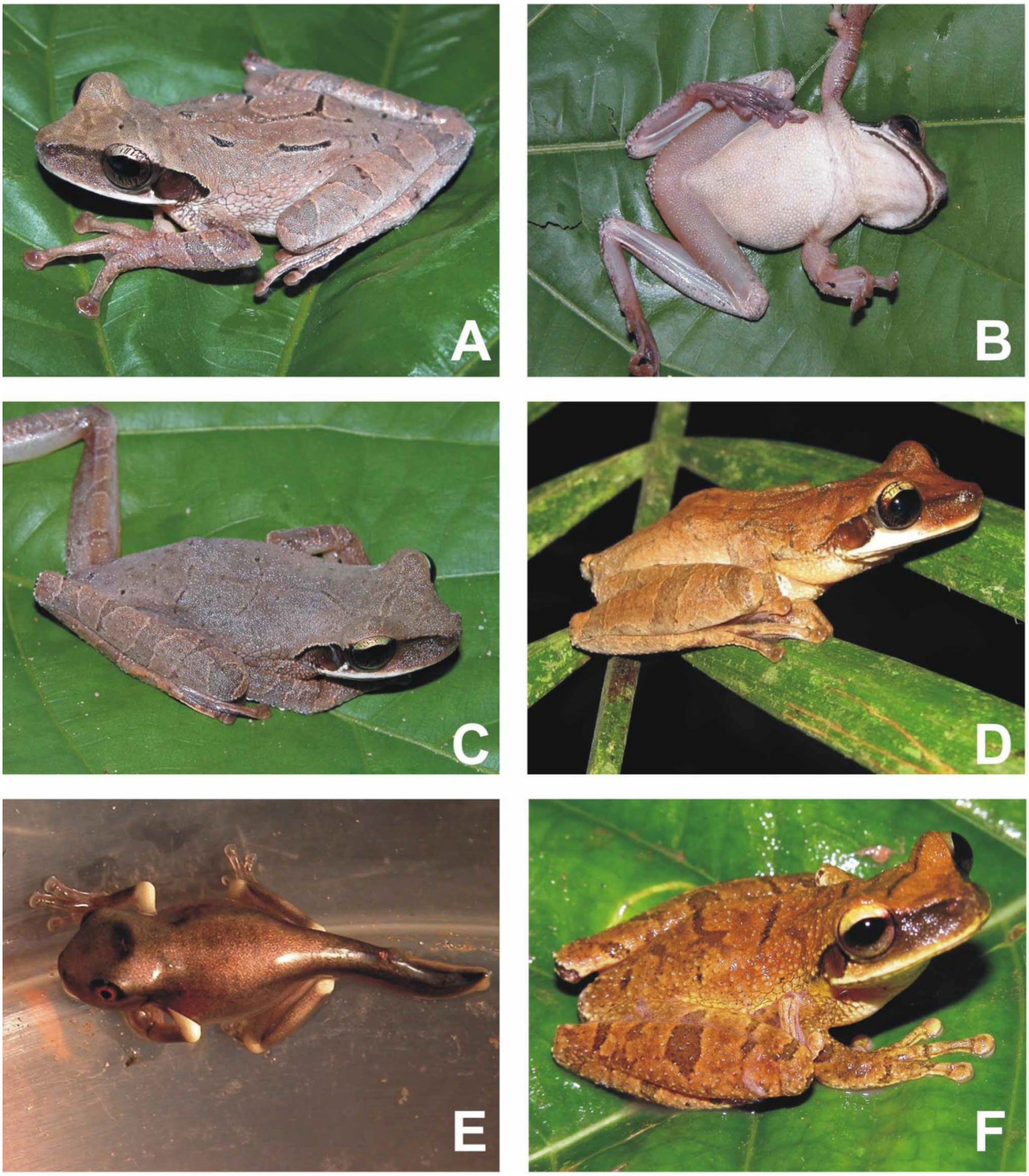

Figure 3.1.2. Holotype of *Osteocephalus castaneicola* **sp. n.** (CBF 6051) in life, (A) dorsal, and (B) ventral views. (C) Adult female paratype of *Osteocephalus castaneicola* **sp. n.** (CBF 6052) in life. (D) Night colouration of adult male paratype of *Osteocephalus castaneicola* **sp. n.** (NMP6V 73810/2) under natural conditions. (E) Newly metamorphosed juvenile of *Osteocephalus castaneicola* **sp. n.** (F) Adult male of *Osteocephalus* sp**.** (B) (NMP6V 73105) from Canadá (Bolivia, Pando) in life.

inner metatarsal tubercle large, ovoid; subarticular tubercles single, round, protuberant; supernumerary tubercles present; toes three fourths webbed; webbing formula of toes I1^{+}—2^{-}II1—2^{-}III1—2^{-}IV2^{-}—1^{-}V. Skin on dorsum, head, and dorsal surfaces of limbs smooth, with numerous minute tubercles; skin on flanks shagreen; skin on venter coarsely granular; skin on throat slightly granular; proximal two thirds of lower surfaces of thighs slightly granular. Cloacal opening directed posteriorly at upper level of thighs; short simple cloacal sheath covering cloacal opening; rounded tubercles around vent and on posterior surface of proximal third of thigh. Tongue ovoid, widely attached to floor of mouth; vomerine odontophores angular, separated medially, between choanae, bearing 8 and 9 (left/right) vomerine teeth; choanae rhomboidal, oblique; vocal slits absent; vocal sac indistinct.

Measurements of the holotype: SVL 51.3; HL 17.7; HW 16.6; EN 5.3; ED 6.1; TD 4.0; ELW 4.9; IOD 5.4; TL 27.3; FL 33.4.

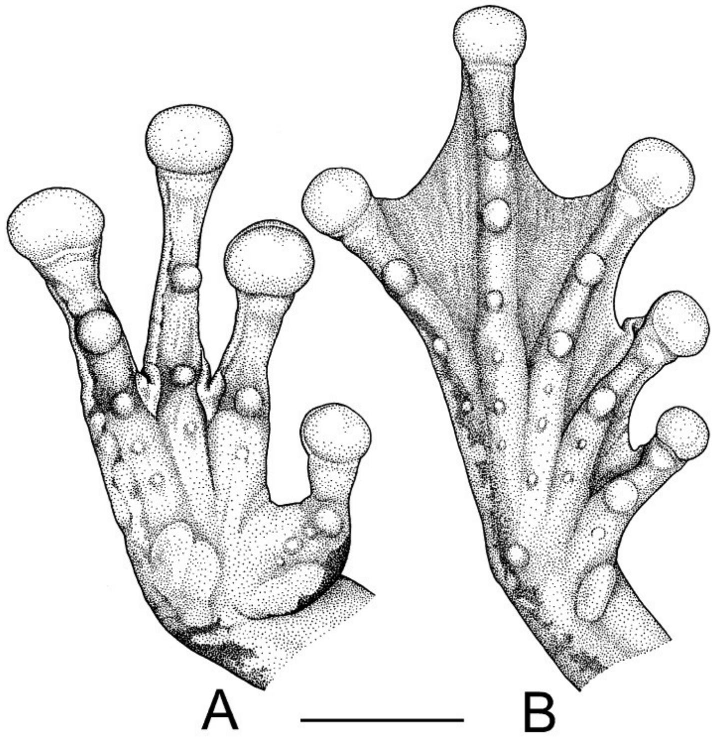

Figure 3.1.3. (A) Palmar, and (B) plantar views of right hand and foot of the holotype of *Osteocephalus castaneicola* sp. n. (CBF 6051). Scale bar equals 5 mm.

In alcohol, head and dorsum tan with several narrow irregular darker tan to dark brown markings (including an indistinct interorbital stripe) narrowly outlined by pale brown line; dorsal surfaces of limbs tan with darker tan crossbars outlined by a pale brown line. A narrow pale supralabial line expanding in a subocular spot; a dark canthal stripe extending from nostril to the anterior margin of eye; a broad dark brown postocular stripe extending from posterior margin of eye across the tympanum to insertion of arm. Flanks pale with several inconspicuous small darker markings; a dark supracloacal spot; hidden surfaces of thighs tan. Throat and belly creamy white; a narrow dark line along the lower jaw; ventral surfaces of thighs yellowish white; plantar surfaces pale brown. Tibiae green.

In life, dorsal and lateral colouration differed only slightly from the preserved specimen in having a slight purple-red tint by day. Ventral surfaces of forearms and thighs fleshy pink; tibiae green. Iris bicoloured with dark brown horizontal stripe, golden above, bronze below, both parts with fine dark reticulate to radiate lines (Fig. 3.1.2A).

Variation. Variation of measurements of the type series is given in Table 3.1.3. *Osteocephalus castaneicola* exhibits sexual dimorphism in body size, but sexual dimorphism of dorsal skin texture is absent. Both breeding males and females bear similar minute flat to round tubercles on dorsal surfaces of head, body and limbs. The most conspicuous dorsal tubercles are present in female paratopotype CBF 6052 (Fig. 3.1.2C), having SVL 47.7 mm and containing numerous small immature eggs. The new species shows considerable variation in number of vomerine teeth (6–14 on each odontophore). Vomerine odontophores are separated in holotype, paratopotype NMP6V 72810/1 and paratypes CBF 6054 and NMP6V 73820, but in contact in the remaining types. Some variation seems to be evident in distinctiveness of lateral margins of the frontoparietals. They are not visible through skin in smaller individuals (SVL up to 47 mm; paratopotype CBF 6052 and paratype CBF 6053) and best pronounced in largest individuals (SVL above 59 mm; female paratopotype NMP6V 73810/3 and female paratypes CBF 6054 and NMP6V 73820). Some differences can be found in shape of distal subarticular tubercle of the fourth finger. It is single in holotype and four other type specimens, but it shows a slight tendency to bifidity in the paratopotype NMP6V 73810/3 and paratypes CBF 6053 and NMP6V 73820. The finger and toe webbing formulae vary as follows: II $(2^{-}–2^{+})$—$(3^{-}–3^{+})$ III $(3^{-}–3)$—$(2^{2}/_{3}$–

3^{-}) IV and I (1–$1^{1}/_{4}$)—($1^{2}/_{3}$–2^{-}) II (1–1^{+})—(2^{-}–2) III (1–1^{+})—($1^{2}/_{3}$–2) IV ($1^{2}/_{3}$–2^{-})—(1^{-}–1) V.

General dorsal colouration in alcohol varies from light tan to dark tan with purple-red tint or to reddish brown. Dorsal pattern varies mostly regarding distinctness and shape of the irregular darker markings. A more or less distinct interorbital streak narrower than the diameter of the eye is present in all individuals. Dorsal markings are fused in a large, irregular, indistinct dorsal spot in the male paratype CBF 6053, whereas dorsal pattern of paratopotypes CBF 6052, NMP6V 73810/1, 73810/3 and paratype 73820 is almost missing. Ventral colouration in alcohol varies from cream white to yellowish-white. A fine dark brown mottling is present on the throat and pectoral area of the female paratype NMP6V 73820. Colour of tibiae seems to vary independently of age or size of individual specimens. The bones are green in the holotype and paratopotypes NMP6V 73810/1–3 (SVL 48.4–59.1 mm) and white in

Table 3.1.3. Variation of measurements (in mm) of the type series of *Osteocephalus castaneicola* sp. n.). See text for abbreviations.

Measurement	Males (N=4)	Females (N=4)
	Mean ± SD; Range	Mean ± SD; Range
SVL	49.3 ± 1.56; 47.8–51.3	57.6 ± 6.83; 47.7–63.3
HL	16.9 ± 0.87; 15.7–17.7	19.4 ± 2.18; 16.6–21.9
HW	16.2 ± 0.67; 15.4–16.9	18.4 ± 1.92; 15.6–20.0
EN	5.0 ± 0.36; 4.5–5.3	6.1 ± 0.87; 4.9–7.0
ED	5.9 ± 0.29; 5.1–6.1	6.1 ± 0.71; 5.1–6.8
TD	3.7 ± 0.22; 3.5–4.0	4.3 ± 0.70; 3.5–5.2
ELW	4.8 ± 0.08; 4.7–4.9	5.5 ± 0.79; 4.6–6.4
IOD	5.0 ± 0.30; 4.7–5.4	5.8 ± 0.83; 4.8–6.6
TL	26.5 ± 0.70; 25.7–27.3	31.9 ± 3.28; 27.2–32.9
FL	32.5 ± 1.35; 30.5–33.4	38.5 ± 4.46; 31.9–41.3

paratopotype CBF 6052 and paratypes CBF 6053, 6054 and NMP6V 73820 (SVL 47.7–63.3 mm). In life, dorsal colouration varies from tan to brown. A slight purple-red tint observed in most specimens by day turns into ochre by night (Fig. 3.1.2D).

Newly metamorphosed juveniles are light brown dorsally with a dark interorbital spot, bright orange iris, and creamy white upper arms, knees and heels (Fig. 3.1.2E).

Distribution, ecology and threat status. The known localities of *Osteocephalus castaneicola* lie in western and central part of the Departamento Pando, northern Bolivia (Fig. 3.1.4). This area is located in the south-western Amazon basin within the zone of tall evergreen lowland rainforest. *O. castaneicola* was encountered in more or less undisturbed terra firme forest with frequent occurrence of large climax forest trees [e.g. *Bertholletia excelsa* Humb. & Bonpl., *Ceiba pentandra* (L.) Gaertn., *Cedrela odorata* L., *Ficus* sp.]. The forest was characterised by relatively well defined tree strata and a dense canopy at ca. 25–35 m above the ground. The understory was dominated by various tree seedlings, young trees, herbaceous lianas, palms and ferns. The forest floor was covered by leaf litter with scattered large fruit capsules of the Brazil nut tree (*Bertholletia excelsa*) and other species of Lecythiadaceae. All observed individuals of *O. castaneicola* were sitting on vegetation in ca. 0.5–2 m height. No calling males were located. Other hylid species found in sympatry with *O. castaneicola* included *Hypsiboas lanciformis* Cope, *H. punctatus* (Schneider), *Phyllomedusa camba* De la Riva, *P. tomopterna* (Cope), *P. vaillantii* Boulenger, *Trachycephalus coriaceus* (Peters), and *T. resinifictrix* (Goeldi). *O. castaneicola* is apparently known (as *O.* sp.) to occur also in the Region Madre de Dios (exact localities not provided) in adjacent southern Peru (von May *et al.* 2007). Life history of *O. castaneicola* is closely associated with fruit capsules of the Brazil nut tree, which are opened by agoutis (*Dasyprocta* sp.) or indigenous Brazil nut collectors and abandoned on the forest floor. At both known localities of *O. castaneicola* some of water filled capsules contained tadpole assemblages numbering up to tens of individuals. Rarely the same tadpoles were found also in water-filled palm bracts lying on the ground. In some cases the assemblages consisted of larvae of markedly different sizes and different stage of development. The largest tadpoles reached a total length of 33–35 mm. Occasionally, white ingested eggs were visible through the transparent venter of the larger larvae. The tadpoles were raised until metamorphosis (Fig. 3.1.2E) and their determination was verified by genetic comparison with the adult specimens (Fig. 3.1.1). According to the sparse data available we here classify *O. castaneicola* as “Data Deficient” according to the IUCN red list criteria. In Peru, the species occurs within protected areas (von May *et al.* 2007).

Etymology. The specific name is a compound from the Latin *castanea* (Horse Chestnut, *Aesculus*) from which the Spanish *castaña* (vernacular name of the Brazil nut tree) was derived and the Latin *colō* (to inhabit). The name is used as a noun in apposition and refers to the life history of the new species.

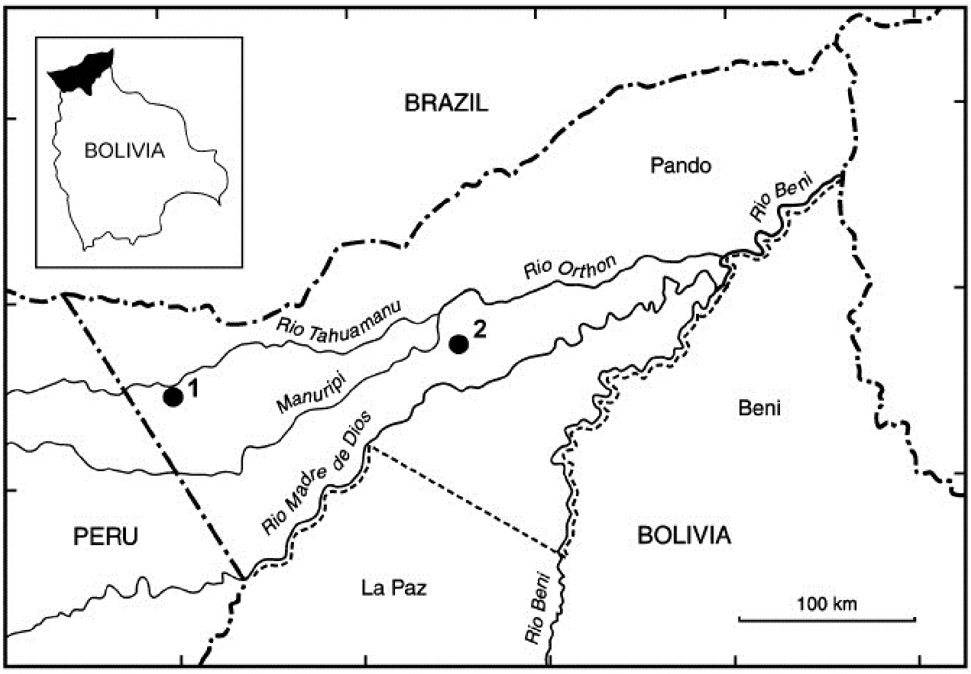

Figure 3.1.4. Schematic map of northern Bolivia showing the known distribution of *Osteocephalus castaneicola* sp. n. in Bolivia: (1) San Antonio del Matti, (2) San Antonio de Filadelfia (type locality).

Discussion

The obtained phylogeny demonstrates existence of several distinct lineages within the genus *Osteocephalus*. Nevertheless, the fact that representatives of two nominal species (*O. leprieurii* and *O. oophagus*) cluster independently within two different clades indicates that more complete sampling and accurate determination of analysed taxa are necessary to obtain a more exact picture of phylogenetic relationships within the given genus. Some of the GenBank sequences represent obviously misidentified species or even a chimerical sequence (see Table 3.1.1). Also the high genetic similarity of the GenBank sequences of *O. cabrerai, O. verruciger* and *O.* "*oophagus*" argue more likely for erroneous original determination of the sequenced animals than for close or even nearly identical phylogenetic positions of these morphologically well differentiated species. However, despite of the rather preliminary character of the obtained phylogeny of the genus, it is evident that *O. castaneicola* forms a separate monophylum with *O. deridens*, *O. planiceps* and the GenBank sample from Venezuela determined as *O. leprieurii* (sensu Faivovich *et al.* 2004, 2005) (Fig. 3.1.1).

Both *O. castaneicola* and *O. deridens* lay eggs in phytotelmata and take care of their oophagous tadpoles. Similarly, *O. planiceps* breeds in various phytotelmata (pers. obs. KHJ). In contrary, *O. leprieurii* forms explosive breeding congregations around temporal free waters (Jungfer & Hödl 2002). Considering these huge differences in reproductive mode, the position of Venezuelan "*leprieurii*" in this clade seems to be questionable. In the past, the name *O. leprieurii* has been widely used for many forms of *Osteocephalus* and it is likely that the Venezuelan sample represents a misidentified taxon (this sample was used later also by Wiens *et al.* 2005, 2006, Fouquet *et al.* 2007 and Moen & Wiens 2009). This possibility is supported by the fact that the GenBank sample of *O. leprieurii* from French Guiana (EF376066; Salducci *et al.* 2005), where the type locality of this species (Cayenne) is located, is embedded in a different clade together with morphologically similar *O. mutabor*, *Osteocephalus* sp. (B) and other species. A similarly doubtful situation can be found in the case of two GenBank samples of *O.* "*oophagus*" from French Guiana (Salducci *et al.* 2002, Faivovich *et al.* 2005; the latter sample was used also by Wiens *et al.* 2006, and Moen & Wiens 2009), which cluster separately in two different clades. However, the GenBank sample AF467267 was labelled without further explanation as *O. cabrerai* in Fouquet *et al.* (2007), contrary to the original (Salducci *et al.* 2002, 2005) and GenBank data. The sample really clusters with *O. cabrerai* (AY843705; Faivovich *et al.* 2005), and thus, may represent rather *O. cabrerai* than *O. oophagus*. Anyway, both clades containing *O.* "*oophagus*" comprise species, which breed in free water bodies and do not take care of their tadpoles, although *O. oophagus* is known by reproducing in phytotelmata and feeding its tadpoles with fertilized eggs (Jungfer

& Weygoldt 1999). Considering egg deposition in free water plesiomorphic (Duellman & Trueb 1986), we can suppose the tendency to utilize phytotelmata as breeding place to be a derived state. Therefore, one may expect that *Osteocephalus* species with this derived reproductive mode could cluster together. However, this pattern is not supported by current data considering any of the ambiguous positions of *O.* "*oophagus*" in our tree, suggesting that this reproductive strategy may have evolved more than once within *Osteocephalus*. Nevertheless, specific determination of the "*oophagus*" samples should be verified to have a clearer picture on the life history evolutionary scenario in this genus.

Breeding in phytotelmata is one of many possible ways to avoid competition and predator pressure in the tropics (e.g. Duellman 1978, Krügel & Richter 1995). In this respect, fruit capsules of the Brazil nut tree may offer an excellent shelter. In addition, water trapped in the capsules dries up much more slowly than free water in small puddles appearing on the forest floor after heavy rains. Therefore, frogs specialized to breeding in abandoned Brazil nut tree capsules may profit both from the protection and from relatively stable water conditions provided by these unusual phytotelmata. Although *O. castaneicola* represents the first evidence of a hylid frog breeding in fruit capsules of the Brazil nut tree, at least three other frog species are known to use the same breeding place: two dendrobatids, *Adelphobates castaneoticus* (Caldwell & Myers) and *A. quinquevittatus* (Steindachner), and one bufonid, *Rhinella castaneotica* (Caldwell) (Caldwell 1993, Lötters *et al.* 2007). Complex life history responses to predation are described in two of these species by Caldwell (1993). There are no similar available data in the case of *Osteocephalus castaneicola*. Absence of vocal slits and absence of an obvious vocal sac is the most characteristic morphological feature of the males of *O. castaneicola*. Jungfer & Hödl (2002) suppose that the relatively small subgular vocal sac of bromeliad-breeding species of *Osteocephalus* might have evolved from ancestral (for the genus) lateral or both lateral and subgular vocal sac as an adaptation towards limited space in a narrow leaf axil.

Therefore, an interesting question is, if disappearance of vocal slits as well as a distinct vocal sac can be seen as an advanced adaptation for breeding in limited space inside the Brazil nut tree fruit capsule. Observation of sporadic breeding also in fallen water-filled palm bracts indicates some degree of plasticity in the breeding strategy of the new species. It appears that at least in the case of *Rhinella castaneotica* the fruit capsules are not obligatory for the breeding. This species has subgular vocal sac and can reproduce also in small waterfilled holes in the soil (see Köhler & Lötters 1999). Therefore, more detailed research should be further done to understand the unusual life history of *O. castaneicola.*

As mentioned in the introduction, the taxonomic status of the Bolivian populations referred to as *Osteocephalus* sp. (A) (Jungfer & Lehr 2001) remains to be solved. It was reported as *O. leprieurii* or *O.* cf. *leprieurii* from the Departamento Santa Cruz by De la Riva *et al.* (2000). According to the scarce information available, this taxon resembles *O. leprieurii*, but differs from it by its bicoloured iris with dark reticulation, yellow venter and absence of sexual size dimorphism (Jungfer & Hödl 2002). On the other hand, Jungfer & Lehr (2001) mentioned that the bicoloured iris of this species lacks reticulation and also the specimen from Los Fierros figured by De la Riva *et al.* (2000, p. 107) lacks an obvious reticulation in the iris. A formal description of this taxon should be in press since 2000 (see De la Riva *et al.* 2000, Jungfer & Lehr 2001, Jungfer & Hödl 2002). Unfortunately, no tissue samples of *Osteocephalus* sp. (A) were at disposal for our molecular comparison with populations of similar *Osteocephalus* sp. (B) from Pando (Fig. 3.1.2F). The latter form shows relatively high variation in iris colouration (bicoloured to uniform with dark horizontal stripe and dark vermiculation). It has creamy to yellowish white venter and it is slightly dimorphic in sexual size (Moravec & Aparicio 2004). Morphologically, *Osteocephalus* sp. (B) cannot be differentiated clearly from *O. leprieurii,* redescribed by Jungfer & Hödl (2002). It appears to be conspecific with the Brazilian population discovered recently ca. 600 km east of the Bolivian border in municipality of Aripuanã (10°09' S, 59°28' W; state of Mato Grosso) and determined as *O. leprieurii* (Santana *et al.* 2008). According to our molecular results, *Osteocephalus* sp. (B) forms a discrete unit with the sample of *O. leprieurii* from French Guiana. Nevertheless, it is difficult to judge if it is really conspecific with *leprieurii* or not (obtained divergence 1.3– 1.8 % uncorrected *p*-distances in 16S rRNA; 1.2 % in the among-all species comparable fragment, Table 3.1.2). Therefore, a more thorough study focused on phylogeography and bioacoustics of *O. leprieurii* including populations of *Osteocephalus* sp. (A) and *Osteocephalus* sp. (B) is necessary to solve the systematic status and mutual position of these forms.

Acknowledgments

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Appendix. Additional specimens examined

Osteocephalus “*ayarzaguenai*”: VENEZUELA: Amazonas: Marakapiwei, MBUCV 6632.

Osteocephalus buckleyi: BOLIVIA: Pando: Santa Crucito, NMP6V 73945; Pando: CBF 1262, 2150–51.

Osteocephalus cabrerai: PERU: Loreto: 21 km W of Iquitos, NMP6V 71144/1–2.

Osteocephalus castaneicola sp. n.: BOLIVIA: Pando: San Antonio de Filadelfia, NMP6d 28/2009.

Osteocephalus deridens: PERU: Loreto: Anguilla, NMP6V 71263; 35 km SW of Iquitos, NMP6V 71262/1–5.

Osteocephalus elkejungingerae: PERU: Huánuco/Ucayali: El Boquerón del Padre Abad, ZFMK 33352 (holotype), 36319 (paratype).

Osteocephalus fuscifacies: ECUADOR: Napo: Aliñahuí (5 km W of Ahuano), ZFMK 68660 (paratype).

Osteocephalus mutabor: ECUADOR: Napo: Río Chaloyacu on Carretera Narupa – Coca, ZFMK 66237 (paratype).

Osteocephalus oophagus: BRAZIL: Amazonas: Reserva Forestal Adolfo Ducke, ZFMK 57137–38 (paratypes).

Osteocephalus planiceps: PERU: Loreto: Anguilla, NMP6V, 71264/1–2; 21 km W of Iquitos, NMP6V 71204/1–2; Puerto Almendras, NMP6V 71174/1–5.

Osteocephalus taurinus: BOLIVIA: Pando, Nacebe, NMP6V 72172/1–2; Pando: CBF 1281, 1300–02, 2147–48, 43333;

PERU: Loreto: Puerto Almendras, NMP6V 71184.

Osteocephalus sp. (B): BOLIVIA: Pando: Canadá, NMP6V 73105; Nacebe, CBF 5589–93, NMP6V 72173/1–4; Palmira, NMP6d 41/2009.

3.1.2. *Osteocephalus duellmani* Jungfer, 2011

This part was published in *The Herpetological Journal* as follows:

Jungfer, K.-H. (2011): **A new tree frog of the genus *Osteocephalus* from high altitudes in the Cordillera del Cóndor, Ecuador (Amphibia: Anura: Hylidae)**. *Herpetological Journal*, 21(4): 247-253.

ABSTRACT

A new *Osteocephalus* is described from the Ecuadorian part of the Cordillera del Cóndor, an isolated sub-Andean mountain range along the Ecuadorian – Peruvian frontier. Apparently an endemic to these mountains, it is one of the few species in the genus reaching an altitude of almost 2000 m. It can be distinguished from other species in the *O. buckleyi* complex by lacking spinous dorsal tuberculation, a relatively small tympanum, uniformly coloured posterior surfaces of the thighs, lack of a row of tubercles on the lower jaw and smooth fringes on the inner side of Finger III and outer edge of Finger IV.

Key words: *Osteocephalus* new species; Ecuador, Peru, Cordillera del Cóndor.

INTRODUCTION

The Cordillera del Cóndor is one of several sub-Andean mountain ranges stretching north to south for about 150 km parallel to the Andes along the border between Ecuador and Peru, its highest peaks reaching an altitude of about 2900 m. Unlike the main eastern cordillera of the Andes, which is built up of metamorphic and volcanic rock, it consists of sand- and limestone, basically sediments uplifted in the Mesozoic and early Tertiary at about the same time as the Andes, but apparently disjunct from the Andean Cordillera Oriental (Neill, 2005; Missouri Botanical Garden, 2007). Several expeditions have shown the Cordillera del Cóndor to be a region of high biodiversity and endemism, not only botanically, as could be expected by the different geological formations (Schulenberg & Awbrey, 1997; Neill, 2005; Missouri

Botanical Garden, 2007; Conservation International, 2009). Several amphibian species have been described from the Cordillera del Cóndor, mainly based on material collected by an expedition to the headwaters of Río Piuntza in 1972 (Lynch, 1974; 1976; 1979; Lynch & Duellman, 1980; Duellman & Lynch, 1988; Duellman & Simmons, 1988; Duellman & Pramuk, 1999). More recent expeditions to the Cordillera del Cóndor (e. g. Schulenberg & Awbrey, 1997; Conservation International, 2009), are also beginning to have impact on the number of new species known from the area (e. g. Duellman, 2004; Cisneros-Heredia & McDiarmid, 2006; Cisneros-Heredia & Morales-Mite, 2008; Cisneros-Heredia et al., 2008; Teran-Valdez & Guayasamin, 2010). For species lists see also Duellman & Lynch (1988), Almendáriz (1997), Reynolds (1997) and Reynolds & Icochea M. (1997).

Tree frogs in the genus *Osteocephalus* are not typically inhabitants of high elevations, but predominantly of Amazonian and Guianan lowland rainforests. Few species reach 1200 m in elevation, and there are only five species that surpass 1500 m. One of these is *O. phasmatus* (1550 m) from Mount Ayanganna in the Guiana Highlands (MacCulloch & Lathrop, 2005). On the eastern Andean slopes, *O. carri* reaches 1600 m in Colombia (specimens at ICN, Jungfer, 2010), *O. mimeticus* ascends to 1650 m in Peru (Jungfer, 2010), and *O. verruciger* from Ecuador and southern Colombia is reported from 1840 m asl (Trueb & Duellman, 1971). Some specimens of *O. verruciger* at KU collected later than 1971 are from 1910 m. A species similar to *O. verruciger* occurring in the Cordillera Oriental in northern Peru and southern Ecuador (*O.* "*festae*" of Ron et al., 2010) reaches an altitude of 2200 m (Jungfer, 2010: 41; Ron et al., 2010). The aim of this paper is to describe a new species in the *O. buckleyi* complex from similarly high elevations (1910 m), that is known only from the Cordillera del Cóndor.

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. Terminology of skin texture is as described by Duellman & Lehr (2009) for strabomantid 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-to-vent length; TD: tympanum diameter; TE: distance between tympanum and eye; TL: tibia length. Measurements were made using digital callipers or the ocular micrometer of a dissecting microscope if less than 5 mm; all measurements are in mm. Museum abbreviations follow Frost (2011). The appendix of specimens examined lists those species not already included in Jungfer (2010).

Results

Osteocephalus duellmani n. sp.

Holotype: KU 147172, an adult male of 48.6 mm SVL (Fig. 3.2.1), collected in the Cordillera del Cóndor, Río Piuntza, 1910 m asl, about 3°25'S, 78°27'W, Provincia Morona-Santiago, Ecuador, by John E. Simmons on 5 January 1972.

Paratype: KU 147171, a subadult of 34.0 mm SVL (Fig. 3.2.2), collected on 4 January 1972, otherwise with same data as holotype.

Diagnosis and comparisons. The coarse dorsal skin, areolate flanks, angular dentigerous processes of the vomers and size distinguish *O. duellmani* from other hylid frog genera in southeastern Ecuador and northeastern Peru. Within the genus it resembles *O. buckleyi* and *O. festae* in having a rounded and curved canthus rostralis and coarsely areolate flanks (Jungfer, 2010). It may be diagnosed as (1) a medium sized species in males (48.6 mm SVL) (females unknown); (2) skin on dorsum of (non-breeding) males shagreen; (3) skin on flanks coarsely areolate; (4) rounded canthus rostralis curved inward; (5) frontoparietal ridges not visible externally; (6) dentigerous processes of vomers angular; (7) moderately thick, tuberculate supratympanic fold from the posterior edge of the orbit sloping in an arch towards the arm insertion; (8) web on inner edge of third finger reaching to penultimate subarticular tubercle, continued to ultimate subarticular tubercle as a fringe; (9) distal subarticular tubercle on Finger IV barely bifid or single; (10) dorsum tan with irregular dark tan blotches, posterior part sometimes with minute light spots ; (11) throat, chest and venter creamy tan to creamy white with irregular tan spots; (12) one or two white supralabial marks; (13) flanks creamy white without dark tan blotches, areolae outlined dark tan; (14) position of vocal sacs paired, protruding ventral to angles of jaws; (15) juvenile colouration unknown; (16) tadpole habitat (most likely in streams) and labial tooth row formula unknown; (17) colour of tibiofibular bones white in preservative.

Osteocephalus duellmani differs from other species in the *O. buckleyi* complex (Jungfer 2010) as follows (characters of *O. duellmani* in parentheses): *Osteocephalus buckleyi* has a large tympanum with TD/HL 0.23-0.26 in males (medium-sized, TD/HL 0.15-0.16), posterior surfaces of the thighs tan with or without dark brown and/or light marbling or irregular crossbars (light tan, uniform), and webbing on the inner side of Finger III without fringe from penultimate subarticular tubercle to intercalary tubercle (fringe present). *Osteocephalus cabrerai* has a row of tubercles on the lower jaw (absent) and an irregular, deep fringe on the outer edge of Finger IV (smooth, shallow fringe). *Osteocephalus festae* has a large tympanum in males with TD/ED 0.23-0.25 (medium-sized, TD/HL 0.15-0.16) and a row of low tubercles on the outer edge of Finger IV (smooth, shallow fringe). The dorsal surface of the head, inclusive of the orbits, of *O. festae* is tuberculate interspersed with several larger tubercles (uniformly tuberculate). *Osteocephalus* sp. (*O.* "*festae*" sensu Ron et al., 2010) from the Andes of southern Ecuador and northern Peru has large tubercles on the dorsum in breeding and non-breeding condition (shagreen without large tubercles in non-breeding male). It further differs in having a rounded lower jaw (slightly pointed tip of lower jaw) and a protruding snout in ventral view (less protruding) (Fig. 3.2.3). In *O. inframaculatus* the dorsal surfaces of the head and canthus rostralis are covered with small, irregular tubercles and there are larger tubercles on the orbits (uniformly tuberculate). The posterior surfaces of the thighs are tan with light, short vermiculation (light tan, uniform).

Other species of *Osteocephalus* from the Andean slopes between 600 and 2000 m differ as follows: *Osteocephalus carri* is shagreen to weakly tuberculate in the subcloacal area (warty). Males of *Osteocephalus mimeticus*, *O. mutabor* and *O. verruciger* have tuberculate dorsa with spinous tubercles with (breeding) or without keratinized tips (non-breeding) (shagreen in non-breeding male) (Jungfer, 2010; Jungfer & Hödl, 2002; Trueb & Duellman, 1971).

Other *Osteocephalus* species in the western Amazonian lowlands adjacent to the Cordillera del Cóndor differ from *O. duellmani* as follows: *Osteocephalus deridens* differs by smaller size in males, to 40.0 mm SVL (48.6 mm), dorsum with scattered low tubercles (absent) and axillary membrane absent (present) (Jungfer *et al*., 2000); *O. fuscifacies* by the absence of an axillary membrane (present), and less webbing on the foot that does not reach the intercalary tubercle on the outer side of Toe III (to intercalary tubercle) (Jungfer *et al*., 2000); *O. leoniae* by a straight, angular canthus rostralis (curved inward, rounded), a thin dark line on the lower lip (absent), and less webbing, just or barely reaching proximal edge of proximal subarticular tubercle on the inner side of Finger III (to proximal subarticular tubercle and continued to intercalary tubercle as a fringe) (Jungfer & Lehr, 2001). *Osteocephalus planiceps* is considerably larger, males up to 67.8 mm SVL, and with a straight, angular canthus rostralis (concave, rounded). *Osteocephalus taurinus* with males up to 89.3 mm SVL and *O. yasuni* with males up to 56.0 mm SVL are larger species (48.6 mm) and males of both species have tuberculate dorsa with (breeding) or without keratinized tips (non-breeding) (shagreen in non-breeding male) (Trueb & Duellman, 1971; Ron & Pramuk, 1999; Jungfer, 2010).

Description of holotype: The snout is bluntly rounded in dorsal and lateral view. The head is longer than wide (HL/HW 1.06). The lateral edges of the frontoparietals are not visible through the skin. The canthus rostralis is concave, rounded. The loreal region is oblique, concave. The nostrils are elevated, opening posterolaterally. The lips are flared. The dentigerous processes of the vomers are angular, separated from each other, bearing 9 teeth on the left and 10 on the right. The processes are situated between the choanae, their anterior edges at midlevel of the choanae, their posterior edges reaching beyond the posterior edges of the choanae. They are somewhat asymmetrical (length on the right 2.3 mm, on the left 1.8 mm) in this specimen. Together, they are slightly wider than the narrowest interchoanal distance. The choanae are large, oblique, ovoid, and somewhat angular anteriorly. The tongue is elliptical, about 1.3 times wider than long.

The postocular area is barely oblique, almost vertical. There is a moderately heavy, tuberculate supratympanic fold from posterior to the orbit following the shape of the tympanum from 11 to 3 (tympanum of the left side visualised as a clock face), and then curving towards the midlevel of the arm insertion. The tympanum is elliptical (height 89% of width), with a distinct tympanic annulus that is partly concealed dorsally by the supratympanic fold. It is medium-sized, its diameter about 93% of the

Fig. 3.2.1. Holotype of *Osteocephalus duellmani* n. sp. (KU 147172) in dorsal and ventral view, lateral view of the head and cloacal region with posterior surface of the thigh.

width of the disc of Finger III and 49% of the eye diameter. Dorsal surfaces of the head, orbits, loreal region and postorbital area are evenly weakly tuberculate. Posteroventral to the tympanum, tubercles are larger than those anteriorly. Dorsally, the skin of the body is shagreen. The flanks are coarsely areolate from above the arm insertion to the groin. The gular area is shagreen anteriorly, becoming areolate posterolaterally. The vocal sacs are paired and protrude ventral to the angles of the jaws. The arms are finely shagreen dorsally and ventrally. A few outer ulnar tubercles are flat and indistinct. An axillary membrane is conspicuous in ventral view, covering one fourth of the upper arm proximally in dorsal view. The proximal two thirds of the thighs are finely areolate ventrally and lateral from the cloacal opening, shagreen dorsally, the other surfaces are smooth. There are three to four minute, flat tubercles on the heel. The outer edge of the metatarsus is smooth. A few minute tubercles are present on the outer edge of Toe V. Lateral to the cloacal opening, which is situated almost at the upper level of the thighs and opens posteriorly, there are numerous tubercles that extend to the posterior surfaces of the thighs. The subcloacal area is warty. A cloacal sheath is weak (Fig. 3.2.1).

The finger discs are ovoid. A large elliptical thenar tubercle is present. Small, flat supernumerary tubercles are present on the bases of all fingers. The distal subarticular tubercle on Finger IV is barely bifid. The inner side of Finger III and the outer edge of Finger IV bear narrow, smooth fringes. The relative lengths of the adpressed fingers are I < II < IV < III. The webbing formula is **I** basal **II** 2 — 3 $^{1}/_{4}$ **III** 3 $^{+}$ — 2 $^{2}/_{3}$ **IV** (Fig. 3.2.4).

On the foot there is a large elliptical inner and a small flat, rounded outer metatarsal tubercle. The plantar tubercles are low and flat. Supernumerary tubercles on the proximal segments of Toes III–IV are small and low. There are a few small tubercles on the metatarsus to the penultimate subarticular tubercle. The subarticular tubercles are single and conical. Distally a narrow smooth fringe extends at least to the intercalary on the inner side of Toe II and both sides of Toe III and IV. The relative lengths of the adpressed toes are I < II < V < III < IV. The webbing formula is **I** 1 $^{1}/_{3}$ — 2 **II** 1 $^{+}$ — 2 **III** 1 $^{1}/_{3}$ — 2 $^{-}$ **IV** 2 $^{-}$ — 1 $^{+}$ **V**. (Fig. 3.2.4).

Measurements: SVL 48.6; HL 17.2; HW 16.8; TL 26.1; FL 34.2; ED 5.1; TD 2.8; FD 2.6; EN 4.6; IN 4.1; TE 3.5.

Colour in preservative: The ground colour of head and dorsum is tan, irregularly interspersed by darker tan blotches. There is creamy white supralabial mark. Postocular, sub- and posttympanic areas are dark tan, the tympanum is lighter tan. Dark tan blotches are present anteroventrally from the eye, on the orbits, medially on the head posterior to the orbits, and there are two paired median blotches in the shoulder area. Posteriorly the pattern becomes an anastomosis of tan interspersed by minute light tan spots. The shoulders are lighter tan towards the arm insertions. Transversal furrows on the shoulders are dark brown. The flanks are creamy white with areolae outlined dark brown. There is a light tan crossbar on each wrist. Dorsal surfaces of the arms and legs are, like the posterior part of the back, an anastomosis of tan, interspersed by light tan spots. Irregularly shaped, slightly darker tan crossbars are visible. Hidden surfaces of the limbs are creamy tan to creamy white, except for the posterior surfaces of the thighs, which are uniformly light tan (Fig. 3.2.1). Ventrally, the frog is creamy tan to creamy white with a few irregular tan spots on throat, chest and abdomen. Large subcloacal warts are creamy white (Fig. 3.2.1).

Paratype. A subadult specimen of 34.0 mm SVL varying little from the holotype in morphology and proportions. Some of the differences might be explained by smaller size. Characters of the holotype are in parentheses for comparison. The snout is truncate (bluntly rounded) in dorsal and bluntly rounded in lateral view. The choanae are ovoid (angular). The supratympanic fold is smooth (tuberculate). The tympanum diameter is about 70 % (93 %) the width of the disc on Finger III. The head is finely shagreen dorsally (areolate). Outer ulnar tubercles are absent (indistinct). The distal subarticular tubercle on Finger IV is barely bifid, as in the holotype, on the left, but single on the right. Measurements: SVL 34.0; HL 13.4; HW 12.6; TL 18.1; FL 24.3; ED 4.2; TD 2.0; FD 1.4; EN 3.5; IN 3.3; TE 2.8.

In preservative, the paratype is more boldly blotched dark tan dorsally, and the crossbars on the limbs are conspicuous. There are two white supralabial marks on both sides, the latter extending to the posterior edge of the upper lip. Bold tan blotches also extend to the flanks (Fig. 3.2.2). Two photos of the live paratype, though not good enough for publication, indicate that live colouration more or less equals that of the preserved specimen.

Fig. 3.2.2. Subadult paratype of *Osteocephalus duellmani* n. sp. (KU 147171). Note bold dark brown dorsal blotches and light supralabial markings.

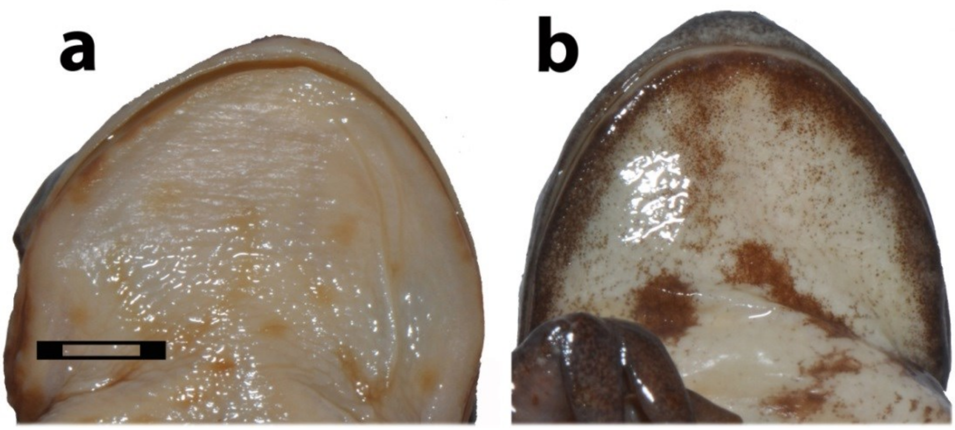

Fig. 3.2.3. Ventral view of head of a. *Osteocephalus duellmani* (holotype, 48.6 mm SVL) and b. *Osteocephalus* sp. (*O*. "*festae*" of Ron et al., 2010) (MUSM 19224, 49.9 mm SVL). Note the pointed lower jaw and less protruding snout in *O. duellmani*, which also has a proportionately wider head. Bar equals 5 mm.

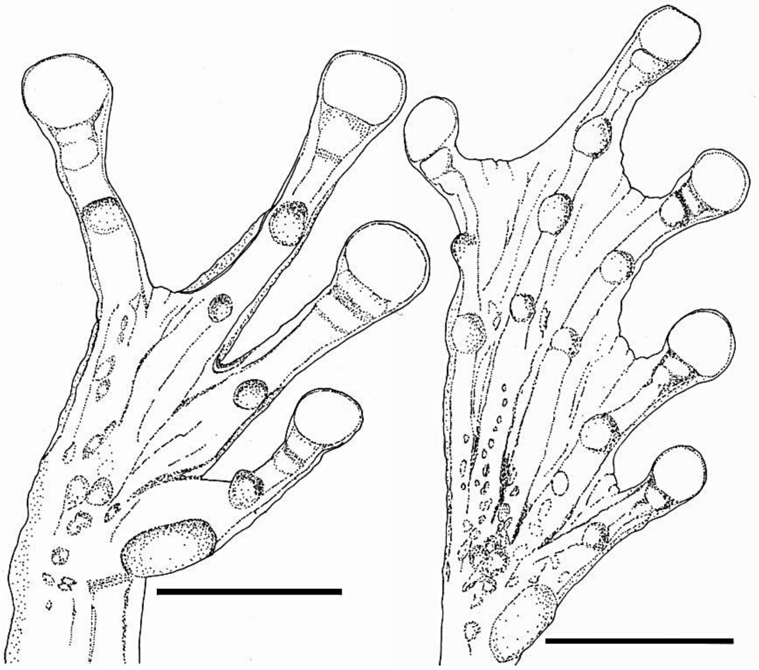

Fig. 3.2.4. Hand (left) and foot of *Osteocephalus duellmani* n. sp. in ventral view (KU 147172, holotype). Bars equal 5 mm.

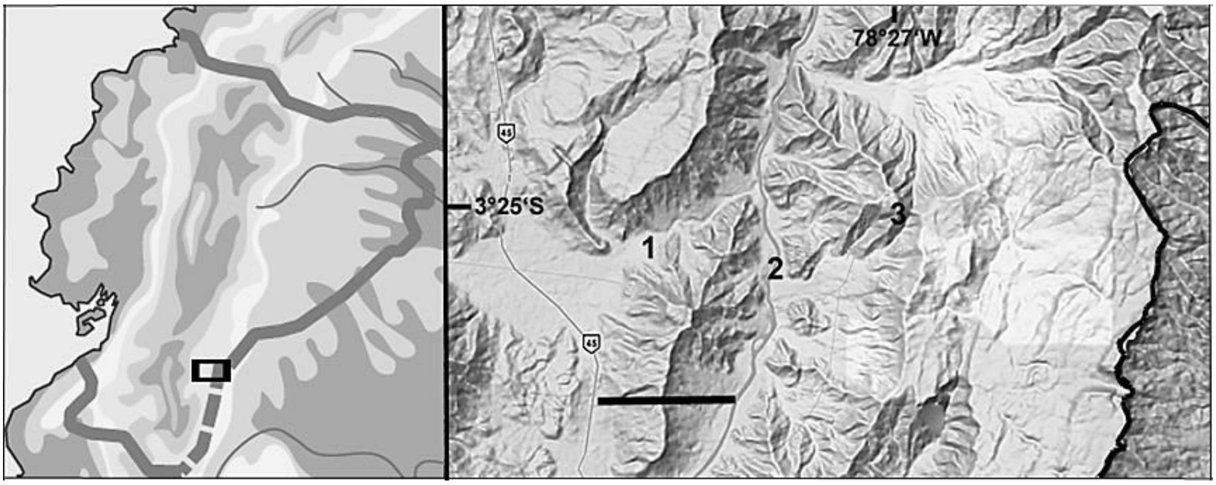

Fig. 3.2.5. Map of Ecuador (left). The rectangle indicates the position of the enlarged region, the middle Río Zamora area, Morona-Santiago Province, Ecuador (right). 1. Town of Bomboiza (3°26'S, 78°31'W). 2. Río Zamora. 3. Area of type locality at about 3°25'S, 78°27'W. Bar equals 5 km. Solid black line on the right indicates the international border with Peru.

Distribution and habitat. The new species is only known from the type locality in the Cordillera del Cóndor in Ecuador, close to the Peruvian border. Duellman & Simmons (1988) provided a map of the area that showed the position of their campsite to be very near the type locality of *O. duellmani*, but 80 m lower in elevation, indicating its coordinates as "approx. 3 30'S, 78 20'W (…) Provincia Morona Santiago, Ecuador". While these coordinates indicate a site in Peruvian territory, the map allows their position to be corrected slightly to the northwest of their coordinates, at about 3°25'S, 78°27'W, by Google Earth (Fig. 3.2.5).

The area 80 m lower in elevation was described as wet, dense cloud forest with branches of trees covered by spongy mosses and supporting many epiphytes (Duellman & Simmons, 1988; see more details there).

Etymology. The specific name is a patronym for William E. Duellman on the occasion of his 80th birthday on 6th September 2010 for his outstanding achievements in Neotropical herpetology.

Discussion

There are only two specimens available of the new species. Therefore data on the variation of the species remain barely known. The more so, since adult male *Osteocephalus* bear a number of characteristics that may be species specific or allow the allocation with related species, namely tuberculate dorsa, sometimes tipped by keratinized spines and nuptial excrescences of various extent and colouration. Although the adult male holotype was not preserved while in breeding condition and therefore characters are lacking, the species is tentatively placed with the *O. buckleyi* complex, because of the rounded and curved canthus rostralis and the coarsely areolate flanks that most closely resemble two other members of the complex, *O. buckleyi* and *O. festae* (Jungfer, 2010). Given the isolated locality and occurrence at high elevation, together with the morphological differences found in *O. duellmani*, there can be no doubt that it is a species distinct from all the others in the *buckleyi* complex and the whole genus.

There are several more species of anurans collected during the memorable Río Piuntza expedition and later described as new, whose type locality data might be affected by the changed coordinates, namely *Oreobates simmonsi* (Lynch, 1974), *Noblella lochites* (Lynch, 1976), *Pristimantis condor* (Lynch and Duellman, 1980), *P. pecki* (Duellman and Lynch, 1988), *Hyloxalus mystax* and *H. shuar* (Duellman and Simmons, 1988), *Pristimantis exoristus* and *P. infraguttatus* (Duellman and Pramuk, 1999). At least the Ecuadorian type locality of the latter two species, indicated as 3°52'S, 78°15'W, actually in Peruvian territory, has to be amended.

Acknowledgements

I am indebted to Ana Almendáriz (EPN-H), Rafe Brown, Linda Trueb and William E. Duellman (KU), Jesús Córdova and César Aguilar (MUSM), Alexander Haas and Jakob Hallermann (ZMH), Gunther Köhler (SMF), John D. Lynch (ICN), Ross MacCulloch (ROM), Andreas Schmitz (MHNG), Harold K. Voris and Alan Resetar (FMNH) for allowing me to inspect the *Osteocephalus* in their care. John E. Simmons (Museologica) provided additional information on the colouration of the species and gave valuable comments on the position of the type locality. Conservation International allowed me to use the map (https://rap.conservation.org/rap/). I thank

Diego Cisneros-Heredia (USFQ), Ross MacCulloch (ROM), Jiří Moravec (NMPC) and Ulrich Sinsch (University of Koblenz-Landau) for helpful comments on the manuscript.

Appendix

Specimens examined not listed yet by Jungfer (2010)

Osteocephalus deridens

ECUADOR: *Napo:* Estación Biológica Jatun Sacha: EPN-H 6655 (holotype); EPN-H 6656 (paratype); SMF 78742-3 (paratypes).

PERU: *Loreto*: Río Napo at Río Mangua: KU 192021; Carretera Iquitos – Nauta km 26.5-30.5: MUSM uncat. (6 ex.).

COLOMBIA: *Amazonas:* Carretera Leticia – Tarapaca km 15: ICN 11300; Leticia: Río Calderón: ICN 35636, ICN 35640, ICN 35648-9; Tarapaca: Rio Putumayo, caño Alambre: ICN 35642; Leticia, Río Pure: ICN 46518-21; Leticia: Comunidad Jitoma: ICN 46884.

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 fuscifacies

ECUADOR: *Napo*: Estación Biológica Jatun Sacha: EPN-H 6657 (holotype); Rucullacta, 2 km NNW Archidona: EPN-H 4774-5 (paratypes). *Sucumbíos*: San Pablo de Kantesiya: MHNG 2366.73, 2373.91 (paratypes).

PERU: *Loreto*: Teniente Lopez, 310 m: KU 221943.

Osteocephalus leoniae

PERU: *Pasco*: Pozuzo (10°04’10’’S/75°31’42’’W, 1000 m NN): MUSM 20350 (holotype), SMF 80365 (paratype). *Huánuco*: Panguana: ZMH 915-916. *San Martín*:

Río Cainarache, 33 km NE Tarapoto on road to Yurimaguas: KU 209447-53; 14 km ESE Shapaja, 360 m: KU 212180.

Osteocephalus mutabor

ECUADOR: *Napo*: 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. *Pastaza*: Canelos, 530 m: KU 120915; Locación Petrolera Garza 1, NE Montalvo, 300 m: KU 217747-9. *Sucumbíos*: 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 phasmatus

GUYANA: *District 7*: NE plateau of Mount Ayanganna, 1490-1550 m: ROM 43855, 43858.

Osteocephalus sp. (*O*. "*festae*" of Ron et al., 2010)

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 verruciger

COLOMBIA: *Huila*: Acevedo, Río Suaza, Río Aguas Claras near San Adolfo, 1400 m: FMNH 69709-10; Palestina: ICN 01542. *Caquetá*: Municipio de Florencia: Escuela Tarqui, carretera Altamira-Florencia km 48-49: ICN 23648; Municipio de Florencia: 35.2 km. arriba de Florencia: ICN 23943; Municipio de Florencia: Vereda Tarqui 38.8-39.0 km: ICN 23944-5, ICN 23948, ICN 23952, ICN 23954; Municipio de Florencia: Vereda Tarqui 13.2 km arriba de Florencia: ICN 23946; Municipio de Florencia: 39.3 km arriba de Florencia: ICN 23947. *Putumayo*: 10.3 km W El Pepino, 1440 m: KU 169586-7, 169589-93, 169595-6,169599, 169601-4, 169606-7.

ECUADOR: *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; 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 Agrio 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. No specific locality: ZMH-A946.

Osteocephalus yasuni

ECUADOR: Orellana : Río Yasuní, 150 km upstream from Río Napo, 180 m: KU 175196, KU 175198; Río Yasuní, 200 km upstream from Río Napo, 180 m: KU 175205-6.

PERU: *Loreto*: Explorama Lodge, jct. Río Yanamono and Río Amazonas, 210 m: KU 220894.

COLOMBIA: *Amazonas*: Parque Nacional Natural Amacayacu, quebrada Matamata: ICN 20493, ICN 46478; Río Pure: ICN 46477, ICN 46479-87; Carretera Leticia – Tarapaca km 14: ICN 46506.

3.1.3. *Osteocephalus camufatus* Jungfer, Verdade, Faivovich & Rodrigues

This part has been submitted for publication to *Zootaxa* as follows:

Jungfer, K.-H., Verdade, V. K., Faivovich, J. & M.T. Rodrigues (submitted): **A new species of spiny-backed treefrog (*Osteocephalus*) from Central Amazonian Brazil (Amphibia: Anura: Hylidae)**.

ABSTRACT

A new species of treefrog of the genus *Osteocephalus* is described from the Rio Abacaxis, a southern tributary of the Amazon in the state of Amazonas, Brazil. A member of the *O. buckleyi* group, it is a small to medium-sized species with a known snout-vent length of 39.5-40.4 mm in males (females are unknown). The species is characterized by green dorsal coloration 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 and merely 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. n.

INTRODUCTION

Spiny-backed treefrogs of the genus *Osteocephalus* are widespread in the Amazonian and Guianan regions of South America. A recent 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 in that paper following the terminology of Vieites *et al.* (2009). Frogs of the *Osteocephalus buckleyi* group are stream-breeding, most of them occurring along the eastern Andean edge up to elevations of about 2000 m, although several species also inhabit the lowlands eastward to the mouth of the Amazon. Among them there are species that are partly or predominantly green dorsally and laterally, 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 orbits. These three characters, absent in all other *Osteocephalu*s, are present in the new species which was identified molecularly (Jungfer *et al.* 2013) using tissues from specimens obtained along the Rio Abacaxis, south of the Amazon. Herein, on the basis of the same specimens, we proceed to their 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 strabomantid 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; F: finger; FD: diameter of finger disc on third finger; FL: foot length; HL: head length; HW: head width; IN: internarial distance; SVL: snout-to-vent length; T: toe; TD: tympanum diameter; TE: distance between tympanum and eye; TL: tibia length. Measurements were made using digital callipers or the ocular micrometer of a dissecting microscope if less than 5 mm; all measurements are in mm. Museum abbreviations follow Frost (2013). The numerical code used for the new species by Jungfer *et al.* (2013) refers to a similar species, “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).

Fig. 3.3.1. Adult male holotype of *O. camufatus* n. sp. from Igarapé-açu, Rio Abacaxis, Estado Amazonas, Brazil. Enclosure: close-up of the eye.

RESULTS

Osteocephalus camufatus **sp. n.** (Figs. 3.3.1-4)

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, collected by Miguel T. Rodrigues, Sergio Marques de Souza, José Cassimiro and José Mário Guellere, on 9 January 2007.

Paratype: MZUSP 142390 (field number MTR 13147), an adult male with well-developed nuptial excrescences from Brazil: Amazonas: Areal, left bank of Rio Abacaxis (04°35'49''S 58°13'14''W), 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 in males (39.5 – 40.4 mm SVL) (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. No phenotypic synapomorphies are yet known from this group. 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 orbits 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 species from the eastern Andean slopes between 600 and 2200 m differ as follows: in *Osteocephalus carri* the canthus rostralis and orbits are smooth (strongly tuberculate) and the iris is black with golden spots in life (light); in O. *duellmani* the posterior surfaces of the thighs are uniform tan (spotted) and the canthus and orbit weakly tuberculate (strongly tuberculate); *O. festae* exhibits brown ground colour (green), a dark brown iris in life (light) and uniform tan posterior thigh surfaces (spotted). Males of *Osteocephalus mimeticus*, *O. mutabor* and *O. verruciger* have heavily tuberculate dorsa with numerous spinous tubercles bearing keratinized tips during breeding (a few irregular small tubercles, few of them with keratinization). Other species of the *O. buckleyi* group from lower regions, that in some cases may share the greenish ground colour of *O. camufatus*, differ as follows: *Osteocephalus buckleyi* from the western Amazon Basin in eastern Ecuador and northern to central Peru has a weakly tuberculate or smooth orbit (strongly tuberculate), and low or absent tarsal tubercles (prominent), an axillary membrane covering about one fourth of the length of the upper arm (absent), and the tympanum appears to be slightly larger with TD/HL 0.23-0.26 in males (TD/HL 0.22-0.23 in the small sample of n = 2). Breeding males of *O. buckleyi* exhibit dorsal tubercles, many with keratinized tips (few keratinized tips, if at all). *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 the western Amazon Basin in northern Colombia, eastern Ecuador and northern Peru is a distinctly larger frog of 38.5-57.2 mm SVL (mean, 46.8 mm) (Ron *et al.* 2012) in males (to 40.4 mm), differing 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* is a variable frog throughout its range from Santa Cruz, Bolivia, to the coastal Guianas. 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 Amazon in Estado Amazonas, Brazil are larger, males reaching 47.8 mm SVL (40.4 mm), 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. 3.3.4a). Specimens from near Rio Branco, Estado Acre, Brazil, roughly 1100 km WSW of the type locality of *O. camufatus*, are also larger in males, to 46.3 mm (40.4 mm), have posterior thigh surfaces brown, finely mottled with cream (bold dark brown markings on light ground) and lack tubercles on the orbits (present).

Frogs in the closely related genus *Dryaderces* differ in exhibiting bold dark ventral reticulation (dark spotting) and uniform dark iris (light iris) in *D. pearsoni*, 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 *D.* sp. (*Dryaderces pearsoni* [Ca1_MTR13158_2768] of Jungfer *et al.* 2013). The inspection of a fresh specimen of *"Osteocephalus" inframaculatus*, a species until recently only known from the holotype and placed with the *O. buckleyi* group by Jungfer (2010), leads us to suggest that it should be placed in *Dryaderces*, as already proposed by Hoogmoed (2013). It is easily distinguishable 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). Its proper name is *Dryaderces inframaculata*.

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, 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, medium-sized, 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 $^{3}/_{4}$ **III** 2 $^{1}/_{3}$ — 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 adpressed toes I < II < III ≤ 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 dorsal and lateral sides of the head and the body laterally. 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. Anterior part of midbody almost without them. Although there are light areas on the upper lip, there are no discrete supralabial marks distinguishable from the rest of the pattern. Tympanum tan. Arms dorsally and laterally with irregular dark brown crossbars, with irregular brown spotting ventrally.

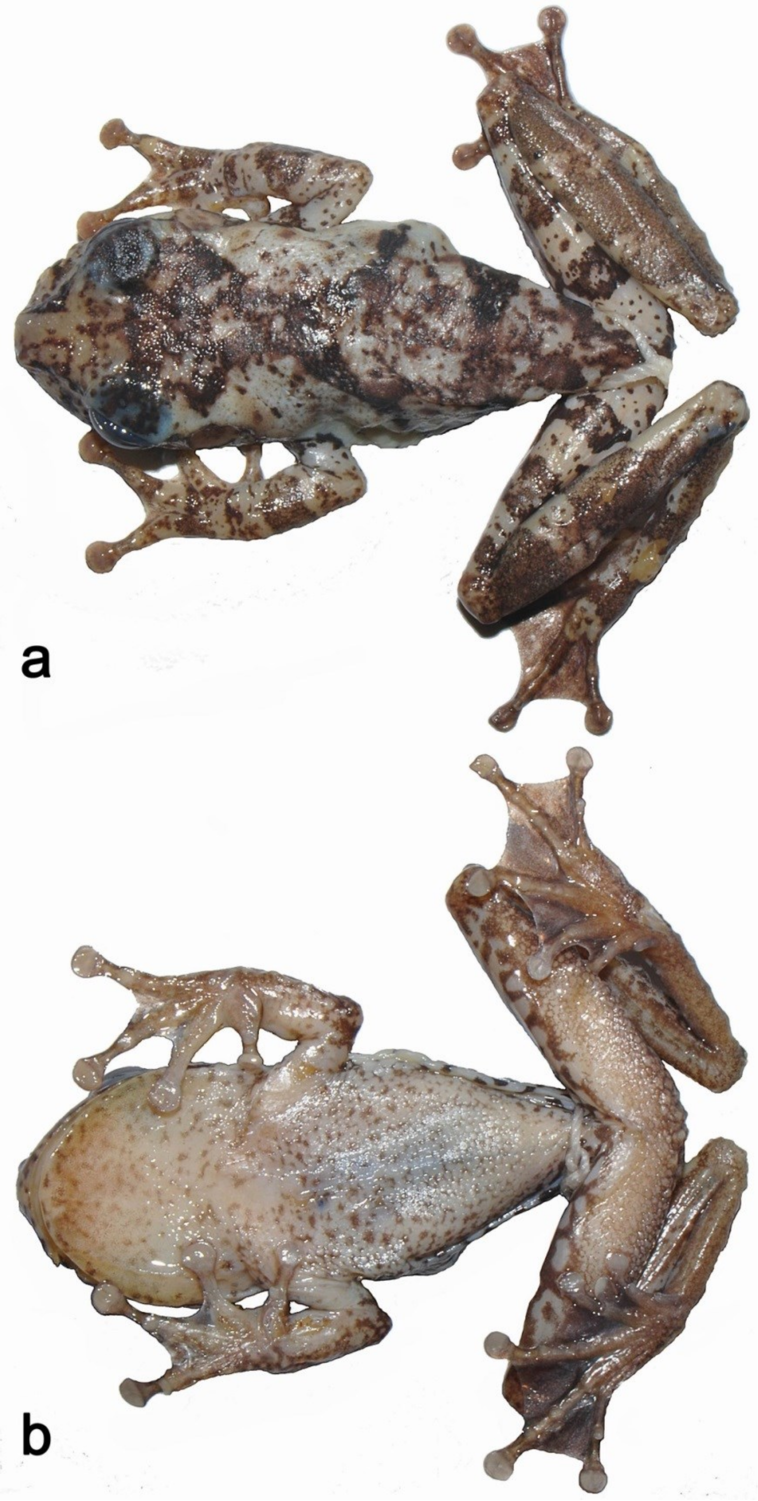

Fig. 3.3.2. a. Dorsal, b. ventral view of the preserved holotype of *O. camufatus* n. sp.

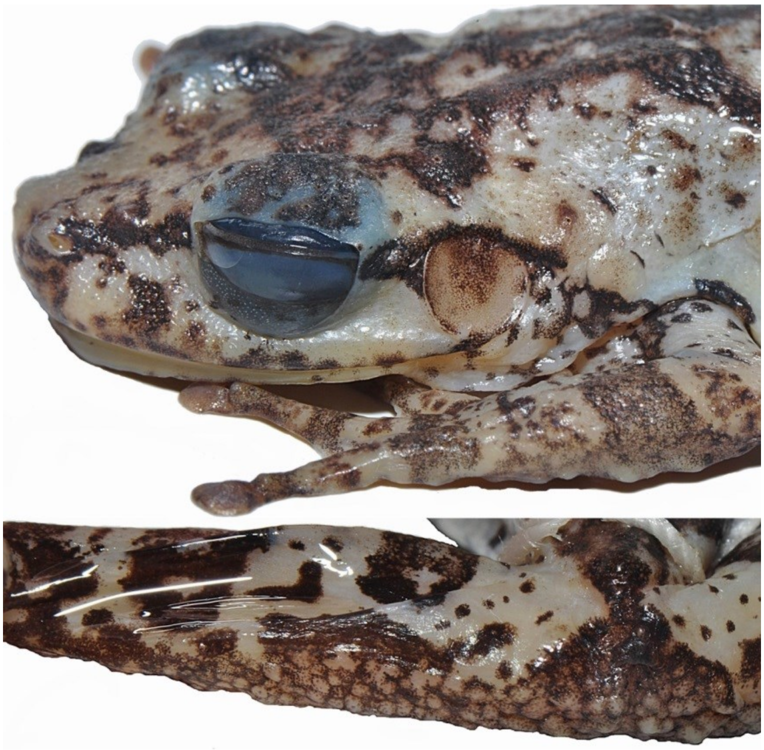

Fig. 3.3.3. Lateral view of the head, circumcloacal area and posterior surface of thigh of the preserved holotype of *O. camufatus* n. sp.

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.

Colour in life: Colours were taken from photographs (Fig. 3.3.1). 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 dark brown. 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. The hidden surfaces of the thighs appear to be or be bordered light blue. Outer tarsal and heel as well as ulnar tubercles are tipped white.

Variation in the paratype. An adult frog slightly larger than the holotype (40.4 mm SVL) with well-developed nuptial excrescences. The snout is bluntly rounded in

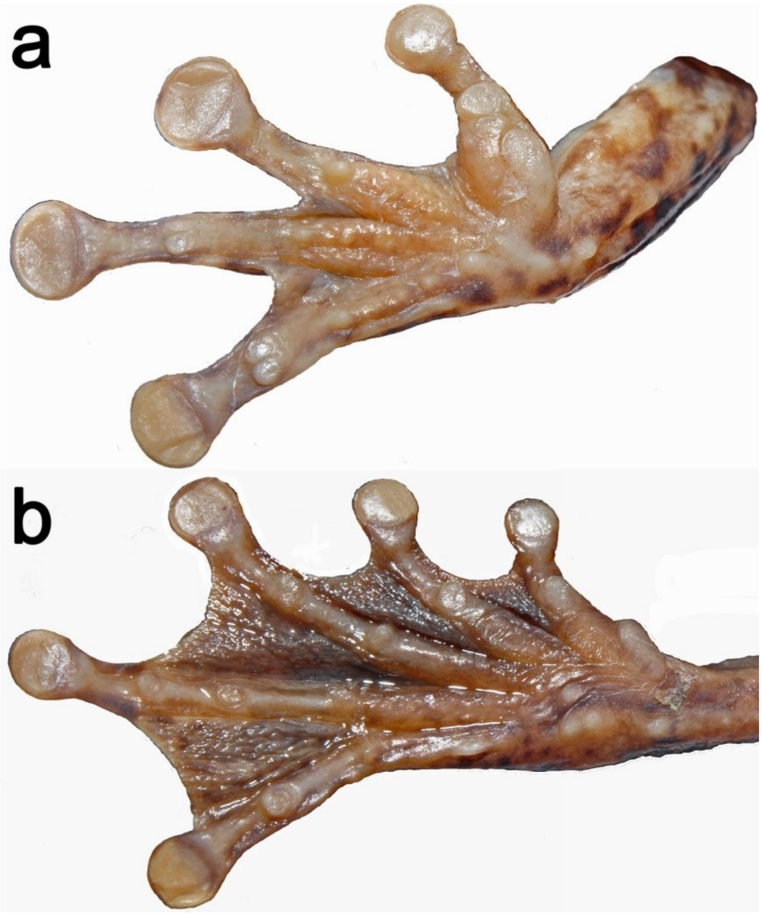

Fig. 3.3.4. a. Right hand and forearm and b. right foot of the preserved holotype of *O. camufatus* n. sp. Not to scale.

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 $^{2}/_{3}$ — 2 $^{2}/_{3}$ **III** 2 — 2 **IV** and little variation on the foot: **I** 1^{+} — 2 **II** 1 — 2^{-} **III** 1 — 1 $^{1}/_{3}$ **IV** 1 $^{1}/_{3}$ — 1 **V**. There is also little variation in proportions.

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.

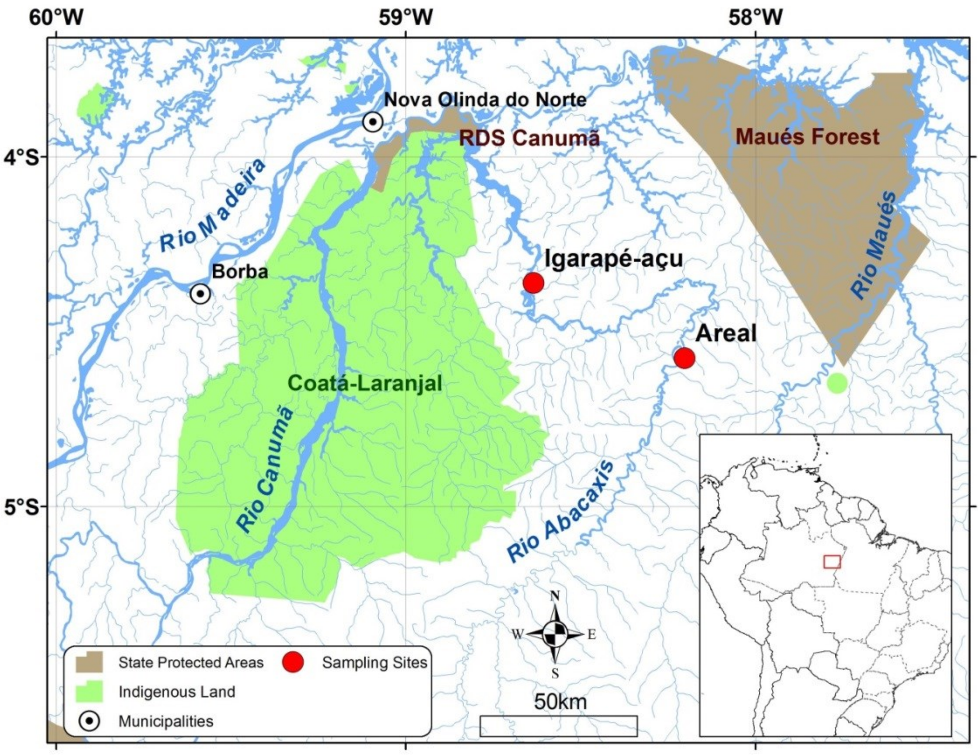

Fig. 3.3.5. Map of the collecting sites of *Osteocephalus camufatus* n. sp. in Estado Amazonas, Brazil. The type locality is Igarapé-açu.

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 to the Amazon that discharges in Paraná do Arariá, a white water channel delimiting the southern border of Ilha de Tupinambarana (Fig. 3.3.5). This is a huge island (about 300 km long) extending between Nova Olinda do Norte in the lower Madeira river to Parintins in 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 is 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.

Relationships. A molecular phylogenetic study (Jungfer *et al.* 2013) revealed that the new species is most closely related and sister to a clade consisting of the polymorphic and widely distributed *O. helenae*, a species occurring from coastal Guyana in the north throughout most of Amazonia, to Bolivia in the southwest, but is only distantly related to the morphologically similar *O. buckleyi*.

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3.2. Taxonomy of problematic hylid species referable to *Osteocephalus*

This part was published in *Zootaxa* as follows:

Jungfer, K.-H. (2010): **The taxonomic status of some spiny-backed treefrogs, genus *Osteocephalus* (Amphibia: Anura: Hylidae)**. *Zootaxa*, 2407: 28-50.

Abstract

A reassessment of some Amazonian spiny-backed treefrogs (*Osteocephalus*) either considered to be junior synonyms or not associated yet with *Osteocephalus* reveals that *O. cabrerai* (Cochran and Goin, 1970) from lowland Colombia and Peru is distinct from a frog previously used to revalidate the species, that *O. festae* (Peracca, 1904) is a valid species from the foothills of the Andes in Ecuador, and that *Hyla inframaculata* Boulenger, 1882, from the lower Amazon in Brazil, is a member of this genus. The oldest available name for *O. elkejungingerae* (Henle, 1981) from the Andean foothills in Peru is *O. mimeticus* (Melin, 1941). Another Melin (1941) species, *Hyla vilarsi* from the Rio Negro watershed in Brazil, is also an *Osteocephalus* revalidated from the synonymies of several other frogs.

Key words: Amphibia, Anura, Hylidae, *Osteocephalus*, taxonomy, revalidation, *Osteocephalus cabrerai*, *Osteocephalus elkejungingerae*, *Osteocephalus festae* nov. comb., *Osteocephalus inframaculatus* nov. comb., *Osteocephalus mimeticus*, *Osteocephalus vilarsi* nov. comb., Amazonia, Brazil, Colombia, Ecuador, Peru.

Introduction

The Neotropical hylid genus *Osteocephalus* is presently comprised of 21 species distributed in Amazonia and on the Guiana Shield (Frost 2009). The last review (Trueb and Duellman 1971) was published almost 40 years ago. Several species were named subsequently (Henle 1981, Martins and Cardoso 1987, Jungfer and Schiesari 1995, Ron and Pramuk 1999, Jungfer *et al.* 2000, Jungfer and Lehr 2001, Smith and Noonan 2001, Jungfer and Hödl 2002, Lynch 2002, MacCulloch and Lathrop 2005, Moravec *et al.* 2009), two were transferred to *Osteocephalus* from *Hyla* (Lynch 2006, Wiens *et al.* 2006), one transferred from *Osteocephalus* to the new genus *Itapotihyla* (Faivovich *et al.* 2005), and two species were resurrected from the synonymies of other *Osteocephalus* species (Duellman and Mendelson 1995). But still the genus is far from being well understood on an alpha taxonomic level. This hampers studies of the phylogeny of the genus. Recently, Moravec *et al.* (2009) have shown that misidentifications have had effects on a phylogenetic tree with respect to the relationships among *Osteocephalus* (Faivovich *et al.* 2005). Due to their overall similarity in adult frogs of the same sex, but also because of sexual dimorphisms and considerable ontogenetic change within species, many are difficult to identify, especially when they are only known as preserved specimens, one sex, or one age class (Trueb and Duellman 1971, Jungfer and Hödl 2002).

During the last few years I have accumulated life history data and undescribed species. Several species in various museum collections also await description. Before adding more new species it is necessary to address the taxonomic status of some frogs that are currently considered to be junior synonyms of other species or have not yet been assigned to the genus *Osteocephalus* at all. Comparisons and, where necessary, detailed descriptions are provided of five species in this study. Three of them belong to the *Osteocephalus buckleyi* complex (within a more inclusive *O. buckleyi* group; Jungfer *et al.*, in prep.): frogs camouflaged in shades of brown, gray, and green, with dermal appendages such as toe fringes or tubercles and also tubercles on tarsus, upper eyelid and other parts of the body, areolate skin on the flanks, and posterior surfaces of the thighs often not uniform in coloration. Although they exhibit some sexual dimorphism in dorsal tuberculation, breeding males lack or have fewer keratinized tips on tubercles than many other species, e. g. *O. leprieurii* (Jungfer and Hödl 2002), *O. taurinus* or *O. verruciger* (Trueb and Duellman 1971), and females may also be tuberculate to a lesser extent. These frogs are usually associated with streams. Males call from streamside bushes, usually at times of no rain, and tadpoles live in slow-moving water or streamside pools. Two species, *O. buckleyi* and *O. cabrerai*, are currently recognized. One of them is reanalyzed here. Trueb and Duellman (1971), in reviewing the genus, were explicitly conservative in their concept of species. This holds especially true for the *O. buckleyi* complex. They synonymized no less than three taxa with *O. buckleyi*. One of them, *Hyla carri* Cochran and Goin, 1970, was shown to be a distinct species of *Osteocephalus* by Lynch (2006). With more material and data at hand, it is possible to revalidate the other two taxa here. Another taxon, *Hyla inframaculata* Boulenger, 1882, from the lower Amazon, previously not associated with *Osteocephalus*, also has its relationship with the *O. buckleyi* complex and is compared with the other species here. A fourth species with extremely spiny-backed males is widespread along the Andean foothills in Amazonian Peru. The oldest available name, *Hyla mimetica* Melin, 1941, is revalidated here. A fifth species, similar to *O. taurinus* and *O. planiceps*, from the Rio Negro drainage in Brazil, *Hyla vilarsi* Melin, 1941, is resurrected from the synonymies of several other species. All in all, this paper adds another three species to the genus.

Materials and Methods

Measurements were taken following Duellman (1970), except that foot length is the distance from the bent tibiotarsal articulation to the tip of the fourth toe. Webbing formula is that of Savage and Heyer (1967), as modified by Myers and Duellman (1982). Species of *Osteocephalus* are considered small when they are less than 40 mm in snout-to-vent length, medium-sized in between 40 and 70 mm, and large when they exceed 70 mm. Since there is considerable sexual dimorphism in size, the different sexes may belong to different size categories. 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-to-vent length; TD: tympanum diameter; TE: distance between tympanum and eye; TL: tibia length. Museum abbreviations are as follows: AMNH: American Museum of Natural History, New York; BM: Natural History Museum, London; EPN: Escuela Politécnica Nacional, Quito; FMNH: Field Museum of Natural History, Chicago; GNM: Göteborg Natural History Museum; ICN: Instituto de Ciencias Naturales, Bogotá; INPA: Instituto Nacional de Pesquisas da Amazônia, Manaus; KU: University of Kansas Museum of Natural History, Lawrence; MHNG: Muséum d’Histoire naturelle, Genève; MUSM: Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MPEG: Museu Parense Emilio Goeldi, Belém; MZUSP: Museu de Zoologia da Universidade de São Paulo; MZUT: Museo

Zoologico, Università di Torino (at Museo Regionale di Scienze Naturali, Torino); NMW: Naturhistorisches Museum Wien; SMF: Senckenberg-Museum, Frankfurt am Main; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMH: Zoologisches Museum, Hamburg.

Results

***Osteocephalus cabrerai* (Cochran and Goin, 1970)** (Figs. 3.4.1, 3.4.2, 3.4.8a)

Hyla cabrerai Cochran and Goin, 1970

Osteocephalus buckleyi – Trueb and Duellman 1971 (synonymized *cabrerai* with *buckleyi*)

Osteocephalus cabrerai – Duellman and Mendelson 1995 (revalidated *cabrerai*, nov. comb.)

Osteocephalus cabrerai – Lynch 2002

Osteocephalus cabrerai – Frost 2009

The holotype of *O. cabrerai* (USNM 152759) is from the Caño Guacayá, a tributary of the lower Río Apaporis, Departamento Amazonas, Colombia. Cochran and Goin (1970) described it in detail and differentiated it from *O. buckleyi* by chest and throat coloration, a variable character in *O. buckleyi*, and by more webbing. Trueb and Duellman (1971) synonymized *O. cabrerai* with *O. buckleyi* stating that its morphological characters were within the variation of the latter. Duellman and Mendelson (1995) revalidated *O. cabrerai* on the basis of a green male with nuptial excrescences from San Jacinto, Departamento Loreto, Peru. Subsequently, most authors dealing with *O. buckleyi*-like frogs that were predominantly green called them *O. cabrerai* (Gorzula and Señaris 1998, Lescure and Marty 2000, Lynch 2002). I was able to examine the holotype and also the specimen from San Jacinto (KU 221927), among others, and identified the latter as *O. buckleyi*. Nonetheless, *O. cabrerai* is considered a valid species here. I have seen Colombian and Peruvian material and concur with Lynch (2002) that frogs he collected near Leticia, Departamento Amazonas, Colombia, are *O. cabrerai*. Figure 1

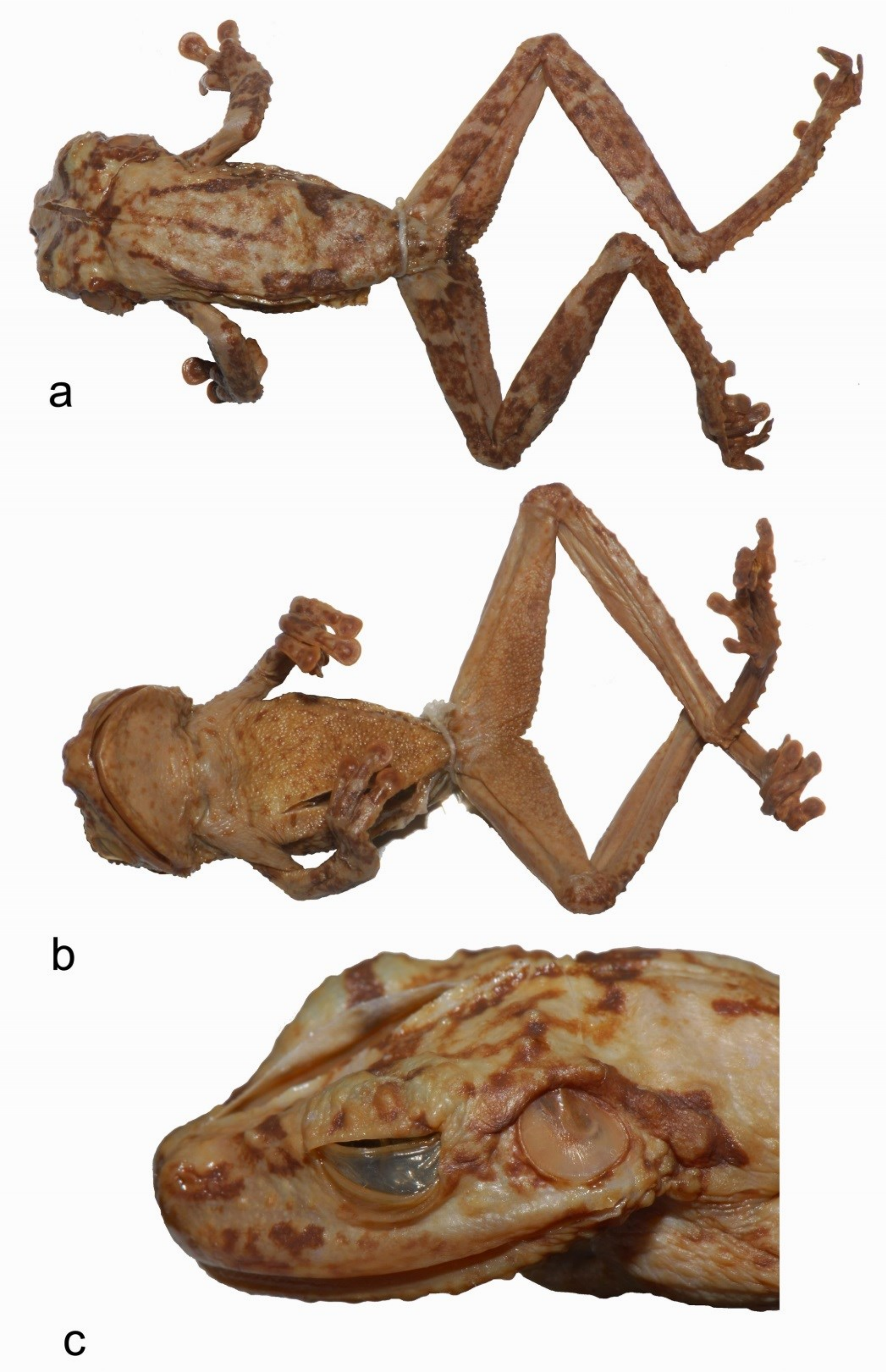

Fig. 3.4.1. *Osteocephalus cabrerai* (holotype): a. dorsal, b. ventral, c. lateral view of the head. Not to scale.

in Lynch (2002) lower right (not as stated upper left) depicts a specimen. Cochran and Goin (1970), Trueb and Duellman (1971) and Duellman and Mendelson (1997) provide details of the morphology of the holotype, so no detailed description is given here. These authors all agree that *O. cabrerai* has more webbing and is much more tuberculate than *O. buckleyi*.

Comparisons: The holotype and additional material is compared with *O. buckleyi* from northwestern Amazonia (Colombia, Ecuador, northern Peru) (see Appendix for specimens examined). Females of *O. cabrerai* (SVL up to 71.4 mm) from Colombia and Peru are much larger than those of *O. buckleyi* (SVL up to 54.2 mm). Males are up to 54.8 mm (up to 46.7 in *O. buckleyi*).

There are several tubercles ventrally on the posterior part of the lower jaw (absent in *O. buckleyi*). The webbing (Fig. 3.4.8a) between Finger I and II of *O. cabrerai* reaches beyond the subarticular tubercle on Finger I and is continued to the disc as a smooth fringe. It reaches the subarticular tubercle on Finger II and is continued to the disc as a smooth fringe. In *O. buckleyi* (Fig. 3.4.8b) it is basal (i. e. considerably lower than the only subarticular tubercle on Finger I and the proximal subarticular tubercle on Finger II). In *O. cabrerai* webbing on the inner side of Finger III reaches the proximal part of the ultimate subarticular tubercle and continues as a fringe to the finger disc. In *O. buckleyi* webbing on the inner side of Finger III varies. It reaches the penultimate subarticular tubercle or less than half way between the penultimate and the ultimate subarticular tubercle. In *O. cabrerai*, the outer edge of Finger IV is irregularly fringed (either smooth, tuberculate, a smooth fringe, or a fringe with a few slightly raised tubercles in *O. buckleyi*) and the ulna bears several large tubercles posteriorly (several low tubercles in *O. buckleyi*). A row of tubercles along the posteroventral margin of the tarsus is very prominent in *O. cabrerai* (variable, i.e. low to prominent, in *O. buckleyi*). Only the disc is free of webbing on Toe I, while the intercalary tubercle is free in *O. buckleyi*. An axillary membrane extends for about one third or slightly more the length of the upper arm (one fourth in *O. buckleyi*). The tympanum is elliptical (its height about 90% its width in the holotype) to round (same as in *O. buckleyi*). Both species can be predominantly green, but while this is almost exclusively so in *O. cabrerai*, *O. buckleyi* may have dorsal and lateral colorations of all shades of brown, grey and green.

The iris color of *O. cabrerai* is whitish to light golden with dark venation that varies with light from fine to wide. There is a dark brown horizontal bar and a dark brown

Fig. 3.4.2. Amplecting pair of *Osteocephalus cabrerai* from Quebrada Negra, Río Iauasiyacu, Loreto, Peru.

vertical streak in the lower half of the iris (Fig. 3.4.2).The iris coloration varies in *O. buckleyi*. There are specimens with almost clear golden or yellow irises, but also darker ones (golden tan), with irregular venation, some with a hue of radiating dark lines. There is usually a dark horizontal mid-eye bar varying in intensity, and often a dark vertical streak in the lower half of the iris (Fig. 3.4.3).

The posterior surfaces of the thighs of *O. cabrerai* are light tan with dark tan spots or irregular tan markings in preservative. In life, they are bright blue with tan spots or irregular tan markings. The hidden surfaces of tibia, tarsus, parts of Toe I and II, axillary membrane and posterior part of upper arm are bright blue. In *O. buckleyi* the posterior surfaces of the thighs are variable: in preservative tan with or without dark brown and/or light marbling or irregular crossbars. In life they are tan to dark purple with or without black and/or green marbling or ill-defined crossbars. Breeding males of *O. cabrerai* with well-developed nuptial excrescences found in amplexus lack

Fig. 3.4.3 Amplecting pair of *Osteocephalus buckleyi* from Jatun Sacha, Napo, Ecuador.

keratinized tips on dorsal tubercles (present in *O. buckleyi*).

The tibiofibular bones are green in life in both species. Bones of some preserved specimens of *O. buckleyi* are pale with no green visible.

Snout-to-vent lengths are similar in *O. festae* (males up to 48.1 mm, females up to 78.9 mm) and *O. cabrerai* (males up to 54.8 mm SVL, females up to 71.4 mm), but the latter differs from *O. festae* (in parentheses) in a truncate snout in dorsal and lateral aspect (rounded), in a larger tympanum in females of *O. cabrerai* with TD/HL = 0.20–0.22 and TD/FD = 1.11–1.31 (TD/HL = 0.16–0.19 and TD/FD = 0.87–1.08 in females of *O. festae*), tubercles ventrally on the posterior part of the lower jaw (smooth), a tuberculate supratympanic fold (smooth) and more extensive webbing. On the hand the webbing reaches at least the proximal end of the ultimate subarticular tubercle on the inner side of Finger III (the penultimate subarticular tubercle). The outer edge of Finger IV is irregularly fringed (a row of low tubercles). The tibiofibular bones are green (white).

Reaching an SVL of 71.4 mm in females, *O. cabrerai* appears to be a much larger species than *O. inframaculatus* (41.9 mm in the only known female specimen). The latter species also lacks tubercles ventrally on the posterior part of the lower jaw. The posterior surfaces of the thighs are tan with light short vermiculation (light with tan spots or irregular tan markings in *O. cabrerai*). Webbing of *O. inframaculatus* (see below) is similar to that of *O. buckleyi*, i.e. considerably less extensive than in *O. cabrerai*.

Osteocephalus cabrerai may be diagnosed as (1) a medium to large-sized species with considerable sexual dimorphism in SVL (71.4 mm in females, 54.8 mm in males) and minor differences in dorsal tuberculation; (2) skin on dorsum granulate in females, tuberculate in males; tubercles lacking keratinized tips in breeding males; (3) skin on flanks areolate; (4) canthus rostralis weakly angular, strongly curved inward; (5) frontoparietal ridges not visible from outside; (6) dentigerous processes of vomers angular; (7) a tuberculate supratympanic fold from midlevel of eye to midlevel of tympanum posteriorly, sloping towards arm insertion up to lower tympanum level; (8) web on inner edge of third finger reaching proximal part of ultimate subarticular tubercle or beyond, continued as a fringe to finger disc; (9) distal subarticular tubercle on Finger IV broad-edged to bifid; (10) dorsum variable in shades of green with tan and brown blotches, streaks, or a reticulate pattern; (11) venter creamy white with or without tan spots; (12) a pale supralabial mark posteroventrally from eye to mid-tympanum; (13) flanks light with or without tan blotches; (14) position of vocal sacs paired, protruding posteroventral to angles of jaws; (15) juvenile coloration unknown; (16) tadpoles in streams, labial tooth row formula unknown; (17) color of tibiofibular bones green in preservative.

Distribution: *Osteocephalus cabrerai* is known from several lowland sites below 250 m a.s.l. in Amazonian Colombia (Departamento Amazonas) and Peru (Departamentos Loreto and Ucayali). There are also specimens from the Guiana Shield and the Orinoco Delta in Venezuela (Gorzula and Señaris 1998, Lescure and Marty 2000, Lima *et al.* 2005 [as *O. buckleyi*]) that I refrain from including in the present study.

***Osteocephalus festae* (Peracca, 1904) nov. comb.** (Figs. 3.4.4, 3.4.8c)

Hyla festae Peracca, 1904

Hyla festae – Nieden 1923

Osteocephalus buckleyi – Trueb and Duellman 1971 (synonymized *festae* with *buckleyi*)

This large frog was described on the basis of one specimen. The holotype, MZUT An. 208, is a female of 73.6 mm SVL with minute, immature eggs in the ovaries, from Valle de Santiago (= lower Río Zamora according to Trueb and Duellman 1971), Provincia Morona-Santiago, Ecuador. Trueb and Duellman (1971) synonymized *festae* with *O. buckleyi*. Their concept of the latter species then encompassed four species as understood here (*O. buckleyi*, *cabrerai*, *carri*, *festae*). Females of *O. festae* are considerably larger than those of *O. buckleyi*, similar in size to *O. cabrerai*, but much less tuberculate than the latter. A full description of the type specimen and variation in some additional material is given here.

Redescription of the holotype: The snout is rounded in dorsal and lateral view. The head is slightly wider than long. The lateral edges of the frontoparietals are not raised. The canthus rostralis is curved inward, weakly angular. The loreal region is oblique, concave. The nostrils are not elevated, opening anterolaterally. The lips are flared. The dentigerous processes of the vomers are angular, separated from each other, bearing 10 teeth on the left and 11 on the right. The vomers are situated between the choanae, their anterior edges at midlevel of the choanae, their posterior edges reaching slightly beyond the posterior edges of the choanae. Together, the dentigerous processes are slightly wider than the narrowest interchoanal distance. The choanae are large, oblique, ovoid, but somewhat angular. The tongue is elliptical, about 1.3 times wider than long. The postocular area is oblique. There is a strong, smooth supratympanic fold from the posterior edge of the orbit sloping slightly arched towards the flanks almost to the lower tympanum level. The tympanum is elliptical (height 87% of width), with a distinct tympanic annulus that is partly concealed dorsally by the supratympanic fold. The tympanum is medium-sized, its diameter about 80% of the width of Finger III and 53% of the eye diameter. The orbit, however, has received pressure and the eye is difficult to measure. A flat tubercle on top of the orbit is still discernible. Dorsal surfaces of the head, loreal region and postorbital area are shagreened, and tuberculate posteroventral to the tympanum. The skin of the body dorsally and dorsolaterally is smooth, as well as the dorsal and lateral surfaces of the extremities. Anterior to the arm insertion, ventrolaterally

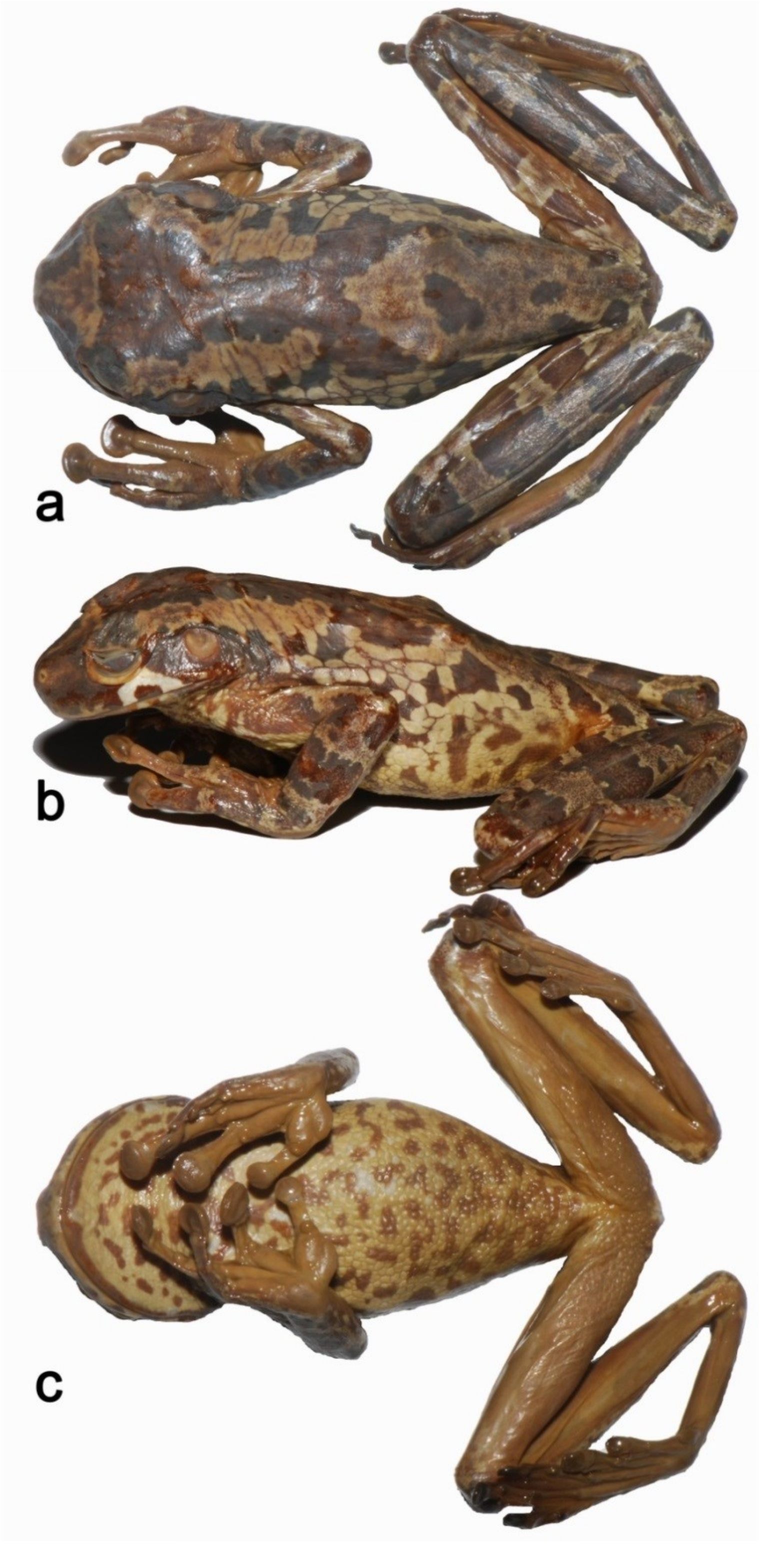

Fig. 3.4.4. *Osteocephalus festae* (holotype): a. dorsal, b. lateral, c. ventral view. Not to scale.

and ventrally (including the posterior gular area) the skin is areolate. The anterior gular area is granulate. The arms are smooth to slightly shagreen dorsally, otherwise smooth and without tubercles. An axillary membrane covers the proximal fourth of the upper arm posteriorly. Ventrally, the proximal half of the thighs is granulate, the other surfaces of the hind legs are smooth except for about three low elliptical tubercles on the inner ventrolateral edge of the tarsus. There are numerous minute circumcloacal warts. An anal sheath is absent.

The finger discs are ovoid. The diameter of the disc of Finger III is about 115% of that of the tympanum. The thumb bears a large elliptical thenar tubercle. The distal subarticular tubercle on Finger IV is single, but with a wide upper edge. The outer edge of Finger IV is fringed. The relative length of the adpressed fingers is I < II < IV < III. The webbing formula is I basal II 2^{-} — 3^{+} III 2 ¾ — 2 ½ IV. The plantar tubercles are low and flat. There is a large elliptical inner metatarsal tubercle. The outer edge of Finger I is fringed. The subarticular tubercles are single and conical. The proximal segments of Toes II–IV bear 2–4 low supernumerary tubercles. The relative length of the adpressed toes is I < II < III ≤ V < IV. The webbing formula is I 1^{+} — 2^{+} II 1 — 2 ½ III 1^{+} — 2 ½ IV 2 ½ — 1 V.

Measurements of the holotype (in mm): SVL 73.6; HL 24.9; HW 26.0; TL 43.2; FL 53.5; ED 7.3; TD 4.0; FD 4.6; EN 7.2; IN 5.5; TE 4.6.

Coloration: The dorsum is tan with bold dark brown blotches, the largest of them reaching from the anterior corners of the orbits posteriorly narrowing towards the posterior end of the occiput, widening then to form a Y-shaped mark with its both ends almost reaching the sacrum. There is another smaller blotch on the sacrum and another one posterior to it. Dark spots or lines are also present on the head anterior to the eyes. The head is dark brown laterally. There is a white subocular mark in the shape of an inverted V. The iris coloration is no longer visible. The postocular area is dark brown, the tympanum light brown. There are three dark irregular marks on the dorsal surfaces of the thighs as well as on the tibiae and two of them on the tarsus. The posterior and anterior parts of the hind legs and dorsal surface of the foot are uniform brown, ventrally light brown. The long bones of the tibia are green. Dorsal surfaces of the legs and posterior parts of arms with some dark blotches, ventral and anterior parts as well as hands ventrally light brown. There are some dark markings on palm and fourth finger. The lateral sides of the body are finely reticulate forming a mosaic of creamy yellow and brown spots. The ventral surfaces of throat and abdomen are creamy yellow marbled with brown irregular spots.

Variation: I have seen five more specimens, from Napo and Sucumbíos Province, Ecuador, but no live ones. Two additional females (EPN 5578 and MHNG 2560.60) are similar in size. The largest specimen with 78.9 mm SVL is EPN 5578. In this specimen the head is slightly longer than wide (HL/HW 1.01). The dorsal skin is smooth in MHNG 2560.60 and shagreen in EPN 5578. There are a few low tubercles on the dorsal surfaces of body and extremities of EPN 5578 that are lacking in MHNG 2560.60. Both specimens bear some low tubercles in the loreal and posttympanic area. On the eyelid there are one (MHNG 2560.60) and three (EPN 5578) tubercles. Both specimens have more webbing on the hand than the holotype, especially on the inner edge of the third finger, where the web almost reaches the ultimate subarticular tubercle. The distal subarticular tubercle on Finger IV is broadly rimmed distally like the holotype in MHNG 2560.60, but slightly bifid in EPN 5578.

Both specimens are similar to the holotype in their dorsal coloration, with bold dark bands between the eyes and large blotches on the back. Some of these are outlined creamy yellow on the head in EPN 5578 and also on the back in MHNG 2560.60. The venter is uniform light tan or tan.

Three males (EPN 5577, EPN AA-5611, EPN 5607) are 44.1–48.1 mm in SVL. The head is as long as wide in all specimens. The tympana in males are proportionately larger than in females (TD/HL 0.23–25 in females, 0.16–0.19 in males). All dorsal surfaces, the dorsolateral area of the flanks and the head laterally are more tuberculate than in the females. Although at least one of them (EPN AA-5611) has well-developed nuptial excrescences, none bears tubercles with keratinized tips on the dorsum. There are numerous tubercles on the posteroventral edge of tarsus and metatarsus and up to five ones on the orbit. The axillary membrane is more extensive than in females and covers about ½ of the upper arm proximally. The dorsal coloration is variable, with tan blotches, irregular streaks or a reticulum of tan on grey (most likely green in life) ground. The ventral surfaces of the body are creamy white with numerous speckles of brown. The tibiofibular bones are white in both males and females.

Comparisons: *Osteocephalus festae* differs from *O. buckleyi* (in parentheses) in larger size of the females of up to 78.9 mm SVL (up to 54.1 mm), dorsal

tubercles without keratinized tips in breeding males (with tips), a medium-sized tympanum in females with TD/HL 0.16–0.19 (tympanum larger: TD/HL 0.20–0.23), a smooth supratympanic fold (tuberculate) and an axillary membrane covering about $^3/_8$ (females) to ½ (males) of the proximal part of the upper arm (one fourth).

The species differs from *O. cabrerai* (in parentheses) in lacking a row of tubercles on the lower jaw (present), a row of low tubercles on the outer edge of Finger IV (an irregular deep fringe), webbing on the inner side of Finger III reaching the penultimate subarticular tubercle (proximal part of the ultimate subarticular tubercle, and continued as fringe to the finger disc), medium tympanum size in females with TD/HL = 0.16–0.19 and TD/FD = 0.87–1.08 (large size with TD/HL 0.20–0.22 and TD/FD = 1.11–1.31), a smooth supratympanic fold (tuberculate) and uniform brown posterior surfaces of thighs in preservative (light tan with dark tan spots or irregular tan markings).

Osteocephalus inframaculatus (in parentheses) is a much smaller species. Female *O. festae* reach 78.9 mm SVL (41.9 mm). In addition, *O. festae* has a smooth supratympanic fold (tuberculate) and posterior surfaces of thighs in preservative are uniform brown (tan with light short vermiculation).

Osteocephalus festae may be diagnosed as (1) a medium to large-sized species with considerable sexual dimorphism in SVL (78.9 mm in females, 48.1 mm in males) and minor differences in dorsal tuberculation; (2) skin on dorsum of females smooth with or without a few granules, granulate in males; (3) skin on flanks areolate; (4) weakly angular canthus rostralis curved inward; (5) frontoparietal ridges not visible from outside; (6) dentigerous processes of vomers angular; (7) strong supratympanic fold from the posterior edge of the orbit sloping in an arch towards a point posterior to the jaw joint; (8) web on inner edge of third finger reaching distal end of penultimate subarticular tubercle or beyond, almost reaching the ultimate subarticular tubercle; (9) distal subarticular tubercle on Finger IV broad-edged to slightly bifid; (10) dorsum variable in shades of tan or grey (green in life?), with dark brown blotches, streaks, or a reticulate pattern; (11) venter creamy white with or without brown marbling or numerous brown speckles; (12) a large white subocular mark; (13) flanks marbled irregularly with light, tan and dark brown; (14) position of vocal sacs paired, protruding posteroventral to angles of jaws; (15) juvenile coloration unknown; (16) tadpole habitat and labial tooth row formula unknown (most likely in streams); (17) color of tibiofibular bones green or white in preservative.

Distribution: *Osteocephalus festae* is known from the Andean foothills in the provinces of Sucumbíos, Napo and Morona-Santiago, Ecuador.

***Osteocephalus inframaculatus* (Boulenger, 1882) nov. comb.** (Fig. 3.4.5)

Hyla inframaculata Boulenger, 1882

Hyla inframaculata – Nieden 1923

Hyla inframaculata – Duellman 1977

Hyla inframaculata – Frost 2009

This species, known only from the holotype, BM 1947.2.13.10, has only appeared in species lists after its description. Its type locality is “Santarem”, Estado do Para, Brazil. Although there are few characters found in species of *Osteocephalus* that are not present in other hylid genera (Jungfer and Hödl 2002), the combination of angular vomers, a bifid ultimate subarticular tubercle of Finger IV and tuberculate dorsal skin characterize *Hyla inframaculata* as a species of *Osteocephalus*. The tuberculate dorsal skin in a female specimen together with areolate skin on the flanks, non-uniform coloration of the posterior surfaces of the thighs and a row of tubercles on the tarsus indicate that the species is a member of the *buckleyi* complex. With only one undissected specimen at hand, neither sex, identified by lack of nuptial excrescences, lack of vocal sac apertures and externally visible vocal sacs, nor adult size can be taken for completely granted.

Redescription of the holotype: Snout rounded in dorsal and lateral view, as long as the diameter of the orbit. Head slightly wider than long, without raised lateral edges of the frontoparietals. Canthus rostralis rounded, indistinct; loreal region slightly concave; interorbital space as broad as the upper eyelid. Dorsal surfaces of head and canthus rostralis covered with small, irregular tubercles; larger tubercles on the orbits. Tympanum distinct, large, about 70% of the diameter of the eye. A heavy tuberculate supratympanic fold from the midlevel of the eye to a point at about 2 h (when tympanum is thought as a clock face), sloping towards the flanks to a point at about midlevel of the tympanum. Tongue circular, vomers angular, almost between the large choanae. Anteriorly, the choanae reach slightly beyond the anterior parts of the vomers, posteriorly it is vice versa.

Dorsum tuberculate. Two dorsal folds not mentioned in the original description, but shown in Plate XXIII (Boulenger 1882) and still present, are irregular and obviously artefacts of preservation. Anterior two thirds of the flanks areolate. Ventrally granulate. Cloacal opening at about midlevel of the thighs. Anal sheath absent. Circumanal tubercles present, low. Axillary membrane weak. Upper surfaces of limbs weakly tuberculate. A row of irregular tubercles on the outer ventrolateral edge of the lower arm and the tarsus. Hidden surfaces of limbs smooth. When bent forward, the tibiotarsal articulation reaches nearly the tip of the snout. Finger discs rounded. Disc on Finger III about 70% the diameter of the tympanum. The relative lengths of the adpressed fingers is I < II < IV < III. Finger webbing formula is I basal II 1 ½ — $2\,{}^{2}/_{3}$ III 3^{-} — 2^{+} IV. Webbing on the inner edge of Finger III reaches halfway between penultimate and ultimate subarticular tubercle. The distal subarticular tubercle on Finger IV is bifid. The relative length of adpressed toes is I < II < III ≤ V < IV. The webbing formula is I 1^{+} — 2 II 1^{+} — 2 ½ III $1\,{}^{1}/_{3}$ — $2\,{}^{1}/_{3}$ IV 2 ½ — 1 V.

Measurements of the holotype (in mm): SVL 41.9; HL 14.2; HW 14.5; TL 22.4; FL 27.6; ED 5.2; TD 3.7; FD 2.2; EN 4.6; IN 3.1; TE 2.2.

Coloration: Dorsally grayish brown, indistinctly marbled with dark brown; Flanks marbled white and brown; throat and chest with bold brown blotches on cream ground; posterior half of abdomen and ventral surfaces of thighs light brown; hidden surfaces of arms and legs boldly marbled with brown and cream. The tibiofibular bones are white.

Comparisons: The only known female is much smaller than both female *O. festae* (78.9 mm) and *O. cabrerai* (71.8 mm), and smaller than female *O. buckleyi* (54.1 mm). Other differences to *O. cabrerai* include the outer edge of Finger IV, which is tuberculate in its proximal half and smooth in the distal half (with an irregular fringe in *O. cabrerai*) and there are no tubercles on the lower jaw (present in *O. cabrerai*). It

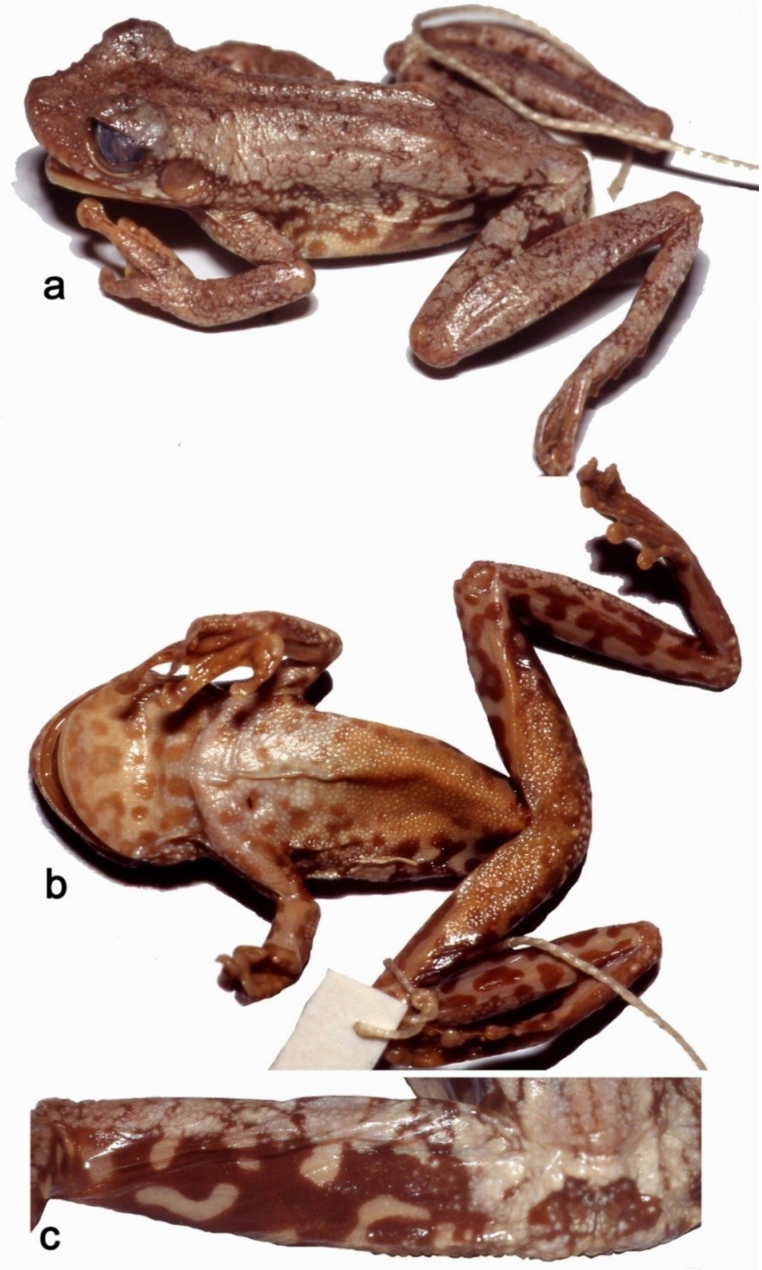

Fig. 3.4.5. *Osteocephalus inframaculatus* (holotype): a. dorsolateral, b. ventral view, c. posterior surface of thigh and cloacal area. Not to scale.

differs from *O. festae* in the coloration of the posterior surfaces of thighs in preservative, which are tan with light short vermiculation (uniform brown). It differs from *O. buckleyi*, *O. cabrerai* and *O. festae* in having a longer snout. The snout is round in dorsal view, while *O. buckleyi* usually has a bluntly rounded to truncate snout.

Osteocephalus inframaculatus may be diagnosed as (1) a medium-sized species with sexual dimorphism unknown; (2) skin on dorsum of female tuberculate; (3) anterior two thirds of the flanks areolate; (4) canthus rostralis indistinct, rounded, curved inward; (5) frontoparietal ridges not visible through skin; (6) dentigerous processes of vomers angular; (7) tuberculate supratympanic fold from the midlevel of the eye sloping posterior to the tympanum towards the flanks up to about midlevel of the tympanum; (8) web on inner edge of third finger reaching halfway between penultimate and ultimate subarticular tubercle; (9) distal subarticular tubercle on Finger IV bifid; (10) dorsum grayish brown, indistinctly marbled with dark brown; (11) ventrally anterior half with large brown blotches on cream ground, posterior half light brown; (12) several light markings on the upper lip, the largest one posteroventral to the midlevel of the eye to the tympanum; (13) flanks marbled white and brown; (14) position of vocal sacs unknown; (15) juvenile coloration unknown; (16) tadpole habitat and labial tooth row formula unknown; (17) color of tibiofibular bones white in preservative.

***Osteocephalus mimeticus* (Melin, 1941)** (Fig. 3.4.6)

Hyla mimetica Melin, 1941

Osteocephalus pearsoni – Trueb & Duellman 1971 (partim)

Hyla triangulum – Duellman 1974 (synonymized *mimetica* with *triangulum*)

Hyla elkejungingerae Henle, 1981

Hyla elkejungingerae – Henle *et al.* 1983

Hyla elkejungingerae – Frost 1985

Osteocephalus verruciger – Schütte & Spieler 1986

Osteocephalus elkejungingerae – Henle 1992 (nov. comb.)

Osteocephalus mimeticus – Smith & Noonan 2001 (nov. comb.)

Osteocephalus elkejungingerae – Frost 2009

Hyla mimetica was described from two syntypes both bearing GNM “no. 469” from the village of Roque, Departamento San Martín, Peru. I designate the specimen that coincides in details of coloration with Melin’s (1941) Fig. 10a, which his description apparently is based on, a subadult specimen of 34.0 mm SVL, as the lectotype.

This frog has been confused many times since its description. One reason may be the fact that the type specimens are juvenile frogs with rows of bold paravertebral spots on the dorsum lacking many characteristic features of adult male *Osteocephalus*. Trueb & Duellman (1971) referred an adult specimen from Yaupi, Río Paucartambo, Departamento Pasco, Peru (KU 136312) to *O. pearsoni* and illustrated it as such. The dorsal coloration of the holotype apparently led Duellman (1974) to synonymize *Hyla mimetica* with *Hyla triangulum* Günther, 1869 (= *Dendropsophus triangulum*). However, the lectotype (he mentions a frog of 23.5 mm SVL; apparently the other syntype) lacks the axillary membranes and glandular thoractic patches of frogs of the *Dendropsophus leucophyllatus* group, which *triangulum* is a member of. Henle (1981) described *Hyla elkejungingerae* on the basis of juveniles collected as tadpoles and raised in captivity from Boquerón del Padre Abad, Departamento Ucayali, Peru. He later transferred it to *Osteocephalus* when frogs raised to adult size and more specimens were available (Henle 1992). Before, Frost (1985) had listed the taxon under *Hyla elkejungingerae*, but added a note by Hoogmoed that it was likely to be a synonym of *Osteocephalus taurinus*. Eric Smith (pers. comm. 2002) and I independently inspected the holotype of *Hyla mimetica* and agree that it is a valid taxon in the genus *Osteocephalus*. Earlier, Smith & Noonan (2001), without further comment, had referred to material examined by them as *Osteocephalus mimeticus* in their description of *Osteocephalus exophthalmus*. The species (as *Osteocephalus elkejungingerae*) was described in detail by Henle (1992), so it need not be repeated here. The lectotype agrees with the holotype of *Hyla elkejungingerae*, also a subadult (22 mm SVL) as well as with the large series of “topotypes” at the ZFMK, namely the subadult specimens (e. g. ZFMK 39164, 40152–3). The lectotype of *Hyla mimetica* has still retained some juvenile characters: Large white supralabial spots (reduced to a large subocular mark in many adults), dark paravertebral markings (a uniform dorsum or variable markings on the entire dorsum in adults), light elbows, knees and tibiotarsal articulations (dark like the rest of the extremities in adults). But the iris coloration, black with some golden blotches (a character shared among the genus only with the allopatric Colombian *O. carri*) is already reminiscent of that of an adult. In contrast, recently

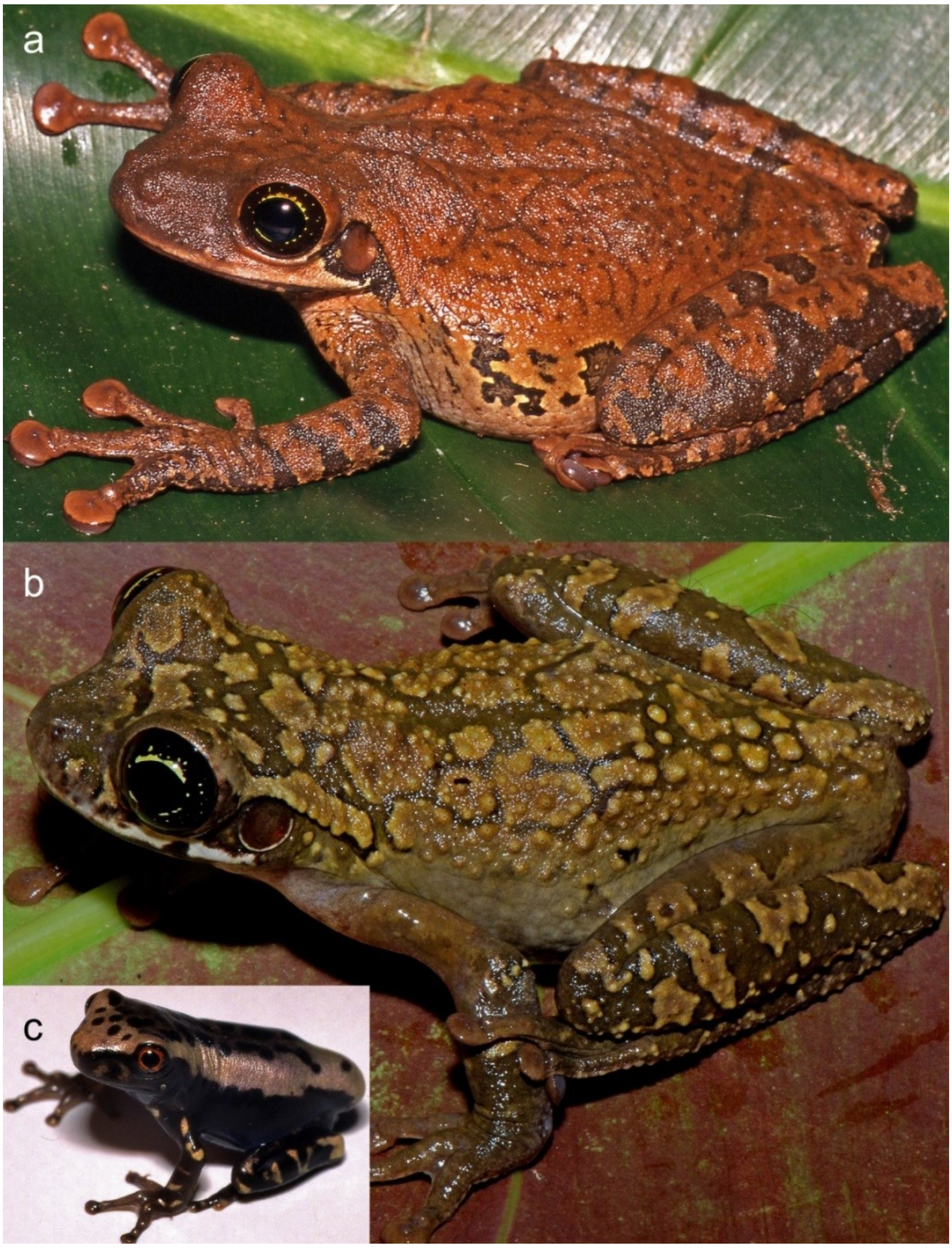

Fig. 3.4.6. *Osteocephalus mimeticus*. a. Adult female, 75 mm SVL, from Boquerón del Padre Abad, Ucayali, Peru. b. Adult male, 63 mm SVL, not in breeding condition. c. Recently metamorphosed juvenile, 19 mm SVL, b and c both from Tarapoto, San Martín, Peru.

metamorphosed juveniles have bright red irises. Live subadults have intermediate irises with black blotches on light red ground. The red color quickly fades in preserved frogs. Sexes at this stage can already be identified by dorsal skin structure. The specimen’s back is smooth, indicating that it is a female. The ontogenetic change in this species has been described and illustrated several times (Henle 1981, Henle *et al.* 1983, Schütte and Spieler 1993) under various names. Females from the type locality of *Hyla elkejungingerae* that I placed together with a male from Tarapoto, about 45 km east of the type locality of *Hyla mimetica*, laid eggs that were fertile. Frogs raised from these eggs were also fertile. The maximum size for males measured is 62.7 mm SVL from Boquerón del Padre Abad, Departamento Ucayali, Peru (Henle 1992), the largest female, KU 209454 from the Río Cainarache, 33 km NE Tarapoto, San Martín, Peru, is 82.7 mm in SVL.

Measurements of the lectotype of *Hyla mimetica* (in mm): SVL 34.0; HL 12.5; HW 12.0; TL 23.0; FL 12.6; ED 4.3; TD 2.1; FD 1.8; EN 3.6; IN 2.8; TE 1.9.

Distribution: *Osteocephalus mimeticus* is a widespread species in the Andean foothills from about 260 to 1650 m a.s.l. from the Huancabamba Depression southward from Departamento San Martín, Peru, at least to Departamento Cuzco, Peru. I have seen photographs of a preserved specimen from Pilon Lajas, Departamento Beni, Bolivia, that I tentatively identified as *O. mimeticus*. This would be the southernmost locality record of the species. Similar frogs from north of the Huancabamba Depression in the Departamentos Amazonas and Cajamarca, Peru, and adjacent Provincia de Loja, Ecuador, represent an undescribed species most closely related to *O. verruciger*.

***Osteocephalus vilarsi* (Melin, 1941) nov. comb.** (Fig. 3.4.7)

Hyla (Trachycephalus) vilarsi Melin, 1941

Osteocephalus taurinus – Bokermann 1966 (synonymized *vilarsi* with *taurinus*)

Osteocephalus leprieurii – Cochran and Goin 1970 (synonymized *vilarsi* with *leprieurii*)

Osteocephalus taurinus – Trueb and Duellman 1971

Osteocephalus taurinus – Frost 2009

Hyla vilarsi (GNM 488) was described by Melin (1941) from a single female that he had obtained from indigenous people at Taracuá (on modern maps also Taracua or Missão Taraquá; for information on the type locality see Caldwell *et al.* 2002), about 100 m a.s.l., Rio Uaupés, in the upper Rio Negro drainage of Estado Amazonas, Brazil, on 7 April 1924. The holotype is a female of 62.2 mm snout-to-vent length (SVL) that contains eggs and therefore must be an adult. A striking feature are two distinct, almost parallel longitudinal frontoparietal ridges on the head, a character found in a few species of *Osteocephalus*.

Bokermann (1966) listed the taxon without explanation as a synonym of *Osteocephalus taurinus* Steindachner, 1862. Cochran and Goin (1970) considered *vilarsi* and *Osteocephalus planiceps* Cope, 1874, to be synonymous with *Osteocephalus leprieurii* (Duméril and Bibron, 1841). Trueb and Duellman (1971) included *vilarsi* and *O. planiceps*, among others, in the synonymy of *O. taurinus*, a widespread species ranging from the Guyanas and southern Venezuela throughout the Amazon Basin southward to Bolivia. Duellman and Mendelson (1995) resurrected *O. planiceps* as a valid species. The status of *vilarsi* was not addressed by them. Thus, according to those previous authors, the taxon should either be a synonym of *O. leprieurii, O. planiceps*, or *O. taurinus*.

Redescription of the holotype: Melin (1941) described the species in some detail. This is expanded here in order to facilitate the comparison between species, for while he mentioned the similarity between *vilarsi* and *O. taurinus*, he did not explicitly state the differences between them.

Adult female of 62.2 mm SVL. Snout bluntly rounded in dorsal and lateral view. Head slightly longer than wide. Lateral edges of frontoparietals raised, forming two almost parallel ridges. Canthus rostralis very distinct, almost straight (very slightly curved inwardly). Loreal region deeply concave. Nostrils elevated, opening laterally. Dentigerous processes of vomers in contact with each other, bearing 11 teeth on the left and 15 on the right, angular, in between choanae, their anterior edges at about midlevel of the choanae, their posterior edges reaching slightly beyond the posterior edges of the choanae. The latter are large, oblique and bean-shaped though somewhat angular. Tongue elliptical, about 1.4 times longer than wide. Supratympanic fold from the anterior edge of the tympanum sloping towards the

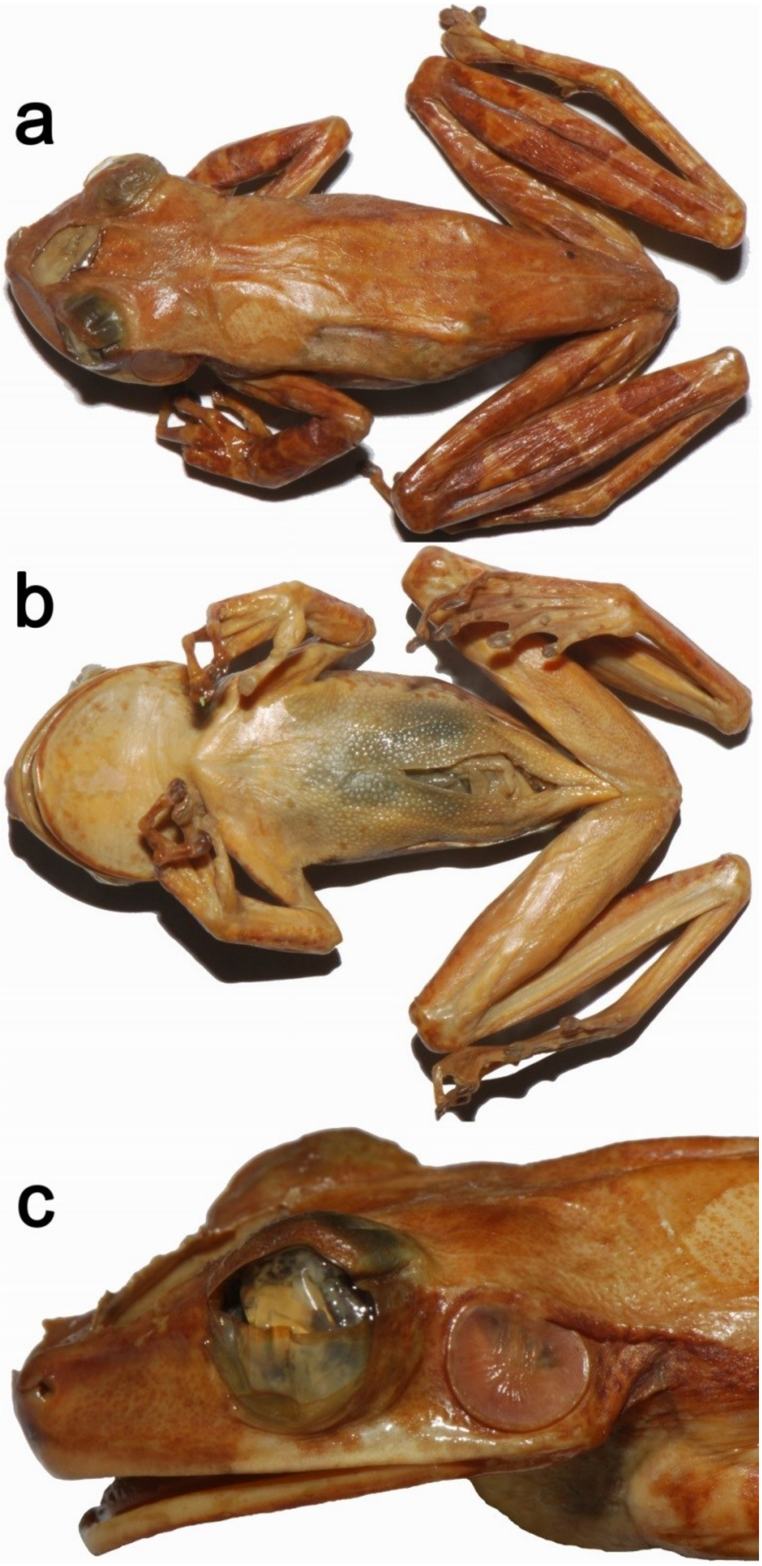

Fig. 3.4.7. *Osteocephalus vilarsi* (holotype): a. dorsal, b. ventral, c. lateral view of head. Not to scale.

upper edge of the arm insertion in an almost straight line. Tympanum large, conspicuous, elliptical, slightly wider than high and about 77 % of the eye diameter.

Skin on dorsum smooth with a few scattered, small, flat tubercles (under magnification) in the posterior half of the back. Dorsal surfaces of head rugose. Loreal region granulate. Skin loose or missing (removed) above the sphenethmoid and on the right nostril. Skin of body smooth laterally and on lateral and dorsal surfaces of the extremities. Ventrally smooth in thoracic area and on chin, granulate on belly and posterior two thirds of the thighs. Axillary membrane absent. Cloacal opening at about three fourths of thigh height.

The finger and toe discs are desiccated. Melin described them as being scarcely half the size of the tympanum and slightly oblong, but it is not clear whether they were in a better state then. The disc of Finger III is 52 % of the tympanum width. The thumb bears a large elliptical thenar tubercle and there is a prominent supernumerary tubercle proximal to the proximal subarticular tubercle. A few low tubercles are present on the outer edge of the fourth finger. The distal subarticular tubercle on Finger IV is barely bifid, the others are simple. The relative length of the adpressed fingers is I < II < IV < III. The webbing formula is I basal II 2 — 3^+ III 2 ¾ — 2 ¾ IV.

On the foot there is a large elliptical inner metatarsal tubercle and a small rounded median plantar tubercle. The subarticular tubercles are single and conical. The proximal segments of Toes III-V bear numerous supernumerary tubercles. The relative length of the adpressed toes is I < II < III = V < IV. The webbing formula is I 1 ¼ — 2 ¼ II 1^+ — 2 $^{2}/_{3}$ III 1^+ — 2 ¾ IV 2 ¾ — 1 ¼ V.

Measurements of the holotype (in mm): SVL 62.2; HL 20.1; HW 19.6; TL 34.5; FL 42.0; ED 6.2; TD 4.8; FD 2.3; EN 6.2; IN 4.6; TE 2.5.

Coloration of the holotype: Dorsum uniform tan. Broad dark tan bars on the limbs, two on lower arms, one on hands, two on thighs, one across the knee, two on the tibia, two on the tarsus. A dark tan horizontal supracloacal stripe. A few indistinct dark tan spots laterally. A thin white supralabial line from the posterior edge of the tympanum around the snout, greatly expanded as a subocular spot from anterior edge of eye to midlevel of tympanum on the left, from posterior third of eye level almost to posterior edge of tympanum (reaching eye on lower eyelid) on the right. Throat creamy yellowish with some small tan mental spots. Lower jaw bordered by a thin tan sublabial line. Belly creamy yellowish. A few small tan spots bordering the chest posterior to the clavicles. Arms and legs ventrally light brownish white. Posterior surfaces of thighs uniform tan. Iris color not clearly visible (there are a few black spots on grey ground, straight radiating lines are not visible). The bones, which have been in preservative for 85 years, are white, but may have been green as in many other *Osteocephalus*.

Comparisons: *Osteocephalus leprieurii* is a medium-sized species with spiny-backed males up to 53 mm and females with smooth dorsa reaching 63 mm (Lescure and Marty 2000, Kok and Kalamandeen 2008). Unlike *vilarsi*, there are no frontoparietal ridges on the head of this species (Jungfer and Hödl 2002).

Osteocephalus taurinus is a large species of the genus with distinct frontoparietal ridges. Melin (1941) had obtained "*Hyla taurina*" at Taracuá and at the Rio Uaupés, north of Rio Japú (about 60 km WNW of Taracuá). His female specimens were 82–98 mm in SVL. I have not seen them, but from his description there can be no doubt they are *O. taurinus*. No other similar frog is known from there. The largest preserved female of *O. taurinus* I have seen is the holotype, NMW 16492, with 103.9 mm SVL, from Barra do Rio Negro, Manaus, Brazil. I have measured a live female of 105 mm SVL at Reserva Adolpho Ducke, 25 km north of Manaus. Thus, the sympatric females of *O. taurinus* are 30–58 % larger than the adult female holotype of *vilarsi*, and other *O. taurinus* from the Rio Negro watershed are up to 69 % larger.

Apart from the considerably larger size, *O. taurinus* differs from *vilarsi* in the following characters: The canthus rostralis is more or less straight, distinct and rounded rather than angular, as in *vilarsi*. The supratympanic fold begins anterior to the tympanum at about 2/3 height of it and curves around the tympanum down towards the arm. In *vilarsi* it begins at the upper level of the tympanum and continues as a fairly straight sloping fold towards the arm insertion. The back of females is uniformly slightly granulate (smooth anteriorly, a few small granules posteriorly in *vilarsi*). The distal subarticular tubercle on Finger IV is distinctly bifid. Although there is some variation in the extent of webbing throughout the range of *O. taurinus*, there is always more webbing, especially on the outer edge of Finger II and on the inner side of Toe II and both sides of Toe IV. For example, female ZFMK 55900 (77.5 mm SVL) from Manaus, Brazil, has a hand formula of I basal II 1 ½ — 3^{-} III 2 $^{2}/_{3}$ — 2 ½ IV and a foot formula of I 1 — 2 II 1 — 2^{+} III 1 — 2 $^{1}/_{3}$ IV 2 $^{1}/_{3}$ — 1 V. The bones are green.

Osteocephalus planiceps is known from the western Amazon Basin in Colombia, Peru and Ecuador and a locality south of the Amazon in Brazil, about 300 km WSW Manaus (Duellman and Mendelson 1995, Jungfer *et al.* 2000, Lehr 2001, Lynch 2008, unpublished data). Its northernmost locality in Colombia is in the Río Guaviare drainage, other northern localities are in the Río Caquetá drainage (Lynch 2008). A single Brazilian locality is from the lower Rio Negro (Gordo and Neckel-Oliveira 2004). No other records exist from the Rio Negro drainage.

Eleven adult females of *O. planiceps* from Ecuador and Peru are 67.0 – 88.2 (x = 74.7) mm in SVL. The species shares many characters with *vilarsi*, especially the frontoparietal ridges, a straight, very prominent canthus rostralis, a more or less straight supratympanic fold, a large white subocular spot and white supralabial line, a dark tan sublabial line on the lower jaw, a few tan spots laterally and bold tan bars on the limbs, and a barely bifid distal subarticular tubercle on Finger IV. The webbing is very similar. That of the hand of *vilarsi* is almost within the range of that of *O. planiceps*, which has slightly more webbing on the outer edge of Finger II (1 $^{3}/_{4}$ – 2^{-}). On the foot *O. planiceps* has slightly more webbing on the inner edge of Toe II (2 – 2^{+}) and on Toe V (1 – 1^{+}).

Both species can be distinguished by a few characters: The dorsum of *O. planiceps* females is smooth. Tubercles are lacking on the posterior two thirds of the back. The discs on the fingers of *O. planiceps* are round and large. Their diameter is about 80 % of the tympanum width. Even though the discs of the holotype of *vilarsi* are somewhat desiccated, they seem to have been smaller than those of *O. planiceps*. The tibiofibular bones are green. They are white in *vilarsi*, but they might just be discolored after such a long time in preservative.

Six other species of *Osteocephalus* are known from north of the Amazon in Brazil and on the Guaina Shield. *Osteocephalus oophagus* has two cranial ridges that are not visible superficially, as in *vilarsi*. The largest known female is 55.6 mm in SVL and thus considerably smaller (Jungfer and Schiesari, 1995). *Osteocephalus* cf. *buckleyi* and *O.* cf. *cabrerai* both have rows of tubercles on the tarsus and areolate skin on the flanks. Both characters are absent in *vilarsi*. A species from Guyana, *O. exophthamus* Smith and Noonan, 2001, is considerably smaller (up to 42.5 mm SVL) and lacks cranial ridges (Kok and Kalamandeen 2008).

Another Guyanan species, *O. phasmatus* MacCulloch and Lathrop, 2005, from high elevations >1400 m on Mount Ayanganna has about the same size as *vilarsi* and also shares cranial ridges, but *vilarsi* lacks an axillary fold (one half of humerus length in *phasmatus*) and the width of the disc of Finger III is about half the tympanum width (larger than tympanum).

Since *vilarsi* can be distinguished from all other species in the area it is here considered a valid member of the genus *Osteocephalus* characterized by (1) medium size (female 62.2 mm SVL), sexual dimorphism unknown; (2) skin on dorsum of females smooth anteriorly, interspersed with small flat tubercles on the posterior 2/3 of the back, unknown in males; (3) skin on flanks smooth; (4) very prominent, almost straight canthus rostralis; (5) frontoparietal ridges present, well visible through skin; (6) dentigerous processes of vomers angular; (7) straight supratympanic fold, sloping in a fairly straight line posterior to the tympanum; (8) web on inner edge of third finger reaching distal end of penultimate subarticular tubercle; (9) distal subarticular tubercle on Finger IV barely bifid; (10) dorsum uniform tan; (11) venter cream with some small brown spots posterior to the clavicle; (12) narrow white labial stripe to posterior edge of tympanum, extended into large subocular spot; (13) flanks brown with a few small irregular tan spots; (14) position of vocal sacs unknown; (15) juvenile coloration unknown; (16) tadpole habitat and labial tooth row formula unknown; (17) color of bones white (?).

Distribution: *Osteocephalus vilarsi* is still only known from the type locality in the extreme northwest of Brazil, close to the Colombian border.

Discussion

Years ago, *O. buckleyi* was believed to be a widespread Amazonian and Guianan species (Trueb and Duellman 1971), but in fact it is a complex of several species. Four species in the *buckleyi* complex are dealt with here. While it is relatively easy to distinguish between *O. buckleyi*, *O. cabrerai* and *O. inframaculatus*, males of two species living sympatrically in the Andean foothills of Ecuador, *O. buckleyi* and *O. festae*, may be difficult to tell apart, because variation of the former encompasses most of the morphological features of the latter. Females, however, differ so markedly in size and some proportions, that there can be no doubt that two species

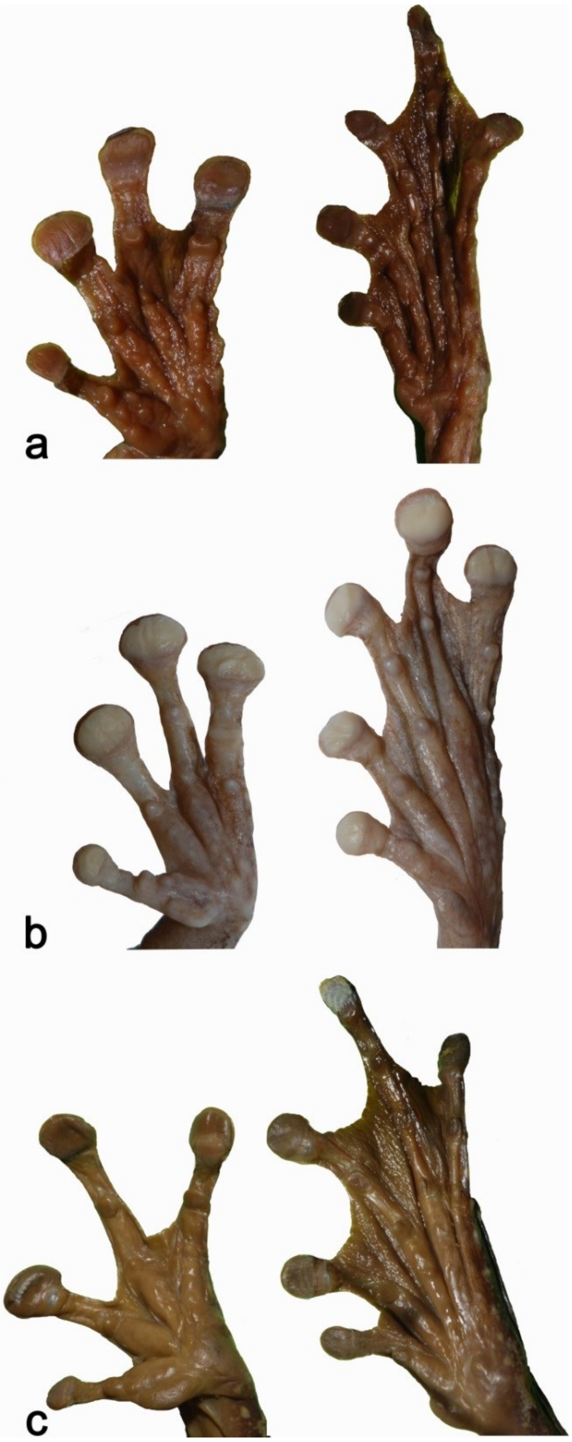

Fig. 3.4.8. Hand and foot of a. *Osteocephalus cabrerai* (female holotype), b. *O. buckleyi* (SMNS 13713, female from Jatun Sacha, Napo, Ecuador), c. *O. festae* (female holotype). Some fingers and toes are spread with needles (not entirely shown), that may cover parts of the discs or intercalary tubercles. Not to scale.

Table 3.4.1. Some distinguishing characters among frogs of the *O. buckleyi* complex in northwestern (*O. buckleyi*, *O. cabrerai*, *O. festae*) and eastern (*O. inframaculatus*) Amazonia.

	O. buckleyi	*O. cabrerai*	*O. festae*	*O. inframaculatus*
maximum SVL females males	 54.1 mm 46.7 mm	 71.4 mm 54.8 mm	 78.9 mm 48.1 mm	 41.9 mm (?) ?
row of tubercles on lower jaw	absent	present	absent	absent
outer edge of Finger IV	smooth, tuberculate, a smooth fringe, or a tuberculate fringe	an irregular deep fringe	a row of low tubercles	proximal half tuberculate, distal half smooth
webbing on inner side of Finger III	to penultimate subarticular tubercle or less than half way between penultimate and ultimate subarticular tubercle	to proximal part of ultimate subarticular tubercle, continued as fringe to finger disc	to distal end of penultimate subarticular tubercle or beyond, almost reaching the ultimate subarticular tubercle	to half way between penultimate and ultimate subarticular tubercle
snout length (EN/HL)	short (females 0.29–0.31; *n* = 4; males 0.23–0.28; *n* = 6)	short (females 0.30; *n* = 2; males 0.27–0.31; *n* = 4)	short (females 0.30–0.31; *n* = 3; males 0.30; *n* = 3)	medium-sized (female 0.33)
tympanum size	large (TD/HL in females 0.20–0.23; *n* = 4); in males 0.23–0.26; *n* = 6)	large (TD/HL in females 0.20–0.22; *n* = 3; in males 0.23–0.26; *n* = 4)	medium-sized (females) to large (males) (TD/HL in females 0.16–0.19; *n* = 3; in males 0.23–0.25; *n* = 3)	large (TD/HL in female 0.26)

Table 3.4.1 continued.

supratympanic fold	tuberculate; from midlevel of eye to 2 h, sloping towards flanks or arm insertion up to lower tympanum level or almost so	tuberculate; curving from midlevel of eye to midlevel of tympanum posteriorly, sloping towards arm insertion up to lower tympanum level	smooth; from midlevel of eye to 2 h, sloping towards flanks almost to lower tympanum level	tuberculate; from midlevel of eye to 2 h, sloping towards flanks for about half of tympanum diameter
dorsal tubercles with keratinized tips in breeding males (with well developed nuptial excrescences)	present	absent	absent	?
color of posterior surfaces of thighs (in preservative)	tan with or without dark brown and/or light marbling or irregular crossbars	light tan with dark tan spots or irregular tan markings	uniform brown	tan with light short vermiculation

are involved. I have raised numerous *O. buckleyi* from several localities to adult size, but no matter how much food was offered, females never exceeded 54 mm SVL normal for *O. buckleyi* (in contrast to the known SVL of 72.5 – 78.9 mm in *O. festae*). It is obvious that more data, especially of live frogs, are needed of *O. festae* to facilitate identification.

Most *Osteocephalus* have green tibiofibular bones in life. Preserved *O. buckleyi* and *O. festae* may have either green or white bones. I have never observed white bones in the numerous live specimens of *O. buckleyi* I have seen, so I assume that discolored bones in some specimens are an artefact of preservation. Earlier, Jungfer *et al*. (2000) had described *O. deridens* and distinguished them from *O*. sp. of Rodríguez and Duellman (1994) and Duellman and Mendelson (1995) by their green bones instead of white ones in *O*. sp. Moravec *et al.* (2002) later stated that only one species with green bones was involved. Apparently, the same phenomenon of discoloration in preservative occurs in this species as well, so the diagnostic value of white bones in preserved specimens is questionable.

The only known locality of *O. planiceps* north of the Amazon in Brazil is Jaú National Park, Estado do Amazonas, on the lower Rio Negro (Gordo and Neckel-Oliveira 2004). After resurrection of *O. vilarsi* the specimens from there should be compared with the description of the latter species. They might as well represent unidentified *O. vilarsi*.

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Appendix

Material examined

Osteocephalus buckleyi

COLOMBIA: *Putumayo*: Rumiyacu, 1000 m: FMNH 54765.

ECUADOR: *Sucumbíos*: San Pablo de Kantesiya: MHNG 2366.39–2366.40; Santa Cecilia: KU 105208–9, 150492–3, 152477, 175500; Shushufindi: MHNG 2560.61. *Napo*: Hacienda Primavera, 40 km S Coca: MHNG 2556.58; Jatun Sacha: KU 217746, SMNS 13713-5. *Pastaza*: Canelos: BM 1947.2.13.40–1947.2.13.41, 1947.2.13.43, 1947.2.13.44 (lectotype), 1947.2.13.45.

PERU: *Loreto*: Nanay, Río Mishana: KU 174916; Runtusapa: MUSM 22197–9, 22202; Sabaloyacu Nuevo: MUSM 22195–22196; San Jacinto: KU 221927; 1.5 km N Teniente Lopez: KU 221926. *Huánuco*: Panguana, RíoYuyapichis, 260 m: SMNS 7269.

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 (08º12'16.4''S/73º52'58.3''W): MUSM 24411, 24413–4.

Osteocephalus carri

COLOMBIA: *Meta*: Villavicencio, parte alta Caño Maizazo: ICN 26988. *Huila*: Acevedo, Río Suaza, Río Aguas Claras, near San Adolfo, 1400 m: FMNH 69702 (holotype). *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.

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. *Sucumbíos*: Cuyabeno, Campamento Concienti: EPN AA-5611, AA-5607.

Osteocephalus inframaculatus

BRAZIL: *Para*: Santarem: BM 1947.2.13.10 (holotype).

Osteocephalus mimeticus

PERU: *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. *Ucayali*: Boquerón del Padre Abad: ZFMK 33352 (holotype of *Hyla elkejungingerae*), 39614–5, 39748–50, 39752–3, 40152–3. *Huánuco*: Fundo Flor, Río Pachitea, 300 m: SMNS 6515. *Pasco*: Pozuzo, 770 m: MUSM 20351; Puerto Bermudez: MUSM 17801; Santa Isabel: MUSM 17847–52, 18022, 18024; Yaupi, Río Paucartambo, 1600 m: KU 136312. *Ayacucho*: San José on Río Santa Rosa, 1005 m: KU 196994–5; Sivia, Río Apurimac, 760 m: FMNH 39853. *Cuzco*: Pozo Pagoreni, Comunidad Kirigueti: MUSM 21872; Zona Reservada Nahua Kugapakori: MUSM 23179–80, 23188, 23207, 23218, 23226.

Osteocephalus oophagus

BRAZIL: *Amazonas*: Reserva Florestal Adolpho Ducke: MZUSP 69852 (holotype), MZUSP 69853, NMW 32925.1–2, MPEG 4845–6, AMNH 136183–4, INPA 01446–8, SMNS 10801–2, ZFMK 57137–8.

Osteocephalus planiceps

COLOMBIA: *Amazonas*: 50 km N de Chorrera, carretera sobre el Igara-Parana: ICN 04803; Leticia – Tarapaca, km 13.8: ICN 46488–46489; Leticia – Tarapaca km 14: ICN 46504–46506; Puerto Nariño: KU 153387–8, 153391.

ECUADOR: *Sucumbíos*: Lago Agrio, 370 m: KU 126649–51, 126655; Limoncocha, 200 m: KU 99208, 175502–3, 178803, 183677–8; San Pablo de Kantesiya: MHNG 2258.15, 2260.95–96, 2264.85, 2373.92,2260.7, 2366.74, 2366.41–42, 2366.44, 2366.49–52, 2366.54–60, 2366.6466, 2366.68–72, 2366.86, 2366.89, 2373.85, 2373.88–90, 2373.98, 2468.75–76, 2468.78–83, 2556.44–52, 2560.58; Pañacocha: MHNG 2560.59; RFC Punto Bolívar: MHNG 2468.85; Reserva Indígena

Sequoias/Sionas, Río Aguarico: MHNG 2212.38; Santa Cecilia, 340 m: KU 105233, 123173, 123175, 150496–8, 152478–9; Shushufindi: MHNG 2560.53–57; Tarapoa: MHNG 2468.77. *Orellana*: Estación Científica PUCE, Trail 3: KU 289450; Río Yasuní, 150 km upstream from Río Napo, 180 m: KU 175197, 175199; Río Yasuní, 200 km upstream from Río Napo, 180 m: KU 175203–4, 175207–13. *Napo*: Hacienda Primavera, 40 km S Coca: MHNG 2366.46, 2556.53–56, KU 221663–4. *Pastaza*: Arutam: SMF Ecu-I 71, SMF ECU-536, SMF ECU-565; Canelos: BM 1947.2.13.42.

PERU: *Loreto*: ACEER on Quebrada Grande ca. mouth Río Sucusari into Río Napo, 210 m: KU 220319, 220892; Explorama Lodge, mouth Río Sucusari into Río Napo, 210 m: KU 220430; Explorama Lodge, mouth Río Yanamono into Río Amazonas, 210 m: KU 220893; La Florida, Río Marañon: KU 220427; 1.5 km S Libertad, S bank Río Napo, 80 km N Iquitos, 120 m: KU 206155; Lindero, Río Sucusari: MUSM 21600; Quebrada Orán, ca. 5 km N Río Amazonas, 85 km NE Iquitos, 110 m: KU 206153–4; Mishana, Río Nanay: KU 174917–9; Sabaloyacu Nuevo: MUSM 22194; San Jacinto, 175 m: KU 221933–6; Singasapa: MUSM 22204; Teniente Lopez, 310 m: KU 22939; 1.5 km N Teniente Lopez, 310 m: KU 221937–8. *Ucayali*: Campamento Bolognesi: SMF 80367; Parque Nacional A. von Humboldt: ZFMK 41408. *Huánuco*: Panguana, Río Yuyapichis ZMH A-2127; *Cuzco*: Campamento Miaria, Comunidad de Miaria: MUSM 23918. *Madre de Dios*: Cocha Cashu, Río Manu between Río Panagua and Río Cachiri, 400 m: KU 154742.

Osteocephalus taurinus

VENEZUELA: *Bolívar*: 13 km S, 1 km E Puente Cuyuni, 140 m: KU 167144–7.

GUYANA: *Rupununi*: N of Acarahy Mountains, W of New River: KU 69747–8.

SURINAM: *Paramaribo*: Paramaribo: ZMH A-3456; Zanderji No. 1: KU 221528.

FRENCH GUYANA: *Saint Laurent du Maroni*: Acarouany: ZMH A-3471; *Cayenne*: Regina: ZMHA-3467.

BRAZIL: *Amazonas*: Barra do Rio Negro, Manaus: NMW 16492 (holotype); Reserva Ducke: ZFMK 55900. *Pará*: Belém: KU 129866. *Rondônia*: Igarapé Marmelo, Rio Abunã: KU 92243–6.

ECUADOR: *Sucumbíos*: Lago Agrio, 370 m: KU 126648, 126652; Limoncocha, 200 m: KU 99420, 99422–3, 99425; Reserva Cuyabeno, S Jesenia Batava: MHNG 2264.76–77; San Pablo de Kantesiya: KU 221665–6, MHNG 2468.84, 2485.71–72, 2354.91–93, 2366.81–85, 2366.87–88, 2373.93–97; Santa Cecilia, 340 m: KU 105230–2, 123174. *Orellana*: Río Yasuní, 200 km upstream from Río Napo, 180 m: KU 175200–2. *Napo*: Hacienda Primavera, 40 km S Coca: MHNG 2206.83, 2212.39–40. *Morona-Santiago*: Río Zamora, 760 m KU 147173.

PERU: *Loreto*: Quebrada Coto: MHNG 2088.3; Balta, Río Curanja: KU 196954; Explorama Lodge, mouth Río Yanamono into Río Amazonas, 210 m: KU 220327, 220890, 220891, 222336–7; Estación Biológica de Pithecia, Río Saimiria: KU 192022–3, MHNG 2088.4–6; San Jacinto, 175 m: KU 221940; Singasapa: MUSM 22192–3; Teniente Lopez, 210 m: KU 221941–2. *Huánuco*: Panguana, Río Yuyapichis: ZMH A-917–8, 920, 2129, 2911. *Ucayali*: Campamento Bolognesi, 230 m (10°06’13’’S/73°49’02’’W): MUSM 20352. *Cuzco*: Campamento Miaria, Comunidad de Miaria: MUSM 23917, 23919. *Madre de Dios*: Cuzco Amazonico, 15 km E Puerto Maldonado, 200 m: KU 194925–8, 205403–8, 205410–3, 207641–9, 209161, 215358–69.

BOLIVIA: *La Paz*: 11.4 km S Caranavi, 900 m: KU 183433. *Santa Cruz*: 169 km N Santa Rosa de la Roca: ZFMK 60317.

Osteocephalus vilarsi

BRAZIL: *Amazonas*: Taracuá: GNM 488 (holotype).

3.3. Systematics, diversity and distribution of treefrogs of the genus *Osteocephalus*, the closely related genus *Tepuihyla*, and description of a new genus (*Dryaderces*)

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Abstract

Spiny-backed tree frogs of the genus *Osteocephalus* are conspicuous components of the tropical wet forests of the Amazon and the Guiana Shield. Here, we revise the phylogenetic relationships of *Osteocephalus* and its sister group *Tepuihyla*, using up to 6134 bp of DNA sequences of nine mitochondrial and one nuclear gene for 338 specimens from eight countries and 218 localities, representing 89% of the 28 currently recognized nominal species. Our phylogenetic analyses reveal (1) the paraphyly of *Osteocephalus* and *Tepuihyla* with respect to each other; (2) the placement of “*Hyla*” *warreni* as sister to *Tepuihyla*; (3) the non-monophyly of several currently recognized species within *Osteocephalus*; (4) the presence of low (< 1%) and overlapping genetic distances among phenotypically well characterized nominal species (e.g. *O. taurinus* and *O. oophagus*) for the 16S gene fragment used in amphibian DNA barcoding. We propose a new taxonomy, securing the monophyly of

Osteocephalus and *Tepuihyla* by rearranging and redefining the content of both genera and also erect a new genus for the sister group of *Osteocephalus*. The colouration of newly metamorphosed individuals is proposed as a morphological synapomorphy for *Osteocephalus*. We recognize and define five monophyletic species groups within *Osteocephalus*, synonymize three species of *Osteocephalus* (*O. germani, O. phasmatus, O. vilmae*) and three species of *Tepuihyla* (*T. celsae, T. galani, T. talbergae*) and reallocate three species (*Hyla helenae* to *Osteocephalus*, *O. exophthalmus* to *Tepuihyla* and *O. pearsoni* to *Dryaderces* gen. n.). Furthermore, we flag nine putative new species (an increase to 138% of the current diversity). We conclude that species numbers are largely underestimated, with most hidden diversity centred on widespread and polymorphic nominal species. The evolutionary origin of breeding strategies within *Osteocephalus* is discussed in the light of this new phylogeny and a novel type of amplexus (gular amplexus) is described.

Key words: Amazonia, barcoding, candidate species, cryptic species, *Dryaderces* gen. n., Guiana, *Osteocephalus*, species paraphyly, *Tepuihyla*.

Introduction

Treefrogs of the genus *Osteocephalus* constitute an important component of the amphibian fauna of the Amazonian and Guianan regions of South America. Their distributions range from the coastal areas of Venezuela and the Guianas south to central Brazil (Mato Grosso) and central Bolivia, and from north-eastern Brazil (Piauí) west to the eastern Andean slopes from Colombia to Bolivia. Their altitudinal distribution ranges from sea level up to about 2000 m a.s.l., although most species are restricted to the lowlands (Trueb & Duellman 1971; Jungfer 2010, 2011; La Marca *et al.* 2010a, b; Ron *et al.* 2010). They are inhabitants of primary or old secondary forests in most of their range (with a few species also present in human-modified landscapes), entering some gallery forests in the drier habitats especially at the edge of their ranges (Trueb & Duellman 1971; Lynch 2006; La Marca *et al.* 2010b; Valdujo *et al.* 2012).

Species of *Osteocephalus* are diverse in their use of different kinds of water bodies for reproduction and exhibit a variety of reproductive modes. There are species that deposit eggs in lentic water, others in lotic waters, and some deposit their eggs in water-holding plant leaf axils and tree holes and exhibit various degrees of parental care (Jungfer & Weygoldt 1996; Jungfer *et al.* 2000; Moravec *et al.* 2009; pers. obs. KHJ). Males of most species exhibit tuberculate dorsal skin, with tubercles often tipped by dark, heavily keratinized spicules in breeding males (hence, spiny-backed treefrogs), while the females exhibit a more or less smooth dorsum. Generalized omnivorous stream and pond dwelling tadpoles of *Osteocephalus* share similar numbers of tooth rows (Trueb & Duellman 1970; Henle 1981; Hero 1990; Ron *et al.* 2010; Menin *et al.* 2011), while phytotelm adapted larvae, at least in two cases, are highly specialized feeders of conspecific nutritive eggs and have reduced numbers of labial tooth rows (Jungfer & Schiesari 1995; Schiesari *et al.* 1996; pers. obs. KHJ).

The genus *Osteocephalus* was originally coined by Fitzinger (1843) in combination with the specific epithet *taurinus*, but he neither designated nor illustrated any specimen, so both names are *nomina nuda*. Steindachner (1862) reused both names, described *O. taurinus,* and defined *Osteocephalus*. Cope (1867, 1874), Goin (1961) and Trueb (1970) included more species. The first and only thorough revision of the genus performed to date is that of Trueb & Duellman (1971). Subsequently, numerous species were described and named, rearranged to or from other genera, or resurrected (Duellman 1974; Henle 1981, 1992; Martins & Cardoso 1987; Duellman & Mendelson 1995; Jungfer & Schiesari 1995; Ron & Pramuk 1999; Jungfer *et al.* 2000; Jungfer & Lehr 2001; Smith & Noonan 2001; Jungfer & Hödl 2002; Lynch 2002, 2006; Faivovich *et al.* 2005; MacCulloch & Lathrop 2005; Wiens *et al.* 2006; Moravec *et al.* 2009; Jungfer 2010, 2011). Six species (*O. aecii, O. edelcae, O. galani, O. luteolabris*, *O. rimarum, O. rodriguezi*) from the Venezuelan Guiana Shield were transferred to a new genus, *Tepuihyla* (Ayarzagüena *et al.* 1993). Although a combination of characters distinguishes *Tepuihyla* from *Osteocephalus*, no putative phenotypic synapomorphy has yet been reported. Thus, the generic assignment of several *Osteocephalus*-like species from the Guiana Shield has been problematic (e.g. *O. exophthalmus* Smith & Noonan, 2001; *T. talbergae* Duellman & Yoshpa, 1996). More recently, Salerno *et al.* (2012) have shown that *Osteocephalus* might not be monophyletic because *O. exophthalmus* is the sister taxon of *Tepuihyla*.

Osteocephalus is plagued with species-level taxonomic problems. Several reasons make species taxonomy in this genus particularly difficult. One of them is a drastic ontogenetic colour change between recently metamorphosed juveniles and adults, with most juveniles having bright red eyes and light areas on upper arm, elbow, knee, and heel (Appendix S1), while adults have golden to brown irises with ornamentation consisting of venation or radiating lines. As a result of these differences, *O. mimeticus* (Melin, 1941) was named twice as new species of *Hyla* on the basis of juveniles (Jungfer 2010). Apart from the ontogenetic changes in *Osteocephalus*, sexual dimorphism in dorsal skin structure makes males and females look distinctly different in some species. In collections we have frequently seen females of different species grouped under one name and males under a different one. A third source of misidentification is the considerable morphological variation within apparently widespread species, e.g. in *O. taurinus* (Trueb & Duellman 1971). On the other hand, diagnostic morphological characters useful to distinguish some species, such as amount of webbing, tuberculation or maximum snout–vent length, appear to be insufficient to identify putative closely related species such as those of the *O. buckleyi* complex (Jungfer 2010). This taxonomic conundrum casts doubts on our ability to develop an accurate and complete taxonomy of *Osteocephalus* on the basis of currently available morphological data alone and encourages the use of other types of data. Indeed, the use of different lines of evidence (e.g., behaviour, bioacoustics, ecology, morphology, molecules) in alpha taxonomy, although not new (see the works of Myers & Daly 1976a, b, 1979, 1980), has recently gained attention because of its potential to solve long standing taxonomic problems (e.g. Padial & De la Riva 2010; Köhler *et al.* 2010; Brown *et al.* 2011; Castroviejo-Fisher *et al.* 2011).

The phylogenetic relationships within *Osteocephalus* and with closely related groups remain poorly understood. Faivovich *et al*. (2005) presented a phylogenetic analysis of the hylid subfamily Hylinae. Their results indicated the polyphyly of *Osteocephalus*, inasmuch as *O. langsdorffii*, the only species of the genus present in the Atlantic Forest of south-eastern Brazil, was not related to the other four species. On the basis of these results, Faivovich *et al.* (2005) erected the new monotypic genus *Itapotihyla* for *O. langsdorffii* and continued with the recognition of *Osteocephalus* for the remaining species. *Tepuihyla edelcae* was found to be sister taxon to *Osteocephalus*, and that clade in turn was found to be sister to *Osteopilus*. Two species in this analysis (*O. leprieurii* and *O. oophagus*) turned out to be misidentified (Moravec *et al*. 2009), although this fact was irrelevant for their conclusions.

Wiens *et al.* (2006) combined most sequences generated by Faivovich *et al.* (2005) with those of Wiens *et al.* (2005), added 12S sequences of a few other hylid species and obtained a clade composed of *O. cabrerai*, *O. buckleyi*, *O. mutabor* and *O. verruciger*, a clade composed of *O. oophagus* + *O. taurinus* and a clade composed of *O. leprieurii* and *O. planiceps*. An important point of their results was that "*Hyla*" *alboguttata*, a species considered *incertae sedis* by Faivovich *et al.* (2005), was embedded within *Osteocephalu*s. The contributions by Wiens *et al.* (2006) and Moen & Wiens (2009) represented increasingly stringent tests of the monophyly of *Osteocephalus*.

Phylogenetic analyses presented by Moravec *et al.* (2009), Ron *et al.* (2010), and Wiens *et al.* (2010) and Pyron & Wiens (2011) added more information on the relationships of *Osteocephalus*. Salerno *et al.* (2012) recently presented a phylogenetic analysis of *Tepuihyla* and included several species of *Osteocephalus* as outgroups. A more in-depth analysis of genetic diversity among tepui dwelling vertebrates, including frogs currently referred to *Osteocephalus* and *Tepuihyla,* additionally sheds light on their genetic diversity (Kok *et al.* 2012). Ron *et al.* (2012) presented an analysis of north-western Amazonian stream-breeding species called the *O. buckleyi* species complex by them and described three new species. In this paper, we present the first densely sampled phylogenetic analysis of *Osteocephalus.* The goals of this study are to: (1) test the monophyly of *Osteocephalus* and identify its sister group, (2) explore relationships among its species, (3) elucidate the potential number of unnamed species in the genus on the basis of molecular data, (4) develop a monophyletic taxonomy, and (5) study the evolution of the various reproductive modes observed in the group in the context of our phylogenetic hypothesis.

Materials and Methods

Taxon sampling and terminology

In a combined effort by numerous colleagues, we tried to obtain as many samples as possible from throughout the range of the genus. We obtained tissue samples from Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, and Venezuela; thus covering most of the Guiana Shield, Amazonia and the north-western part of the Brazilian Cerrado where the genus occurs. Nevertheless, not all of the countries have been sampled sufficiently yet. Data are lacking especially for parts of Colombia, Amazonian Venezuela and Brazil. All in all, we included sequences of up to 6134 bp of nine mitochondrial and one nuclear gene from 338 individuals, including 25 of the 28 presently known species of *Osteocephalus*, plus a large number of unidentified specimens. The species for which tissues are unavailable for this study are *O. duellmani*, *O. inframaculatus* and *O. vilarsi* which are known only from their type material. We also included six species of *Tepuihyla* (*T. aecii*, *T. edelcae, T. galani, T. rodriguezi, T.* sp., *T. talbergae*), and *“Hyla” warreni*, a species that could not be associated with any of the genera recognized by Faivovich *et al.* (2005), because preliminary analyses and morphological data suggest that it could be related to the *Osteocephalus* + *Tepuihyla* clade (e.g. Kok *et al.* 2012). *“Hyla” warreni* was recently considered a species of *Tepuihyla* by Aubrecht *et al.* (2012) without mentioning any supporting evidence. As outgroups we included exemplars of several genera of Lophyohylini, and *Myersiohyla kanaima*, of Cophomantini, was used to root the trees, following the results of a previous phylogenetic analysis (Faivovich *et al.* 2005). Newly generated sequences are deposited in GenBank under accession numbers KF001880–KF002004 and KF002006–KF002249. For a list of species, voucher specimens, localities, and detailed GenBank accession numbers of the data used in the phylogenetic analyses, see Appendix S2. Unnamed species are referred to as candidate species following the terminology of Vieites *et al*. (2009): for unnamed species for which evidence is conclusive we use the term Confirmed Candidate Species (CCS), and when evidence is inconclusive (i.e. mostly molecular data only), we use the term Unconfirmed Candidate Species (UCS). We follow the system of Padial *et al.* (2010) to refer to particular candidate species, where the candidate species name results from the combination of the binomial species name of the most similar or closely related nominal species, followed (in square brackets) by the abbreviation “Ca” (for candidate) with an attached numerical code referring to the particular candidate species (e.g. Ca1, Ca2, etc.), and terminating with the GenBank accession numbers of one of the sequences that revealed the putative species.

Character sampling and lab protocols

The mitochondrial gene sequences produced for this project include portions of cytochrome oxidase I (COI), cytochrome b (cytb), 12S, two non-overlapping fragments of the 16S, NADH dehydrogenase subunit 1 (ND1), and the intervenings tRNA^{Val}, tRNA^{Leu}, and tRNA^{Ile}. The primers employed are the same used by Faivovich *et al.* (2005), with the addition of AnF1-AnR1 for cytochrome oxidase I (ML, unpublished), and 16S-frog and tMet-frog for the fragment containing the downstream fragment of 16S, RNA^{Leu}, ND1 and tRNA^{Ile} (Wiens *et al.* 2005). We also included sequences of these genes and of the mitochondrial control region and the nuclear gene pro-opiomelanocortin (POMC) recently produced by Kok *et al.* (2012), Ron *et al.* (2012) and Salerno *et al.* (2012).

DNA extraction, amplification, and sequencing methods are those described in a recent paper by Blotto *et al.* (2013). All samples were sequenced in both directions. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 3.0. (Gene Codes, Ann Arbor, MI). Complete sequences were edited with BioEdit (Hall 1999).

Phylogenetic analyses

The phylogenetic analyses included treatment of sequences both as dynamic homologies (simultaneus tree searches and aligment) and as static homology hypotheses. The consideration of sequences as dynamic homologies simultaneously with tree searches has been discussed and justified by Wheeler (1996, 2002) and De Laet (2005). Static alignments (multiple alignments) independent of tree searches are the most common procedure in molecular phylogenetics, regardless of the omnipresent and always ignored problem of the lack of an optimality criterion to choose among competing alignments. We also performed a multiple sequence alignment and analyzed it using both maximum parsimony (MP) and likelihood (ML) inference. The rationale for using parsimony as an optimality criterion was advanced by Farris (1983) and discussed, among others, by Goloboff (2003), Goloboff & Pol (2005), and Kluge & Grant (2006), Grant & Kluge (2009), and Wheeler (2012) for its conceptualization in a dynamic homology framework. Within this framework, the phylogenetic analysis under direct optimization was performed with POY4.1.1 (Varon *et al.* 2009), using equal weights for all transformations (substitutions and insertion/deletion events). Sequences of 12S, 16S, and intervening tRNA^{Val} were preliminarily delimited in sections of putative homology (Wheeler *et al.* 2006), and equal-length sequences of protein-coding genes were considered as static alignments to accelerate the searches. Searches were performed using the command "Search". This command implements a driven search building Wagner trees using random addition sequences (RAS), Tree Bisection and Reconnection (TBR) branch swapping followed by Ratchet (Nixon 1999), and Tree Fussing (Goloboff 1999). The command (Search) stores the shortest trees of each independent run and performs final tree fusing using the pooled trees as a source of topological diversity. Two 144-hour runs of Search were implemented in parallel at the American Museum of Natural History Cluster using 32 processors. The resulting trees were submitted to a final round of swapping using iterative pass optimization (Wheeler 2003a). Parsimony Jackknife (Farris *et al.* 1996) absolute frequencies were estimated from the implied alignment (Wheeler 2003b) with T.N.T., Willi Hennig Society Edition (Goloboff *et al.* 2008), generating 50 RAS + TBR per replicate, for a total of 1000 replicates. Tree edition was performed with Winclada (Nixon 2002), and character optimizations and reconstructions with T.N.T.

We performed a multiple sequence alignment with Clustal-W (Thompson *et al.* 1997) under default parameters. For the phylogenetic analysis using parsimony we employed T.N.T. Willi Hennig Society Edition (Goloboff *et al.* 2008). Tree searches were done with a driven new technology search, using 100 as the initial level. The strategy included sectorial searches, tree drift, and tree fusing (Goloboff 1999). The driven search was requested to hit the minimum length 500 times. Gaps were considered as a fifth state. Parsimony Jackknife estimation was performed as done with the implied alignment. Trees were edited with Winclada (Nixon 2002).

Maximum likelihood analyses were performed on the static alignment with 16 partitions (see Appendix S3). All partitions were analyzed simultaneously and unlinked, and model parameters were optimized during tree search. We used the program jModeltest 1.0 (Posada 2008) under ML to select the model of nucleotide evolution for each partition according to the Akaike Information Criterion (Akaike

1974). Maximum likelihood analyses were performed in Garli 2.0 (Zwickl 2006; available at http://www.nescent.org/informatics/download.php?software_id=4). The following parameters values differ from default conditions and were modified to improve tree search intensity following Zwickl (2006): 5,000,000 generations each replicate (stopgen = 5,000,000), with random starting addition (streefname = random), 677 attachment per taxon (attachmentspertaxon = 677), a threshold of 40,000 generations without topology improvement for termination (genthreshfortopoterm = 40,000), and a threshold of 30 for the maximum number of branches away from its original location for a branch to be reattached during subtree pruning and regrafitting (limsprrange = 30). We did a total of 100 independent searches to reduce the probability of inferring a suboptimal likelihood solution. Node support was assessed by 1000 bootstrap pseudoreplicates under the same search conditions explained above. Sequence variation of the static alignment of 551characters of 16S gene, corresponding to the most used DNA barcode in amphibians (e.g. Vieites *et al.* 2009; Crawford *et al.* 2010) was assessed with uncorrected proportional distances (p-distances) calculated in PAUP* 4.0b10 (Swofford 2002).

Inferences on species numbers

We consider a species as the single lineage segment of ancestor-descendant populations or metapopulations delimited by one splitting event. Under this theoretical perspective, species exist and evolve regardless of our ability to discover them, and are discoverable to the degree that footprints of their evolutionary history allow us to infer their existence (Ghiselin 1975; Wiley 1978; Hull 1976; Frost & Kluge 1994). We used two criteria to infer the existence of distinct species using DNA data and to guide the recognition of candidate species: monophyly and genetic distances. Reciprocal monophyly supported by the congruent phylogenetic optimization of neutral and unlinked molecular character states can be considered evidence of species divergence (e.g. Vences & Wake 2007), since the recovered congruent pattern will reflect the shared history of gene genealogies among populations (the species history) rather than the history of particular gene genealogies (gene trees)

(Avise & Ball 1990; reviewed by Sites & Marshall 2004). In addition, fixed diagnostic traits across populations are indicative of lineage divergence, since character fixation across populations requires limited or absent gene flow (see review by Padial *et al.* 2010). Therefore, reciprocally monophyletic groups recovered by the total evidence analysis of DNA sequences, and for which distinct phenotypic characters have been described, are herein considered distinct species. Paraphyly of species inferred by total evidence analyses of DNA sequences that, yet, include morphologically distinct groups, is considered indicative of the presence of more than one species. The second criterion, based on genetic divergences, assumes that genetic divergence among populations within a species tends to be relatively small because of gene flow, whereas divergence among species increases with time due to lack of gene flow (reviewed by Avise 2000). When large gaps in genetic divergences were detected between populations of the same nominal species, morphological and behavioural evidence was revised in order to determine if genetic divergences were indicative of otherwise overlooked divergence in phenotypic traits and hence, of the presence of unnamed species. However, for the reasons exposed by Padial *et al.* (2009) and Padial & De la Riva (2010), we refrain from using thresholds of genetic divergences to avoid creating artificially established species (or candidate species) numbers.

Results

Phylogenetic relationships

The combined dataset included 338 terminals and 6134 aligned characters (Clustal-W alignment), of which 3509 were constant, 533 were variable but parsimony uninformative, and 2092 were parsimony informative. No ambiguously aligned regions were detected (Data deposited in the Dryad Repository http://dx.doi.org/10.5061/dryad.j04vf). Models of sequence evolution for each partition used in the ML analyses are in Appendix S3.

All optimality criteria produced quite similar results and no strongly supported conflicting topologies were recovered (Figs. 3.5.1–4, Appendices S5–S6). Maximum parsimony with direct optimization recovered four most parsimonious trees (length = 12865), see Figs. 3.5.1–4. For the static alignment, the MP new technology search hit 500 times the best length. It recovered 4232 most parsimonious trees (MPT length = 13254), see Appendix S6. Further TBR revealed that there were more MPT (>10000), but successive strict consensus converged on the same topology as that obtained with the initial 4232 MPTs, and so we considered that further effort to find equally parsimonious trees was unnecessary (Goloboff 1999). The ML analysis recovered one tree with ln Likelihood = -54492.326409. Most of the conflict among the most parsimonious trees (both from dynamic and static alignments) and the ML analysis occurs among shallow clades of closely related terminals of *Osteocephalus,* and among the poorly supported relationships between the five major clades that we recognize in this paper as species groups of *Osteocephalus*.

Relationships among outgroups (not shown in Fig. 3.5.1; see Appendix S5 and S6) differ from previous analyses (Faivovich *et al.* 2005; Moen & Wiens 2009; Wiens *et al.* 2006, 2010). However, outgroup relationships in general are poorly supported. This analysis has not been designed (in terms of character and taxon sampling) to assess internal relationships of Lophyohylini and the results involving them should not be interpreted as a test of previous hypotheses.

The strict consensus of the best hypotheses indicates that *Osteocephalus* and *Tepuihyla* as currently defined are paraphyletic. The most basal clade in the ingroup (Fig. 3.5.1) includes species of *Tepuihyla*, the Guiana Shield species of *Osteocephalus* (*O. exophthalmus* and *O. phasmatus*), and "*Hyla" warreni*. This clade is the sister taxon of a clade composed of *O. pearsoni* and a candidate species from Amazonian Brazil (see below) plus a clade composed of all remaining species of *Osteocephalus* (Figs. 1–4). To remediate the paraphyly of *Osteocephalus* and *Tepuihyla*, we transfer *O. exophthalmus*, and *O. phasmatus* to *Tepuihyla* and "*Hyla warreni*" is placed in *Tepuihyla* (see Systematics section).

The bulk of species of *Osteocephalus* are divided into five main clades: (1) a clade including *O. taurinus*, *O. oophagus* and five candidate species, that we call the *O. taurinus* Species Group (Fig. 3.5.2); (2) a clade composed of *O. alboguttatus*, *O. heyeri*, and *O. subtilis*, that we call the *O. alboguttatus* Species Group (Fig. 3.5.3); (3) a clade composed of *O. leprieurii*, *O. yasuni*, and two candidate species that we call the *O. leprieurii* Species Group (Fig. 3.5.3) (4) a clade composed of *O. castaneicola*,

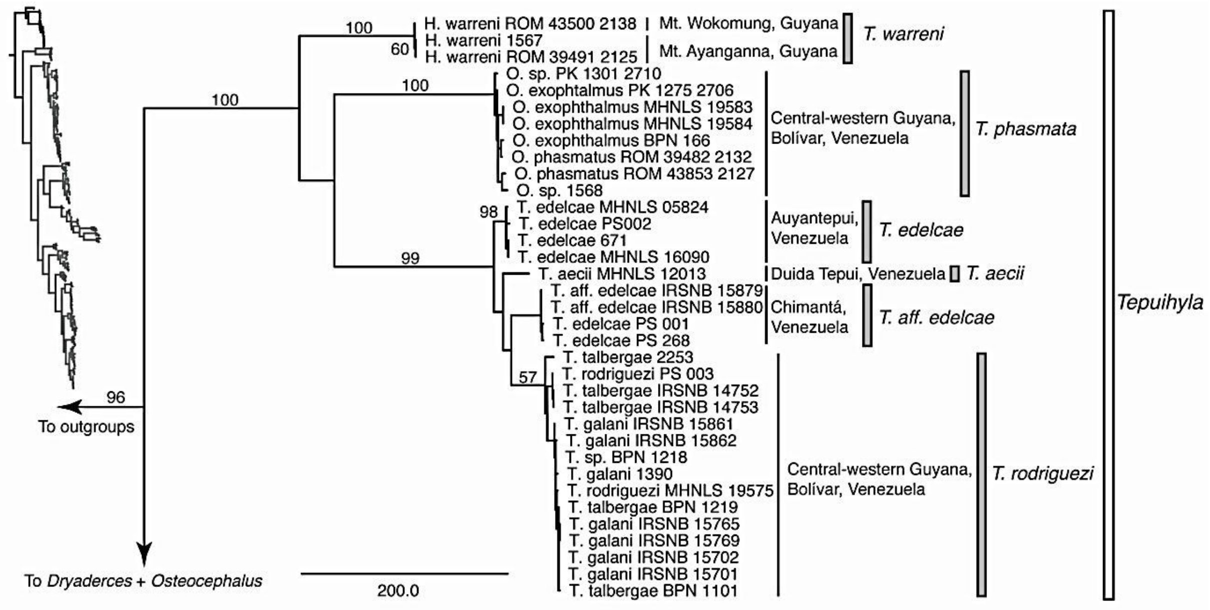

Figure 3.5.1. Phylogenetic relationships of *Osteocephalus* and *Tepuihyla* inferred from maximum parsimony analysis under dynamic homology in the program POY4.1.1. This topology reflects one of the four most parsimonious trees (length 12865 steps) with branch lengths proportional to the number of unambiguous transformations and black dots on nodes indicate clades collapsed in the strict consensus tree; not all loci are available for all terminals. For brevity the outgrous are not shown. Their relationships are identical to those shown in Appendix S5 for the static parsimony analysis. The taxonomy proposed in this work and distribution of clades mentioned in the main text is shown. Numbers on branches are parsimony jackknife absolute frequencies calculated for the static parsimony analysis and shown only for nodes in common between optimal trees of both analyses. A skeletal topology for reference, with the magnified section marked in black, is shown on the left side.

O. deridens, *O. fuscifacies*, *O. leoniae*, *O. planiceps*, and a candidate species, that we call the *O. planiceps* Species Group (Fig. 3.5.3); and (5) a clade composed of *O. buckleyi*, *O. cabrerai*, *O. cannatellai*, *O. helenae*, *O. mimeticus*, *O. mutabor*, *O. verruciger*, and one candidate species, that we call the *O. buckleyi* Species Group (Fig. 3.5.4). Each of these five clades is in general well supported, but the

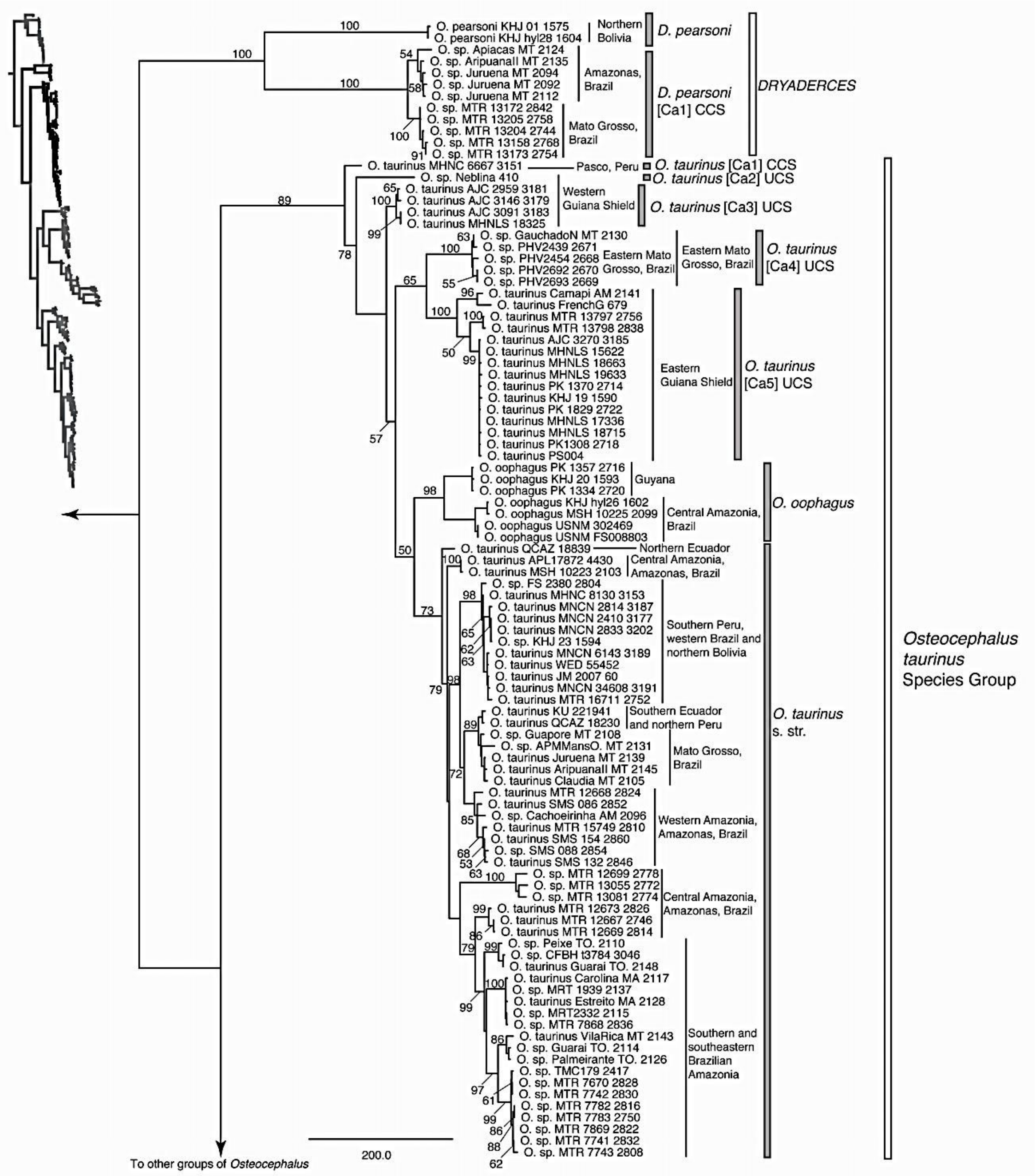

Figure 3.5.2. Continuation of the phylogenetic tree of Fig. 3.5.1. Phylogenetic relationships of *Dryaderces* gen. n. and the *Osteocephalus taurinus* Species Group. For details see Fig. 3.5.1.

relationships among most of them received poor support (Figs. 3.5.1–4, Appendix S5, S6). Furthermore, in both the static parsimony and ML analyses the relationships

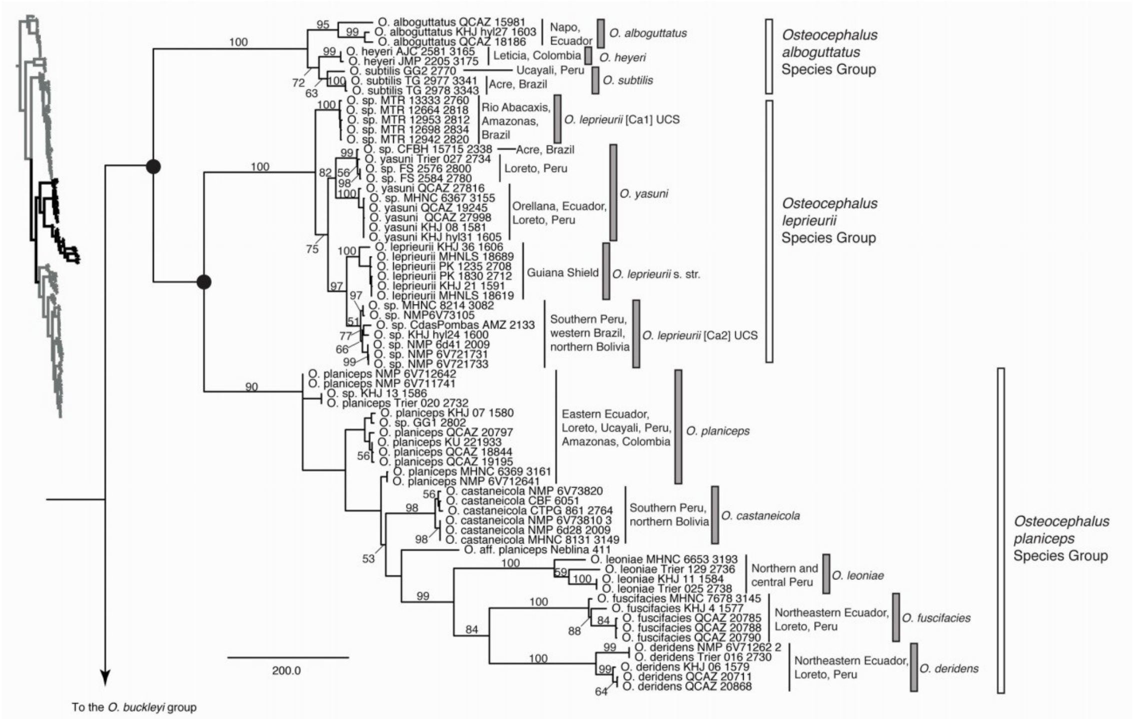

Figure 3.5.3. Continuation of the phylogenetic tree of Fig. 3.5.1. Phylogenetic relationships of the *Osteocephalus alboguttatus, O. leprieurii* and *O. planiceps* species groups. For details see Fig. 3.5.1.

among these clades differ from that obtained in the dynamic homology analysis. The *O. alboguttatus* Group is the sister taxon of all other species groups of *Osteocephalus,* while in the latter analysis this is one of the possible positions, the other being the sister taxon of the *O. planiceps* Group. In the three analyses the alternative positions of the *O. alboguttatus* Group is poorly supported. We also observed that in most cases clades received higher node support in the ML analysis. This should be interpreted with caution because several recent studies have reported a patological inflation of bootstrap values in ML analyses (Simmons & Freudenstein 2011; Simmons 2012; Simmons & Norton 2013 and references therein). See Systematics section for definitions and diagnoses of these groups.

Species diversity

Non-monophyly of nominal species was inferred for *O. buckleyi*, *O. leprieurii*, *O. planiceps*, *O. taurinus* and most likely for *O. mutabor* (Figs. 3.5.2–4). Several geographically restricted and well-supported lineages were inferred within *O. taurinus*, *O. buckleyi* and *O. leprieurii*, which are the most widely distributed nominal taxa in the Amazon Basin. Specimens identified as *O. planiceps* were recovered as a monophyletic group, although without support in the ML analysis (Appendix S5), but as a paraphyletic group with respect to *O. castaneicola*, *O. deridens*, *O. fuscifacies*, and *O. leoniae* in the maximum parsimony trees (Fig. 3.5.3, Appendix S6).

Within species placed in *Tepuihyla* (Fig. 3.5.1), "*Hyla warreni*" samples are monophyletic. Samples of "*O. phasmatus*" from Mt. Ayanganna and Mt. Wokomung in Guyana cluster together, and are sister to "*O. exophthalmus*" from Kaieteur, Guyana. Interspecific genetic divergences ranged from 0.0–0.2% between "*O. exophthalmus*" and "*O. phasmatus*", to 6.1–6.2% between "*Hyla warren*" and "*O. phasmatus*". Sequence divergence between *T. edelcae* and *T. galani*, was 0.9%. The 16S barcode fragment was missing for *T. talbergae* in this study, but Kok *et al.* (2012) found a sequence divergence ranging from 0.0–0.7% between different and geographically distant populations (some from different tepui summits) of *T. galani*, *T. rodriguezi* and *T. talbergae* , although no taxonomic decision was taken. The same authors found relatively low sequence divergence (0.9–1.6%) between populations of the *T. galani*/*rodriguezi*/*talbergae* clade and *T. edelcae* from its type locality (Auyantepui, Bolívar, Venezuela) and found *T. edelcae* to be non-monophyletic suggesting that specimens previously identified as *T. edelcae* from the Chimantá Massif (Bolívar, Venezuela) belong to a distinct, unnamed species (*T.* aff. *edelcae*).

Two samples of *Osteocephalus pearsoni* from near the type locality in northern Bolivia cluster together, and are sister to a highly supported monophyletic lineage from Mato Grosso and Amazonas (Brazil) (Fig. 3.5.2), which is morphologically distinct, and show large genetic divergences with respect to *O. pearsoni* (3.9–4.2%). This lineage is considered a CCS and is referred here to as *O. pearsoni* [Ca1_MTR13158_2768]. Within this lineage, two distinct geographically restricted

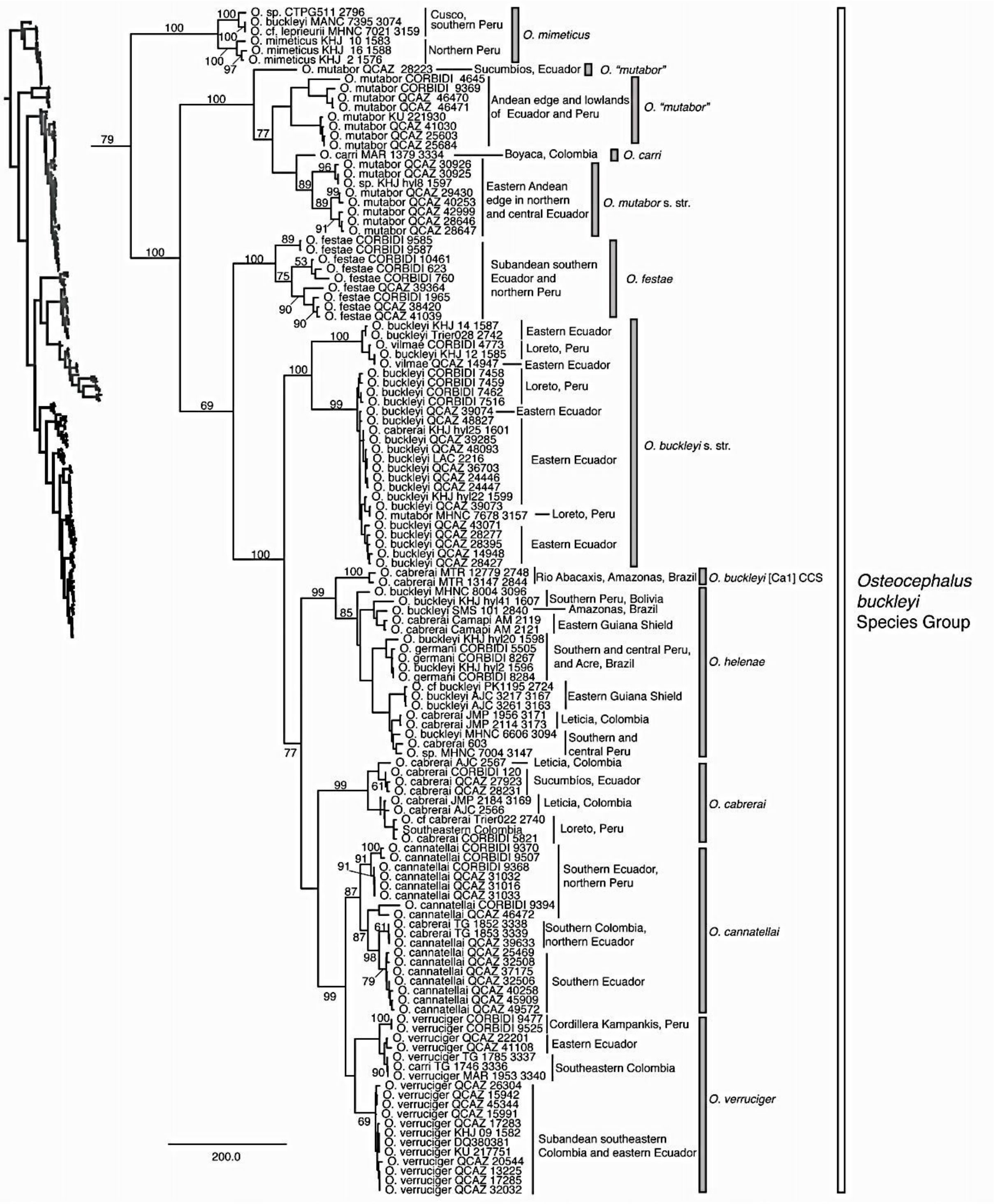

Figure 3.5.4. Continuation of the phylogenetic tree of Fig. 3.5.1. Phylogenetic relationships of the *Osteocephalus buckleyi* Species Group. For details see Fig. 3.5.1.

clades are recovered (Mato Grosso and Amazonas), showing genetic divergences of 2.0%.

Within the *O. alboguttatus* Species Group, the three species were all monophyletic (although with low support for *O. subtilis* in the MP trees). Genetic divergences are 4.2% between *O. alboguttatus* and *O. heyeri*, 3.1% between *O. alboguttatus* and O. *subtilis*, and 1.8% between *O. subtilis* and *O. heyeri*. No candidate species are proposed for this group. Within the *O. taurinus* Species Group (Fig. 3.5.2), *O. taurinus* is found paraphyletic with respect to *O. oophagus*. Samples from the type locality of *O. oophagus* from Reserva Ducke in central Amazonia cluster together and are sister to a clade containing samples from the eastern Guiana Shield, with genetic divergences among populations reaching 2.0%. The genetic structuring of *O. taurinus*, and its paraphyly with respect to *O. oophagus*—an easily distinguishable species with single vocal sac and breeding in bromeliads in contrast to the paired lateral sacs and pond breeding of nominal *O. taurinus* and allies (Appendix S9, S10)—suggest the existence of unnamed species within this species group. Interestingly, despite large morphological divergences, genetic distances between these two species range between 0.9–2.2%, overlapping with the range of their respective intraspecific divergences (Appendix S4a). These results support bioacoustical data suggesting the existence of multiple species-level lineages within nominal *O. taurinus* (De la Riva *et al.* 1995). However, analyses of call data are hampered by misidentifications, e.g. by Duellman & Lescure (1973) and Schlüter (1979) with *O. planiceps*. On the basis of phylogenetic position (Fig. 3.5.2) and genetic divergences, we flag five candidate species for four geographically restricted and supported clades within the large clade including nominal *O. taurinus* and *O. oophagus*.

The type locality of *O. taurinus* is “Barra do Rio Negro”, an old name for Manaus, in central Amazonia. Therefore, we consider our sample from Conjunto Pedro, a central-western urban district of Manaus close to the ancient Barra do Rio Negro, as nominal *O. taurinus*, and refer to it as *O. taurinus sensu stricto* (s. str. hereafter). *Osteocephalus taurinus* [Ca1_MHNC6667_3151] from Pasco, Central Peru, represents a lineage that is basal to all other lineages within *O. taurinus* and *O. oophagus*. Genetic divergences (Appendix S4a) range between 1.5–2.2% and 2.1–2.6% with respect to *O. taurinus* s. str. and *O. oophagus*, respectively. This Central

Peruvian lineage is considered herein as a CCS for being basal to all other lineages in the *O. taurinus* Group. *Osteocephalus taurinus* [Ca2_Neblina410] from Cerro de la Neblina (the southern tip of Venezuela bordering Brazil) shows genetic divergences of 0.9–1.8 and 2.0–2.2 with respect to *O. taurinus* s. str. and *O. oophagus*, respectively. This species is recovered in the ML tree as sister to *O. taurinus* [Ca3_AJC2959_3181] from the western lowlands of the Guiana Shield, but as sister to all *O. taurinus* and *O. oophagus* included in the analyses but *Osteocephalus taurinus* [Ca1_MHNC6667_3151] in the MP trees. Due to incomplete evidence and uncertain phylogenetic position we consider it a UCS. The three other candidate species within *O. taurinus* are considered UCSs. Although there is some morphological evidence suggesting that they may be different species (pers. obs. KHJ), evidence at hand is still fragmentary and we refrain from proposing them as CCS at this time (see Discussion for details of an analysis of available morphological evidence). *Osteocephalus taurinus* [Ca3_AJC2959_3181] is endemic to the lowlands of the western portion of the Guiana Shield in Venezuela. Genetic divergences range between 0.9–2.2% and 1.8–2.6% with respect to *O. taurinus* s. str. and *O. oophagus*, respectively. *Osteocephalus taurinus* [Ca4_PHV2439_2671] is restricted to eastern Mato Grosso (Brazil). Genetic divergences range between 1.1–2.2% and 2.2–2.8% with respect to *O. taurinus* s. str. and *O. oophagus*, respectively. It is sister to *O. taurinus* [Ca5_SMNS12063] from the eastern Guiana Shield, east of the Sierra de Maigualida. Both lineages are allopatric, showing genetic divergences between 1.3–2.2%, and intervening areas are occupied by *O. taurinus* s. str. *Osteocephalus taurinus* [Ca5_SMNS12063] shows genetic divergences between 1.1–2.6% and 1.3–3.1% with respect to *O. taurinus* s. str. and *O. oophagus*, respectively. Interestingly, this lineage is not sister to *O. taurinus* [Ca3_AJC2959_3181], the other Guiana Shield lineage, inhabiting the area west of the Sierra de Maigualida, but to *O. taurinus* [Ca4_PHV2439_2671] from eastern Mato Grosso.

Osteocephalus taurinus s. str. shows variable interpopulational genetic divergences (0.0–1.7%) partially associated with particular geographic regions (Fig. 3.5.2), although haplotypes from central Amazonia are intermixed with haplotypes of other geographic areas. One of the main clades within *O. taurinus* s. str. contains haplotypes from eastern Brazilian Amazonia in the states of Amazonas, Mato Grosso, Tocantins, Piauí and Maranhão. Members of this lineage occur in sympatry or almost so with two other haplotypes from central Amazonia grouped under other lineages, both from Amazonas, Brazil. Likewise, members of a lineage from the central-western Amazon Basin in Amazonas, Brazil, occur in sympatry with a relatively densely sampled lineage occurring in southern Peru, northern Bolivia and north-westward to the Rio Purus, Brazil. The northernmost lineage, represented by a single specimen from the Cordillera del Cóndor, southern Ecuador (Ron *et al.* 2010), occurs at an unusually high elevation (940 m). Poor resolution of relationships among phylo-groups nonetheless hampers a detailed phylogeographic interpretation.

Nominal species within the *O. planiceps* Species Group are inferred as monophyletic except *O. planiceps* (Fig. 3.5.3). *Osteocephalus planiceps* is retrieved as non-monophyletic in MP analyses, but as monophyletic in ML (Fig. 3.5.3, Appendices S5–S6). Neither of those analyses shows high support values for their respective topologies. Given the relative homogeneity of the habitat, the clustering of samples of *O. planiceps* from near its type locality in Loreto (Peru) with other samples from nearby areas of Colombia, Ecuador and Peru, the low resolution of the trees, the relatively low and greatly overlapping genetic distances (0.0–1.3%, Appendix S4b) between the MP clades of *O. planiceps* and, to the best of our knowledge, the absence of phenotypic data supporting the split of this lineage, we prefer to maintain *O. planiceps* as a single nominal species until more evidence is collected. Samples from the type locality of *O. castaneicola* in northern Bolivia cluster with other samples from the area and with samples from Madre de Dios in southern Peru. Samples of *O. leoniae* from near the type locality in Pasco, northern Peru, cluster with other samples from San Martín and Amazonas in north-western Peru. Samples of *O. deridens* from the lowlands of Ecuador near the type locality cluster with samples from adjacent Loreto in Peru. Samples from the type locality of *O. fuscifascies* cluster with samples from nearby areas in Ecuador and adjacent Peru. A divergent lineage from the western Guiana Shield (from the Cerro de la Neblina area), does not cluster with any of the nominal species. We consider this lineage as a CCS due to its basal position to three supported nominal species, and refer to it as *O. planiceps* [Ca1_Neblina411]. Genetic divergences among this lineage and other nominal species in the *O. planiceps* Group range between 2.6–5.9%, while intraspecific genetic divergences within species of the group range between 0.0–4.0% (Appendix S4b).

Within the *O. leprieurii* Species Group, *O. leprieurii* is paraphyletic with respect to *O. yasuni* (Fig. 3.5.3). Samples of *O. leprieurii* from the eastern Guiana Shield in Guyana cluster together and are considered herein as representative for the type locality (Cayenne, French Guiana), and as *O. leprieurii* s. str. Samples of *O. yasuni* from the type locality in Orellana, Ecuador, cluster together with a sample from adjacent Loreto, Peru and are sister to a clade containing samples from western Amazonia in Acre, Brazil and Loreto, Peru. Genetic divergences between *O. leprieurii* s. str. and *O. yasuni* range between 0.7–1.8%, while intraspecific divergences in the *O. leprieurii* Group range between 0.7–2.0%, taking into account the candidate species proposed below (Appendix S4c). Nonetheless, since O. *leprieurii* s. str. and *O. yasuni* are morphologically distinct (Ron & Pramuk 1999), we interpret the paraphyly of *O. leprieurii* as indicative of the putative existence of multiple unrecovered species-level lineages. A lineage composed of samples from Rio Abacaxis in Amazonas, Brazil, is inferred as basal to the lineage including *O. leprieurii* s. str. and *O. yasuni*. Due to its basal position, allopatry, and genetic divergences with respect to *O. leprieurii* s. str. and *O. yasuni* (1.7–1.8% and 0.9–1.3%, respectively) we consider this lineage as a UCS pending additional evidence, and refer to it as *O. leprieurii* [Ca1_MTR12698_2834]. A second well-supported lineage is sister to *O. leprieurii* s. str. This lineage contains samples from eastern Bolivia, northern Bolivia, southern Peru and adjacent Brazil, and is allopatric to *O. leprieurii*. Both lineages show genetic divergences between 0.9–1.8%. Published morphological data are not available and despite the large geographical gap between nominal *O. leprieurii* and this clade, we prefer to consider it a UCS pending further research. We refer to this lineage as *O. leprieurii* [Ca2_NMP6d41/2009].

Four of the nominal species included in the *O. buckleyi* Species Group, *O. cabrerai*, *O. festae*, *O. mimeticus*, and *O. verruciger*, are monophyletic and well-supported (Fig. 3.5.4). Interspecific genetic distances within this clade are the highest recorded within *Osteocephalus* (Appendix S4d), up to 6.1% between *O. helenae* and *O. mimeticus*. Samples of *O. mimeticus* from near the type locality in San Martín, Peru, group with other samples from the Amazonian foothills of the Andes in San Martín and Huánuco, Peru. Three samples from Cusco, in southern Peru, cluster together and are sister to topotypic and Huánuco samples. A large geographic distance and large genetic divergences (2.8%) separate these two clades. Nonetheless, given the lack of samples from intervening areas and the morphological similarity of specimens from both areas we refrain from flagging any candidate species within *O. mimeticus*. Samples of *O. festae* from northern Peru and Ecuador included in this analysis are those used by Ron *et al*. (2010). This lineage is morphologically distinct from other members in the group. Unfortunately, sequences of the 16S barcode were not available for representatives of this lineage.

A sample of *O. mutabor* from the type locality at Volcan Sumaco, Ecuador, clusters together with samples from Napo, Orellana and Pastaza in Ecuador. We refer to this clade as *O. mutabor* s. str. There are several more lineages phenetically referable to *O. mutabor* distributed from northern Ecuador to northern Peru along the Andean edge and adjacent lowlands (Appendix S8.3b). Surprisingly, one of them is sister to *O. carri*, (Fig. 3.5.4) rendering several lineages of "*O. mutabor*" outside the clade including sequences of topotypes. Although we clearly identified a picture of the specimen of *O. carri* used here from Boyacá, Colombia as belonging to that species, we consider it premature to postulate several candidate species of *O. mutabor*, but rather refer to them as "*O. mutabor*" in the trees and the map until additional material is available to us.

Unfortunately, sequences of the 16S barcode were only available for representatives of *O. mutabor* s. str. and *O. carri;* these show a genetic divergence of 2.6% (Appendix S4d).

The type locality of *Osteocephalus buckleyi* is Canelos, Ecuador. Multiple samples assignable to *O. buckleyi* from the lowlands of Ecuador and adjacent Peru group together in a well-supported clade that we consider here as nominal *O. buckleyi* and refer to it as *O. buckleyi* s. str. This clade shows genetic divergences ranging between 0.0–1.5%, and is subdivided in two well-supported subclades sharing haplotypes from the same regions. One of these subclades is considered a distinct species by Ron *et al.* (2012). We do not follow their taxonomic arrangement for reasons given in the Appendix. Recognizing this clade as nominal *O. buckleyi* leaves a large and well-supported clade, which is part of the more inclusive clade containing *O. buckleyi* s. str., *O. cabrerai*, *O. cannatellai*, and *O. verruciger.* This clade includes samples from the eastern Guiana Shield (Guyana, Delta Amacuro in Venezuela and Amapá in Brazil) across central Amazonia in Brazil and eastern Colombia, to south-western Amazonia in Acre (Brazil), Cusco (Peru) and the southern limit of Amazonia at Mataracú (Santa Cruz, Bolivia). Intra-lineage divergences are high among geographically restricted lineages (up to 2.6%), but absence of sufficient phenotypic information from parts of its range and the presence of shared haplotypes among distant populations prevent us from recognizing more than two species. Two samples from the Abacaxis River south of the Amazon River in Amazonas, Brazil, are basal to a larger and well-supported subclade including samples from all other areas. We consider the Abacaxis population as a distinct candidate species, *O. buckleyi* [Ca1_MTR12779_2748] with morphological characters sufficient to consider it a CCS. The relationships of geographically restricted lineages within the other subclade are not resolved. However, some interesting patterns are observable. Samples from Amazonian Colombia cluster with distant samples from southern Peru and Acre. Also, samples from the Guiana Shield (Amapá, Delta Amacuro) cluster together, although support for this relationship is low (Fig. 3.5.4). For the time being and given the evidence at hand, we consider this whole subclade as a single species referred here to *O. helenae* nov. comb.

A sample of *Osteocephalus cabrerai* from south-eastern Colombia, the one closest to the type locality on the Río Apapóris, clusters with samples from adjacent Loreto, Peru, and Sucumbíos, Ecuador (Fig. 3.5.4), and shows no genetic divergences. We consider this well-supported lineage as nominal *O. cabrerai*.

The type locality of *Osteocephalus verruciger* is “Ecuador”. Multiple samples from Ecuador assigned to this taxon cluster together in a well-supported clade (Fig. 3.5.4) that is subdivided into four main subclades showing large variation in genetic divergences (0.0–1.7%).

Systematics

On the basis of our results we provide a new monophyletic taxonomy where we redefine *Osteocephalus* and *Tepuihyla* and describe a new genus for *Osteocephalus pearsoni* and an unnamed species considered here as CCS. Additionally, we comment on the species diversity of these genera, propose and define five species groups within *Osteocephalus*, and discuss the distribution and taxonomic situation of species and candidate species in these groups.

Genus *Dryaderces* gen. n.

Type species. *Hyla pearsoni* Gaige, 1929, by original designation.

Diagnosis. No phenotypic synapomorphies are known for this genus. A number of molecular synapomorphies are listed in Appendix S7. *Dryaderces* species differ from most *Osteocephalus* in sexual dimorphism of dorsal skin structure. Albeit being pond breeders (pers. obs. SR), males have only scattered non-spinous tubercles on the dorsum (heavily tuberculate dorsa and tips of tubercles keratinized in pond breeding *Osteocephalus*). Females have smoother backs. Recently metamorphosed juveniles of *D. pearsoni* are coloured like the adults and lack the juvenile coloration typical of *Osteocephalus* (see below and Appendix S1). Frogs in the genus *Dryaderces* are medium-sized with males attaining snout–vent lengths of 43–50 mm and females 53–68 mm. Odontophores are oblique to angular. The distal subarticular tubercle on Finger IV is single to bifid. Posterior surfaces of thighs are mottled. The iris of adults is a deep dark reddish brown or light with fine dark venation and a broad dark horizontal band.

Content. One described species, *Dryaderces pearsoni* (Gaige, 1929) new combination. A second species from Brazilian Amazonia is currently being described.

Etymology. A noun of feminine gender derived from Ancient Greek *dryad* (tree) and *aderces* (unseen, invisible) in the sense of “unseen in a tree”.

Distribution. Lowlands of the states of Amazonas and Mato Grosso, Brazil, south of the Amazon to northern La Paz, Bolivia (Appendix S8.1).

Remarks. The only described species has its type locality on the upper Río Beni below the mouth of Río Mapiri, Beni, Bolivia (Gaige 1929) and was originally placed in *Hyla* until Goin (1961) removed it and placed it in *Osteocephalus*. In their review of the genus, Trueb & Duellman (1971) used (and illustrated) one specimen of *O. mimeticus* among *O. pearsoni* (Jungfer 2011). Subsequent reports might therefore include misidentifications as well. A picture of an adult is found in De la Riva *et al.* (2000) and Padial *et al.* (2000).

Genus *Osteocephalus*

Osteocephalus Fitzinger, 1843 (nomen nudum)

Osteocephalus Steindachner, 1862

Type species: *Osteocephalus taurinus* Steindachner, 1862, by subsequent designation of Kellog (1932).

Diagnosis. The only known putative phenotypic synapomorphy of *Osteocephalus* is the distinctive juvenile colouration (see discussion below and Appendix S1). A number of molecular synapomorphies are listed in Appendix S7.

Content. Twenty-four species: *Osteocephalus alboguttatus* (Boulenger, 1882), *O. buckleyi* (Boulenger, 1882), *O. cabrerai* (Cochran & Goin, 1970*), O. cannatellai* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012, *O. carri* (Cochran & Goin, 1970), *O. castaneicola* Moravec, Aparicio, Guerrero-Reinhard, Calderón, Jungfer & Gvoždík, 2009, *O. deridens* Jungfer, Ron, Seipp & Almendáriz, 2000, *Osteocephalus duellmani* Jungfer, 2011, *O. festae* (Peracca, 1904), *O. fuscifacies* Jungfer, Ron, Seipp & Almendáriz, 2000, *O. helenae* (Ruthven, 1919), *O. heyeri* Lynch, 2002, *O. inframaculatus* (Boulenger, 1882), *O. leoniae* Jungfer & Lehr, 2001, *O. leprieurii* (Duméril & Bibron, 1841), *O. mimeticus* (Melin, 1941), *O. mutabor* (Jungfer & Hödl, 2002), *O. oophagus* Jungfer & Schiesari, 1995, *O. planiceps* Cope, 1874, *O. subtilis* Martins & Cardoso, 1987, *O. taurinus* Steindachner, 1862, *O. vilarsi* (Melin, 1941), *O. yasuni* Ron & Pramuk, 1999, *O. verruciger* (Werner, 1901).

Osteocephalus vilmae Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012 is placed in the synonymy of *O. buckleyi* (Boulenger, 1882) (see Appendix) and *O. germani* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012 in the synonymy of *O. helenae* (Ruthven, 1919) nov. comb., a species previously not assigned to the genus (see Appendix).

Distribution. From coastal northern South America in Venezuela and the Guianas to the mouth of the Amazon and north-eastern Brazil (Piauí) in the East, to central Brazil (Mato Grosso) and central Bolivia in the south and to the eastern Andean slopes from Bolivia to Colombia up to about 2000 m a.s.l. (Appendix S8.2–8.6).

Remarks. Thirteen species of *Osteocephalus* for which data were available show a similar pattern in the colouration of juveniles that radically differs from adult colouration. Ten species share a red iris colour, white elbow and distal part of upper arm, small white knee spot and large white heel spot in juveniles. *Osteocephalus verruciger* and *O. buckleyi* lack the red iris (iris black and reddish golden, respectively) and *O. mutabor* lacks white markings on limbs (Appendix S1), but they all show a similar juvenile colour pattern that differs from that of adults. The *O. alboguttatus* Species Group is the only one of which we have not seen any recently metamorphosed juveniles. A photo, however, of a subadult *O. subtilis* taken by A. J. Cardoso and deposited at the Biodiversity Institute, University of Kansas, has the typical intermediate colouration with orange iris and black venation (uniform, deep dark brown in adults) and faded cream elbow, knee, and heel spot (absent in adults) that leaves no doubt that juveniles are coloured like the other *Osteocephalus* as described above. *Dryaderces pearsoni* differs from *Osteocephalus* in that it already exhibits adult colouration immediately after metamorphosis. Most other Lophyohylini also lack an ontogenetic colour change, e.g. *Aparasphenodon brunoi* (pers. obs. CFBH), *Argenteohyla siemersi* (D. Baldo, pers. com), *Itapotihyla langsdorffii* (Appendix S1), *Nyctimantis rugiceps*, *Osteopilus crucialis*, *O. wilderi* (pers. obs. KHJ), *Phyllodytes luteolus* (pers. obs. MTR), while in others juvenile patterns remain, but only slightly dissolve, as in *Trachycephalus hadroceps* (pers. obs. KHJ) and *T. resinifictrix* (Jungfer & Proy 1998). Juvenile *T. typhonius* are as polymorphic in colouration and pattern as their adult phases (pers. obs. KHJ). Distinctly deviating juvenile colourations are only known to us in *Trachycephalus jordani* (green with white dorsolateral and supralabial stripes, iris golden) and *Osteopilus ocellatus* (green, transversal bands on limbs, iris coppery red), both of which lack the light limb spots of *Osteocephalus*. In general, with respect to colouration, juveniles of most *Osteocephalus* species resemble one another more than their interspecific adult stages, so that we consider the juvenile colouration a synapomorphy of *Osteocephalus* sensu this work. With the exception of the *O. buckleyi* Group (Ron *et al.* 2012), species groups in *Osteocephalus* so far have not been recognized. According to the results of phylogenetic analyses and morphological data, we recognize five species groups within *Osteocephalus*; these are defined below.

Osteocephalus alboguttatus Species Group

Content. O. alboguttatus (Boulenger, 1882), *O. heyeri* Lynch, 2002, and *O. subtilis* Martins & Cardoso 1987.

Diagnosis. Males in this clade are small (< 40 mm snout–vent length) and females are medium sized (< 50 mm). The dorsum in males and females is smooth or, in males of *O. heyeri*, nearly so. Hand webbing is reduced or absent. Vocal sacs are subgular and single or slightly bilobed. Nuptial excrescences are present in breeding males. Information on breeding sites and reproduction is missing. Amplexus is axillary in *O. subtilis* and unknown in the other members of the group. Iris colouration is golden with irregular black reticulation, dark grey or deep dark brown in adults (Duellman 1978; Martins & Cardoso 1980; Lynch 2002).

Distribution. Osteocephalus alboguttatus is known from sites along the Andean edge in north-eastern Ecuador below 600 m in elevation (Almendáriz *et al.* 2004a); *O. heyeri* from the upper Amazon in Loreto, Peru and Amazonas, Colombia (Lynch 2002). *Osteocephalus subtilis* occurs in Acre, Brazil and adjacent Ucayali, Peru (Martins & Cardoso 1980; this study). See Appendix S8.2 for sampled localities.

Remarks. No morphological synapomorphies are known for this group. There is little variation within species in this group and the advertisement calls are unknown.

Osteocephalus buckleyi Species Group

Content. Osteocephalus buckleyi (Boulenger, 1882), *O. cabrerai* (Cochran & Goin, 1970), *O. cannatellai* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012, *O. carri* (Cochran & Goin, 1970), *O. festae* (Peracca, 1904), *O. helenae* (Ruthven, 1919), *O. mimeticus* (Melin, 1941), *O. mutabor* (Jungfer & Hödl, 2002), *O. verruciger* (Werner, 1901). *Osteocephalus duellmani* Jungfer, 2011 and *O. inframaculatus* (Boulenger, 1882) are also included tentatively here on the basis of their morphological similarity, as no synapomorphies involving adult morphology are known for the group, and no tissues of these two species were available for this study.

Diagnosis. Stream-breeding is a putative synapomorphy of this group. Reproduction is usually associated with streams in all species for which data are available, although we found *O. buckleyi* (pers. obs. GGU) and *O. mutabor* (pers. obs. KHJ) exceptionally breeding in stagnant pools of water. Dorsal skin texture in males varies from strongly tuberculate with tubercles bearing keratinized tips (e.g. in *O. verruciger*) to granulate (*O. duellmani*), while females are smoother. Vocal sacs are paired, situated laterally, with a subgular expansion (Appendix S9). Amplexus is axillary (Appendix S11). Nuptial pads are brown.

Distribution. As currently defined, *O. buckleyi* covers a huge area from the coastal Guianas to southern Venezuela, most of Amazonian Colombia, Ecuador and Peru and in the east from the mouth of the Amazon to Santa Cruz, Bolivia (La Marca *et al.* 2010a; Appendix S8.3a). However, *O. buckleyi* s. str. is restricted to Amazonian Ecuador and north-western Loreto, Peru (type locality restricted to Canelos, Provincia Pastaza, Ecuador by Trueb & Duellman 1971). *Osteocephalus festae* is known from montane sites from Morona Santiago, Ecuador to Amazonas and Cajamarca, Peru (Jungfer 2010 as *O.* sp., Ron *et al.* 2010). The CCS *O. buckleyi* [Ca1_MTR12779_2748] is known from a few sites along the Rio Abacaxis in Amazonas, Brazil, where it might occur in sympatry with *O. helenae*. The latter is a widely distributed species from the Delta Amacuro in Venezuela and the eastern Guiana Shield, through central Amazonia across Amapá, Amazonas, Acre, and Mato Grosso, Brazil, reaching the Andean foothills in central and northern Bolivia and southern and northern Peru.

Osteocephalus cabrerai has been reported from Amazonas, Colombia (Cochran & Goin 1970; Lynch 2002), Loreto and Ucayali, Peru (Jungfer 2010; Ron *et al.* 2012), Sucumbíos, Ecuador (Ron *et al.* 2011) and also from the Delta Amacuro and the Guiana Shield area in Venezuela, French Guiana and Amazonas, Brazil (Gorzula & Señaris "1998" [1999]; Lescure & Marty 2000; Lima *et al.* 2006 as *O. buckleyi*; Jungfer 2010; Menin *et al.* 2011). Frogs in this study are all from the upper Amazon in Sucumbíos, Ecuador, Amazonas, Colombia and Loreto, Peru (Appendix S8.3a).

Apart from *O. festae*, several species are known from the eastern Andean slopes and foothills (Appendix S8.3b): *O. carri* in Colombia (Cochran & Goin 1970; Lynch 2006; Jungfer 2010), *O. verruciger* in southern Colombia and northern Ecuador (Angulo *et al.* 2004) , *O. duellmani* from the Cordillera del Cóndor in Ecuador (Jungfer 2011), *O.*

mimeticus from San Martín southward to Cusco, Peru (Jungfer 2010). *Osteocephalus mutabor* occurs along the eastern Andean foothills of central and northern Ecuador, while phenetically similar frogs, here referred to as "*O. mutabor*" are known from lowland Amazonian Ecuador in Sucumbíos, Ecuador, the eastern Andean edge of southern Ecuador and northern Peru and adjacent lowlands as far east as the Iquitos and Leticia areas in Peru and Colombia (Jungfer *et al.* 2000; Ron *et al*. 2012; this study). *Osteocephalus inframaculatus* is known from the type locality, Santarem, Pará, Brazil on the Amazon River (Boulenger 1882; Jungfer 2010).

Remarks. As currently defined, *Osteocephalus buckleyi* is a widespread and largely polymorphic taxon. Jungfer (2010) included only specimens from north-western Amazonia for comparisons with related species to avoid confounding morphological characters without first assessing the possible existence of putative new species. Populations vary in degree of tuberculation and webbing, snout–vent length, especially in females, and other characters. Some populations are also difficult to distinguish from *O. cabrerai* despite a recent redescription of the latter (Jungfer 2010). La Marca *et al.* (2010a) assumed that *O. buckleyi* might be a complex of more than one species. Ron *et al.* (2012) attempted to resolve parts of this complex in Ecuador and Peru and described three new species, only one of which we consider valid: *Osteocephalus cannatellai* occurs in eastern Ecuador and north-eastern Peru. It also occurs in Caquetá, southern Colombia (this study). The second one, *O. germani*, is preoccupied by *O. helenae* (Ruthven, 1919). We do not recognize the third one, *O. vilmae*, as distinct from *O. buckleyi* for reasons given in the Appendix. Morphological characters of *O. cabrerai* are also polymorphic and partially overlap with those of *O. buckleyi*. Probably for this reason, specimens listed as *O. buckleyi* by Ron *et al.* (2010) were later used to report the first record of *O. cabrerai* for Ecuador by Ron *et al.* (2011) on the basis of molecular data. Jungfer (2010) also refrained from using material from north of the Amazon for a redescription of this species. The rest of species in this group, and those with more restricted distributions, are morphologically more uniform.

Osteocephalus leprieurii Species Group

Content. O. leprieurii (Duméril & Bibron, 1841) and *O. yasuni* Ron & Pramuk, 1999.

Diagnosis. Males and females in this clade are highly dimorphic in dorsal skin structure with females being smooth or bearing few low tubercles and males being heavily tuberculate. During breeding, tubercles bear keratinized tips. Keratinized excrescences, apart from the large dark brown nuptial pad, are also present on parts of the limbs, hands, feet and lower jaw in some populations of *O. leprieurii* (Jungfer & Hödl 2002). Vocal sacs are paired, lateral with subgular expansion (Appendix S9). Amplexus is axillary (Appendix S11). Both species are explosive breeders congregating at ponds or flooded areas. During that time males become yellow dorsally and light yellow ventrally (Ron & Pramuk 1999; Lescure & Marty 2000; Jungfer & Hödl 2002; Deichmann & Williamson 2007; Kok & Kalamandeen 2008). Irises of adult frogs in the *O. leprieurii* clade are golden to golden brown with fine irregular dark venation and a broad dark brown horizontal midline.

Distribution. As currently defined, *Osteocephalus leprieurii* is widely distributed from the Guianas and northern Venezuela to eastern Colombia, eastern Peru, northern Bolivia and the northern and eastern Brazilian Amazon including Amazonas and Amapá (La Marca *et al.* 2010c; this study).The nominal species s. str. occurs in the Guianas and southern Venezuela (Appendix S8.4); its type locality is “Cayenne”, French Guiana. The UCS *Osteocephalus leprieurii* [Ca1_MTR12698_2834] occurs allopatrically from *O. leprieurii* s. str. in Brazilian central Amazonia. Our samples are from three localities on the Rio Abacaxis (Appendix S8.4), but there are also specimens from further south-east in Pará, Brazil. The UCS *O. leprieurii* [Ca2_NMP6d41/2009] has long been considered a distinct unnamed species occurring in northern Bolivia and south-western Amazonas, Brazil, apparently in allopatry from all other lineages within the *O. leprieurii* Group. *Osteocephalus yasuni* is known from lowland sites in north-eastern Ecuador, northern Peru, Acre, Brazil, and north of the Amazon in Amazonas, Colombia (Ron & Pramuk 1999; Lynch 2002; this study). Sampled localities are shown in Appendix S8.4.

Remarks. No morphological synapomorphies are known for this group. *Osteocephalus leprieurii* is a polymorphic species with considerable variation especially in snout–vent length, colouration and degree of keratinized structures in breeding males. The advertisement calls of this species are highly complex and not as stereotyped as in most frogs (Jungfer & Hödl 2002), making bioacoustic comparisons among populations difficult. That *O. leprieurii* might be a composite of several species has already been hypothesized by Jungfer & Hödl (2002) and Moravec *et al.* (2009). The latter authors also presented some molecular evidence to support this.

Osteocephalus planiceps Species Group

Content. Osteocephalus castaneicola Moravec, Aparicio, Guerrero-Reinhard, Calderón, Jungfer & Gvoždík, 2009, *O. deridens* Jungfer, Ron, Seipp & Almendáriz, 2000, *O. fuscifacies* Jungfer, Ron, Seipp & Almendáriz, 2000, *O. leoniae* Jungfer & Lehr, 2001, and *O. planiceps* Cope, 1874.

Diagnosis. Phytotelm breeding (see below) and a single, subgular vocal sac are putative synapomorphies of this group. All species in this clade breed in phytotelmata such as leaf axils, fruit capsules, bamboo and tree holes (Jungfer *et al.* 2000; Moravec *et al.* 2009; pers. obs. KHJ). Except for *O. planiceps*, dorsal skin is not sexually dimorphic and more or less smooth in both sexes. Breeding males identified as *O. planiceps* vary from tuberculate to almost smooth. Nuptial excrescences in breeding males are dark brown (*O. planiceps*), light brown (*O. castaneicola*), or white (*O. deridens*, *O. fuscifacies*, *O. leoniae*). The vocal sac is white, single and subgular. Amplexus is axillary or gular (Appendix S11).

Distribution. Sampled localities are in Appendix S8.5. *Osteocephalus planiceps* has a wide distribution in the western Amazon Basin from Meta in south-western Colombia through Ecuador to Madre de Dios in south-western Peru (Lehr 2001; Lynch 2008; this study). There is also a record from the central Amazon in Amazonas, Brazil (Gordo & Neckel-Oliveira 2004). The other species have smaller ranges. *Osteocephalus castaneicola* occurs in Pando, Bolivia and adjacent Madre de Dios, Peru (Moravec *et al.* 2009); *O. deridens* ranges from north-eastern Ecuador, south-eastward through northern Loreto, Peru, to the Leticia area, Amazonas, Colombia and adjacent Amazonas, Brazil (Moravec *et al.* 2002; Almendáriz 2004b; this study).

Osteocephalus fuscifacies is known from north-eastern Ecuador in Orellana, Sucumbíos and Napo, and adjacent Loreto, Peru (Jungfer *et al.* 2000; this study). *Osteocephalus leoniae* occurs from the Rio Marañon area in Amazonas, Peru southward to Cusco, Peru (Jungfer & Lehr 2001; Chávez *et al.* 2008; this study). An allopatric population from the western Guiana Shield is considered herein a CCS (*O. planiceps* [Ca1_Neblina411]).

Remarks. There is little morphological variation in those species with small ranges. *Osteocephalus planiceps*, however, exhibits considerable variation in snout–vent length, dorsal skin structure in breeding males, and call structure (Duellman & Lescure 1973 as *O. taurinus*; Schlüter 1979 as *O. leprieurii*; pers. obs. KHJ). The latter may be due to variation in types of calls or the presence of cryptic species.

Osteocephalus taurinus Species Group

Content. Osteocephalus oophagus Jungfer & Schiesari, 1995, *O. taurinus* Steindachner, 1862, and *O. vilarsi* (Melin, 1941). The latter is tentatively associated with this group because of its close external similarity with *O. taurinus* (Jungfer 2010).

Diagnosis. Frogs in the group are medium-sized to large with frontoparietal ridges variably present (extremely pronounced to inconspicuous), iris golden with uniformly radiating dark lines and a broad dark horizontal midline, sexually dimorphic tuberculate and spiculate dorsum present or absent, nuptial excrescences dark, vocal sacs paired, lateral, with subgular expansion, or single, subgular (Appendix S9) and oviposition in pools or phytotelmata (Appendix S10). Amplexus is axillary (Appendix S11).

Distribution. Osteocephalus oophagus is primarily Guianan, ranging from central Guyana, Suriname and northern French Guiana southward to the Amazon and Rio Negro and slightly beyond into Pará, Brazil. To the west it reaches Guainía, Colombia (Hoogmoed & Avila-Pires 1991; Jungfer & Schiesari 1995; Lescure & Marty 2000; Lynch & Vargas-Ramírez 2000; Ernst *et al.* 2005; Azevedo-Ramos 2010). As currently defined, the nominal species *Osteocephalus taurinus* occupies a large range, from Amazonian and Guianan Venezuela throughout Amazonia to

Bolivia and Mato Grosso, Tocantins, Piauí and Maranhão, Brazil (Trueb & Duellman 1971; La Marca *et al.* 2010b). However, as explained above, in addition to *O. taurinus* s. str., we recognize five candidate species (Fig. 3.5.2). Our data suggest that these have restricted non-overlapping ranges. However, we have not included samples from the western Amazon Basin yet (Appendix S8.6). The CCS *O. taurinus* [Ca1_MHNC6667_3151] is a large species only known from one site in Pasco, Peru that does not appear to be in sympatry with any other lineage within *O. taurinus.* The UCS *O. taurinus* [Ca2_Neblina410] is known from an isolated site in the Pico de Neblina area in extreme southern Venezuela. The UCS *O. taurinus* [Ca3_AJC2959_3181] occurs in lowlands at the western edge of the Guianan region and is not known to occur sympatrically with any other lineage within the *O. taurinus* group either. The UCS *O. taurinus* [Ca4_PHV2439_2671] occurs in eastern Mato Grosso, Brazil, where it might occur in sympatry with *O. taurinus* s. str. both to the east and west. The UCS *O. taurinus* [Ca5_SMNS12063] occurs in the Guianan region from eastern Venezuela to the Guianas and the mouth of the Amazon in Brazil. There is a large collection gap for samples between Ca5 and *O. taurinus* s. str., although *O.* “*taurinus*” is known to occur there (La Marca 2010b).

Remarks. As currently defined, *Osteocephalus taurinus* is an extremely polymorphic species. Snout–vent length of mature females ranges from 56.4–109.8 mm and from 50.3–91.1 mm in breeding males, with neighbouring populations sometimes exhibiting extreme size differences. The presence of frontoparietal ridges, sexually dimorphic dorsal skin and an iris with radiating dark lines in all populations assigned to this species apparently led Trueb & Duellman (1971) to consider *O. taurinus* a single polymorphic species. The fact that *O. oophagus*, a species with single subgular vocal sac and other distinct characters, is nested within *O.* “*taurinus*”, which has paired lateral sacs, suggests the existence of several unrecognized species. A detailed morphological and bioacoustic study of populations within *O.* “*taurinus*” is needed in order to unravel species diversity within this taxon.

Genus *Tepuihyla* Ayarzagüena, Señaris & Gorzula, 1993

Type species. Hyla rodriguezi Rivero, 1968, by original designation.

Diagnosis. No phenotypic synapomorphies are known for *Tepuihyla* (see discussion below). A number of molecular synapomorphies are listed in Appendix S7. Recently metamorphosed juveniles of *T. rodriguezi* (population from Guadacapiapu-tepui, Venezuela), *T.* aff. *edelcae* (undescribed species from the Chimantá Massif, Venezuela), and *T. rimarum* (Ptari-tepui, Venezuela) lack the juvenile coloration typical of *Osteocephalus* and usually have granular skin (PJRK, pers.obs., see below and Appendix S1); likewise Myers & Donnelly (2008) do not report ontogenetic colour change between recently metamorphosed juveniles and adults of *T. edelcae* from Auyantepui, Venezuela.

Content. Seven species: *Tepuihyla aecii* (Ayarzagüena, Señaris & Gorzula, 1993)*, T. edelcae* (Ayarzagüena, Señaris & Gorzula, 1993)*, T. exophthalma* (Smith & Noonan, 2001) new combination, *T. luteolabris* (Ayarzagüena, Señaris & Gorzula, 1993)*, T. rimarum* (Ayarzagüena, Señaris & Gorzula, 1993)*, T. rodriguezi* (Rivero, 1968)*,* and *T. warreni* (Duellman & Hoogmoed, 1992).

Tepuihyla galani (Ayarzagüena, Señaris & Gorzula, 1993) and *T. talbergae* Duellman & Yoshpa, 1996 are considered junior synonyms of *T. rodriguezi*, *Tepuihyla celsae* Mijares-Urrutia, Manzanilla & La Marca, 1999 a synonym of *T. luteolabris*, and *Osteocephalus phasmatus* MacCulloch & Lathrop, 2005 a junior synonym of *T. exophthalma*; see Appendix.

Distribution. Eastern and south-eastern Venezuela and western Guyana (Appendix S8.7).

Remarks. Two alternatives were considered to remediate the non-monophyly of *Osteocephalus*; placing *Tepuihyla* in the synonymy of *Osteocephalus* or including *O. exophthalmus, O. phasmatus*, and *“Hyla” warreni* in *Tepuihyla*. We chose the latter. *Tepuihyla* was originally defined by Ayarzagüena *et al.* (“1992” [1993]) by a number of character states, whose polarity was uncertain at the time. Of these, the reduction of webbing between toes I and II has been suggested as a putative synapomorphy by Faivovich *et al.* (2005), who also noticed instances of homoplasy in the Lophyohylini. The exposition of the frontoparietal fontanelle noted by Ayarzagüena *et al.* (1993) also is a putative synapomorphy overlooked by Faivovich *et al.* (2005), with several instances of homoplasy in the Lophyohylini as well (e.g., some species of *Osteocephalus* and *Osteopilus*; Trueb & Tyler 1974). Our redefinition of *Tepuihyla* dissociates the genus from these putative synapomorphies because *“Hyla” warreni*, “*O”. exophthalmus*, and “*O”. phasmatus* have webbing between toes I and II (Duellman & Hoogmoed 1992; Smith & Noonan 2001; MacCulloch & Lathrop 2005), and at least “*O.*” *exophthalmus* has the frontoparietal fontanelle covered by the frontoparietals (Smith & Noonan 2001). The modification of content and concept of *Tepuihyla* is the less disruptive alternative in terms of deviation from the current taxonomy.

Little is known about the breeding habits of *Tepuihyla* and it is only recently that the tadpole of one species (*T. edelcae*) has been described (Myers & Donnelly 2008). All *Tepuihyla* species for which reproductive ecology is known breed in marsh and relatively shallow rocky pools in upland and highland savannahs (on white sand or sandstone) where several males congregate and call partially immersed in the water or from very low vegetation close to the water (PJRK, pers. obs.). Amplexus is axillary and eggs are laid as gelatinous masses (PJRK, pers. obs.). Tadpoles can tolerate acidic water (pH values ~4). They are opportunistic feeders and have been seen feeding on dead animals including congeners (PJRK, pers. obs.). Virtually nothing is known about the reproductive ecology of *T. exophthalma* and *T. warreni*, which in contrast to other *Tepuihyla* species, are primarily forest dwellers (MacCulloch & Lathrop, 2005). Kok & Kalamandeen (2008) hypothesized that *T. exophthalma* (as *Osteocephalus exophthalmus*) could be a phytotelm breeder, but this remains uncorroborated.

Discussion

Amazonian and Guiana Shield diversity

The Amazonian and Guianan regions (pan-Amazonia) form a continuous area integrating a mosaic of habitats that harbour a significant portion of the global amphibian fauna. About 1039 (18%) of the approximately 6370 amphibian species worldwide listed by the IUCN (2012) (AmphibiaWeb [2012] lists 7083 named species, but see Frost [2013]) are pan-Amazonian, with records of more than 100 species occurring in a few square kilometres (e.g. Lynch 2005). This already outstanding species diversity of amphibians, however, appears to be greatly underestimated because of a number of factors. First, large areas still remain unexplored from a taxonomic perspective. Second, most of the historical species hypotheses are based on brief and cursory phenotypic descriptions often lacking vouchered types (either lost, destroyed or never designated), specific type localities or both; this implies that new species descriptions are hampered by lack of sufficient information. An example is the toad *Rhinella margaritifera* (Laurenti, 1768) with “Brasilia” (= Brazil) as its type locality, but in fact a complex of numerous species occurs within and outside Brazil (Fouquet *et al.* 2007b). Third, many species can be considered morphologically cryptic because they lack clear diagnostic characters, therefore information on behaviour, reproductive biology, ecology and genetics is needed to discover species (e.g. Padial & De la Riva 2009). And fourth, although our understanding of the biogeography and origin of the Amazonian fauna is growing rapidly (Fouquet *et al.* 2012; see also summaries by Antonelli *et al.* 2010; Lovejoy *et al.* 2010; Wesselingh *et al.* 2010), we are still far from having a general understanding of the history and mechanisms responsible for species diversity across groups of organisms and areas (Hoorn *et al.* 2010), which in turn suggests that important hotspots of diversity still remain undetected under the apparently uniform forest cover.

These factors, combined with the realization that pan-Amazonia is biogeographically much more complex than previously thought, led some researchers to wonder if there are amphibian species in the Amazon region with wide distributions (i.e. distributions occupying most of the region) (e.g. Wynn & Heyer 2001). Since then a few studies have specifically addressed this question for amphibians using two different strategies, 1) focussing on the diversity of a relatively small (compared to the total area of the pan-Amazon region), but well sampled location, such as parts of French Guiana (Fouquet *et al.* 2007a) and the Chiquitania of Bolivia (Jansen *et al.* 2011), or 2) studying the diversity of only a few species in genera such as *Adelophryne* and *Phyzelaphryne* (Fouquet *et al.* 2012), *Amereega* (Brown & Twomey 2009), *Engystomops* (Ron *et al.* 2006), *Hyalinobatrachium* (Castroviejo-Fisher *et al.* 2011), *Leptodactylus* (e.g. Heyer 2005; Heyer & de Sá 2011), *Oreobates* (Padial *et al.* 2012), *Pristimantis* (Elmer *et al.* 2007; Padial & De la Riva, 2009), and *Ranitomeya* (Brown *et al.* 2011).

The present contribution, with information from 328 specimens and 218 localities encompassing eight countries, constitutes one of the most extensive sampling efforts of pan-Amazonian amphibian groups. Our results reveal an intriguing pattern where four widespread nominal species (*O. buckleyi*, *O. leprieurii*, *O. planiceps* and *O. taurinus*) are indeed composites of species, with lower than previously reported genetic variability, but with wide distributions in some lineages. This pattern is similar to that found in certain groups of dendrobatids such as species of *Ranitomeya* and *Amereega* with low genetic distances (1–2 %) among species, some of them having very restricted distributions (e.g. *R. summersi*), while others occur throughout thousands of kilometres (e.g. *R. amazonica*) (Brown *et al.* 2011).

Our results support an increase in the species diversity of *Osteocephalus* from 24 recognized species (taking into account three species removed from *Osteocephalus* and two synonymized here) to 27 (12.5% more species), if we only include confirmed lineages, or 33 (37.5%) more species, if we include all candidate species. A high level of overlooked diversity is not exclusive of *Osteocephalus*, but has been found in several amphibian groups in the region (Fouquet *et al.* 2007a, b, 2012; Funk *et al.* 2012; Jansen *et al.* 2011) and in other tropical areas such as Madagascar (Vieites *et al.* 2009; Vences *et al.* 2010), Central America (Crawford *et al.* 2010), or Southeast Asia (Stuart *et al.* 2006). Recent studies of other vertebrates confirm this pattern, e.g. for birds (Milá *et al.* 2012), mammals (Pavan *et al.* 2012), or reptiles (Bergmann & Russel 2007).

Candidate species within *Osteocephalus* are not randomly distributed across the species groups. The *O. taurinus* Group alone contributes five candidate species and accounts for 56% of the previously unrecognized species diversity within the genus. The *O. leprieurii* (two candidate species), *O. buckleyi* (1) and *O. planiceps* (1) Groups contribute more candidate species, while we did not detect any additional diversity in the *O. alboguttatus* Group.

To facilitate comparison, we recognize four geographic areas of unequal size within the pan-Amazon region. Each of these geographic regions harbours important areas of endemism that have been previously recognized in other studies (e.g. da Silva *et al.* 2005). We divide the pan-Amazon longitudinally into a northern and a southern area, along the main course of the Amazon River. Most of the north-eastern region coincides with the Guianan region (Hoogmoed 1979), divided from the north-western area by the Río Orinoco, the Casiquiare Canal and the Rio Negro. The southern area includes the basins of the rivers Tapajos, Tocantins, Xingu, Madeira, and Juruá, and is divided by the Rio Madeira, which separates the lowlands of Bolivia and the south-western part of Brazilian Amazonia from the basins of those rivers originating on the Brazilian Shield. The western area has a strong Andean influence, while the eastern area is more influenced by the uplands and highlands of the Precambrian shields of Guiana and Brazil.

Most of the diversity of the 33 species (24 nominal and 9 candidate species considered here) of *Osteocephalus* is concentrated in the western parts of the Amazon (24 spp.). The *O. buckleyi* Group is much more diverse (10 spp.) in the west than in other regions (one in the NE and two in the SE), especially in species that inhabit elevations above 500 m a.s.l. in the Andean foothills (seven spp.). This diversification is coincidental with the origin of a derived mode of reproduction (breeding in mountain streams; see Reproductive Diversity). The presence of at least five species with mostly allopatric distributions (some overlap at the species' contact zones) suggests vicariance as the origin of speciation. One species in the SW (*O. helenae*) also occurs in the NE and spans a huge area in contrast to the other species in the group.

The *O. leprieurii* Group has one representative in each of the four sections, while all three species in the *O. alboguttatus* Group occur in the NW. The *O. planiceps* Group (six spp.) has a western distribution (five spp.) with one apparently isolated species (*O. planiceps* Ca1) at Pico de Neblina, an outcrop of the Guiana Shield, in the north-eastern sector.

The *O. taurinus* Group (seven spp.) is predominantly northern (six spp.), with five species associated with the Guianan region. Two species occur in the SE and SW sectors, among them *O. taurinus* s. str. that occurs in all four sectors. It is the most widely distributed species in the genus. Our results show that the eastern exemplars of *O. taurinus* s. str., from the gallery forests of the Cerrado, represent those of the most recent divergence in the clade, indicating a recent occupation of the Amazonian periphery.

Our findings of species richness in *Osteocephalus* corroborate the results found in other Amazonian frog groups (Fouquet *et al.* 2007a, b; Jansen *et al.* 2011; Funk *et al.*

2012) that the frog biodiversity in Amazonia is severely underestimated. While Funk *et al.* (2012) locally compared two species of *Engystomops* and two species of *Hypsiboas* with wide pan-Amazonian distributions and found an increase of species to 150-250% and 200-350%, respectively, of the current number, our results show a lower increase of 113-138% for the entire genus, suggesting that *Osteocephalus* was either a well-studied (and well-known) group or that its evolutionary history was different from that of *Engystomops* and *Hypsiboas*. Both assumptions appear to be incorrect. The difference is simply caused by our inclusion of species with smaller ranges. Thus, if we considered only the three widespread nominal species *O. buckleyi*, *O. leprieurii* and *O. taurinus* and added the candidate species, the number of species would increase from three to six CCS (200%), or to 9 CCS + UCS (300%). Considering that 1000+ species of amphibians are currently known to occur in pan-Amazonia, and combining our results with those of other studies, we consider that the diversity of Amazonia is highly understimated. Broad scale taxonomic analyses as the one presented here are much needed for other groups of organisms in order to understand the evolution, distribution patterns and biogeography of Amazonia, as well as to guide effective conservation measures.

Morphological and genetic data in *Osteocephalus*

There are few nominal species of *Osteocephalus* exhibiting fixed qualitative or quantitative characters to separate them from all other species in the genus (e. g. iris colouration in O. *subtilis*). Usually a set of characters is needed to diagnose currently accepted nominal species. The issue becomes more acute with increasing character variability within a supposed species. Most of the morphological characters found in 20 of the 24 nominal species of *Osteocephalus* vary intraspecifically by 7-21% (KHJ, unpublished). The lowest variation is found in species with small ranges that are also represented in low numbers in collections. The three species with the largest ranges, and also the highest numbers of specimens examined, *O. buckleyi*, *O. leprieurii*, and *O. taurinus sensu lato* respectively, also have the highest percentages of variation (57-71 %). These preliminary data substantiate our molecular findings with respect to candidate species. Similarly, the molecular data support the view that a great deal of the morphological variation might be due to the presence of cryptic species. Using morphological data, several (candidate) species can be further subdivided, most of them representing clades also recognizable in the trees (Figs. 3.5.1-4). Likewise, among populations of *O. taurinus* s. str. there are clades that are extremely different. While breeding specimens from near the type locality measure 82 mm snout–vent length in males and 104 mm in females, breeding specimens from some 250 km SW of that site measure 50 and 57 mm, respectively, only slightly more than half the size of the former specimens. This indicates that our molecular view of candidate species is conservative when compared to one focussed on morphology. Unfortunately, few bioacoustical or other data on isolating mechanisms between populations are available to allow a more integrative approach to decipher species diversity in the genus.

Reproductive diversity and evolution of reproductive biology in *Osteocephalus*

Exploitation of different breeding sites may be one reason for the successful colonization and sympatric occurrence of *Osteocephalus* species in pan-Amazonia. Our phylogenetic hypothesis indicates that pond breeding and egg clutches laid as a surface film is the plesiomorphic reproductive mode in *Osteocephalus* (Appendix S10). Both adaptations are advantageous in facilitating rapid development in warm water with low oxygen contents (e.g. Wells 2007). This mode is common in hylids, including many Lophyohylini (Faivovich *et al.* 2005). Males call while floating in water with lateral vocal sacs inflated, but they can also call while out of water. Jungfer & Hödl (2002) speculated that a tuberculate dorsum in large choruses of males, like those of *O. leprieurii* (Lescure & Marty 2000) or *O. taurinus* (Bokermann 1964), may facilitate recognizing that the wrong sex has been clasped. This reproductive mode occurs in all known (candidate) species of the *O. taurinus* Group except *O. oophagus*. The latter is not only the smallest species in the group, it also breeds in narrow phytotelmata. An amplecting pair deposits small clutches of about 250 eggs altogether in short intervals of about five days, and males lack dorsal tubercles and have a subgular vocal sac. All these character states have been proposed to be adaptations to breeding in phytotelmata (Jungfer & Weygoldt 1999). Small size allows for using very small bodies of water such as bromeliad leaf axils. Small sites can only hold few eggs, but if fewer eggs are laid, they can be produced at shorter intervals. Phytotelmata are not available ad libitum, so remembering and re-using them might be an advantage. Females of *O. oophagus* avoid sites where tadpoles of other females are already present. Parents return to phytotelmata where they have oviposited and provide their larvae with nutritive eggs. Larvae are dependent on them and will starve if the female does not return at least five times to feed them. Like other oophagus tadpoles in several anuran families, they have a reduced number of labial tooth rows (Silverstone 1975; Jungfer 1985; Ueda 1986; Lannoo *et al.* 1987; Duellman 2001). A small subgular vocal sac may be advantageous over large paired sacs in the confines of a narrow phytotelm, which in many cases acts as a resonator itself (pers. obs. KHJ).

The shift from pond breeding sites to phytotelmata could be advantageous not only for tadpoles avoiding interspecific competition and numerous predators. The shift in call strategy away from large choruses to spaced individuals scattered in the forest may be seen as an adaptation to avoid predators of adults, too. The cost of a prolonged breeding season appears to be lower than that of explosive breeding.

Members of the *O. leprieurii* Group are pond breeders depositing eggs in surface films. Males of *O. leprieurii* have coloured keratinized nuptial pads, spiny backs, and keratinized structures on other parts of the body (Jungfer & Hödl 2002). Explosive breeding in large choruses after heavy rains is the rule in this group and male nuptial excrescences are advantageous not only on the hands. Dorsal spines in male-male interactions may be analogous to release calls. Furthermore, males become conspicuously yellow during breeding, possibly to warn other males or to attract females. This phenomenon is also known in other explosive breeders in the genera *Scinax*, e.g. *S. elaeochroa* (Duellman 2001), *Dendropsophus*, e.g. *D. microps* (Kwet 2001), *D. minutus* (Marty & Gaucher 1999), *Trachycephalus mesophaeus* (pers. obs. MTR) or *Triprion petasatus* (pers. obs. KHJ). Very often males in the *O. leprieurii* Group call while floating in water. Vocal sacs are lateral, as it occurs in several frog groups that call while floating on the water surface, such as *Pelophylax* or *Pseudis*.

The sister taxon of the *O. leprieurii* Group is the *O. buckleyi* Group, the only clade of stream breeding *Osteocephalus*. Stream breeding is a synapomorphy of this group. Although they breed in moving, oxygen-rich water, most species have retained the ancestral character of a surface film of eggs. However, eggs of this group that become submerged develop normally (pers. obs. KHJ), unlike those of lentic breeding *O. oophagus* (Jungfer & Weygoldt 1999), *O. taurinus* (pers. obs. KHJ) or other hylids (e.g. Kluge 1981) in the field. Vocal sacs in the group do not appear to be different from the lateral ones of the *O. leprieurii* Group, although at least half of the (candidate) species usually call from vegetation along streams (pers. obs. KHJ). The dorsal skin of breeding males ranges from dense keratinized spicules (*O. mimeticus*, *O. verruciger*) to simple, non-keratinized tubercles (*O. cabrerai*). It is not known whether skin texture is correlated with size of choruses or distribution of choruses along streams. Breeding period at least in *O. buckleyi* s. str. is lengthy (Jungfer & Weygoldt 1999).

Members of the *O. planiceps* Group breed in phytotelmata (breeding site unknown in *O. fuscifacies*) and all of them have similar smooth backs (except *O. planiceps*) and single, subgular vocal sacs in males (barely distensible and lacking vocal slits in *O. castaneicola*), similar to *O. oophagus* of the *O. taurinus* Group. Coloured keratinized spines on the nuptial excrescences of the thumb are reduced in most species. *Osteocephalus planiceps* is exceptional for the group in being large, having extensive dark brown keratinized nuptial pads and tuberculate backs in males (although some sexually active males are smooth-backed). Tadpoles, at least of *O. castaneicola* and O. *deridens,* eat conspecific eggs and *O. deridens* larvae have a reduced number of labial tooth rows (Jungfer *et al.* 2000; Moravec *et al.* 2009). As already stated by Moravec *et al.* (2009), our consensus tree confirms that phytotelm breeding and tadpoles feeding on conspecific eggs has evolved independently in *Osteocephalus* at least twice and members of both groups independently evolved similar character states associated with this reproductive mode (subgular vocal sacs, smooth dorsa in males, reduction of tooth rows in tadpoles). They also exhibit nuptial excrescences that are reduced (less keratinization) or absent in males of three species, suggesting a lack of male-male competition by clasping. In one of those, *O. leoniae*, we observed females returning without males to tadpoles and feeding them on unfertilized nutritive eggs (KHJ unpublished). This reproductive mode has so far only been found in a few groups of frogs breeding in phytotelmata (reviewed by Lehtinen *et al.* 2004) or subterranean burrows (Gibson & Buley 2004).

Amplexus is a relatively conservative character in anurans. In most neobatrachians and all hylids the amplexus is axillary (Duellman & Trueb 1986). In some *Osteocephalus*, there is a previously unknown position, in which the male clasps the female exclusively around the female's throat, here termed gular amplexus (Appendix S11). It was observed in two closely related species, *O. deridens* and *O. leoniae*, both in the *O. planiceps* Group, and can be expected in *O. fuscifacies* as well. In both species, this type of amplexus is employed exclusively and we observed it 100+ times, while we have never seen it in other species of *Osteocephalus*. These were always found in axillary amplexus. Gular amplexus may also be considered an adaptation to phytotelm breeding, since in both species, females carry amplecting males around, indicating that it is they who select the breeding site, although a male calling from a phytotelm may “propose” one. This latter behaviour is similar to that of *O. oophagus* (Jungfer & Weygoldt 1999). Being held in the gular region may allow a female to climb more freely. Other females in the genus approach males at or near the breeding site on the ground (except the large *O. planiceps*).

Almost nothing is known about the reproduction of the members of the *O. alboguttatus* Group. However, the smooth backs and subgular vocal sacs of males might indicate that these frogs are phytotelm breeders as well.

Summarizing the evolutionary history of reproduction it can be stated that explosive or opportunistic pond breeding is the ancestral state in *Osteocephalus*, as exhibited in the *O. taurinus* Group and retained in the *O. leprieurii* Group. Phytotelm breeding (partly combined with parental care for tadpoles) evolved in the *O. planiceps* Group and independently in *O. oophagus* (*O. taurinus* Group), and stream breeding in the *O. buckleyi* Group.

Authors' contributions

Designed the work: JF and KHJ. Contributed materials: MTR, KHJ, JMP, SCF, VKV, JCC, CPTG, PHV, PJRK, SR, JM, CFBH, RDM, GGU, DBM, RE, IDR, APL, JCS. Analyzed molecular data: JF, JMP, SCF. Produced sequences: JF, ML, BvMB, PI, CFBH, WCW. Wrote the paper: KHJ, JF, SCF, JMP. Maps were prepared by PHV. All authors read, contributed, and approved the final version of the manuscript.

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Appendix. Synonyms among species of *Osteocephalus* and *Tepuihyla*

Mainly because of differences in juvenile and adult colourations several species of *Osteocephalus* have been described more than once and/or placed into different genera (Jungfer 2010). We are aware of more such cases. While synonymizing junior taxon names and establishing old neglected ones is beyond the scope of this work, we nonetheless deem it unwise to use names that will soon be considered outdated. On the other hand it is hard to follow synonymizations when no sufficient reasons are given. The following account—though still not complete—gives a brief overview of the changes proposed here and why. In the case of old taxon names (such as "*Hyla helenae*"), a more detailed study is in progress.

Likewise, several species of *Tepuihyla* have been described from isolated mountain tops using few specimens for which intraspecific variation was poorly known, but which were treated as distinct species basically because of their isolated distributions. More populations and specimens together with molecular data indicate that several of these taxa have to be treated as junior synonyms.

Osteocephalus helenae (Ruthven, 1919) nov. comb. The holotype of *Hyla helenae* Ruthven, 1919 (MCUM 52681) from Dunoon, Guyana, is a recently metamorphosed juvenile with the typical colouration of most of the members of the *O. buckleyi* Species Group (dark spots on light ground and light colour of distal part of upper arm and elbow, and also of knee and tarsus, compare Appendix S1). Based on molecular data of tissue taken from frogs earlier considered to be *O. buckleyi* (Kok & Kalamandeen 2008) or *O. cabrerai* (Gorzula & Señaris "1998" [1999]; Lescure & Marty 2000) from north-eastern South America we consider it a valid species of *Osteocephalus*. This well-supported clade is widely distributed from north-eastern South America south-westward to southern Peru and Bolivia.

Osteocephalus germani Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012. The type locality of *O. germani* is near Pongo de Mainique, La Convención, Cusco, Peru. Our specimen MHNC7004 from Río Nusiniscato, Cusco, Peru, agrees well morphologically with the holotype and genetically with a paratopotype of *O. germani* included in our tree. They form a large, well-supported clade that also includes specimens from Guyana considered to be *O. helenae*. For this reason we consider

O. germani a junior synonym of *O. helenae*. That *O. germani* and specimens from north-eastern South America were likely to be conspecific was also stated by Ron *et al.* (2012).

Osteocephalus vilmae Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012. Within *O. buckleyi* as presented here there are two clades with low genetic distances (uncorrected *p* distance 1.6%). They were also found by Ron *et al.* (2012). One of these is considered a distinct species, *O. vilmae*, by them. We have seen specimens of the "*vilmae*" clade from Yasuní, Ecuador, and the Iquitos region in Loreto, Peru, one of each locality is contained in our tree. For the following reasons we do not follow their arguments, but consider *O. vilmae* a junior synonym of *O. buckleyi*: Morphologically, we were unable to distinguish "*O. vilmae*" from other *O. buckleyi*. In the original description, "*O. vilmae*" is distinguished from *O. buckleyi* by having scattered and weakly keratinized dorsal tubercles (abundant and keratinized in *O. buckleyi*). We have seen both character states in both males of the "*vilmae*" and the "*buckleyi*" clade. Especially keratinization is strongly dependent on reproductive activity and not a reliable character when breeding and non-breeding frogs are compared. "*Osteocephalus vilmae*" is furthermore characterized by its larger snout–vent length (SVL) in males (50.74 mm ± 3.17 SD; $n = 6$; maximum 55.77 mm), while *O. buckleyi* are stated to have an SVL of 41.12 mm ± 2.49 SD. Five of our males genetically belonging to the "*vilmae*" clade or collected with them are 42.2–50.6 mm in SVL (46.0 ± 3.80) and six more males, like the holotype of "*O. vilmae*" from Loreto, Peru, make the range 38.2 – 50.6 mm (43.3 ± 3.78) SVL, close to the mean given for *O. buckleyi* by Ron *et al.* (2012). Remarkably, our only female in the "*vilmae*" clade, a mature specimen of 54.9 mm, is smaller than the largest male measured by Ron *et al.* (2012), which is exceptional in *Osteocephalus*. In almost all species females are considerably larger than males.

Ron *et al.* (2012) found a more extensive and conspicuous areolate area on the flanks in "*O. vilmae*", reaching from the axilla to the groin (to anterior half of flank in *O. buckleyi*). In our specimens the areolate area covers the first $^{1}/4$ to ¾ of the flanks in "*O. vilmae*" and $^{1}/3$ to ½ in other specimens of *O. buckleyi* from Ecuador, leaving too much overlap to distinguish between both.

At least in captivity specimens ascribed morphologically and genetically to *O. buckleyi* and "*O. vilmae*" (sensu Ron *et al.* 2012) were able to interbreed. The offspring was able to reproduce successfully as well. One such "crossbreed" (Trier 028_2742) was included in our tree and grouped with the "*vilmae*" clade. Ron *et al.* (2012) state that both "species" were sympatric at one site and assume reproductive barriers between them. These apparently do not exist.

It has been demonstrated only recently that Guianan upland and highland species, including populations from different tepui summits, are less divergent genetically than previously thought, suggesting that they have evolved in isolation only for a relatively short time (Kok *et al.* 2012; Salerno *et al.* 2012). Although some morphological differences between *T. exophthalma* and *O. phasmatus* (= *T. phasmata*), namely in snout–vent length, tympanum size and amount of webbing have been reported (Smith & Noonan 2001; MacCulloch & Lathrop 2005; Kok & Kalamandeen 2008), examination of a larger sampling shows that these characters are variable and are not strongly diagnostic. This, coupled with the low interspecific genetic divergence (ranging from 0.0–0.2%), strongly suggests that a single species with a wider morphological and geographical range is involved. Therefore we consider *T. phasmata* a junior synonym of *T. exophthalma*.

Likewise, Kok *et al.* (2012) demonstrated the low genetic divergence between *T. rodriguezi*, *T. galani* and *T. talbergae* even in the rapidly evolving mitochondrial ND1 gene. Descriptions of *T. galani* and *T. talbergae* were based on only four and two specimens, respectively. Examination of additional specimens of these two species, including some from the type localities, showed that the morphological characters used to diagnose *T. galani* and *T. talbergae* are more variable than was stated in the original descriptions. Furthermore, these diagnostic characters exhibit considerable overlap among *T. galani, T. talbergae* and *T. rodriguezi* (PJRK, unpublished). We therefore consider *T. galani* and *T. talbergae* to be junior synonyms of *T. rodriguezi*.

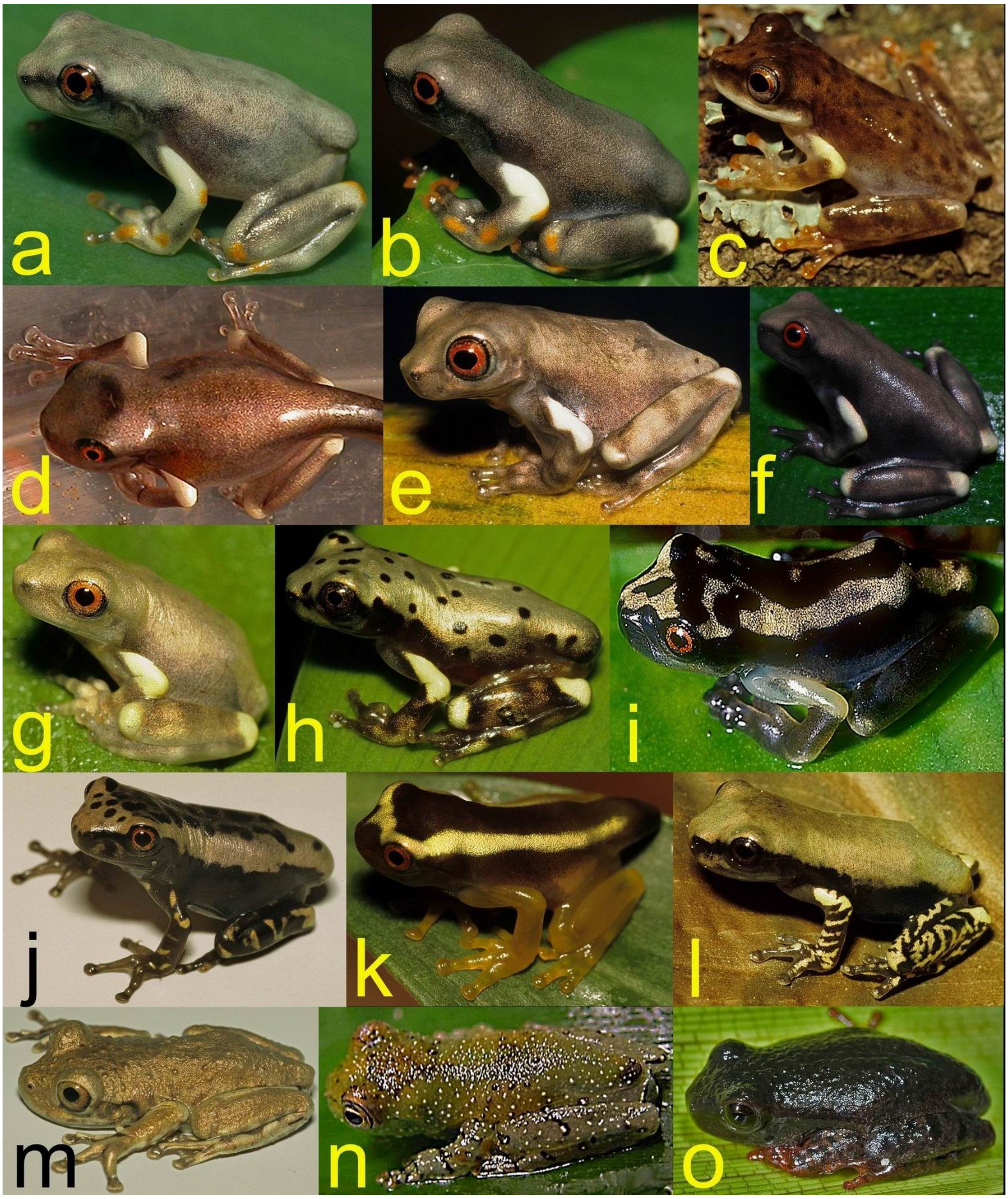
Salerno *et al.* (2012), on the basis of personal communication with César Barrio-Amorós, argued that *T. celsae*, a species purportedly from Falcón, Venezuela (outside the Guiana Highlands and pan-Amazonia) most likely is a junior synonym of *T. luteolabris* based on a specimen with incorrect locality data. We follow this argumentation after inspection of type material of *T. celsae* by one of us (JCS).

Supporting information

(available online at: http://onlinelibrary.wiley.com/store/10.1111/zsc.12015/asset/supinfo/zsc12015-sup-0001-AppendixS1-S11.pdf?v=1&s=efbc7acc98d63b96d5e51cea626f55 bd4d5b94 09)

Appendix S1

Recently metamorphosed juveniles of *Osteocephalus* and of juveniles previously assigned to that genus. The constant pattern in the colouration of juveniles of *Osteocephalus* (*sensu* this work) is proposed as a morphological synapomorphy for the genus. <u>*Osteocephalus taurinus* Species Group</u>: (**a**) *O. taurinus* (Reserva Ducke, Manaus, Amazonas, Brazil); (**b**) *O. oophagus* (Reserva Ducke, Manaus, Amazonas, Brazil). <u>*Osteocephalus leprieurii* Species Group</u>: (**c**) *O. leprieurii* (Arataï, French Guiana). <u>*Osteocephalus planiceps* Species Group</u>: (**d**) *O. castaneicola* (San Antonio, Pando, Bolivia); (**e**) *O. deridens* (Iquitos, Loreto, Peru); (**f**) *O. leoniae* (Tarapoto, San Martín, Peru); (**g**) *O. planiceps* (Jatun Sacha, Napo, Ecuador). <u>*Osteocephalus buckleyi* Species Group</u>: (**h**) *O. buckleyi* (Jatun Sacha, Napo, Ecuador); (**i**) *O. carri* (Picachos, Huila, Colombia); (**j**) *O. mimeticus* (Tarapoto, San Martín, Peru); (**k**) *O. mutabor* (Cordillera Galeras, Napo, Ecuador); (**l**) *O. verruciger* (Reventador, Sucumbíos, Ecuador). *Dryaderces pearsoni* (**m**) (Rurrenabaque, Beni, Bolivia). *Itapotihyla langsdorffii* (**n**) (Rio de Janeiro, RJ, Brazil). *Tepuihyla rimarum* (**o**) (Ptari-tepui, Bolívar, Venezuela) (not to scale).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Appendix S2

Localities, voucher information and GenBank accession numbers for DNA sequences used (in bold: sequences produced for this study). Abbreviations used for vouchers (unless downloaded from GenBank): AMNH: American Museum of Natural History, New York, USA. APL: Albertina P. Lima, Laboratório de Vertebrados da Ecologia - INPA collection, Manaus, Brazil. AJC: Andrew J. Crawford field numbers. CBF: Colección Boliviana de Fauna, La Paz, Bolivia. CFBH Collection Célio F. B. Haddad, Departamento de Zoologia, I.B., UNESP, Rio Claro, SP, Brazil. CPI: Coastal Plains Institute and Land Conservancy (Field numbers of D. Bruce Means), Tallahassee, FL, USA. EPN: Escuela Politecnica Nacional, Quito, Ecuador. GGU: Giussepe Gagliardi-Urrutia field numbers at UNAP (Universidad Nacional de la Amazonía Peruana, Iquitos, Peru). IRSNB: Royal Belgian Institute of Natural Sciences, Brussels, Belgium. JMP: José M. Padial field numbers. KHJ-F: Karl-Heinz Jungfer field numbers, to be divided between MUSM and MTD. MACN: Museo Argentino de Ciencias Naturales “Angel Gallardo”—CONICET, Buenos Aires, Argentina. MAR: Marco Rada field numbers. MHNC Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru. MHNLS: Museo de Historia Natural La Salle, Caracas, Venezuela. MNCN Museo Nacional de Ciencias Naturales, Madrid, Spain. MUSM: Museo de Historia Natural de la Universidad de San Marcos, Lima, Peru. MSH: Marinus S. Hoogmoed field numbers. MTD: Senckenberg Naturhistorische Sammlungen, Dresden, Germany. MTR: Miguel T. Rodrigues field numbers. MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. NMP: National Museum, Zoology, Praha, Czech Republic. PHV: Paula Hanna Valdujo field numbers (to be accessioned in MZUSP)**.** PK: Philippe Kok field numbers deposited at IRSNB. ROM: Royal Ontario Museum, Toronto, Canada. SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany. SMS: Sergio Marques de Souza field numbers (to be accessioned in MZUSP). TG: Taran Grant field numbers. TNHC: Texas Natural History Collections, Austin, USA. UA: Universidad de los Andes, Bogotá, Colombia. Vogt: Richard Vogt field numbers. Locality coordinates are given for specimens newly accessed to GenBank.

Species	Locality	Tissue identification number	Voucher collection number	12+16S	Cytochrome *b*	ND1	COI	Control Region	POMC
Aparasphenodon brunoi	Brazil: Espírito Santo: Aracruz		CFBH 2715	AY843567	AY843789	KF002246	---	---	---
Corythomantis greeningi	Brazil: Alagoas: Represa de Xingó, Piranhas		CFBH 2968	AY843578	AY843800	KF002247	---	---	---
Dryaderces pearsoni	Bolivia: Beni: Rurrenabaque S14°26'00"W67°29'00"	O_pearsoni_KHJ01_1575	SMNS 14187	**KF002006**	**KF001945**	**KF002188**	---	---	---
Dryaderces pearsoni	Bolivia: Beni: Rurrenabaque S14°26'00"W67°29'00"	O_pearsoni_KHJhyl28_1604	SMNS 14188	**KF002007**	**KF001948**	---	---	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13158_2768	MTR 13158	**KF002008**	---	---	**KF001880**	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13172_2842	MTR 13172	**KF002009**	---	---	**KF001881**	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13173_2754	MTR 13173	**KF002010**	---	**KF002189**	**KF001882**	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13204_2744	MTR 13204	**KF002011**	---	**KF002190**	**KF001883**	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13205_2758	MTR 13205	**KF002012**	---	**KF002191**	**KF001884**	---	---
Dryaderces pearsoni	Brazil: Mato Grosso:	O_sp_Aripuan	MZUSP	**KF002013**	**KF001949**	---	---	---	---

[Ca1_MTR13158_2768]	Aripuanã II S10°19'00"W59°23'00"	aII_MT_2135	87697						
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Mato Grosso: Apiacás S09°31'06"W57°19'06"	O_sp_Apiacas_MT_2124	MZUSP 80816	**KF002014**	**KF001950**	---	---	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Mato Grosso: Juruena S10°17'38"W58°29'34"	O_sp_Juruena_MT_2092	MZUSP 86099	**KF002015**	**KF001951**	---	---	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Mato Grosso: Juruena S10°17'38"W58°29'34"	O_sp_Juruena_MT_2112	MTR 9621	**KF002016**	**KF001952**	---	---	---	---
Dryaderces pearsoni [Ca1_MTR13158_2768]	Brazil: Mato Grosso: Juruena S10°17'38"W58°29'34"	O_sp_Juruena_MT_2094	MZUSP 86095	**KF002017**	**KF001953**	---	---	---	---
Itapotihyla langsdorffii	Argentina: Misiones: General Belgrano: 10 km N Bernardo de Irigoyen: Salto Andresito		MACN 38643	AY843706	AY843951	---	**KF001942**	---	**KF002003**
Myersiohyla kanaima	Guyana: District 7: Mt. Ayanganna	Myersiohyla_kanaima_640	ROM 39582	AY843634	AY843868	---	---	---	---
O. alboguttatus	Ecuador: Napo: Jatun Sacha S01°04'00"W77°37'00"	O_alboguttatus_KHJhyl27_1603	SMNS 14189	**KF002018**	**KF001954**	**KF002192**	---	---	---
O. alboguttatus	Ecuador: Pastaza: Canelos	QCAZ 18186	QCAZ 18186	JQ868516	---	---	---	---	---
O. alboguttatus	Ecuador: Pastaza: Canelos	QCAZ 15981	QCAZ 15981	HQ600629	---	HQ600596	---	JX875680	JX875744

O. buckleyi	Ecuador: Napo/Orellana: Jatun Sacha x Yasuní	O_buckleyi_Trier028_2742	SMNS 14192	**KF002019**	---	**KF002193**	**KF001885**	---	---
O. buckleyi	Ecuador: Napo: Ahuano	QCAZ 36703	QCAZ 36703	JX847092	---	JX875625	JX875845	JX875722	JX875778
O. buckleyi	Ecuador: Napo: Cando	QCAZ 24446	QCAZ 24446	HQ600633	---	HQ600600	JX875821	JX875708	JX875753
O. buckleyi	Ecuador: Napo: Cando	QCAZ 24447	QCAZ 24447	HQ600634	---	HQ600601	JX875822	JX875686	JX875754
O. buckleyi	Ecuador: Napo: Jatun Sacha	LAC2216	LAC 2216	DQ380378	---	EU034082	---	---	EU034116
O. buckleyi	Ecuador: Napo: Jatun Sacha	QCAZ 48093	QCAZ 48093	JX847105	---	JX875639	JX875864	JX875702	JX875798
O. buckleyi	Ecuador: Napo: Jatun Sacha	QCAZ 48827	QCAZ 48827	JX847106	---	JX875640	JX875865	JX875703	JX875799
O. buckleyi	Ecuador: Napo: Jatun Sacha S01°04'00"W77°37'00"	O_buckleyi_KHJhyl22_1599	SMNS 13714	**KF002020**	**KF001955**	**KF002194**	---	---	---
O. buckleyi	Ecuador: Napo: Jatun Sacha S01°04'00"W77°37'00"	O_buckleyi_KHJhyl25_1601	SMNS 13715	**KF002021**	**KF001956**	**KF002195**	---	---	---
O. buckleyi	Ecuador: Orellana: Puente del Río Beque	QCAZ 43071	QCAZ 43071	JX847099	---	JX875633	JX875858	JX875724	JX875793
O. buckleyi	Ecuador: Orellana: Yasuní S00°41'00"W76°24'00"	O_buckleyi_KHJ14_1587	SMNS 13713	**KF002022**	**KF001957**	**KF002196**	---	---	---
O. buckleyi	Ecuador: Pastaza: Nuevo Corrientes	QCAZ 14947	QCAZ14947	HQ600628	---	HQ600595	JX875811	JX875663	JX875741
O. buckleyi	Ecuador: Pastaza: Tarangaro	QCAZ 39073	QCAZ 39073	JX847094	---	JX875627	JX875848	JX875714	JX875782
O. buckleyi	Ecuador: Pastaza: Tarangaro	QCAZ 39074	QCAZ 39074	JX847095	---	JX875628	JX875849	JX875672	JX875783

O. buckleyi	Ecuador: Pastaza: Villano	QCAZ 39285	QCAZ 39285	---	---	JX875629	JX875850	JX875694	JX875784
O. buckleyi	Ecuador: Sucumbíos: Playas de Cuyabeno	QCAZ 28277	QCAZ 28277	HQ600639	---	HQ600606	JX875831	JX875720	JX875763
O. buckleyi	Ecuador: Sucumbíos: Playas de Cuyabeno	QCAZ 28395	QCAZ 28395	HQ600640	---	HQ600607	JX875832	JX875677	JX875764
O. buckleyi	Ecuador: Sucumbíos: Tarapoa	QCAZ 14948	QCAZ 14948	JX847081	---	JX875611	JX875812	JX875718	JX875718
O. buckleyi	Ecuador: Sucumbíos: Tarapoa-Puerto Carmen road, Río Cuyabeno	QCAZ 28427	QCAZ 28427	JX847087	---	JX875618	JX875833	JX875689	JX875765
O. buckleyi	Peru: Loreto: 28 km S Iquitos S04°02'00"W73°23'00"	O_buckleyi_KHJ12_1585	KHJ-F 067	**KF002023**	**KF001958**	---	---	---	---
O. buckleyi	Peru: Loreto: Tambo S01°13'50''W75°16'59''	O_buckleyi_MHNC7687_3157	MHNC 7687	**KF002039**	---	---	---	---	---
O. buckleyi	Peru: Loreto: Datem del Marañon: Pampa Hermosa	CORBIDI 4773	CORBIDI 4773	JX847065	---	JX875602	---	JX875653	JX875730
O. buckleyi	Peru: Loreto: Sargento Puño	CORBIDI 7458	CORBIDI 7458	JX847067	---	JX875606	JX875806	---	JX875734
O. buckleyi	Peru: Loreto: Sargento Puño	CORBIDI 7459	CORBIDI 7459	JX847068	---	JX875607	JX875807	---	JX875735
O. buckleyi	Peru: Loreto: Sargento Puño	CORBIDI 7462	CORBIDI 7462	JX847069	---	JX875608	JX875808	JX875657	JX875736
O. buckleyi	Peru: Loreto: Sargento Puño	CORBIDI 7516	CORBIDI 7516	JX847070	---	---	---	---	JX875737
O. buckleyi	Brazil: Amazonas: Areal,	O_cabrerai_M	MTR	**KF002026**	---	**KF002197**	**KF001886**	---	---

[Ca1_MTR12779_2748]	Rio Abacaxis S04°35'49"W58°13'14"	TR13147_2844	13147						
O. buckleyi [Ca1_MTR12779_2748]	Brazil: Amazonas: Igarapé-Açu, Rio Abacaxis S04°20'40"W58°38'06"	O_cabrerai_MTR12779_2748	MTR 12779	**KF002027**	---	**KF002198**	**KF001887**	---	---
O. cabrerai	Colombia: Amazonas: Leticia S04°11'57"W69°57'22"	O_cabrerai_JMP2184_3169	UA-A 931	**KF002028** **KF002029**	---	---	**KF001888**	---	---
O. cabrerai	Colombia: Amazonas: Río Takana 9 km by road from Leticia S04°07'40"W69°56'53"	AJC 2566	AJC 2566	---	---	---	---	JX875650	---
O. cabrerai	Colombia: Amazonas: Río Takana 9 km by road from Leticia S04°07'40"W69°56'53"	AJC 2567	AJC 2567	---	---	---	---	JX875707	---
O. cabrerai	Ecuador: Sucumbíos: Campamento Guepicillo	CORBIDI 120	CORBIDI 120	---	---	JX875600	---	JX875651	JX875727
O. cabrerai	Ecuador: Sucumbíos: Puerto Bolívar	QCAZ 27923	QCAZ 27923	JX847086	---	JX875617	JX875827	JX875709	JX875760
O. cabrerai	Ecuador: Sucumbíos: Puerto Bolívar	QCAZ 28231	QCAZ 28231	HQ600654	---	HQ600621	JX875830	JX875710	JX875762
O. cabrerai	Peru: Loreto: Maynas: Rio Yanayacu, Campamento Curupa	CORBIDI 5819	CORBIDI 5819	JX847066	---	JX875604	JX875804	JX875655	JX875731
O. cabrerai	Peru: Loreto: Maynas: Rio Yanayacu, Campamento Curupa	CORBIDI 5821	CORBIDI 5821	---	---	JX875605	JX875805	JX875656	JX875732

O. cabrerai	Peru: Loreto: Río Iauasiyacu S03°18'48"W72°01'53"	O_cabrerai_Trier022_2740	KHJ-F 082	**KF002030**	---	**KF002199**	---	---	---
O. cannatellai	Colombia: Caquetá: San José del Fragua: Finca Buena Esperanza N01°18'43"W76°04'25"	TG1852_3338	TG 1852	**KF002031**	---	---	---	---	---
O. cannatellai	Colombia: Caquetá: San José del Fragua: Finca Buena Esperanza N01°18'43"W76°04'25"	TG1853	TG 1853	**KF002032**	---	---	---	---	---
O. cannatellai	Ecuador: Morona Santiago: Nuevo Israel	QCAZ 46472	QCAZ 46472	JX847104	---	JX875638	JX875863	JX875717	JX875797
O. cannatellai	Ecuador: Morona-Santiago: Bobonaza	QCAZ 32506	QCAZ 32506	HQ600651	---	HQ600618	JX875843	JX875692	JX875775
O. cannatellai	Ecuador: Morona-Santiago: Bobonaza	QCAZ 32508	QCAZ 32508	HQ600652	---	HQ600619	JX875844	JX875693	JX875776
O. cannatellai	Ecuador: Orellana: El Edén	QCAZ 39633	QCAZ 39633	JX847096	---	JX875630	JX875852	JX875678	JX875786
O. cannatellai	Ecuador: Pastaza, Río Pucayacu near Zanjarajuno Reserve	QCAZ 40258	QCAZ 40258	JX847097	---	JX875631	JX875854	JX875696	JX875788
O. cannatellai	Ecuador: Pastaza, Río Pucayacu near Zanjarajuno Reserve	QCAZ 45909	QCAZ 45909	JX847101	---	JX875635	JX875860	JX875701	JX875795
O. cannatellai	Ecuador: Pastaza, Río Pucayacu near Zanjarajuno Reserve	QCAZ 49572	QCAZ 49572	JX847107	---	JX875641	JX875866	JX875674	JX875800
O. cannatellai	Ecuador: Pastaza: Pomona	QCAZ 25469	QCAZ	HQ600650	---	HQ600617	JX875823	JX875687	JX875755

			25469						
O. cannatellai	Ecuador: Pastaza: Pomona	QCAZ 37175	QCAZ 37175	HQ600653	---	HQ600620	JX875846	JX875713	JX875779
O. cannatellai	Ecuador: Zamora Chinchipe: Centro Shuar Yawi	QCAZ 31016	QCAZ 31016	JX847089	---	JX875621	JX875839	JX875712	JX875771
O. cannatellai	Ecuador: Zamora Chinchipe: Centro Shuar Yawi	QCAZ 31032	QCAZ 31032	JX847090	---	JX875622	JX875840	JX875691	JX875772
O. cannatellai	Ecuador: Zamora Chinchipe: Centro Shuar Yawi	QCAZ 31033	QCAZ 31033	---	---	JX875623	JX875841	JX875668	JX875773
O. cannatellai	Peru: Loreto: Cordillera de Kampankis: Pongo de Chinim	CORBIDI 9368	CORBIDI 9368	JX847072	---	---	---	JX875658	---
O. cannatellai	Peru: Loreto: Cordillera de Kampankis: Pongo de Chinim	CORBIDI 9370	CORBIDI 9370	JX847074	---	JX875643	---	JX875660	---
O. cannatellai	Peru: Loreto: Cordillera de Kampankis: Pongo de Chinim	CORBIDI 9394	CORBIDI 9394	JX847075	---	JX875644	---	JX875661	---
O. cannatellai	Peru: Loreto: Quebrada Kampankis	CORBIDI 9507	CORBIDI 9507	JX847077	---	JX875645	---	JX875662	---
O. carri	Colombia: Boyacá: Pajarito N05°25'00"W72°40'00"	MAR1379	MAR 1379	**KF002033**	---	---	---	---	---
O. castaneicola	Bolivia: Pando: San Antonio	CBF 6051	CBF6051	FJ965300	---	---	---	---	---
O. castaneicola	Bolivia: Pando: San Antonio	NMP 6V73810_3	NMP 6V73810/3	FJ965301	---	---	---	---	---
O. castaneicola	Bolivia: Pando: San Antonio	NMP 6V 73820	NMP 6V 73820	FJ965303	---	---	---	---	---

O. castaneicola	Bolivia: Pando: San Antonio	NMP6d28_2009	NMP6d 28/2009	FJ965302	---	---	---	---	---
O. castaneicola	Peru: Cusco: Miaria S11°20'05"W73°01'16"	O_castaneicola_CPTG561_2764	MUSM 23918	**KF002034**	---	**KF002200**	**KF001889**	---	---
O. castaneicola	Peru: Madre de Dios: Gamitana S12°21'12"W69°02'08"	O_sp_MHNC8131_3149	MHNC 8131	**KF002035**	---	---	---	---	---
O. deridens	Ecuador: Orellana: Estacion Científica Yasuní	QCAZ 20711	QCAZ 20711	JX847083	---	JX875613	JX875817	---	JX875749
O. deridens	Ecuador: Orellana: Yasuní	QCAZ 20868	QCAZ 20868	JQ868501	---	---	---	JX875699	JQ868484
O. deridens	Ecuador: Orellana: Yasuní S00°41'00"W76°24'00"	O_deridens_KHJ06_1579	SMNS 14193	**KF002036**	**KF001959**	**KF002201**	---	---	---
O. deridens	Peru: Loreto: 28 km S Iquitos S04°02'00"W73°23'00"	O_deridens_Trier016_2730	KHJ-F 006	**KF002037**	---	**KF002202**	**KF001890**	---	---
O. deridens	Peru: Loreto: 35 km SW Iquitos	NMP6V71262/2	NMP 6V71262/2	FJ965304	---	---	---	---	---
O. festae	Ecuador: Loja: San Francisco	QCAZ39364	QCAZ 39364	HQ600648	---	HQ600615	JX875851	JX875715	JX875785
O. festae	Ecuador: Morona-Santiago: Río Napinaza	QCAZ38420	QCAZ 38420	HQ600646	---	HQ600613	JX875847	---	JX875781
O. festae	Ecuador: Zamora-Chinchipe: Miasí Alto	QCAZ41039	QCAZ 41039	HQ600647	---	HQ600614	JX875855	JX875716	JX875790
O. festae	Peru: Amazonas: Camñopite	CORBIDI 1965	CORBIDI 1965	JX847064	---	---	JX875803	---	JX875728
O. festae	Peru: Amazonas: Cataratas	CORBIDI 760	CORBIDI		---	---	JX875809	---	JX875738

	de Paraiso-Chonza Alta		760						
O. festae	Peru: Amazonas: Quebrada Goca	CORBIDI 10461	CORBIDI 10461	JX847071	---	JX875649	---	---	---
O. festae	Peru: San Martín: Cataratas de Ahuashiyacu	CORBIDI 9585	CORBIDI 9585	JX847079	---	JX875647	---	---	---
O. festae	Peru: San Martín: Cataratas de Ahuashiyacu	CORBIDI 9587	CORBIDI 9587	JX847080	---	JX875648	---	---	---
O. festae	Peru: San Martín: Río Lejia	CORBIDI 623	CORBIDI 623	HQ600649	---	HQ600616	JX875810	JX875705	JX875733
O. fuscifacies	Ecuador: Orellana: Yasuní	QCAZ 20788	QCAZ 20788	JQ868503	---	---	---	---	JQ868499
O. fuscifacies	Ecuador: Napo: Jatun Sacha S01°04'00"W77°37'00"	O_fuscifacies_KHJ4_1577	SMNS 14194	**KF002038**	**KF001960**	**KF002203**	---	---	---
O. fuscifacies	Ecuador: Orellana: Estación Científica Yasuní	QCAZ 20785	QCAZ 20785	HQ600631	---	HQ600598	JX875818	JX875685	JX875750
O. fuscifacies	Ecuador: Orellana: Yasuní	QCAZ 20790	QCAZ 20790	JQ868502	---	---	---	---	---
O. fuscifacies	Peru: Loreto: Andoas S02°54'19"W76°24'10"	O_fuscifacies_MHNC7678_3145	MHNC7678	**KF002024** **KF002024**	---	---	---	---	---
O. helenae	Bolivia: Santa Cruz: Mataracú S17°37'00"W63°37'00"	O_buckleyi_KHJhyl41_1607	(no voucher)	**KF002040**	---	---	---	---	---
O. helenae	Brazil: Acre: 5 km N Porto Walter S08°13'25"W72°44'40"	O_cabrerai_603	JPC 13178	AY843705	AY843950	---	---	---	---
O. helenae	Brazil: Acre: Catuaba S10°04'00"W63°37'00"	O_buckleyi_KHJhyl2_1596	SMNS 14190	**KF002041**	**KF001961**	---	---	---	---

O. helenae	Brazil: Acre: Catuaba S10°04'00"W63°37'00"	O_buckleyi_KHJhyl20_1598	SMNS 14191	**KF002042**	**KF001962**	**KF002204**	---	---	---
O. helenae	Brazil: Amapá: Igarapé Camaipí, Alto Rio Maracá S00°10'00"W51°42'00"	O_cabrerai_Camapi_AM_2119	MTR 6224	**KF002043**	**KF001963**	---	---	---	---
O. helenae	Brazil: Amapá: Igarapé Camaipí, Alto Rio Maracá S00°10'00"W51°42'00"	O_cabrerai_Camapi_AM_2121	MTR 6226	**KF002044**	**KF001964**	---	---	---	---
O. helenae	Brazil: Amazonas: Campo Tupana S04°09'00"W60°07'00"	O_buckleyi_SMS101_2840	SMS 101	**KF002045**	---	---	**KF001891**	---	---
O. helenae	Colombia: Amazonas: Leticia S04°11'57"W69°57'22"	O_cabrerai_JMP1956_3171	UA-A 745	**KF002046**	---	---	---	---	---
O. helenae	Colombia: Amazonas: Leticia S04°11'57"W69°57'22"	O_cabrerai_JMP2114_3173	UA-A 872	**KF002047**	---	---	---	---	---
O. helenae	Guyana: Potaro-Siparuni: Kaieteur NP N05°08'00"W59°25'00"	O_cf_buckleyi_PK1195_2724	IRSNB 14669	**KF002048**	**KF001892**	**KF002205**	---	---	---
O. helenae	Peru: Cusco: Comunidad Nativa Chokoriari	CORBIDI 8284	CORBIDI 8284	---	---	JX875610	---	---	JX875740
O. helenae	Peru: Cusco: Comunidad Nativa Poyentimari	CORBIDI 8267	CORBIDI 8267	---	---	JX875609	---	---	JX875739
O. helenae	Peru: Cusco: near Pongo de Mainique	CORBIDI 5505	CORBIDI 5505	---	---	JX875603	---	JX875654	---
O. helenae	Peru: Cusco: Rio Nusiniscato S13°07'58"W70°51'47"	O_sp_MHNC7004_3147	MHNC 7004	**KF002049**	---	---	---	---	---

O. helenae	Peru: Madre de Dios: Mazuco S13°06'58"W70°21'32"	O_buckleyi_MHNC8004_3096	MHNC 8004	**KF002050**	---	---	---	---	---
O. helenae	Peru: Pasco: Pampa Pescado S10°22'33"W75°14'36"	O_buckleyi_MHNC6606_3094	MHNC 6606	**KF002051**	---	---	---	---	---
O. helenae	Venezuela: Delta Amacuro: Reserva Forestal Río Grande N08°20'44"W61°41'06"	O_buckleyi_AJC3216_3163	MHNLS 20150	**KF002052**	---	---	---	---	---
O. helenae	Venezuela: Delta Amacuro: Reserva Forestal Río Grande N08°20'44"W61°41'06"	O_buckleyi_AJC3217_3167	MHNLS 20151	**KF002053**	---	---	---	---	---
O. heyeri	Colombia: Amazonas: Leticia S04°07'10"W69°57'04"	O_heyeri_AJC2581_3165	UA-A (number not yet assigned)	**KF002054**	---	---	---	---	---
O. heyeri	Colombia: Amazonas: Leticia S04°07'10"W69°57'04"	O_heyeri_JMP2205_3175	UA-A 948	**KF002055**	---	---	---	---	---
O. leoniae	Peru: Amazonas: Santa María de Nieva S04°37'00"W77°52'18"	O_leoniae_Trier129_2736	KHJ-F_TUN002	**KF002056**	---	**KF002206**	**KF001893**	---	---
O. leoniae	Peru: Pasco: EB Paujil S10°20'12"W75°15'39"	O_leoniae_MHNC6653_3193	MHNC6653	**KF002057**	---	---	---	---	---
O. leoniae	Peru: San Martín: 14 km NE Tarapoto S06°27'20"W76°18'30"	O_leoniae_KHJ11_1584	KHJ-F 112	**KF002058**	**KF001965**	---	---	---	---
O. leoniae	Peru: San Martín: nr.	O_leoniae_Trie	KHJ-F 104	**KF002059**	---	---	---	---	---

	Tarapoto S06°27'20"W76°18'30"	r025_2738							
O. leprieurii	French Guiana: Cayenne: Arataï N04°00'00"W52°34'00"	O_leprieurii_KHJhyl36_1606	SMNS 9278	**KF002060**	**KF001966**	**KF002207**	---	---	---
O. leprieurii	Guyana: Potaro-Siparuni: Kaieteur NP N05°14'00"W60°31'00"	O_leprieurii_PK1830_2712	IRSNB (not yet assigned)	**KF002061** **KF002062**	---	---	**KF001894**	---	---
O. leprieurii	Guyana: Potaro-Siparuni: Mabura Hill Forest Reserve N05°13'00"W58°48'00"	O_leprieurii_KHJ21_1591	SMNS 12056	**KF002063**	**KF001967**	**KF002208**	---	---	---
O. leprieurii	Guyana: Potaro-Siparuni: Wayalayeng Village N05°10'00"W59°30'00"	O_leprieurii_PK1235_2708	IRSNB 14656	**KF002064**	---	---	**KF001895**	---	---
O. leprieurii	Venezuela: Rio Uey, Bolívar N06°11'37"W61°31'30"	MHNLS 18619	MHNLS 18619	JQ868504	---	---	---	---	JQ868498
O. leprieurii	Venezuela: Rio Uey, Bolívar N06°11'37"W61°31'30"	MHNLS 18689	MHNLS 18689	JQ868505	---	---	---	---	JQ868497
O. leprieurii [Ca1_MTR12698_2834]	Brazil: Amazonas: Igarapé-Açu, Rio Abacaxis S04°24'00"W58°38'06"	O_sp_MTR12698_2834	MTR 12698	**KF002065**	---	**KF002209**	**KF001896**	---	---
O. leprieurii [Ca1_MTR12698_2834]	Brazil: Amazonas: Igarapé-Açu, Rio Abacaxis S04°24'00"W58°38'06"	O_sp_MTR12942_2820	MTR 12942	**KF002066**	---	**KF002210**	**KF001897**	---	---
O. leprieurii [Ca1_MTR12698_2834]	Brazil: Amazonas: Igarapé-Açu, Rio Abacaxis S04°24'00"W58°38'06"	O_sp_MTR12953_2812	MTR 12953	**KF002067**	---	---	**KF001898**	---	---
O. leprieurii	Brazil: Amazonas:	O_sp_MTR133	MTR	**KF002068**	---	**KF002211**	**KF001899**	---	---

[Ca1_MTR12698_2834]	Palhalzinho, Rio Abacaxis S04°18'06"W58°38'01"	33_2760	13333						
O. leprieurii [Ca1_MTR12698_2834]	Brazil: Amazonas: Ponta do Apinari, Rio Abacaxis S04º05'46"W58º41'58"	O_sp_MTR12664_2818	MTR 12664	**KF002069**	---	**KF002212**	**KF001900**	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Bolivia: Pando: Canadá	O_sp_NMP6V73105	NMP6V73105	FJ965298	---	---	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Bolivia: Pando: Nacebe	O_sp_NMP6V72173/1	NMP6V72173/1	FJ965298	---	---	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Bolivia: Pando: Nacebe	O_sp_NMP6V72173/3	NMP6V72173/3	FJ965308	---	---	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Bolivia: Pando: Palmira	O_sp_NMP6d41/2009	NMP 6d41/2009	FJ965297	---	---	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Bolivia: Santa Cruz: PN Noel Kempff Mercado S14°33'00"W60°56'00"	O_sp_KHJhyl24_1600	CBF (number not yet assigned)	**KF002070**	**KF001968**	**KF002213**	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Brazil: Amazonas: Cachoeira das Pombas, Rio Aripuanã S06°24'00"W60°21'00"	O_sp_CdasPombas_AMZ_2133	MTR 10220	**KF002071**	---	**KF002214**	---	---	---
O. leprieurii [Ca2_NMP6d41/2009]	Peru: Madre de Dios: Nueva Arequipa S12°54'34"W69°59'34"	O_sp_MHNC8214_3082	MHNC 8214	**KF002072**	---	---	---	---	---
O. mimeticus	Peru: Cusco: Cabecera Mabe	O_mimeticus_	MHNC	**KF002073**	---	---	---	---	---

	S13°06'44"W70°54'51"	MHNC7021_3159	7021						
O. mimeticus	Peru: Cusco: Cabecera Mabe S13°06'44"W70°54'51"	O_ mimeticus _MHNC7395_3074	MHNC 7395	**KF002074**	---	---	---	---	---
O. mimeticus	Peru: Cusco: ZR Nahua Kugapakori S11°51'57"W72°46'20"	O_sp_CPTG51 1_2796	MUSM 23180	**KF002075** **KF002076**	---	---	**KF001901**	---	---
O. mimeticus	Peru: Huánuco: Fundo Flor, Río Pachitea S09°40'30"W74°56'30"	O_mimeticus_ KHJ2_1576	SMNS 14150	**KF002077**	**KF001969**	**KF002215**	---	---	---
O. mimeticus	Peru: Huánuco: Boquerón del Padre Abad S09°04'27"W75°41'00"	O_mimeticus_ KHJ16_1588	KHJ-F 106	**KF002078**	**KF001970**	**KF002216**	---	---	---
O. mimeticus	Peru: San Martín: 14 km NE Tarapoto S06°27'18"W76°18'30"	O_mimeticus_ KHJ10_1583	KHJ-F 105	**KF002079**	**KF001971**	**KF002217**	---	---	---
O. mutabor	Ecuador: Napo: Carretera Jondachi-Coca km 44 S00°42'24"W77°35'54"	O_mutabor_K HJhyl8_1597	EPN-H 6659	**KF002080**	**KF001972**	---	---	---	---
O. mutabor	Ecuador: Napo: Chontapuntas	QCAZ 28646	QCAZ 28646	HQ600641	---	HQ600608	JX875834	JX875721	JX875766
O. mutabor	Ecuador: Napo: Chontapuntas	QCAZ 28647	QCAZ 28647	HQ600642	---	HQ600609	JX875835	JX875675	JX875767
O. mutabor	Ecuador: Napo: Huino	QCAZ 30925	QCAZ 30925	---	---	JX875620	JX875837	JX875690	JX875769
O. mutabor	Ecuador: Napo: Huino	QCAZ 30926	QCAZ 30926	HQ600643	---	HQ600610	JX875838	JX875711	JX875770

O. mutabor	Ecuador: Orellana: Pompeya-Iró Road at km 22	QCAZ 42999	QCAZ 42999	HQ600645	---	HQ600612	JX875857	JX875723	JX875792
O. mutabor	Ecuador: Pastaza: Colonia Mariscal Sucre	QCAZ 40253	QCAZ 40253	HQ600644	---	HQ600611	JX875853	JX875695	JX875787
O. mutabor	Ecuador: Pastaza: Río Pucayacu, Colonia Mariscal Sucre	QCAZ 29430	QCAZ 29430	JX847088	---	JX875619	JX875836	JX875704	JX875768
O. "mutabor"	Ecuador: Sucumbíos: Puerto Bolívar	QCAZ 28223	QCAZ 28223	HQ600638	---	HQ600605	JX875829	JX875682	JX875682
O. "mutabor"	Ecuador: Morona Santiago: Nuevo Israel	QCAZ 46470	QCAZ 46470	JX847102	---	JX875636	JX875861	JX875697	---
O. "mutabor"	Ecuador: Morona Santiago: Nuevo Israel	QCAZ 46471	QCAZ 46471	JX847103	---	JX875637	JX875862	JX875698	JX875796
O. "mutabor"	Ecuador: Pastaza: Canelos	QCAZ 41030	QCAZ 41030	JX847098	---	JX875632	---	JX875673	JX875789
O. "mutabor"	Ecuador: Pastaza: Pomona	QCAZ 25603	QCAZ 25603	HQ600631	---	HQ600598	JX875824	JX875676	JX875756
O. "mutabor"	Ecuador: Pastaza: Pomona	QCAZ 25684	QCAZ 25684	JX847085	---	JX875615	JX875825	JX875700	JX875757
O. "mutabor"	Ecuador: Pastaza: Pomona	QCAZ 25603	QCAZ 25603	HQ600631	---	HQ600598	JX875824	---	JX875756
O. "mutabor"	Peru: Amazonas: Cordillera de Kampankis	CORBIDI 9369	CORBIDI 9369	JX847073	---	JX875642	---	JX875659	---
O. "mutabor"	Peru: Loreto: 1.5 km N Teniente Lopez	KU 221930	KU 221930	DQ380379	---	---	---	---	---
O. "mutabor"	Peru: Loreto: Andoas	CORBIDI 4645	CORBIDI 4645	---	---	JX875601	---	JX875652	JX875729

O. oophagus	Brazil: Amazonas: E. E. Anavilhanas S02°32'00"W60°50'00"	O_oophagus_MSH10225_2099	MSH 10225	**KF002081**	**KF001973**	---	---	---	---
O. oophagus	Brazil: Amazonas: Reserva Ducke S02°55'00"W59°59'00"	O_oophagus_KHJhyl26_1602	SMNS 10802	**KF002082**	**KF001974**	**KF002249**	---	---	---
O. oophagus	Brazil: Roraima: mouth of Rio Branco	USNM 302469	USNM 302469	JQ868514	---	---	---	---	---
O. oophagus	Brazil: Roraima: mouth of Rio Branco	USNM FS008803	USNM FS008803	JQ868515	---	---	---	---	---
O. oophagus	Guyana: Potaro-Siparuni: Kaieteur NP N05°08'00"W59°25'00"	O_oophagus_PK1334_2720	IRSNB 14657	**KF002083**	---	**KF002218**	---	---	---
O. oophagus	Guyana: Potaro-Siparuni: Kaieteur NP N05°08'00"W59°25'00"	O_oophagus_PK1357_2716	IRSNB 14659	**KF002084**	---	**KF002219**	**KF001902**	---	---
O. oophagus	Guyana: Potaro-Siparuni: Mabura Hill Forest Reserve N05°13'00"W58°48'00"	O_oophagus_KHJ20_1593	SMNS 12060	**KF002085**	**KF001975**	**KF002220**	---	---	---
O. planiceps	Colombia: Amazonas: Leticia S04°05'54"W69°58'30"	O_sp_KHJ13_1586	SMNS 14196	**KF002086**	---	**KF002221**	---	---	---
O. planiceps	Colombia: Amazonas: Leticia S04°05'54"W69°58'30"	O_sp_Trier020_2732	SMNS 14196/2	**KF002087**	---	**KF002222**	**KF001903**	---	---
O. planiceps	Ecuador: Napo: Jatun Sacha S01°04'00"W77°37'00"	O_planiceps_KHJ07_1580	SMNS 14195	**KF002088**	---	---	---	---	---
O. planiceps	Ecuador: Orellana: Estación	QCAZ 19195	QCAZ	JQ868521	---	---	---	---	JQ868495

	Científica Yasuní		19195						
O. planiceps	Ecuador: Orellana: Estación Científica Yasuní	QCAZ 20797	QCAZ 20797	HQ600632	---	HQ600599	JX875819	JX875665	JX875751
O. planiceps	Ecuador: Sucumbios: Cuyabeno	QCAZ 18844	QCAZ 18844	JQ868520	---	---	---	---	JQ868496
O. planiceps	Peru: Loreto: Anguilla	O_planiceps_NMP6V71264/1	NMP 6V71264/1	FJ965306	---	---	---	---	---
O. planiceps	Peru: Loreto: Anguilla	O_planiceps_NMP6V71264/2	NMP 6V71264/2	FJ965307	---	---	---	---	---
O. planiceps	Peru: Loreto: Confluence of Ríos Blanco and Negro (= Rio Peneya) S00°19'00"W74°55'51"	O_planiceps_MHNC6369_3161	MHNC 6369	**KF002089** **KF002090**	---	---	---	---	---
O. planiceps	Peru: Loreto: Puerto Almendras	O_planiceps_NMP6V71174/1	NMP 6V71174/1	FJ965305	---	---	---	---	---
O. planiceps	Peru: Loreto: San Jacinto	DQ380380	KU 221933	DQ380380	---	---	---	---	---
O. planiceps	Peru: Ucayali: Imiria S08°51'00"W74°19'00"	O_sp_GG1_2802	GGU 752	**KF002091**	---	---	**KF001904**	---	---
O. planiceps [Ca1_Neblina411]	Venezuela: Amazonas: Neblina Base Camp Rio Mawarinuma (= Rio Baria), 140 m N00°50'00"W66°10'00"	O_aff_planiceps_Neblina_411	AMNH A-131254	AY549361	AY843952	**KF002223**	**KF001905**	---	---
O. subtilis	Brazil: Acre: Cruzeiro do Sul: Mata do BIS S07°36'38"W72°40'39"	TG 2977_3341	TG 2977	**KF002092**	---	---	---	---	---
O. subtilis	Brazil: Acre: Cruzeiro do	TG 2978_3343	TG 2978	**KF002093**	---	---	---	---	---

	Sul: Mata do BIS S07°36'38"W72°40'39"								
O. subtilis	Peru: Loreto/Requena: Río Buncuya S06°14'00"W74°24'00"	GG2_2770	GGU 901	**KF002094**	---	---	**KF001906**	---	---
O. taurinus	Bolivia: Pando: Santa Crucito	O_taurinus_JM 2007/60	JM 2007/60	FJ965296	---	---	---	---	---
O. taurinus	Bolivia: La Paz: Chalalán S14°25'29"W67°55'14"	O_taurinus_MNCN2410_3177	MNCN 2410	**KF002095** **KF002096**	---	---	---	---	---
O. taurinus	Bolivia: La Paz: Chalalán S14°25'29"W67°55'14"	O_taurinus_MNCN2814_3187	MNCN 2814	**KF002146**	---	---	---	---	---
O. taurinus	Bolivia: La Paz: Chalalán S14°25'29"W67°55'14"	O_ taurinus_MNCN2833_3202	MNCN 2833	**KF002097**	---	---	---	---	---
O. taurinus	Bolivia: La Paz: Chalalán, Madidi S14°25'29"W67°55'14"	O_sp_KHJ23_1594	MNCN (number not yet assigned)	**KF002098** **KF002099**	**KF001976**	**KF002224**	---	---	---
O. taurinus	Bolivia: La Paz: Heath River Wildlife Centre S12°40'48"W68°42'42"	O_taurinus_MNCN34608_3191	MNCN 34608	**KF002100**	---	---	---	---	---
O. taurinus	Bolivia: Pando: San Sebastián, EB Tahuamanu S11°24'00"W69°01'00"	O_taurinus_MNCN6143_3189	MNCN 6143	**KF002101**	---	---	---	---	---
O. taurinus	Brazil: Amazonas: Areal, Rio Abacaxis	O_sp_MTR13055_2772	MTR 13055	**KF002102** **KF002103**	---	---	**KF001907**	---	---

O. taurinus	Brazil: Amazonas: Areal, Rio Abacaxis S04°35'49"W58°13'14"	O_sp_MTR13081_2774	MTR 13081	**KF002104**	---	**KF002225**	**KF001908**	---	---
O. taurinus	Brazil: Amazonas: Cachoeirinha, Rio Madeira S05°29'00"W60°49'00"	O_sp_Cachoeirinha_AM_2096	VOGT 2213	**KF002105**	**KF001977**	**KF002226**	---	---	---
O. taurinus	Brazil: Amazonas: Campo Tupana S04°09'00"W60°07'00"	O_sp_SMS088_2854	SMS 088	**KF002106**	---	---	**KF001909**	---	---
O. taurinus	Brazil: Amazonas: Campo Tupana S04°09'00"W60°07'00"	O_taurinus_SMS132_2846	SMS 132	**KF002107**	---	---	**KF001910**	---	---
O. taurinus	Brazil: Amazonas: Campo Tupana S04°09'00"W60°07'00"	O_taurinus_SMS154_2860	SMS 154	**KF002108**	---	---	---	---	---
O. taurinus	Brazil: Amazonas: E. E. Anavilhanas S02°32'00"W60°50'00"	O_taurinus_MSH10223_2103	MSH 10223	**KF002109**	**KF001978**	---	---	---	---
O. taurinus	Brazil: Amazonas: Igarapé-Açu, Rio Abacaxis S04°21'00"W58°38'00"	O_sp_MTR12699_2778	MTR 12699	**KF002110**	---	---	**KF001911**	---	---
O. taurinus	Brazil: Amazonas: Manaus, Conjunto Pedro S03°06'00"W60°01'0"	APL 17872_4430	APL 17872	**KF002111** **KF002112**	---	---	---	---	---
O. taurinus	Brazil: Amazonas: Ponta do Apinari S04°05'46"W58°41'58"	O_taurinus_MTR12667_2746	MTR 12667	**KF002113**	---	**KF002227**	**KF001912**	---	---

O. taurinus	Brazil: Amazonas: Ponta do Apinari S04°35'49"W58°13'14"	O_taurinus_MTR12668_2824	MTR 12668	**KF002114**	---	---	**KF001913**	---	---
O. taurinus	Brazil: Amazonas: Ponta do Apinari S04°35'49"W58°13'14"	O_taurinus_MTR12669_2814	MTR 12669	**KF002115**	---	---	**KF001914**	---	---
O. taurinus	Brazil: Amazonas: Ponta do Apinari S04°35'49"W58°13'14"	O_taurinus_MTR12673_2826	MTR 12673	**KF002116**	---	**KF002228**	**KF001915**	---	---
O. taurinus	Brazil: Amazonas: Samaúma, Lábrea, Rio Purus S07°18'21"W64°48'49"	O_taurinus_MTR15749_2810	MTR 15749	**KF002117**	---	**KF002229**	**KF001916**	---	---
O. taurinus	Brazil: Amazonas: Samaúma, Lábrea, Rio Purus S07°18'21"W64°48'49"	O_taurinus_MTR16711_2752	MTR 16711	**KF002118**	---	**KF002230**	**KF001917**	---	---
O. taurinus	Brazil: Amazonas: Campo Tupana S04°09'00"W60°07'00"	O_taurinus_SMS086_2852	SMS 086	**KF002147**	---	---	**KF001945**	---	---
O. taurinus	Brazil: Maranhão: Carolina S07°15'27"W47°30'50"	O_taurinus_Carolina_MA_2117	MTR (ESTR1186)	**KF002119**	**KF001979**	---	---	---	---
O. taurinus	Brazil: Maranhão: Estreito S05°47'00"W43°15'00"	O_taurinus_Estreito_MA_2128	MTR (ESTR0454)	**KF002120**	**KF001980**	---	---	---	---
O. taurinus	Brazil: Mato Grosso: Aripuanã S10°19'00"W59°23'00"	O_taurinus_AripuanaII_MT_2145	MZUSP 87691	**KF002121**	**KF001981**	**KF002231**	---	---	---
O. taurinus	Brazil: Mato Grosso: Cláudia	O_taurinus_Cl	MZUSP	**KF002122**	**KF001982**	---	---	---	---

	S11°35'06"W55°08'08"	audia_MT_2105	83103						
O. taurinus	Brazil: Mato Grosso: Guaporé S15°06'32"W58°57'21"	O_sp_Guapore_MT_2108	MTR (RGA5739)	**KF002123**	**KF001983**	---	---	---	---
O. taurinus	Brazil: Mato Grosso: Juruena S10°17'38"W58°29'34"	O_taurinus_Juruena_MT_2139	MZUSP 86094	**KF002124**	**KF001984**	---	---	---	---
O. taurinus	Brazil: Mato Grosso: UHE Manso S14°50'55"W55°42'31"	O_sp_APMManso_MT_2131	MTR (AF 717)	**KF002125**	**KF001985**	**KF002232**	---	---	---
O. taurinus	Brazil: Mato Grosso: Vila Rica S09°58'02"W51°06'34"	O_taurinus_VilaRica_MT_2143	MTR 978084	**KF002126**	**KF001986**	---	---	---	---
O. taurinus	Brazil: Piauí: Uruçuí-Una S08°50'00"W44°10'00"	O_sp_MRT2332_2115	MTR 2332	**KF002127**	**KF001987**	**KF002233**	---	---	---
O. taurinus	Brazil: Piauí: Uruçuí-Una S08°50'00"W44°10'00"	O_sp_MRT1939_2137	MTR 1939	**KF002128**	---	---	---	---	---
O. taurinus	Brazil: Tocantins: Peixe S12°14'48"W48°25'43"	O_sp_Peixe_TO_2110	MRT 3939	**KF002129**	**KF001988**	---	---	---	---
O. taurinus	Brazil: Tocantins: Wanderlandia S06°53'07"W47°55'37"	O_sp_TMC179_2417	CFBH 28476	**KF002130**	**KF001989**	---	**KF001918**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7670_2828	MTR 7670	**KF002131** **KF002132**	---	---	**KF001919**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia	O_sp_MTR7741_2832	MTR 7741	**KF002133**	---	---	**KF001920**	---	---

	S07°12'04"W47°45'56"								
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7742_2830	MTR 7742	**KF002134**	---	---	**KF001921**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7743_2808	MTR 7743	**KF002135**	---	---	**KF001922**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7782_2816	MTR 7782	**KF002136**	---	**KF002234**	**KF001923**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7783_2750	MTR 7783	**KF002137**	---	---	**KF001924**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7868_2836	MTR 7868	**KF002138**	---	---	**KF001925**	---	---
O. taurinus	Brazil: Tocantins: Babaçulândia S07°12'04"W47°45'56"	O_sp_MTR7869_2822	MTR 7869	**KF002139**	---	---	**KF001926**	---	---
O. taurinus	Brazil: Tocantins: Guarai S08°36'28"W48°18'14"	O_sp_Guarai_TO_2114	MTR 7132	**KF002140**	**KF001990**	**KF002235**	---	---	---
O. taurinus	Brazil: Tocantins: Guarai S08°38'28"W48°25'24"	O_taurinus_Guarai_TO_2148	MTR 7454	**KF002141**	**KF001991**	**KF002236**	---	---	---
O. taurinus	Brazil: Tocantins: Lizarda S09°35'00"W46°40'30"	O_sp_CFBHt3784_3046	CFBH 13234	**KF002142**	---	---	---	---	---
O. taurinus	Brazil: Tocantins: Palmeirante S07°53'15"W47°54'59"	O_sp_Palmeirante_TO_2126	MTR (ESTR1652)	**KF002143**	---	**KF002237**	---	---	---

O. taurinus	Ecuador: Sucumbíos: Cuyabeno	QCAZ 18839	QCAZ 18839	JQ868513	---	---	---	---	JQ868488
O. taurinus	Ecuador: Zamora Chinchipe: Shaime, Nangaritza	QCAZ 18230	QCAZ 18230	HQ600630	---	HQ600597	---	JX875719	---
O. taurinus	Peru: Loreto: Teniente López	KU 221941	KU 221941	AY819380	EU034065	AY819512	EU034050	---	AY819130
O. taurinus	Peru: Madre de Dios: Gamitana S12°21'12"W69°02'08"	O_taurinus_MHNC8130_3153	MHNC 8130	**KF002144**	---	---	---	---	---
O. taurinus	Peru: Madre de Dios: Cusco Amazonico	WED 55452	WED 55452	AY326041	---	---	---	---	---
O. taurinus	Peru: Madre de Dios: Reserva Nacional Tambopata S12°49'00"W69°18'00"	O_sp_FS2380_2804	FS 2380	**KF002145**	---	---	**KF001927**	---	---
O. taurinus [Ca1_MHNC6667_3151]	Peru: Pasco: EB Paujil S10°19'25"W75°15'50"	O_taurinus_MHNC6667_3151	MHNC 6667	**KF002148** **KF002149**	---	---	---	---	---
O. taurinus [Ca2_Neblina410]	Venezuela: Amazonas: Neblina Base Camp Rio Mawarinuma (= Rio Baria), 140 m N00°50'00"W66°10'00"	O_sp_Neblina_410	AMNH A-131245	AY843709	AY843954	**KF002238**	**KF001928**	---	---
O. taurinus [Ca3_AJC2959_3181]	Venezuela: Amazonas: Puerto Ayacucho N05°39'58"W67°38'04"	MHNLS 18325	MHNLS 18325	JQ868506	---	---	---	---	---
O. taurinus [Ca3_AJC2959_318	Venezuela: Amazonas: Puerto Ayacucho-Gavilan	O_taurinus_AJC3091_3183	MHNLS 20034	**KF002150**	---	---	---	---	---

1]	N05°32'48"W67°26'54"								
O. taurinus [Ca3_AJC2959_3181]	Venezuela: Amazonas: Río Cuao, Salto del Danto N05°02'39"W67°33'38"	O_taurinus_AJC2959_3181	MHNLS 19907	**KF002151**	---	---	---	---	---
O. taurinus [Ca3_AJC2959_3181]	Venezuela: Amazonas: Tobogan de la Selva N05°23'12"W67°37'02"	O_taurinus_AJC3146_3179	MHNLS 20083	**KF002152**	---	---	---	---	---
O. taurinus [Ca4_PHV2439_2671]	Brazil: Mato Grosso: Barra do Garças S15°53'30"W52°15'48"	O_sp_PHV2692_2670	PHV 2692	**KF002153**	---	---	**KF001929**	---	---
O. taurinus [Ca4_PHV2439_2671]	Brazil: Mato Grosso: Barra do Garças S15°53'30"W52°15'48"	O_sp_PHV2693_2669	PHV 2693	**KF002154**	---	---	---	---	---
O. taurinus [Ca4_PHV2439_2671]	Brazil: Mato Grosso: Água Boa S14°03'19"W52°09'31"	O_sp_PHV2439_2671	PHV 2439	**KF002155**	---	---	**KF001930**	---	---
O. taurinus [Ca4_PHV2439_2671]	Brazil: Mato Grosso: Água Boa S14°03'19"W52°09'31"	O_sp_PHV2454_2668	PHV 2454	**KF002156**	---	---	**KF001931**	---	---
O. taurinus [Ca4_PHV2439_2671]	Brazil: Mato Grosso: Gaúcha do Norte S13°11'00"W53°15'23"	O_sp_GauchadoN_MT_2130	MZUSP 83707	**KF002157**	**KF001992**	---	---	---	---
O. taurinus [Ca5_SMNS12063]	Brazil: Amapá: Igarapé Camaipí, Alto Rio Maracá S00°10'00"W51°42`00"	O_taurinus_Camapi_AM_2141	MTR 6365	**KF002158**	**KF001993**	**KF002239**	---	---	---
O. taurinus [Ca5_SMNS12063]	Brazil: Amapá: Serra do Navio N00°52'00"W52°07'00"	O_taurinus_MTR13797_2756	MTR 13797	**KF002159** **KF002160**	---	---	**KF001932**	---	---

O. taurinus [Ca5_SMNS12063]	Brazil: Amapá: Serra do Navio N00°52'00"W52°07'00"	O_taurinus_MTR13798_2838	MTR 13798	**KF002160**	---	---	**KF001933**	---	---
O. taurinus [Ca5_SMNS12063]	French Guiana: Cayenne: Kaw Road N04°33'00"W52°06'00"	O_taurinus_FrenchG_679	MNHN 2001.0828	AY843708	AY843953	---	---	---	---
O. taurinus [Ca5_SMNS12063]	Guyana: Potaro-Siparuni: Kaieteur NP N05°08'00"W59°25'00"	O_taurinus_PK1308_2718	IRSNB 14682	**KF002162**	---	---	---	---	---
O. taurinus [Ca5_SMNS12063]	Guyana: Potaro-Siparuni: Kaieteur NP N05°08'00"W59°25'00"	O_taurinus_PK1370_2714	IRSNB 14704	**KF002163**	---	---	**KF001934**	---	---
O. taurinus [Ca5_SMNS12063]	Guyana: Potaro-Siparuni: Mabura Hill Forest Reserve N05°13'00"W58°48'00"	O_taurinus_KHJ19_1590	SMNS 12063	**KF002164**	**KF001994**	**KF002240**	---	---	---
O. taurinus [Ca5_SMNS12063]	Guyana: Potaro-Siparuni: Wayalayeng Village N05°14'00"W60°31'00"	O_taurinus_PK1829_2722	IRSNB not yet assigned	**KF002165**	---	---	**KF001935**	---	---
O. taurinus [Ca5_SMNS12063]	Venezuela: Bolívar: Río Uey N06°11'37"W61°31'30"	MHNLS 18663	MHNLS 18663	JQ868509	---	---	---	---	JQ868490
O. taurinus [Ca5_SMNS12063]	Venezuela: Bolívar: Río Uey N06°11'37"W61°31'30"	MHNLS 18715	MHNLS 18715	JQ868510	---	---	---	---	JQ868489
O. taurinus [Ca5_SMNS12063]	Venezuela: Bolívar: Las Claritas	PS 004	PS 004	JQ868512.1	---	---	---	---	JQ868487
O. taurinus [Ca5_SMNS12063]	Venezuela: Bolívar: Purumay N05°55'03"W62°45'00"	MHNLS 15622	MHNLS 15622	JQ868507	---	---	---	---	JQ868492

O. taurinus [Ca5_SMNS12063]	Venezuela: Bolívar: Río Atepere N05°43'30"W62°34'55"	MHNLS 17336	MHNLS 17336	JQ868508	---	---	---	---	JQ868491
O. taurinus [Ca5_SMNS12063]	Venezuela: Delta Amacuro: Reserva Forestal Rio Grande N08°19'21"W61°43'32"	O_taurinus_AJ C3270_3185	MHNLS 20201	**KF002166**	---	---	---	---	---
O. taurinus [Ca5_SMNS12063]	Venezuela: Imataca: Río Grande N08°20'44"W61°41'06"	MHNLS 19633	MHNLS 19633	JQ868511	---	---	---	---	---
O. verruciger	Colombia: Caquetá: Florencia: Corregimiento El Caraño, Vereda Las Brisas, Finca Los Lirios, Carretera Florencia–Suiza km 28 N01°46'00"W75°42'00"	TG1785	TG 1785	**KF002167**	---	---	---	---	---
O. verruciger	Colombia: Caquetá: Municipio de Florencia: Vereda Sucre N01°48'05"W75°39'01"	MAR1953	MAR 1953	**KF002168**	---	---	---	---	---
O. verruciger	Colombia: Caquetá: Florencia, Corregi miento El Caraño, Vereda Las Brisas, Carretera Suaza-Florencia, km 46.8 N01°44'57"W75°44'40"	TG1746	TG 1746	**KF002169**	---	---	---	---	---
O. verruciger	Ecuador: Morona Santiago: Río Napinaza	QCAZ 26304	QCAZ 26304	---	---	JX875616	---	---	JX875758
O. verruciger	Ecuador: Napo, 30 km of	QCAZ45344	QCAZ	JX847100	---	JX875634	JX875859	JX875684	JX875794

	Baeza		45344						
O. verruciger	Ecuador: Napo: Cascada de San Rafael	QCAZ 13225	QCAZ 13225	JQ868517	---	---	---	---	JQ868486
O. verruciger	Ecuador: Napo: Cascada de San Rafael	QCAZ 32032	QCAZ 32032	HQ600658	---	HQ600625	JX875842	JX875669	JX875774
O. verruciger	Ecuador: Napo: Cordillera de los Guacamayos	QCAZ 41108	QCAZ 41108	HQ600660	---	HQ600627	JX875856	JX875683	JX875791
O. verruciger	Ecuador: Napo: Cosanga	QCAZ 15942	QCAZ 15942	HQ600659	---	HQ600626	JX875813	JX875679	JX875743
O. verruciger	Ecuador: Napo: km 13 Loreto-Coca road	QCAZ 22201	QCAZ 22201	JX847084	---	JX875614	JX875820	JX875666	JX875752
O. verruciger	Ecuador: Napo: Rio Azuela, 9.5 km W Reventador	KU 217751	KU 217751	DQ380381	---	---	---	---	---
O. verruciger	Ecuador: Napo: Río Salado	QCAZ 17285	QCAZ 17285	JX847082	---	JX875612	---	JX875706	JX875746
O. verruciger	Ecuador: Napo: Río Salado	QCAZ 17283	QCAZ 17283	JQ868518	---	---	---	---	---
O. verruciger	Ecuador: Sucumbios, Rosa Florida	QCAZ 20544	QCAZ 20544	HQ600655	---	HQ600622	JX875816	JX875664	JX875748
O. verruciger	Ecuador: Sucumbíos: Río Azuela	QCAZ 15991	QCAZ 15991	HQ600656	---	HQ600623	JX875814	JX875681	JX875745
O. verruciger	Ecuador: Sucumbíos: Río Azuela S0°04'48'"W77°35'24"	O_verruciger_KHJ09_1582	SMNS 14197	**KF002170**	**KF001995**	**KF002241**	---	---	---
O. verruciger	Peru: Amazonas: Cabecera de la Quebrada Katerpiza	CORBIDI 9477	CORBIDI 9477	---	---	JX847076	---	---	---

O. verruciger	Peru: Loreto: Cabecera de la Quebrada Wee	CORBIDI 9525	CORBIDI 9525	JX847078	---	JX875646	---	---	---
O. yasuni	Brazil: Acre: Tarauacá S08°09'39"W70°45'57"	O_sp_CFBH15715_2338	CFBH 15715	**KF002171**	**KF001996**	---	**KF001936**	---	---
O. yasuni	Ecuador: Orellana: Yasuní	QCAZ 19245	QCAZ 19245	JQ868519	---	---	---	---	JQ868485
O. yasuni	Ecuador: Orellana: Yasuní S00°41'00"W76°24'00"	O_yasuni_KHJ08_1581	SMNS 14198	**KF002172**	**KF001997**	**KF002242**	---	---	---
O. yasuni	Ecuador: Orellana: Yasuní S00°41'00"W76°24'00"	O_yasuni_KHJhyl31_1605	SMNS 14199	**KF002173**	---	---	---	---	---
O. yasuni	Ecuador: Sucumbíos: Playas de Cuyabeno	QCAZ 27816	QCAZ 27816	HQ600636	---	HQ600603	JX875826	JX875688	JX875759
O. yasuni	Ecuador: Sucumbíos: Zábalo	QCAZ 27998	QCAZ 27998	HQ600637	---	HQ600604	JX875828	JX875667	JX875761
O. yasuni	Peru: Loreto: Confluence of Ríos Blanco and Negro (= Rio Peneya) S00°19'00"W74°55'51"	O_sp_MHNC6367_3155	MHNC 6367	**KF002174**	---	---	---	---	---
O. yasuni	Peru: Loreto: Río Iauasiyacu S03°20'25"W71°59'34"	O_yasuni_Trier027_2734	KHJ-F 113	**KF002175**	---	**KF002243**	**KF001937**	---	---
O. yasuni	Peru: Loreto: Río Sucusari	O_sp_FS2576_2800	TNHC-FS 2576	**KF002176**	---	---	**KF001938**	---	---
O. yasuni	Peru: Loreto: Río Sucusari S03°15'54"W72°05'05"	O_sp_FS2581_2780	TNHC-FS 2581	**KF002177**	---	---	**KF001944**	---	---
Osteopilus dominicensis	Pet trade		AMNH A-168410	AY843711	AY843956	---	---	---	---
Osteopilus septentrionalis	Cuba: Guantanamo: Guantanamo Bay		USNM 317830	AY843712	AY843957	---	**KF001943**		**KF002004**

Osteopilus vastus	Pet trade		AMNH A-168415	AY843713	AY843958	---	---	---	---
Phyllodytes luteolus	Brazil: Espírito Santo: Setiba, Guarapri		no voucher	AY843721	AY843966	GQ366314	---	---	GQ366043
Phytotriades auratus	No data	LM 1311		AY819383	DQ403739	AY819515	---	---	AY819133
Tepuihyla aecii	Venezuela: Amazonas: Duida Tepui	MHNLS 12013	MHNLS 12013	JQ868533	---	---	---	---	---
Tepuihyla aff. *edelcae*	Venezuela: Bolívar: Chimantá		IRSNB158 79	JQ742232	---	JQ742399	---	---	---
Tepuihyla aff. *edelcae*	Venezuela: Bolívar: Chimantá		IRSNB158 80	JQ742233	---	JQ742400	---	---	---
Tepuihyla aff. *edelcae*	Venezuela: Bolívar: Chimantá	PS 001	PS 001	JQ868536	---	---	---	---	JQ868476
Tepuihyla aff. *edelcae*	Venezuela: Bolívar: Chimantá	PS 268	PS 268	JQ868538	---	---	---	---	---
Tepuihyla edelcae	Venezuela: Bolívar: Auyantepui	MHNLS 05824	MHNLS 05824	JQ868535	---	---	---	---	---
Tepuihyla edelcae	Venezuela: Bolívar: Auyantepui	MHNLS 16090	MHNLS 16090	JQ868534	---	---	---	---	JQ868477
Tepuihyla edelcae	Venezuela: Bolívar: Auyantepui N05°52'00"W62°34'00"	Tepuihyla_edelcae_671	MNHNP 1998-311	AY843770	---	---	---	---	---
Tepuihyla edelcae	Venezuela: Bolívar: Auyantepui	PS 002	PS 002	JQ868537	---	---	---	---	JQ868475
Tepuihyla exophthalma	Guyana: District 7: Mt. Ayanganna N05°24'00'W59°57'00"	O_phasmatus_ROM39482_2132	ROM 39482	**KF002178**	**KF001998**	**KF002244**	---	---	---

Tepuihyla exophthalma	Guyana: District 7: Mt. Wokomung N05°05'00'W59°50'00"	O_phasmatus_ ROM43853_2127	ROM 43853	**KF002179**	**KF001999**	**KF002245**	---	---	---
Tepuihyla exophthalma	Guyana: Mazaruni-Potaro: Imbaimadai	BPN 166	BPN 166	JQ868523	---	---	---	---	---
Tepuihyla exophthalma	Guyana: Mazaruni-Potaro: First plateau of the Wokomung Massif	O_sp_1568	CPI 10290	**KF002180**	**KF002002**	---	---	---	---
Tepuihyla exophthalma	Guyana: Potaro-Siparuni: Kaieteur NP N05°10'00"W59°30'00"	O_exophtalmus_PK1275_2706	IRSNB 14644	**KF002181**	---	---	**KF001939**	---	---
Tepuihyla exophthalma	Guyana: Potaro-Siparuni: Kaieteur NP N05°10'00"W59°30'00"	O_sp_PK1301_2710	IRSNB 14673	**KF002182**	---	---	**KF001940**	---	---
Tepuihyla exophthalma	Venezuela: Bolívar: Luepa	MHNLS 19583	MHNLS 19583	JQ868524	---	---	---	---	---
Tepuihyla exophthalma	Venezuela: Bolívar: Luepa	MHNLS 19584	MHNLS 19584	JQ868525	---	---	---	---	JQ868483
Tepuihyla rodriguezi	Guyana	BPN 1101	BPN 1101	JQ868541	---	---	---	---	---
Tepuihyla rodriguezi	Guyana	BPN 1219	BPN 1219	JQ868542	---	---	---	---	JQ868473
Tepuihyla rodriguezi	Guyana: Mazaruni-Potaro: Imbaimadai	BPN 1218	BPN 1218	DQ380389	---	EU034094	EU034059	---	EU034131
Tepuihyla rodriguezi	Guyana: Mazaruni-Potaro: Wei Assipu summit N05°13'00"W60°42'30"	Tepuihyla_galani_1390	CPI 10223	**KF002183**	**KF002000**	---	**KF001941**	---	---
Tepuihyla rodriguezi	Guyana: Mazaruni-Potaro:		IRSNB	JQ742223	---	JQ742390	---	---	---

	Wei Assipu Tepui		15861						
Tepuihyla rodriguezi	Guyana: Mazaruni-Potaro: Wei Assipu Tepui		IRSNB 15862	JQ742224	---	JQ742391	---	---	---
Tepuihyla rodriguezi	Guyana: Potaro-Siparuni: Kaieteur NP		IRSNB 14752	JQ742227	---	JQ742394	---	---	---
Tepuihyla rodriguezi	Guyana: Potaro-Siparuni: Kaieteur NP N05°01'01"W60°36'59"		IRSNB 14753	JQ742228	---	JQ742395	---	---	---
Tepuihyla rodriguezi	Guyana: Potaro-Siparuni: Savanna next to Kaieteur Falls N05°10'00"W59°29'00"	PK 1105_2253	IRSNB 14751	**KF002184**	---	---	---	---	---
Tepuihyla rodriguezi	Venezuela: Bolívar: Guadacapiapu Tepui		IRSNB 15702	JQ742226	---	JQ742393	---	---	---
Tepuihyla rodriguezi	Venezuela: Bolívar: Guadacapiapu Tepui		IRSNB 15701	JQ742225	---	JQ742392	---	---	---
Tepuihyla rodriguezi	Venezuela: Bolívar: Luepa	MHNLS 19575	MHNLS 19575	JQ868539	---	---	---	---	---
Tepuihyla rodriguezi	Venezuela: Bolívar: Luepa	PS 003	PS 003	JQ868540	---	---	---	---	JQ868474
Tepuihyla rodriguezi	Venezuela: Bolívar: Uei Tepui		IRSNB 15769	JQ742216	---	JQ742383	---	---	---
Tepuihyla rodriguezi	Venezuela: Bolívar: Uei Tepui		IRSNB 15765	JQ742215	---	JQ742382	---	---	---
Tepuihyla warreni	Guyana: District 7: Mt. Ayanganna	H_warreni_ROM39491_2125	ROM 39491	**KF002185**	---	---	---	---	---
Tepuihyla warreni	Guyana: District 7: Mt. Wokomung	H_warreni_ROM43500_2138	ROM 43500	**KF002186**	---	---	---	---	---

Tepuihyla warreni	Guyana: Mazaruni-Potaro: Little Ayanganna, Wokomung Massif	H_warreni_1567	CPI 10256	**KF002187**	**KF002001**	---	---	---	**---**
Trachycephalus jordani	No data		UMMZ 218914	AY843771	AY844015	**KF002248**	---	---	---
Trachycephalus typhonius	Guyana: Dubulay Ranch on Berbice River, 200 ft		AMNH-A 141142	AY549362	AY843965	GQ366341	**KF001946**	---	GQ366043

Appendix S3

Models of nucleotide substitution for the partitions used in the maximum likelihood phylogenetic analyses.

Gene	Partition	Selected model
12S + tRNA^{Val}+16S	Fragment	GTR+I+G
16S + tRNA^{Leu}	Fragment	SYM+G
tRNA^{Ile}	Fragment	TPM3+I+G
ND1	By codon	TPM1uf+G for 1st, TIM3+G for 2nd and TrN+G for 3rd
cyt-b	By codon	TIM2+G for 1st, HKY+I+G for 2nd and TVM+G for 3rd
COI	By codon	TIM1+I+G for 1st, F81 for 2nd and TPM2uf+G for 3rd
Control Region	Fragment	TIM3+I+G
POMC	By codon	GTR+I+G for 1st, F81 for 2nd and TIM3+G for 3rd

Appendix S4a

Inter- and intraspecific uncorrected genetic distances (diagonal and below the diagonal respectively) within members of the *Osteocephalus taurinus* species group (sample size in parentheses) inferred from 551 aligned characters of a fragment of the mitochondrial 16S gene. ss = *sensu stricto*.

	O. oophagus	*O. taurinus* ss	*O. taurinus* Ca1	*O. taurinus* Ca2	*O. taurinus* Ca3	*O. taurinus* Ca4	*O. taurinus* Ca5
O. oophagus (N=4)	0.2–2.0						
O. taurinus ss (N=47)	0.9–2.2	0.0–1.7					
O. taurinus Ca1 (N=1)	2.1–2.6	1.5–2.2	—				
O. taurinus Ca2 (N=1)	2.0–2.2	0.9–1.8	1.8	—			
O. taurinus Ca3 (N=3)	1.8–2.6	0.9–2.2	1.8–2.2	0.2–0.7	0.2–0.4		
O. taurinus Ca4 (N=5)	2.2–2.8	1.1–2.2	2.0–2.2	1.7–1.8	1.7–2.2	0.0–0.4	
O. taurinus Ca5 (N=8)	1.3–3.1	1.1–2.6	1.7–2.0	1.1–2.2	1.1–2.2	1.3–2.2	0.0–1.8

Appendix S4b

Inter- and intraspecific uncorrected genetic distances (diagonal and below the diagonal respectively) within members of the *Osteocephalus planiceps* species group (sample size in parentheses) inferred from 551 aligned characters of a fragment of the mitochondrial 16S gene.

	O. castaneicola	*O. deridens*	*O. fuscifascies*	*O. leoniae*	*O. planiceps*	*O. planiceps* Ca1
O. castaneicola (N=6)	0.0–0.7					
O. deridens (N=3)	4.0–5.2	0.0–1.5				
O. fuscifascies (N=2)	3.3–4.2	4.4–5.2	0.9			
O. leoniae (N=4)	3.7–5.3	4.4–6.1	4.1–5.9	0.0–4.0		
O. planiceps (N=8)	1.5–2.6	3.3–3.9	2.6–3.7	2.6–4.4	0.0–1.3	
O. planiceps Ca1 (N=1)	3.5–3.9	4.2–4.4	4.4–5.0	4.2–5.9	2.6–2.8	—

Appendix S4c

Inter- and intraspecific uncorrected genetic distances (diagonal and below the diagonal respectively) within members of the *Osteocephalus leprieurii* species group (sample size in parentheses) inferred from 551 aligned characters of a fragment of the mitochondrial 16S gene. ss = *sensu stricto*.

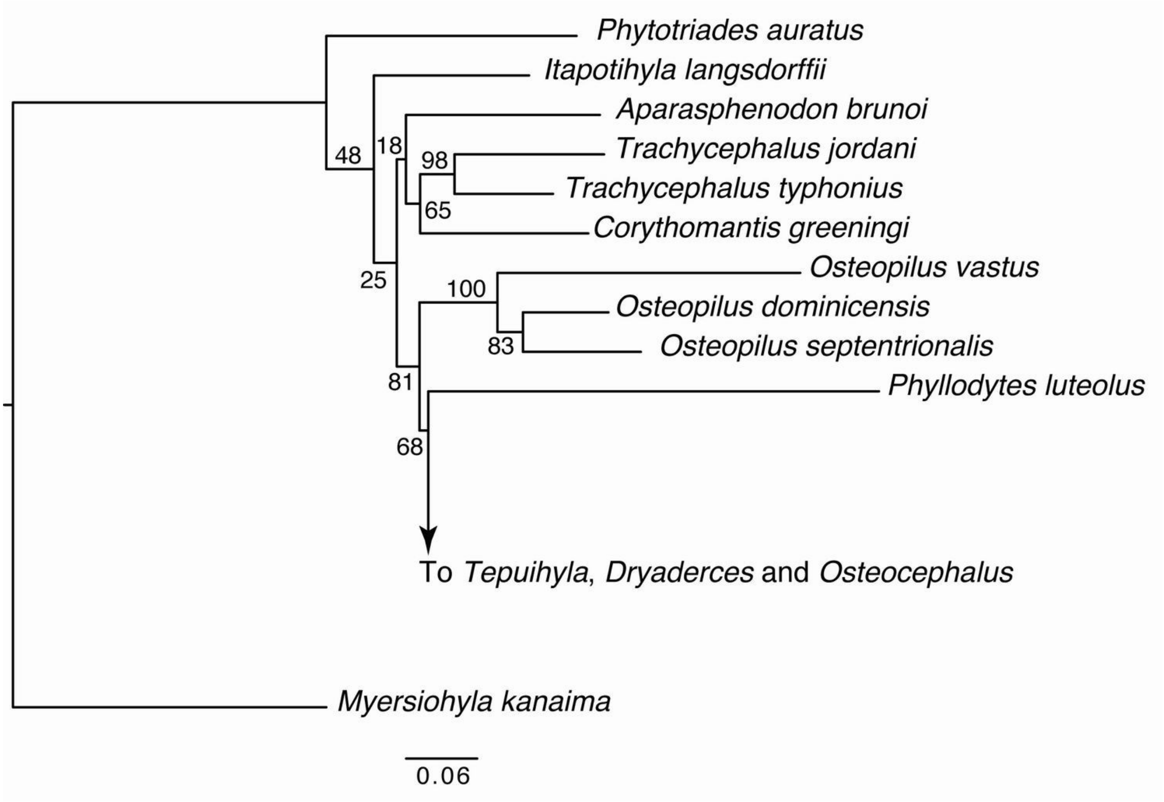
	O. leprieurii ss	*O. leprieurii* Ca1	*O. leprieurii* Ca2	*O. yasuni*
O. leprieurii ss (N=4)	0.0–1.1			
O. leprieurii Ca1 (N=4)	1.7–1.8	0.0		
O. leprieurii Ca2 (N=7)	0.9–1.8	1.5–2.0	0.0–0.6	
O. yasuni (N=7)	0.7–1.8	0.9–1.3	0.6–1.5	0.0–0.7

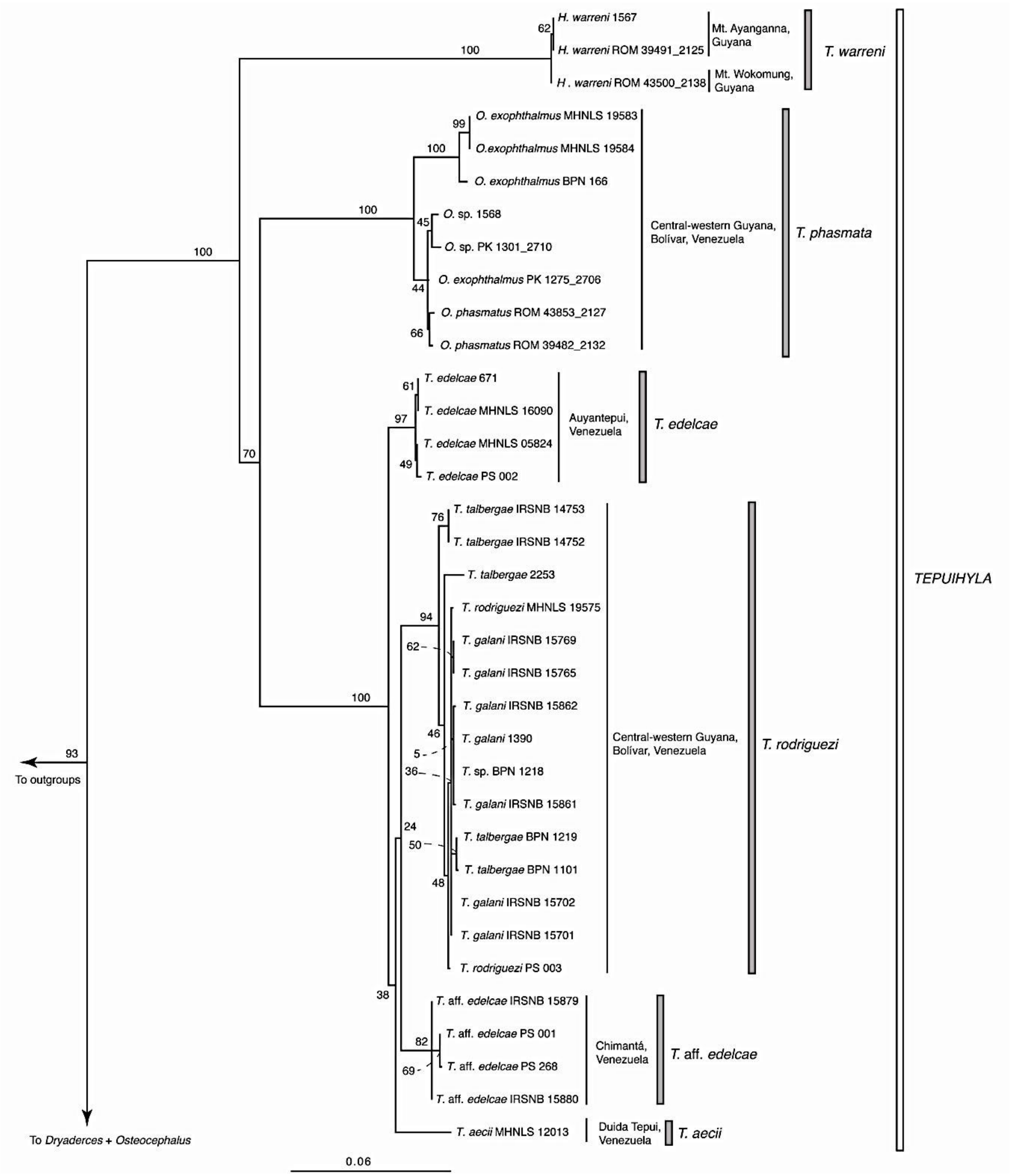
Appendix S4d. Inter- and intraspecific uncorrected genetic distances (diagonal and below the diagonal respectively) within members of the *Osteocephalus buckleyi* species group (sample size in parentheses) inferred from 551 aligned characters of a fragment of the mitochondrial 16S gene. ss = *sensu stricto*.

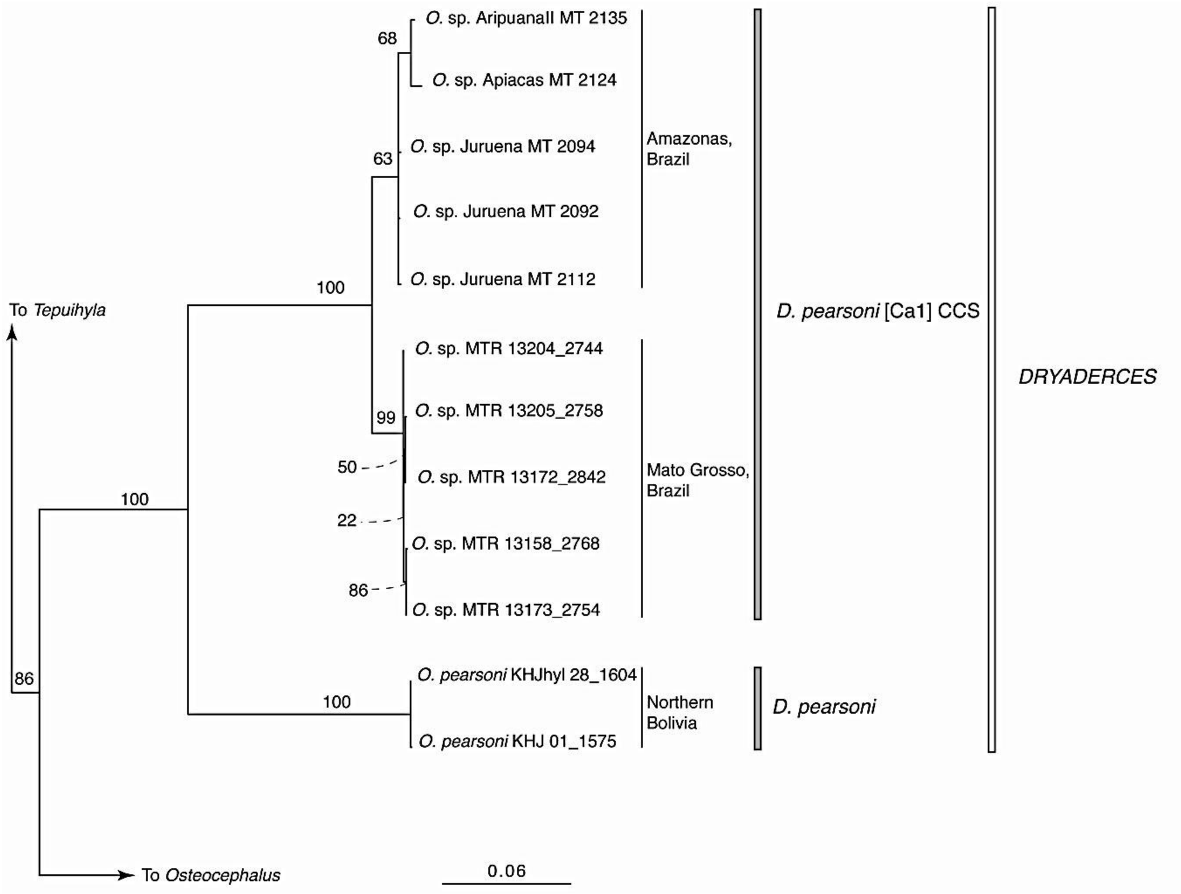
	O. buckleyi ss	*O. buckleyi* Ca1	*O. helenae*	*O. cabrerai*	*O. carri*	*O. mimeticus*	*O. mutabor*	*O. verruciger*
O. buckleyi ss (N=6)	0.0–1.5							
O. buckleyi Ca1 (N=2)	0.7–2.4	0.2						
O. helenae (N=15)	1.3–3.1	1.3–2.6	0.0–2.2					
O. cabrerai (N=2)	0.9–2.0	1.3–1.5	1.5–2.6	0.0				
O. carri (N=1)	3.9–5.0	3.7–3.9	4.0–5.1	4.0	—			
O. mimeticus (N=6)	4.2–5.9	4.2–5.0	4.0–6.1	4.4–5.0	4.6	0.0–2.8		
O. mutabor ss (N=1)	3.9–4.6	3.7–3.9	4.0–5.1	4.0	2.6	4.6–5.1	—	
O. verruciger (N=6)	0.9–2.9	1.3–2.4	1.5–3.5	0.7–1.7	3.7	4.4–5.1	3.7–4.4	0.0–1.7

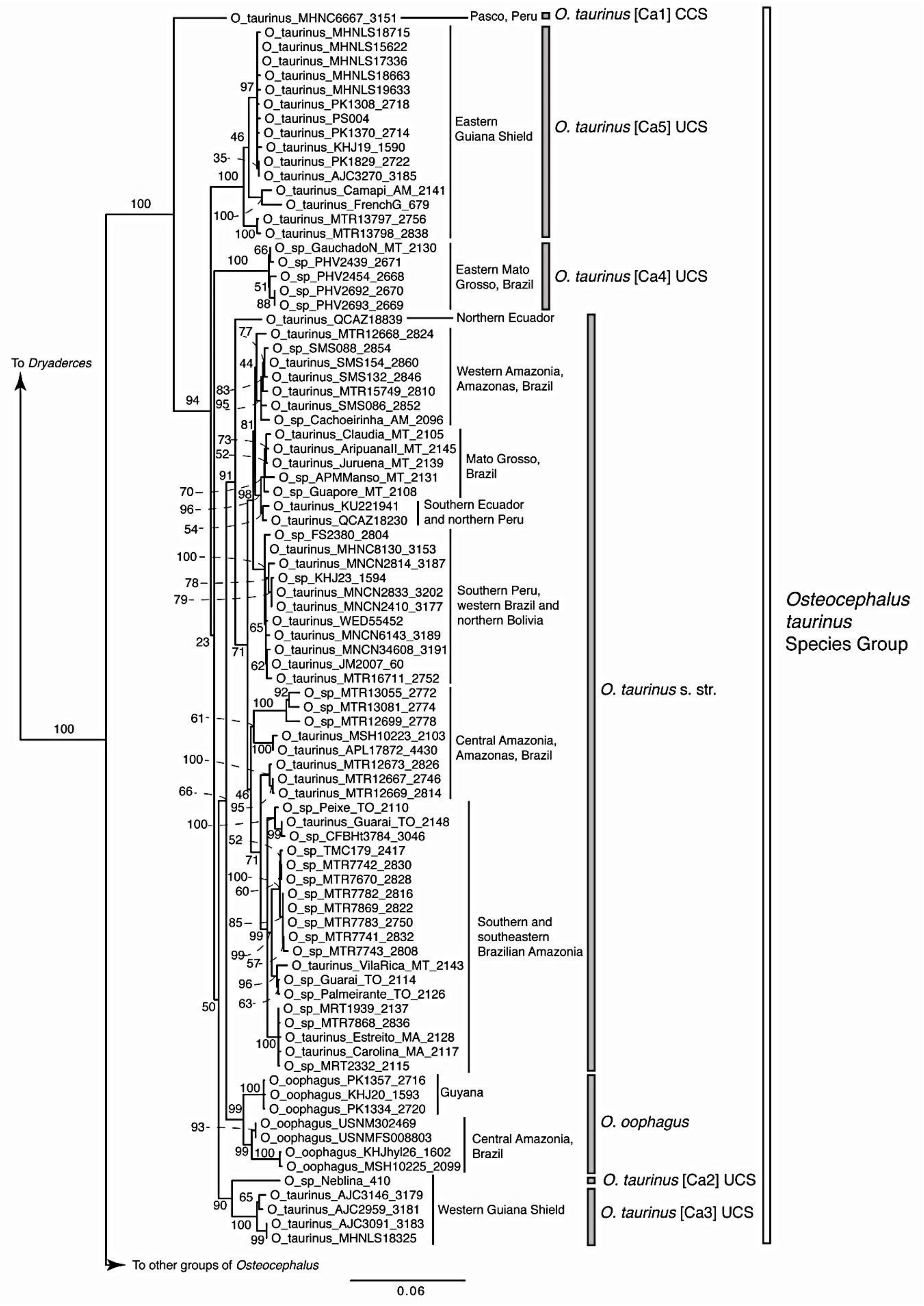
Appendix S5

Phylogenetic relationships of *Dryaderces*, *Osteocephalus*, *Tepuihyla*, and outgroups inferred from a maximum likelihood analysis, executed in the program Garli 2.0, of a partitioned matrix of a static alignment (generated with a multiple sequence alignment in Clustal-W). Partitions and their respective models of sequence evolution are detailed in Appendix S3. Not all loci are available for all terminals.




H. warreni 1567
H. warreni ROM 39491_2125
H . warreni ROM 43500_2138
Mt. Ayanganna, Guyana
Mt. Wokomung, Guyana
T. warreni
O. exophthalmus MHNLS 19583
O.exophthalmus MHNLS 19584
O. exophthalmus BPN 166
O. sp. 1568
O. sp. PK 1301_2710
O. exophthalmus PK 1275_2706
O. phasmatus ROM 43853_2127
O. phasmatus ROM 39482_2132
Central-western Guyana, Bolívar, Venezuela
T. phasmata
T. edelcae 671
T. edelcae MHNLS 16090
T. edelcae MHNLS 05824
T. edelcae PS 002
Auyantepui, Venezuela
T. edelcae
T. talbergae IRSNB 14753
T. talbergae IRSNB 14752
T. talbergae 2253
T. rodriguezi MHNLS 19575
T. galani IRSNB 15769
T. galani IRSNB 15765
T. galani IRSNB 15862
T. galani 1390
T. sp. BPN 1218
T. galani IRSNB 15861
T. talbergae BPN 1219
T. talbergae BPN 1101
T. galani IRSNB 15702
T. galani IRSNB 15701
T. rodriguezi PS 003
Central-western Guyana, Bolívar, Venezuela
T. rodriguezi
T. aff. edelcae IRSNB 15879
T. aff. edelcae PS 001
T. aff. edelcae PS 268
T. aff. edelcae IRSNB 15880
Chimantá, Venezuela
T. aff. edelcae
T. aecii MHNLS 12013
Duida Tepui, Venezuela
T. aecii
TEPUIHYLA
62
100
99
100
100
45
44
66
100
61
97
49
70
76
94
62
46
5
36
24
50
48
100
38
82
69
93
To outgroups
To Dryaderces + Osteocephalus
0.06


68
O. sp. AripuanaII MT 2135
O. sp. Apiacas MT 2124
63
O. sp. Juruena MT 2094
O. sp. Juruena MT 2092
O. sp. Juruena MT 2112
Amazonas, Brazil
100
To *Tepuihyla*
D. pearsoni [Ca1] CCS
DRYADERCES
O. sp. MTR 13204_2744
99
O. sp. MTR 13205_2758
50
O. sp. MTR 13172_2842
Mato Grosso, Brazil
100
22
O. sp. MTR 13158_2768
86
O. sp. MTR 13173_2754
86
O. pearsoni KHJhyl 28_1604
100
O. pearsoni KHJ 01_1575
Northern Bolivia
D. pearsoni
To *Osteocephalus*
0.06


O_taurinus_MHNC6667_3151
Pasco, Peru
O. taurinus [Ca1] CCS
O_taurinus_MHNLS18715
O_taurinus_MHNLS15622
O_taurinus_MHNLS17336
O_taurinus_MHNLS18663
O_taurinus_MHNLS19633
O_taurinus_PK1308_2718
O_taurinus_PS004
O_taurinus_PK1370_2714
O_taurinus_KHJ19_1590
O_taurinus_PK1829_2722
O_taurinus_AJC3270_3185
O_taurinus_Camapi_AM_2141
O_taurinus_FrenchG_679
O_taurinus_MTR13797_2756
O_taurinus_MTR13798_2838
Eastern Guiana Shield
O. taurinus [Ca5] UCS
O_sp_GauchadoN_MT_2130
O_sp_PHV2439_2671
O_sp_PHV2454_2668
O_sp_PHV2692_2670
O_sp_PHV2693_2669
Eastern Mato Grosso, Brazil
O. taurinus [Ca4] UCS
O_taurinus_QCAZ18839
Northern Ecuador
O_taurinus_MTR12668_2824
O_sp_SMS088_2854
O_taurinus_SMS154_2860
O_taurinus_SMS132_2846
O_taurinus_MTR15749_2810
O_taurinus_SMS086_2852
O_sp_Cachoeirinha_AM_2096
Western Amazonia, Amazonas, Brazil
O_taurinus_Claudia_MT_2105
O_taurinus_AripuanaII_MT_2145
O_taurinus_Juruena_MT_2139
O_sp_APMManso_MT_2131
O_sp_Guapore_MT_2108
Mato Grosso, Brazil
O_taurinus_KU221941
O_taurinus_QCAZ18230
Southern Ecuador and northern Peru
O_sp_FS2380_2804
O_taurinus_MHNC8130_3153
O_taurinus_MNCN2814_3187
O_sp_KHJ23_1594
O_taurinus_MNCN2833_3202
O_taurinus_MNCN2410_3177
O_taurinus_WED55452
O_taurinus_MNCN6143_3189
O_taurinus_MNCN34608_3191
O_taurinus_JM2007_60
O_taurinus_MTR16711_2752
Southern Peru, western Brazil and northern Bolivia
O_sp_MTR13055_2772
O_sp_MTR13081_2774
O_sp_MTR12699_2778
O_taurinus_MSH10223_2103
O_taurinus_APL17872_4430
O_taurinus_MTR12673_2826
O_taurinus_MTR12667_2746
O_taurinus_MTR12669_2814
Central Amazonia, Amazonas, Brazil
O_sp_Peixe_TO_2110
O_taurinus_Guarai_TO_2148
O_sp_CFBHt3784_3046
O_sp_TMC179_2417
O_sp_MTR7742_2830
O_sp_MTR7670_2828
O_sp_MTR7782_2816
O_sp_MTR7869_2822
O_sp_MTR7783_2750
O_sp_MTR7741_2832
O_sp_MTR7743_2808
O_taurinus_VilaRica_MT_2143
O_sp_Guarai_TO_2114
O_sp_Palmeirante_TO_2126
O_sp_MRT1939_2137
O_sp_MTR7868_2836
O_taurinus_Estreito_MA_2128
O_taurinus_Carolina_MA_2117
O_sp_MRT2332_2115
Southern and southeastern Brazilian Amazonia
O. taurinus s. str.
O_oophagus_PK1357_2716
O_oophagus_KHJ20_1593
O_oophagus_PK1334_2720
Guyana
O_oophagus_USNM302469
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O_oophagus_MSH10225_2099
Central Amazonia, Brazil
O. oophagus
O_sp_Neblina_410
O. taurinus [Ca2] UCS
O_taurinus_AJC3146_3179
O_taurinus_AJC2959_3181
O_taurinus_AJC3091_3183
O_taurinus_MHNLS18325
Western Guiana Shield
O. taurinus [Ca3] UCS
Osteocephalus taurinus Species Group
To Dryaderces
To other groups of Osteocephalus
0.06
100
94
100
97
46
35
100
100
100
66
100
51
88
77
44
83
95
81
73
52
91
98
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96
54
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78
79
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23
71
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100
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46
95
100
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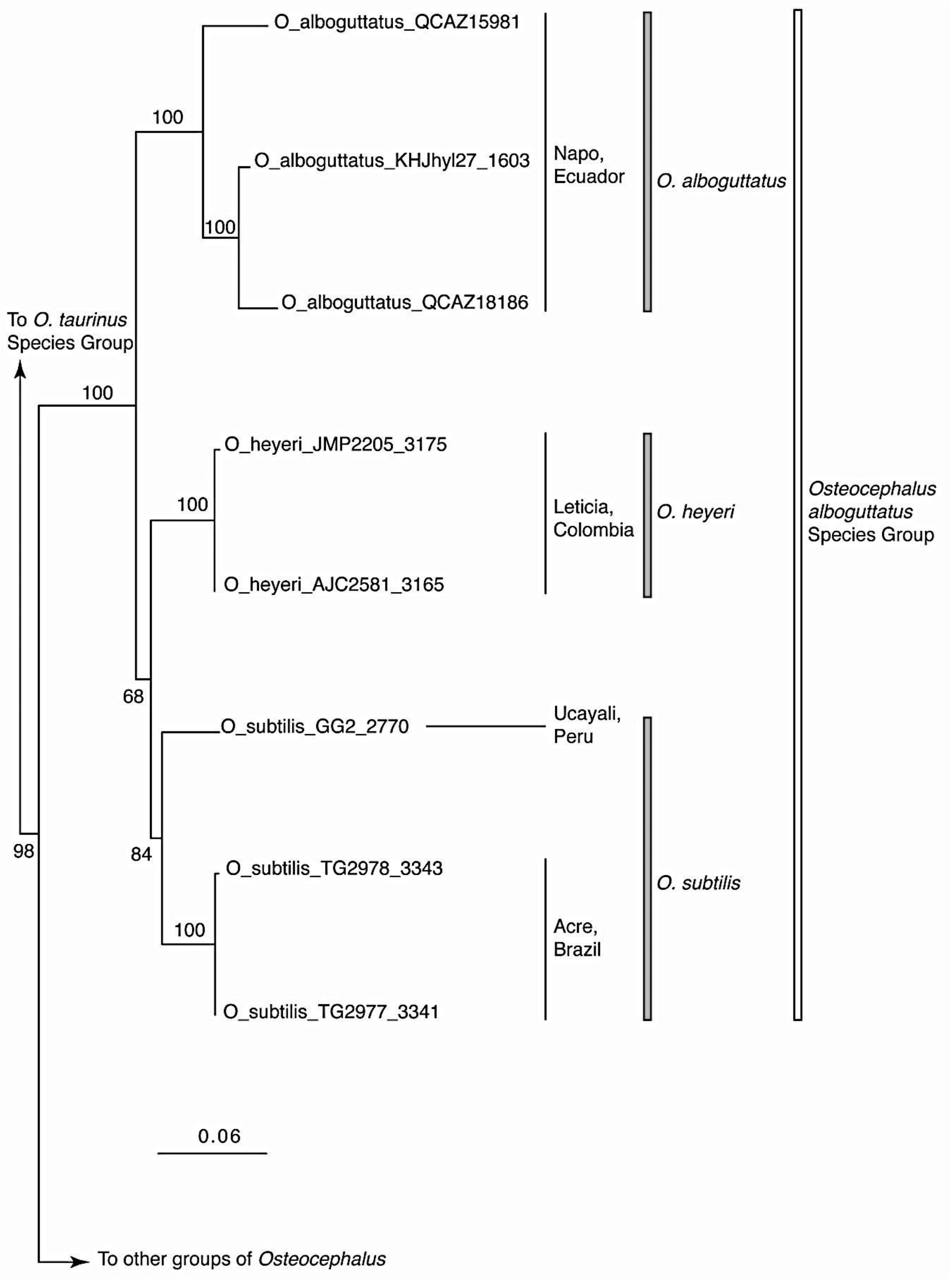
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O_alboguttatus_KHJhyl27_1603
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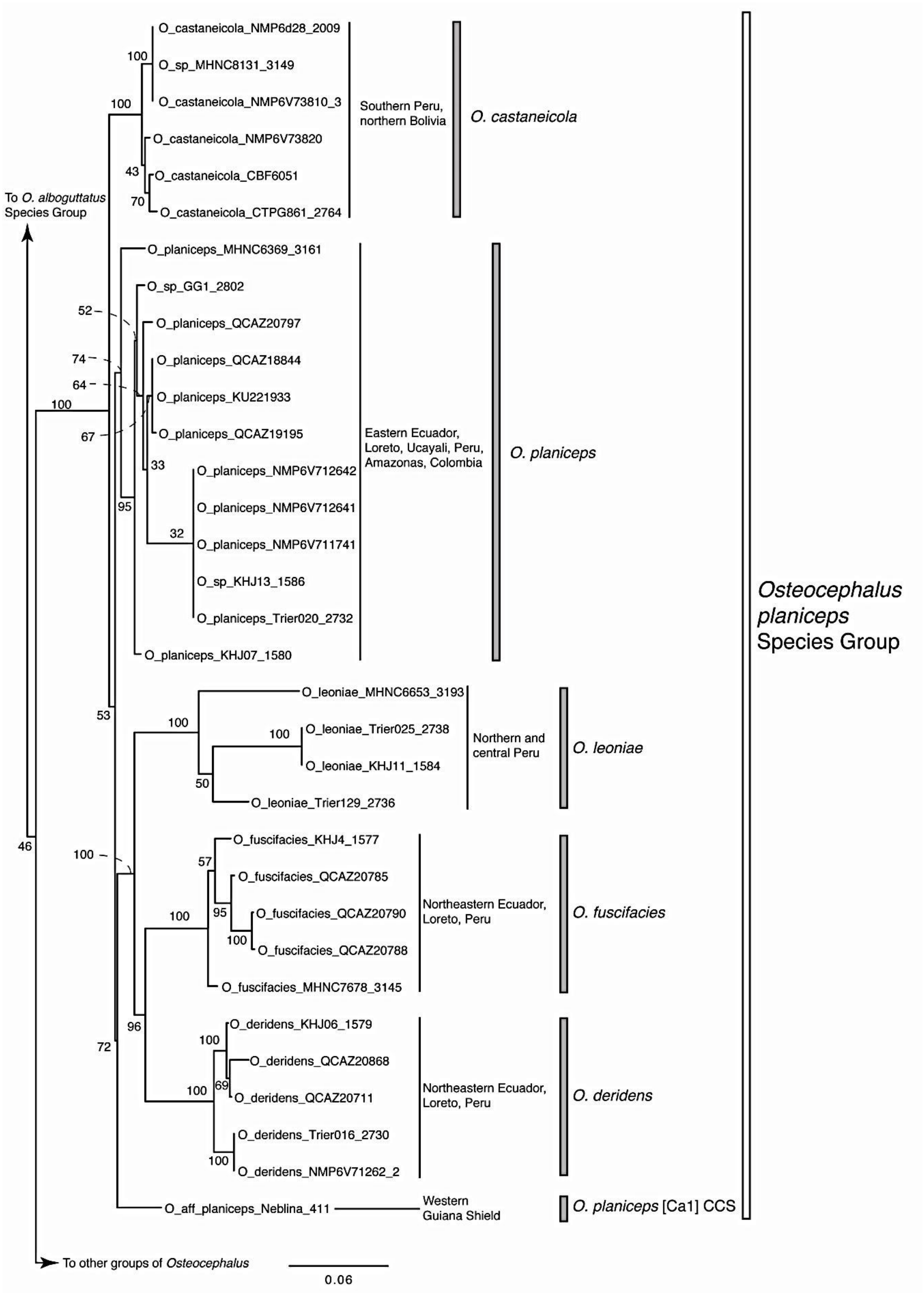
O_alboguttatus_QCAZ18186
Napo, Ecuador
O. alboguttatus
To O. taurinus Species Group
100
O_heyeri_JMP2205_3175
100
O_heyeri_AJC2581_3165
Leticia, Colombia
O. heyeri
Osteocephalus alboguttatus Species Group
68
O_subtilis_GG2_2770
Ucayali, Peru
98
84
O_subtilis_TG2978_3343
100
O_subtilis_TG2977_3341
Acre, Brazil
O. subtilis
0.06
To other groups of Osteocephalus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Southern Peru, northern Bolivia
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To O. alboguttatus Species Group
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O_sp_GG1_2802
52
O_planiceps_QCAZ20797
74
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64
O_planiceps_KU221933
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O_planiceps_NMP6V712642
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95
32
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O_sp_KHJ13_1586
O_planiceps_Trier020_2732
O_planiceps_KHJ07_1580
Eastern Ecuador, Loreto, Ucayali, Peru, Amazonas, Colombia
O. planiceps
Osteocephalus planiceps Species Group
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53
100
100
O_leoniae_Trier025_2738
O_leoniae_KHJ11_1584
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Northern and central Peru
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O_fuscifacies_KHJ4_1577
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O. fuscifacies
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O_deridens_KHJ06_1579
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O_deridens_QCAZ20868
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O_deridens_QCAZ20711
O_deridens_Trier016_2730
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O_deridens_NMP6V71262_2
Northeastern Ecuador, Loreto, Peru
O. deridens
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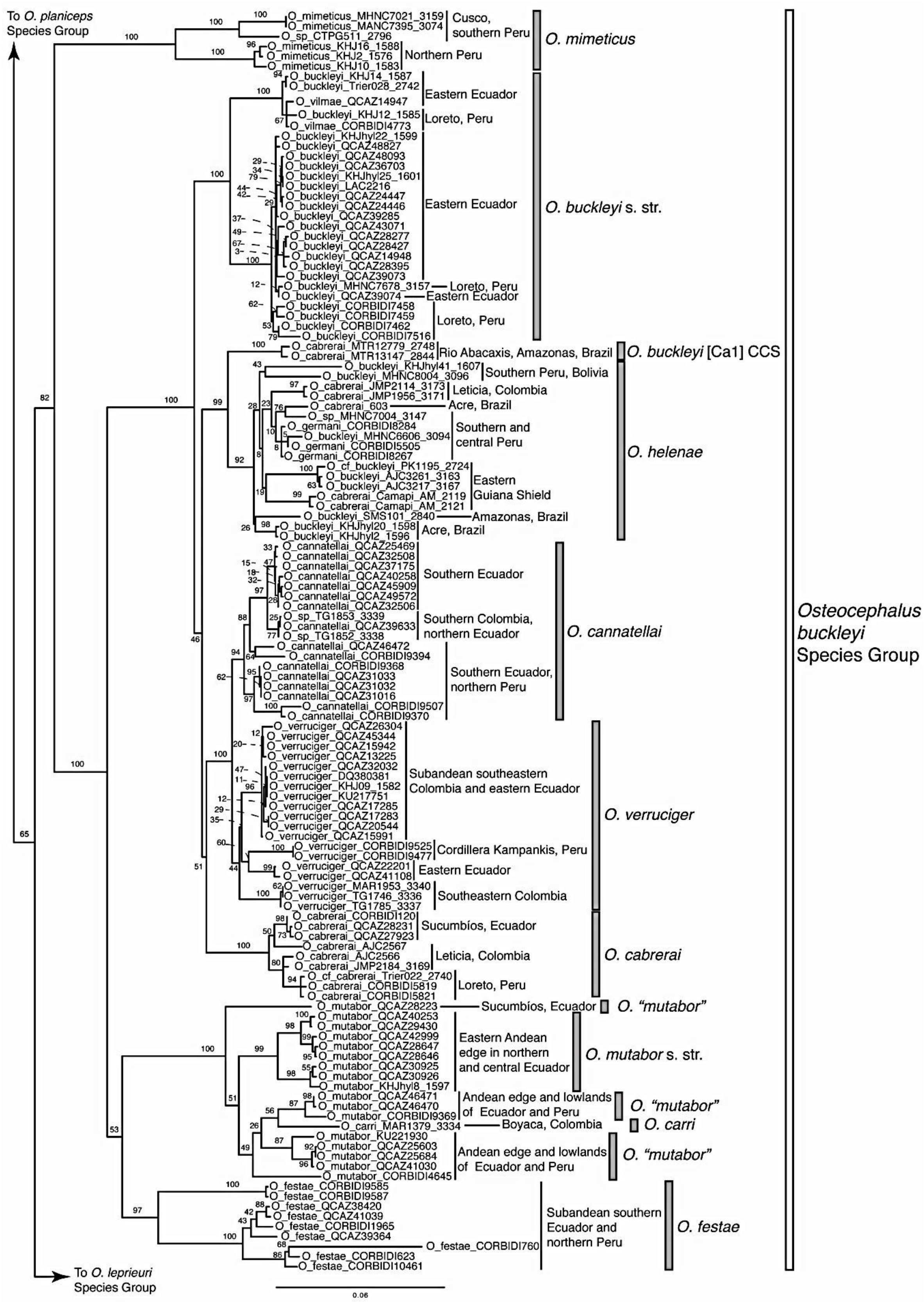
Western Guiana Shield
O. planiceps [Ca1] CCS
To other groups of Osteocephalus
0.06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O_mimeticus_KHJ2_1576
O_mimeticus_KHJ10_1583
Northern Peru
O. mimeticus
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O_buckleyi_Trier028_2742
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O_buckleyi_QCAZ39285
O_buckleyi_QCAZ43071
O_buckleyi_QCAZ28277
O_buckleyi_QCAZ28427
O_buckleyi_QCAZ14948
O_buckleyi_QCAZ28395
O_buckleyi_QCAZ39073
Eastern Ecuador
O. buckleyi s. str.
O_buckleyi_MHNC7678_3157
Loreto, Peru
O_buckleyi_QCAZ39074
Eastern Ecuador
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Loreto, Peru
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Rio Abacaxis, Amazonas, Brazil
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O_cabrerai_JMP1956_3171
Leticia, Colombia
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Acre, Brazil
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O_germani_CORBIDI8284
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O. helenae
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O_buckleyi_AJC3217_3167
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Acre, Brazil
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O. cannatellai
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O_cannatellai_CORBIDI9394
O_cannatellai_CORBIDI9368
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O_verruciger_QCAZ17285
O_verruciger_QCAZ17283
O_verruciger_QCAZ20544
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Subandean southeastern Colombia and eastern Ecuador
O. verruciger
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O_verruciger_CORBIDI9477
Cordillera Kampankis, Peru
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O_verruciger_TG1785_3337
Southeastern Colombia
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Sucumbíos, Ecuador
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O_cabrerai_AJC2566
O_cabrerai_JMP2184_3169
Leticia, Colombia
O. cabrerai
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Loreto, Peru
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Sucumbíos, Ecuador
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O_mutabor_QCAZ29430
O_mutabor_QCAZ42999
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O_mutabor_QCAZ28646
O_mutabor_QCAZ30925
O_mutabor_QCAZ30926
O_mutabor_KHJhyl8_1597
Eastern Andean edge in northern and central Ecuador
O. mutabor s. str.
O_mutabor_QCAZ46471
O_mutabor_QCAZ46470
O_mutabor_CORBIDI9369
Andean edge and lowlands of Ecuador and Peru
O. "mutabor"
O_carri_MAR1379_3334
Boyaca, Colombia
O. carri
O_mutabor_KU221930
O_mutabor_QCAZ25603
O_mutabor_QCAZ25684
O_mutabor_QCAZ41030
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Andean edge and lowlands of Ecuador and Peru
O. "mutabor"
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O_festae_CORBIDI1965
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O_festae_CORBIDI760
O_festae_CORBIDI623
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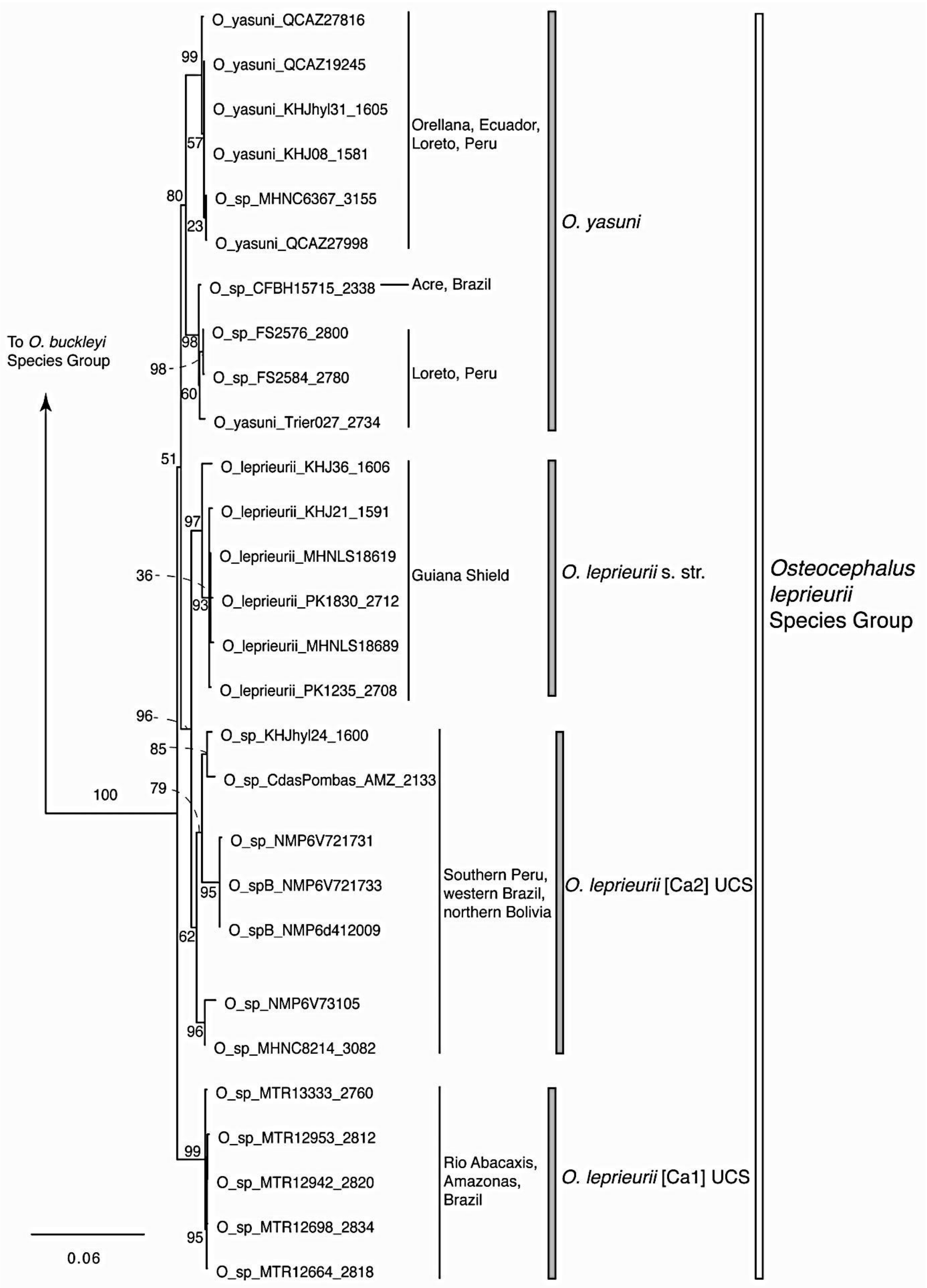
Subandean southern Ecuador and northern Peru
O. festae
Osteocephalus buckleyi Species Group
To O. leprieuri Species Group
0.06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O_yasuni_QCAZ27998
O_sp_CFBH15715_2338
O_sp_FS2576_2800
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O_leprieurii_KHJ21_1591
O_leprieurii_MHNLS18619
O_leprieurii_PK1830_2712
O_leprieurii_MHNLS18689
O_leprieurii_PK1235_2708
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O_spB_NMP6V721733
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O_sp_NMP6V73105
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O_sp_MTR12953_2812
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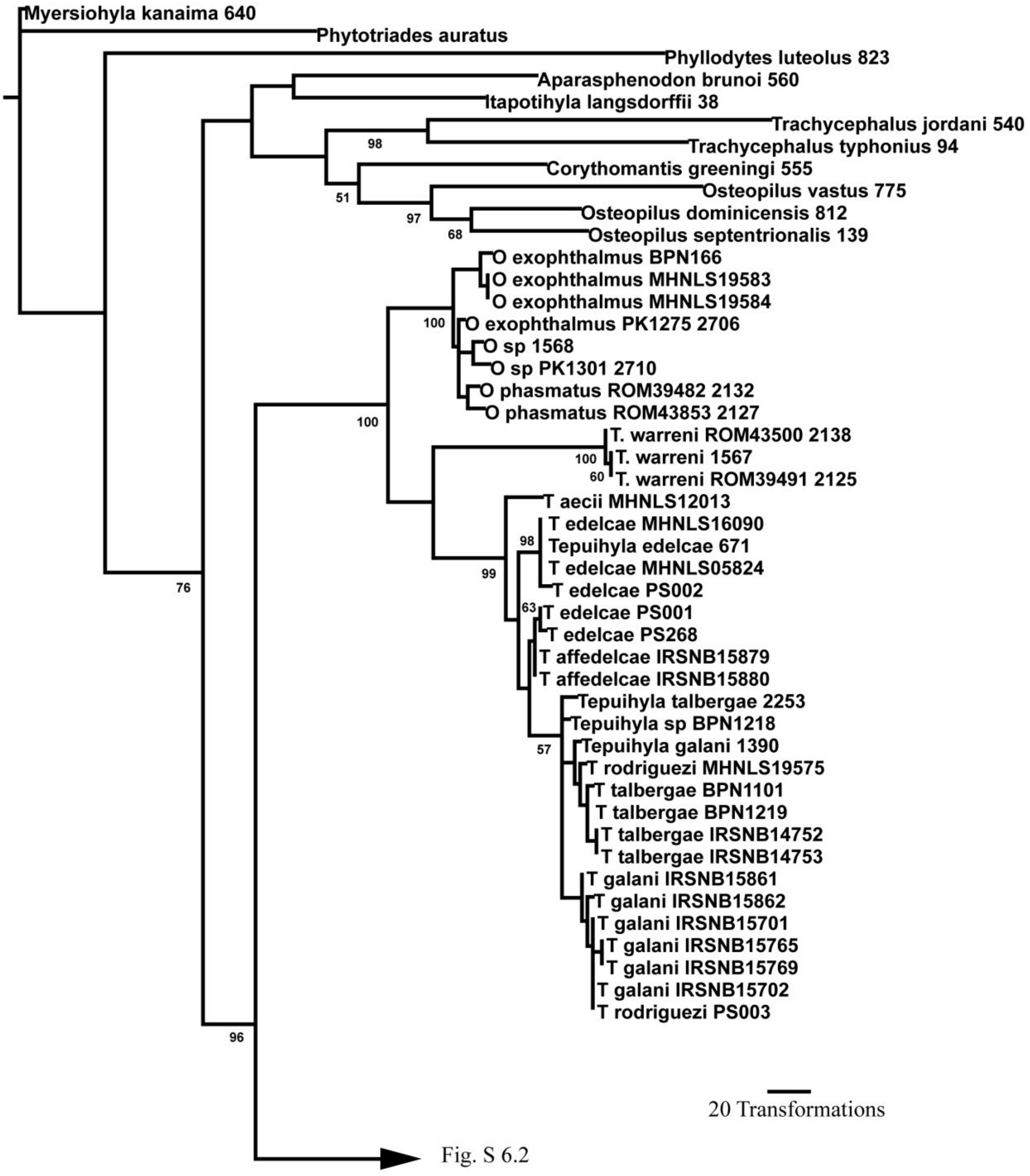
O_sp_MTR12698_2834
O_sp_MTR12664_2818
99
57
80
23
98
98
60
51
97
36
93
96
85
79
100
95
62
96
99
95
To *O. buckleyi* Species Group
0.06
Orellana, Ecuador, Loreto, Peru
Acre, Brazil
Loreto, Peru
Guiana Shield
Southern Peru, western Brazil, northern Bolivia
Rio Abacaxis, Amazonas, Brazil
O. yasuni
O. leprieurii s. str.
O. leprieurii [Ca2] UCS
O. leprieurii [Ca1] UCS
Osteocephalus leprieurii Species Group

Appendix S6.1-6

Phylogenetic relationships of *Dryaderces*, *Osteocephalus*, *Tepuihyla*, and outgroups inferred from maximum parsimony analysis under a static alignment (generated with a multiple sequence alignment in Clustal-W) in the program T.N.T., Willi Hennig Society Edition. This topology reflects one of the 4797 most parsimonious trees (length 13254 steps), with black nodes on dots indicating collapsed clades in strict consensus tree; not all loci are available for all terminals. Tips are labelled with the initial and tentative field identifications. See Appendix S2 and/or Figs 3.5.1–4 for current classification.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Aparasphenodon brunoi 560
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Trachycephalus jordani 540
98
Trachycephalus typhonius 94
Corythomantis greeningi 555
51
Osteopilus vastus 775
97
Osteopilus dominicensis 812
68
Osteopilus septentrionalis 139
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O exophthalmus MHNLS19583
O exophthalmus MHNLS19584
100
O exophthalmus PK1275 2706
O sp 1568
O sp PK1301 2710
O phasmatus ROM39482 2132
100
O phasmatus ROM43853 2127
T. warreni ROM43500 2138
100
T. warreni 1567
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T. warreni ROM39491 2125
T aecii MHNLS12013
T edelcae MHNLS16090
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Tepuihyla edelcae 671
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T edelcae PS002
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T edelcae PS001
T edelcae PS268
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Tepuihyla talbergae 2253
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Tepuihyla galani 1390
T rodriguezi MHNLS19575
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T talbergae BPN1219
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T galani IRSNB15862
T galani IRSNB15701
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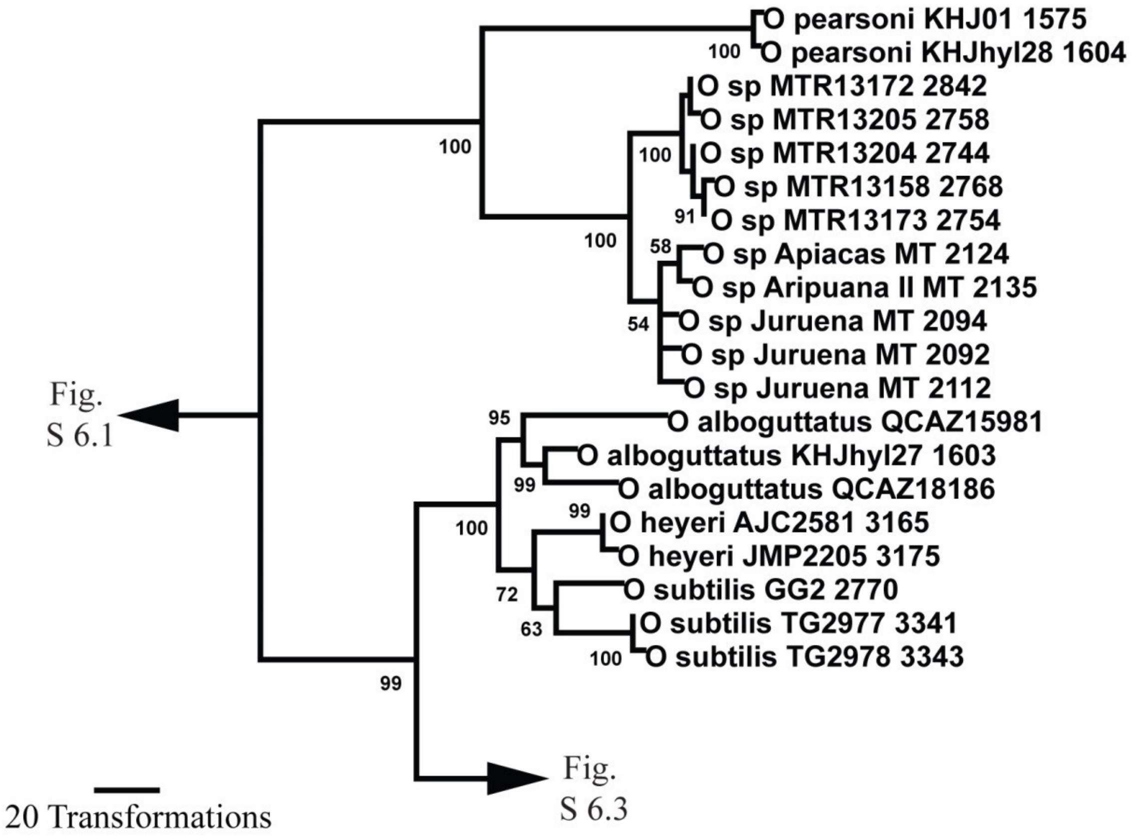
96
20 Transformations
Fig. S 6.2

S 6.2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100
58
O sp Apiacas MT 2124
O sp Aripuana II MT 2135
54
O sp Juruena MT 2094
O sp Juruena MT 2092
O sp Juruena MT 2112
Fig.
S 6.1
95
O alboguttatus QCAZ15981
O alboguttatus KHJhyl27 1603
99
O alboguttatus QCAZ18186
99
O heyeri AJC2581 3165
100
O heyeri JMP2205 3175
O subtilis GG2 2770
72
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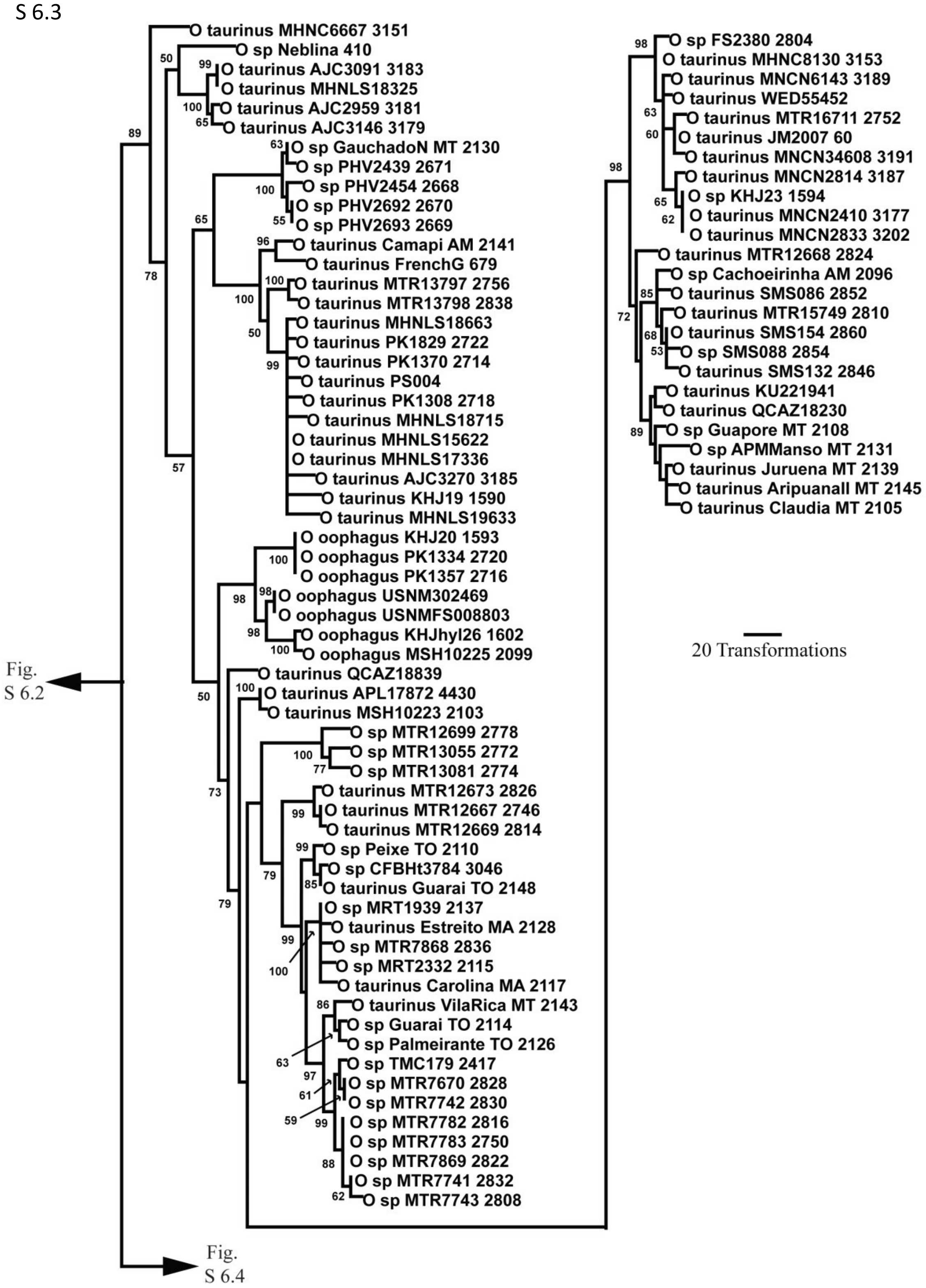
99
Fig.
S 6.3
20 Transformations

S 6.3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O sp PHV2439 2671
O sp PHV2454 2668
O sp PHV2692 2670
O sp PHV2693 2669
O taurinus Camapi AM 2141
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O taurinus MTR13797 2756
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O taurinus MHNLS18663
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O oophagus USNM302469
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O sp Guarai TO 2114
O sp Palmeirante TO 2126
O sp TMC179 2417
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O sp APMManso MT 2131
O taurinus Juruena MT 2139
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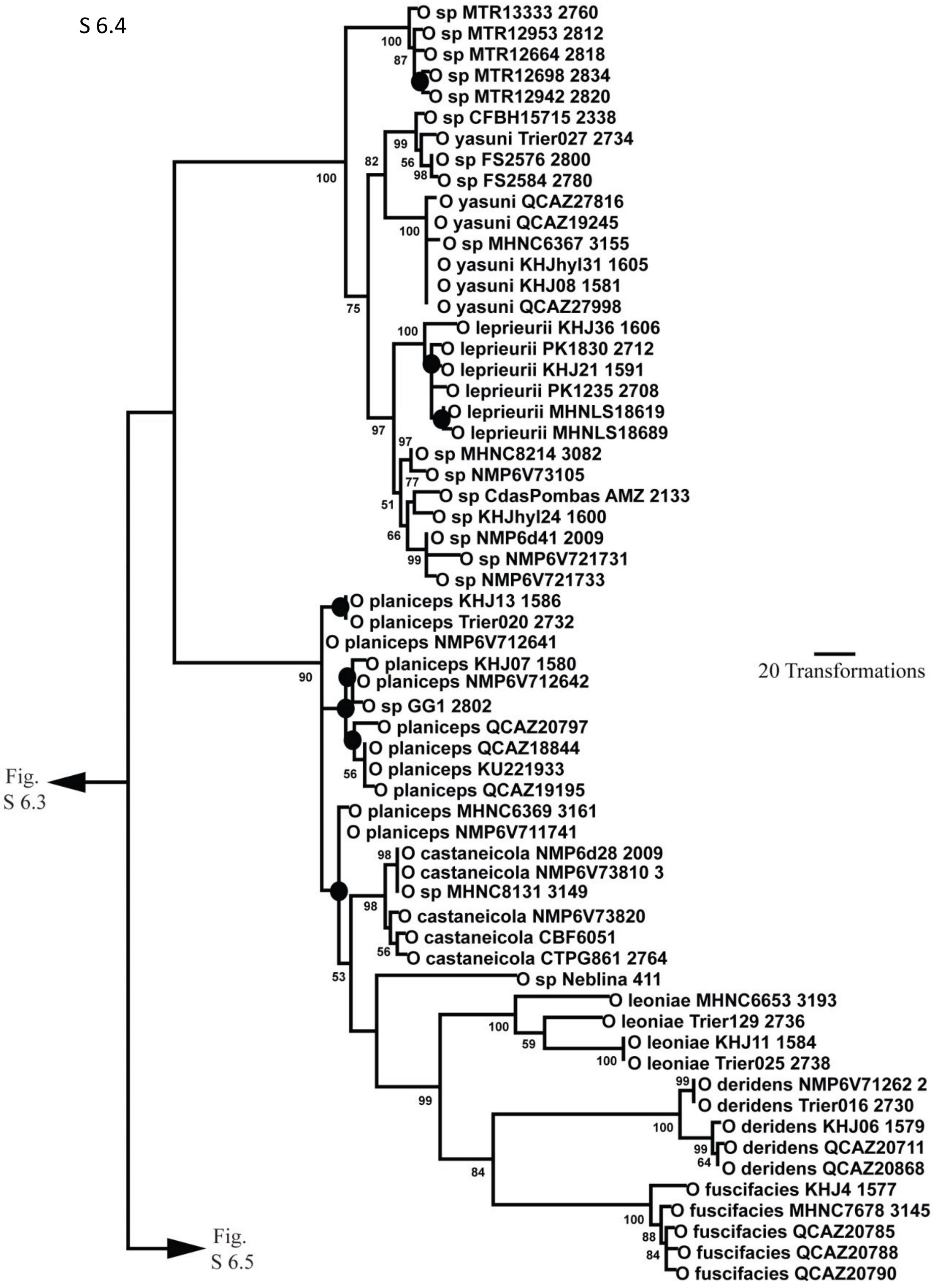
Fig.
S 6.2
Fig.
S 6.4
20 Transformations

S 6.4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56
20 Transformations
Fig.
S 6.3
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O leoniae Trier025 2738
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O deridens KHJ06 1579
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O deridens QCAZ20868
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O fuscifacies KHJ4 1577
O fuscifacies MHNC7678 3145
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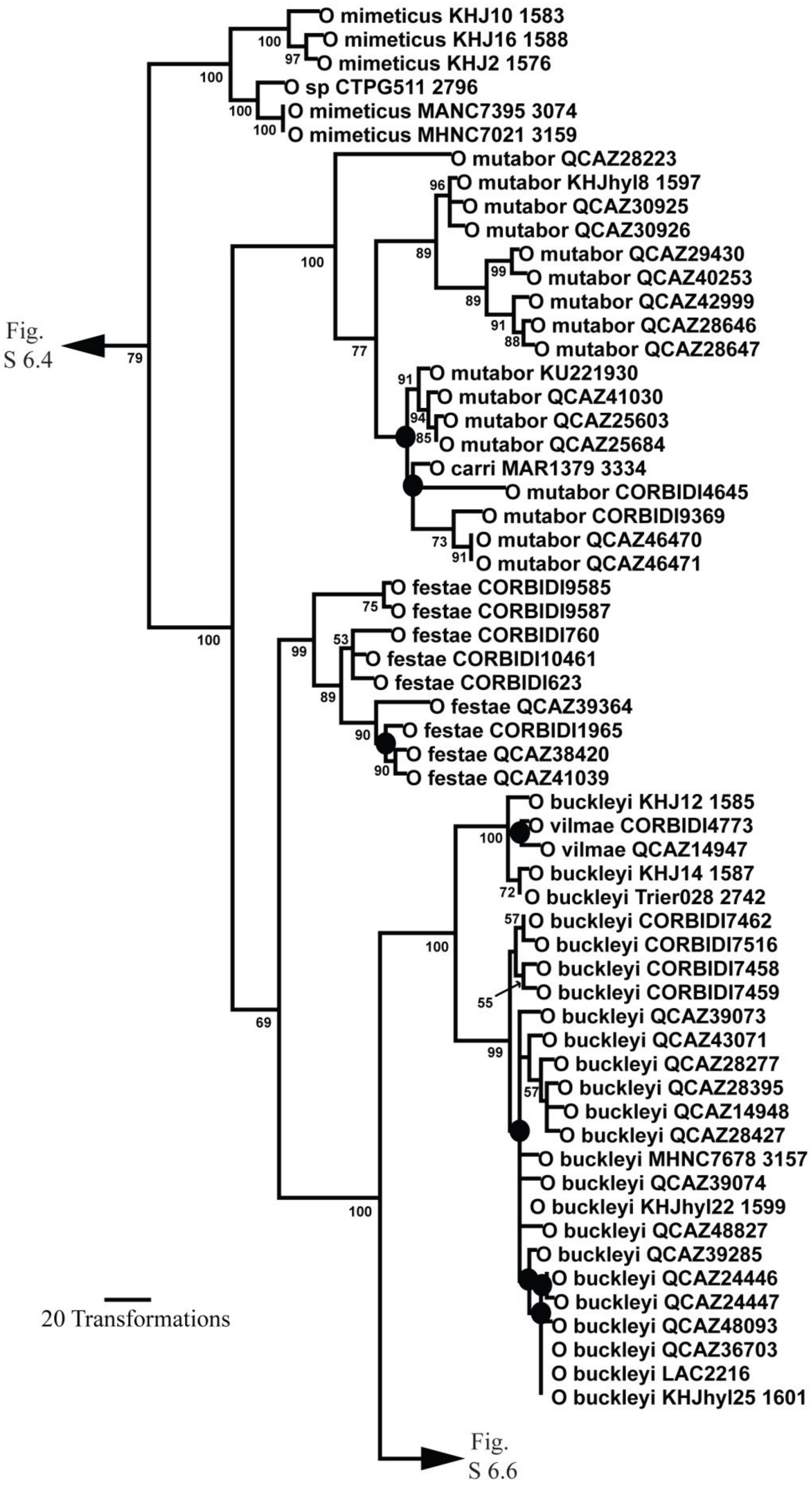
Fig.
S 6.5

S 6.5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O mutabor QCAZ28646
Fig.
S 6.4
79
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O mutabor QCAZ28647
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90
O festae QCAZ41039
O buckleyi KHJ12 1585
O vilmae CORBIDI4773
100
O vilmae QCAZ14947
O buckleyi KHJ14 1587
72
O buckleyi Trier028 2742
57
O buckleyi CORBIDI7462
100
O buckleyi CORBIDI7516
O buckleyi CORBIDI7458
55
O buckleyi CORBIDI7459
O buckleyi QCAZ39073
69
O buckleyi QCAZ43071
99
O buckleyi QCAZ28277
57
O buckleyi QCAZ28395
O buckleyi QCAZ14948
O buckleyi QCAZ28427
O buckleyi MHNC7678 3157
O buckleyi QCAZ39074
O buckleyi KHJhyl22 1599
100
O buckleyi QCAZ48827
O buckleyi QCAZ39285
O buckleyi QCAZ24446
20 Transformations
O buckleyi QCAZ24447
O buckleyi QCAZ48093
O buckleyi QCAZ36703
O buckleyi LAC2216
O buckleyi KHJhyl25 1601
Fig.
S 6.6

S 6.6


O aff. cabrerai MTR12779 2748
100
O aff. cabrerai MTR13147 2844
99
O buckleyi MHNC8004 3096
O buckleyi KHJhyl41 1607
85
O buckleyi SMS101 2840
O cabrerai Camapi AM 2119
81
O cabrerai Camapi AM 2121
O cf buckleyi PK1195 2724
67
O buckleyi AJC3217 3167
O buckleyi AJC3261 3163
O germani CORBIDI8284
O germani CORBIDI5505
O germani CORBIDI8267
O buckleyi KHJhyl2 1596
O buckleyi KHJhyl20 1598
O cabrerai JMP1956 3171
78
O cabrerai JMP2114 3173
Fig. S 6.5
77
O buckleyi MHNC6606 3094
O cabrerai 603
65
O sp MHNC7004 3147
O cabrerai AJC2567
O cabrerai CORBIDI120
O cabrerai QCAZ27923
99
61
O cabrerai QCAZ28231
O cabrerai AJC2566
O cabrerai JMP2184 3169
O cabrerai CORBIDI5819
O cabrerai CORBIDI5821
O cabrerai Trier022 2740
95
O verruciger QCAZ22201
O verruciger QCAZ41108
O verruciger CORBIDI9477
O verruciger CORBIDI9525
100
O verruciger DQ380381
O verruciger KHJ09 1582
O verruciger KU217751
O verruciger QCAZ26304
69
O verruciger QCAZ13225
O verruciger QCAZ15942
O verruciger QCAZ45344
O verruciger QCAZ15991
O verruciger QCAZ17283
99
O verruciger QCAZ20544
O verruciger QCAZ17285
O verruciger QCAZ32032
O verruciger TG1785 3337
90
O verruciger TG1746 3336
O verruciger MAR1953 3340
100
O cannatellai CORBIDI9370
91
O cannatellai CORBIDI9507
O cannatellai CORBIDI9368
91
O cannatellai QCAZ31032
62
O cannatellai QCAZ31016
87
O cannatellai QCAZ31033
O cannatellai CORBIDI9394
O cannatellai QCAZ46472
61
O sp TG1852 3338
87
O sp TG1853 3339
O cannatellai QCAZ39633
98
O cannatellai QCAZ25469
O cannatellai QCAZ32508
79
O cannatellai QCAZ37175
O cannatellai QCAZ32506
O cannatellai QCAZ40258
O cannatellai QCAZ45909
O cannatellai QCAZ49572
20 Transformations

Appendix S7

List of some of the molecular transformations common to all most parsimonious trees of the static parsimony analysis, supporting the monophyly of each of the three genera discussed in the text. Positions correspond to the alignment stored in Dryad Repository DOI (http://dx.doi.org/10.5061/dryad.j04vf).

Dryaderces

ND1

Char. 1018: A --> G
Char. 1034: C --> T
Char. 1048: A --> G
Char. 1153: A --> T
Char. 1180: C --> T
Char. 1234: T --> C
Char. 1267: T --> C
Char. 1324: C --> T
Char. 1327: C --> T
Char. 1375: T --> A
Char. 1412: A --> G
Char. 1429: C --> T
Char. 1432: C --> T
Char. 1624: T --> C
Char. 1636: C --> T
Char. 1670: A --> G
Char. 1679: T --> C
Char. 1693: C --> A
Char. 1739: G --> T
Char. 1755: T --> C
Char. 1756: T --> C
Char. 1798: C --> T
Char. 1810: C --> T
Char. 1816: C --> T
Char. 1828: T --> C
Char. 1861: C --> T
Char. 1880: A --> C

12S

Char. 3726: A --> C
Char. 3734: T --> C
Char. 3901: T --> A
Char. 3967: T --> C
Char. 3968: A --> C
Char. 3969: A --> G
Char. 3970: A --> T
Char. 3978: T --> C
Char. 3996: A --> G
Char. 4005: A --> T
Char. 4021: A --> G
Char. 4056: C --> A
Char. 4103: A --> C
Char. 4209: C --> T
Char. 4317: A --> T
Char. 4399: T --> C
Char. 4479: A --> C
Char. 4519: T --> C
Char. 5919: C --> T
Char. 5947: T --> C

Dryaderces (cont.)

16S

Char. 4657: A --> C
Char. 4677: T --> C
Char. 4699: A --> C
Char. 4713: A --> C
Char. 4723: C --> T
Char. 4725: C --> T
Char. 4839: A --> T
Char. 5086: T --> A
Char. 5181: T --> C
Char. 5256: A --> T
Char. 5257: C --> A
Char. 5272: A --> C
Char. 5294: T --> C
Char. 5295: T --> C
Char. 5381: A --> G
Char. 5422: A --> T
Char. 5429: T --> C
Char. 5573: A --> T
Char. 5757: A --> T
Char. 5810: A --> T
Char. 5942: A --> G

Osteocephalus

ND1

Char. 951: C --> T
Char. 983: A --> G
Char. 1054: C --> A
Char. 1160: T --> C
Char. 1192: C --> A
Char. 1255: T --> C
Char. 1463: A --> G
Char. 1600: T --> A
Char. 1673: A --> G
Char. 1754: G --> C
Char. 1759: T --> C

12S

Char. 3757: C --> T
Char. 3867: A --> T
Char. 3962: C --> T
Char. 4403: A --> G
Char. 4543: C --> T
Char. 4718: T --> A
Char. 4727: T --> C

16S

Char. 4781: T --> G
Char. 4920: T --> C
Char. 4971: A --> G
Char. 5068: T --> A
Char. 5095: C --> T
Char. 5106: A --> T
Char. 5276: T --> A
Char. 5277: A --> T
Char. 5325: C --> A
Char. 5417: A --> C
Char. 5470: T --> A
Char. 5532: T --> C
Char. 5660: C --> T
Char. 5759: A --> C
Char. 5816: C --> T

Tepuihyla

ND1

Char. 1153: A --> C
Char. 1240: A --> T
Char. 1255: T --> A
Char. 1259: T --> C
Char. 1372: C --> T
Char. 1409: A --> G
Char. 1438: A --> T
Char. 1573: A --> T
Char. 1600: T --> C
Char. 1642: T --> C
Char. 1694: C --> A
Char. 1698: T --> C

12S

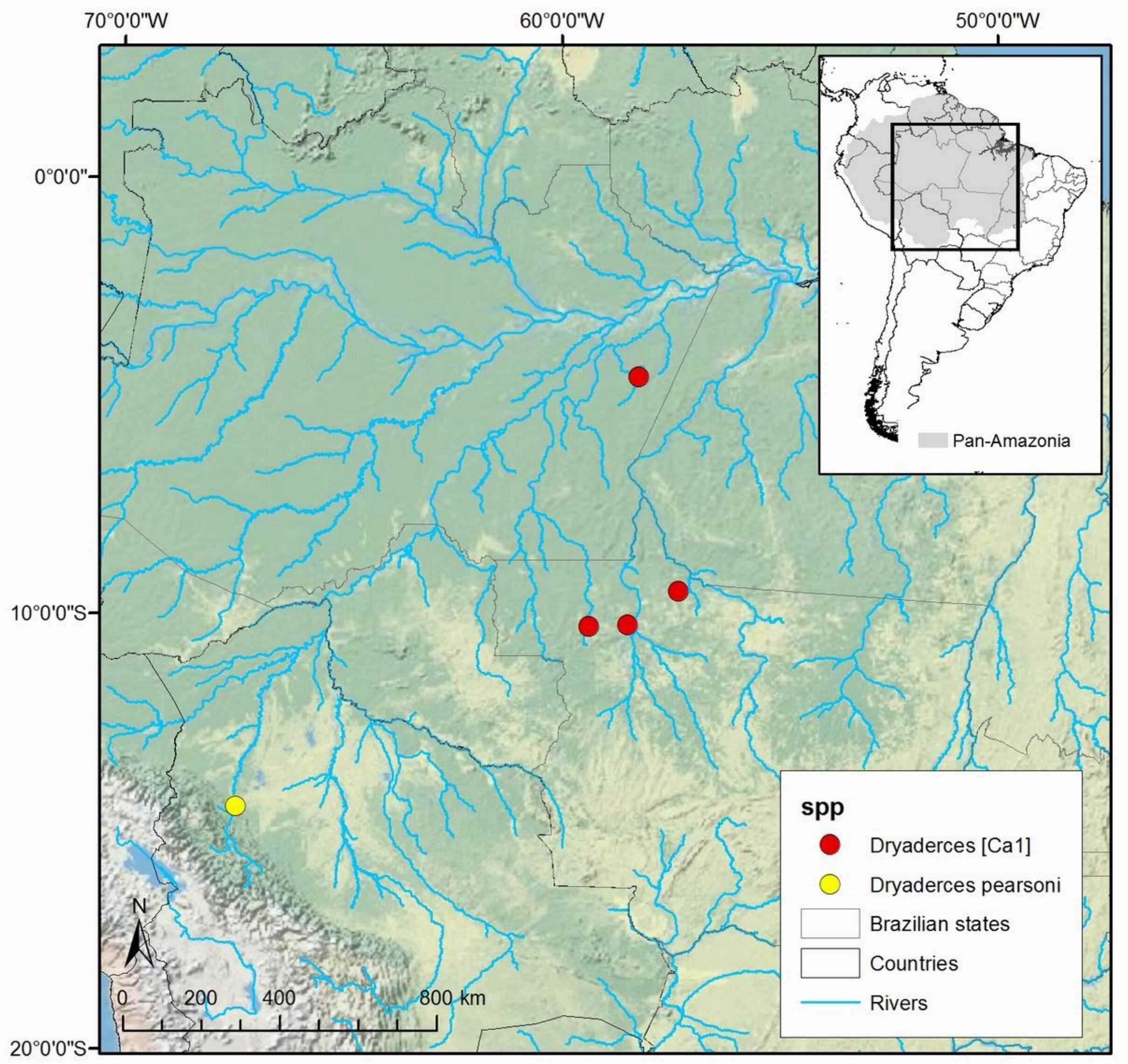
Char. 3760: T --> C
Char. 3950: A --> C
Char. 4053: G --> A
Char. 4086: C --> T
Char. 4197: A --> G
Char. 4206: T --> C
Char. 4308: T --> C
Char. 4553: C --> T

16S

Char. 4730: T --> A
Char. 4780: T --> G
Char. 4781: T --> A
Char. 4797: T --> A
Char. 4852: T --> C
Char. 4894: A --> T
Char. 4920: T --> A
Char. 5106: A --> C
Char. 5252: T --> C
Char. 5257: C --> T
Char. 5258: A --> T
Char. 5272: A --> T
Char. 5279: T --> A
Char. 5317: C --> T
Char. 5456: C --> T
Char. 5833: C --> A
Char. 5840: C --> T
Char. 5845: T --> C
Char. 5896: C --> T
Char. 5906: C --> T
Char. 5919: C --> T
Char. 5947: T --> C

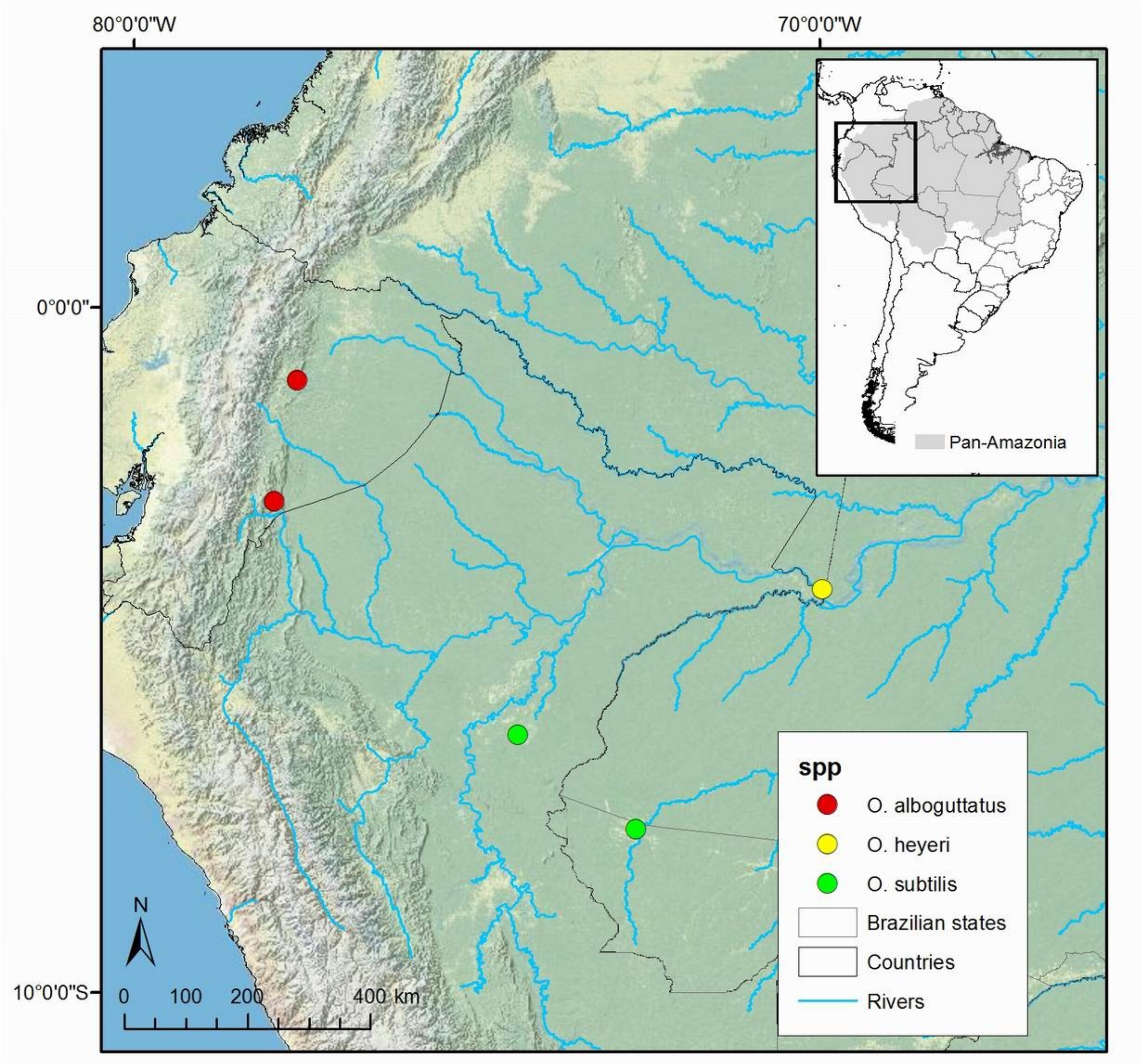
Appendix S8.1

Map of localities of sampled exemplars of *Dryaderces* gen. n. in central and southern Amazonia.



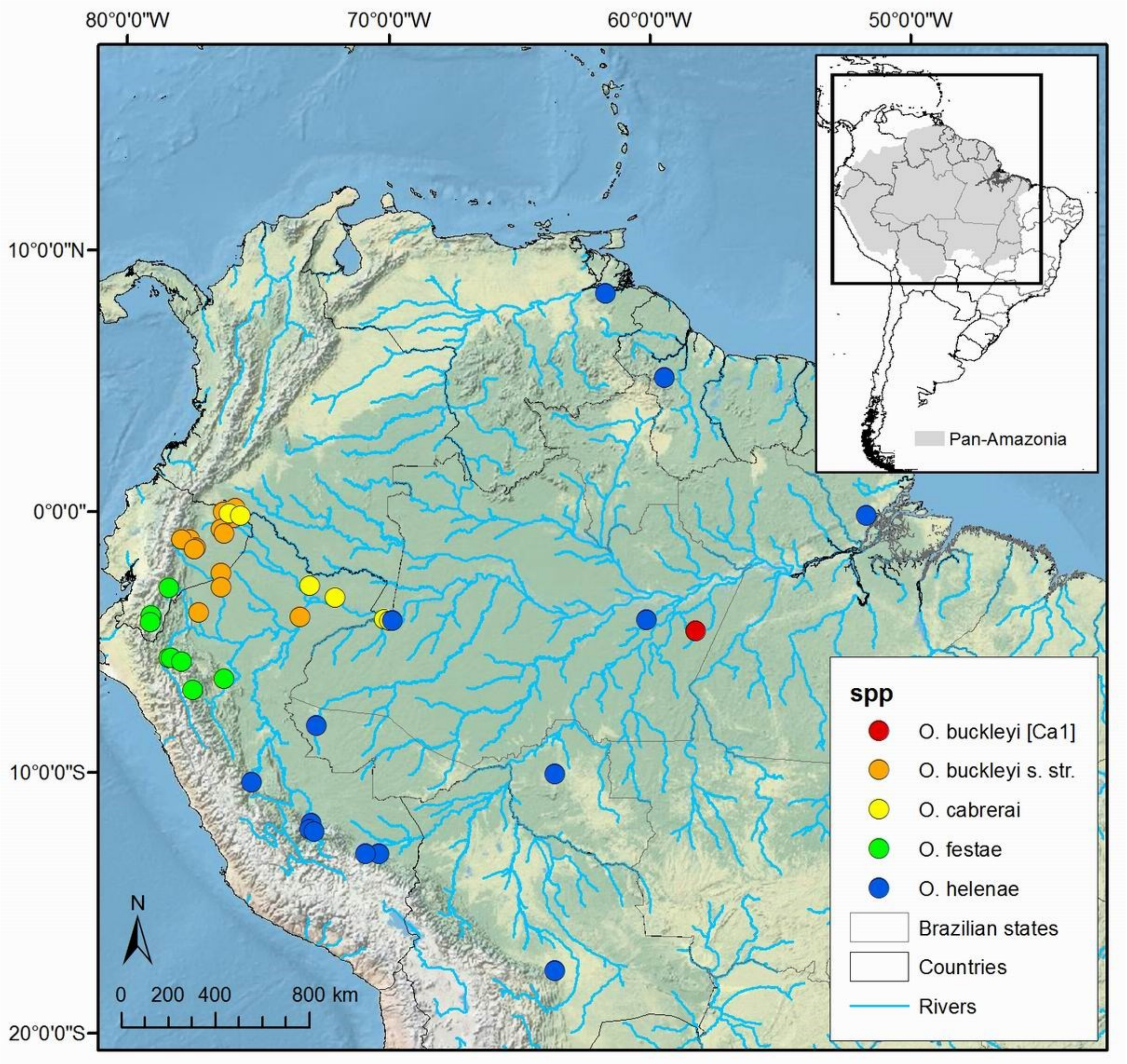
Appendix S8.2

Map of localities of sampled exemplars of the *Osteocephalus alboguttatus* Species Group.



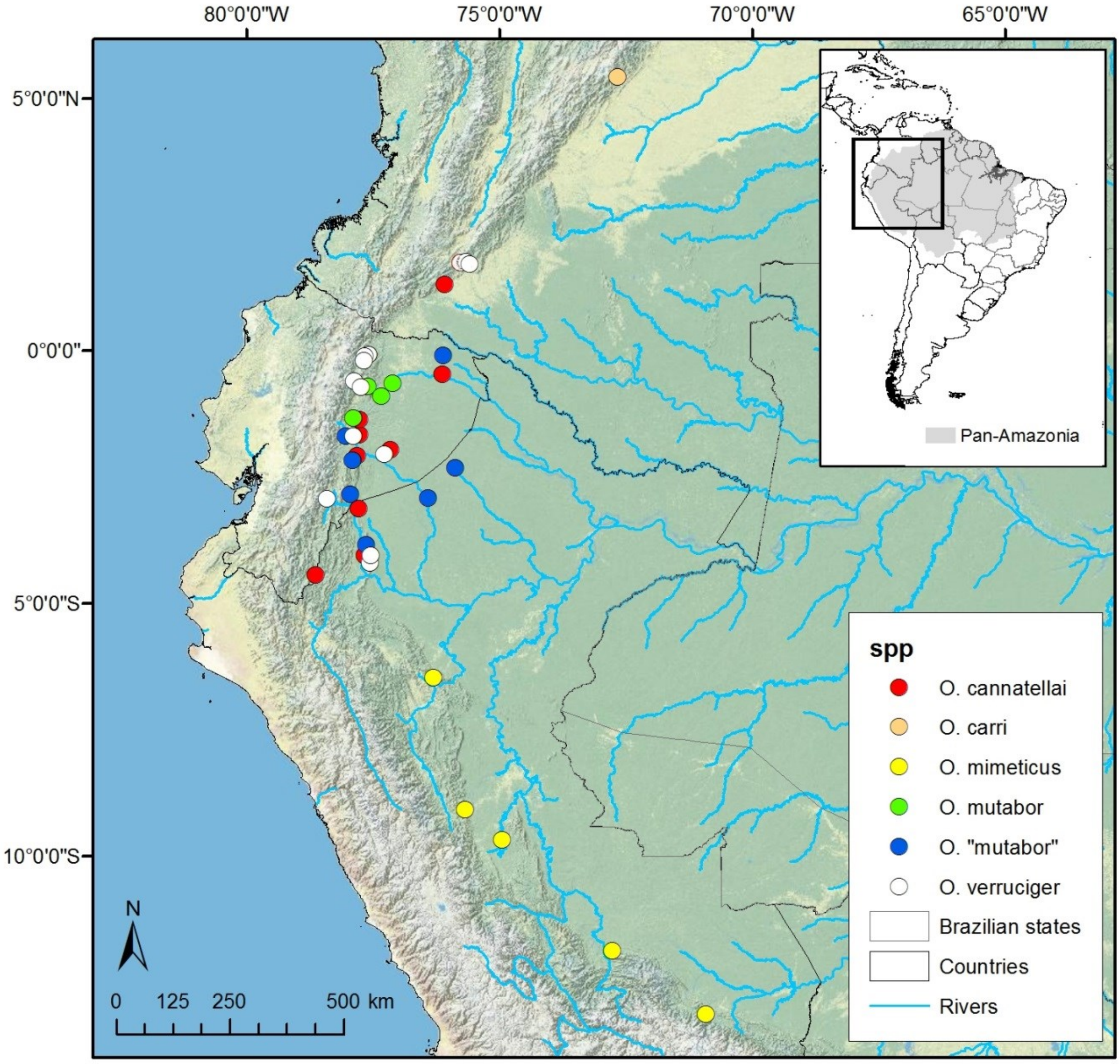
Appendix S8.3a

Map of localities of sampled exemplars of the *Osteocephalus buckleyi* Species Group (part).



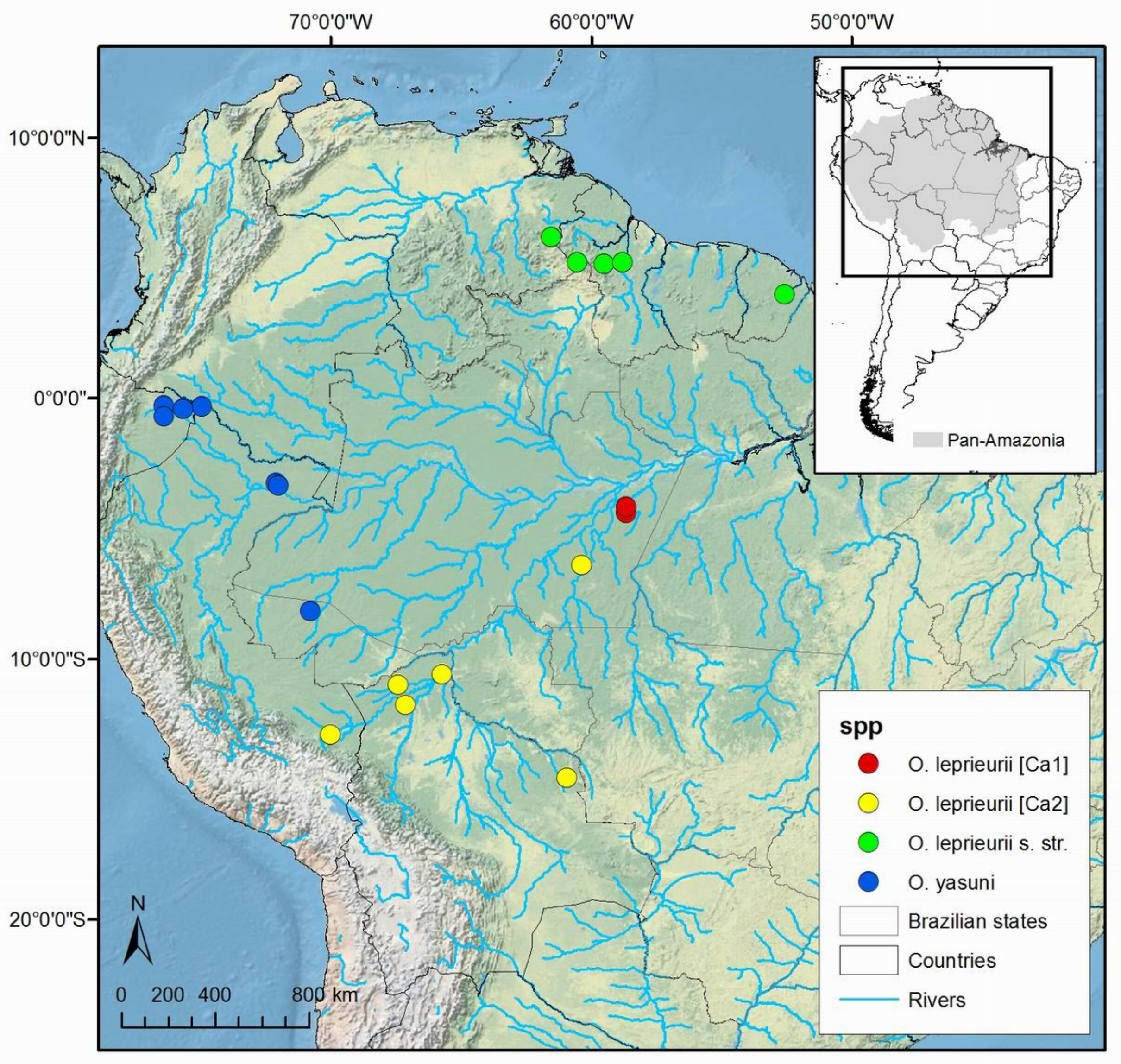
Appendix S8.3b

Map of localities of sampled exemplars of the *Osteocephalus buckleyi* Species Group (part).



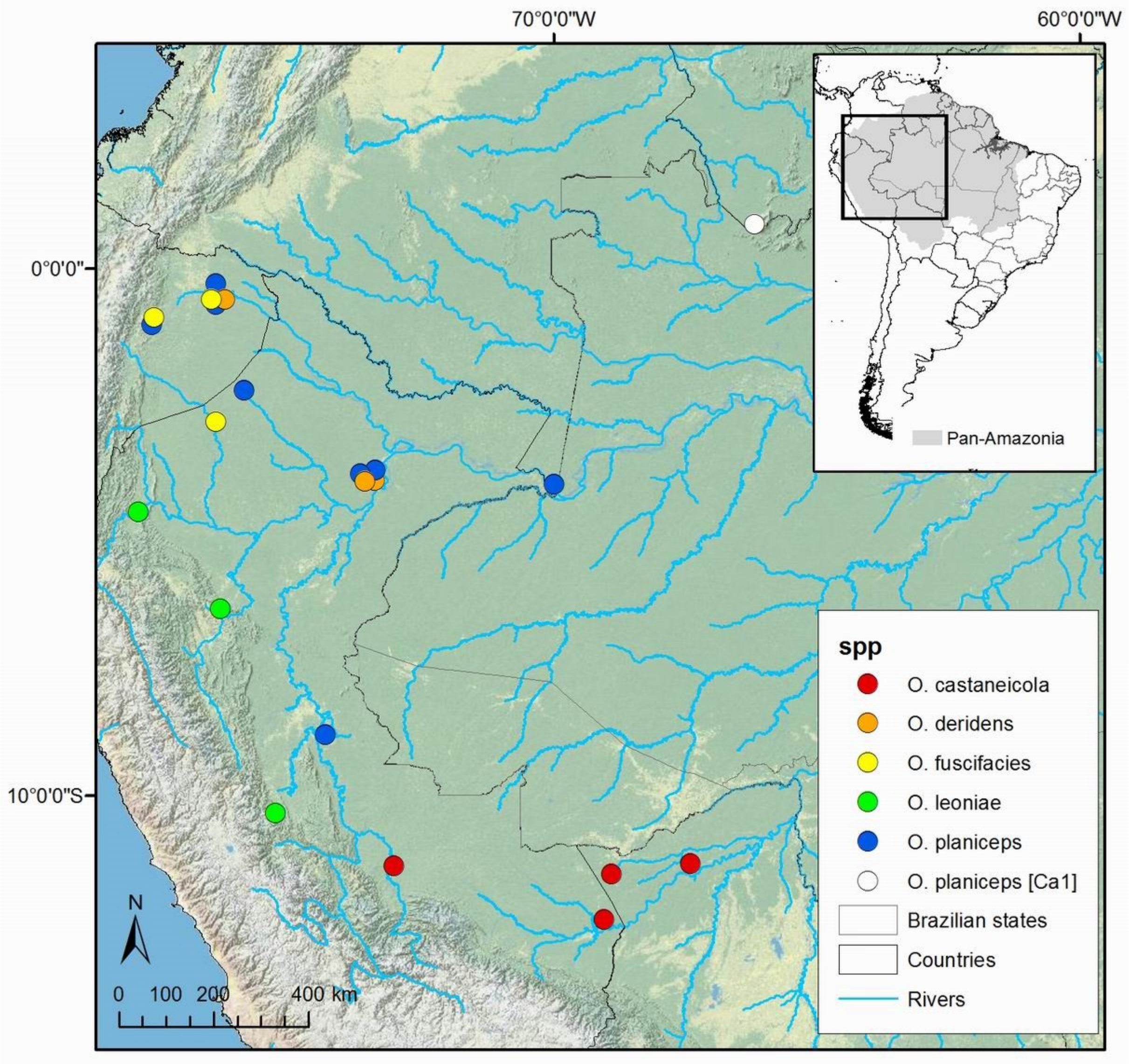
Appendix S8.4

Map of localities of sampled exemplars of the *Osteocephalus leprieurii* Species Group.



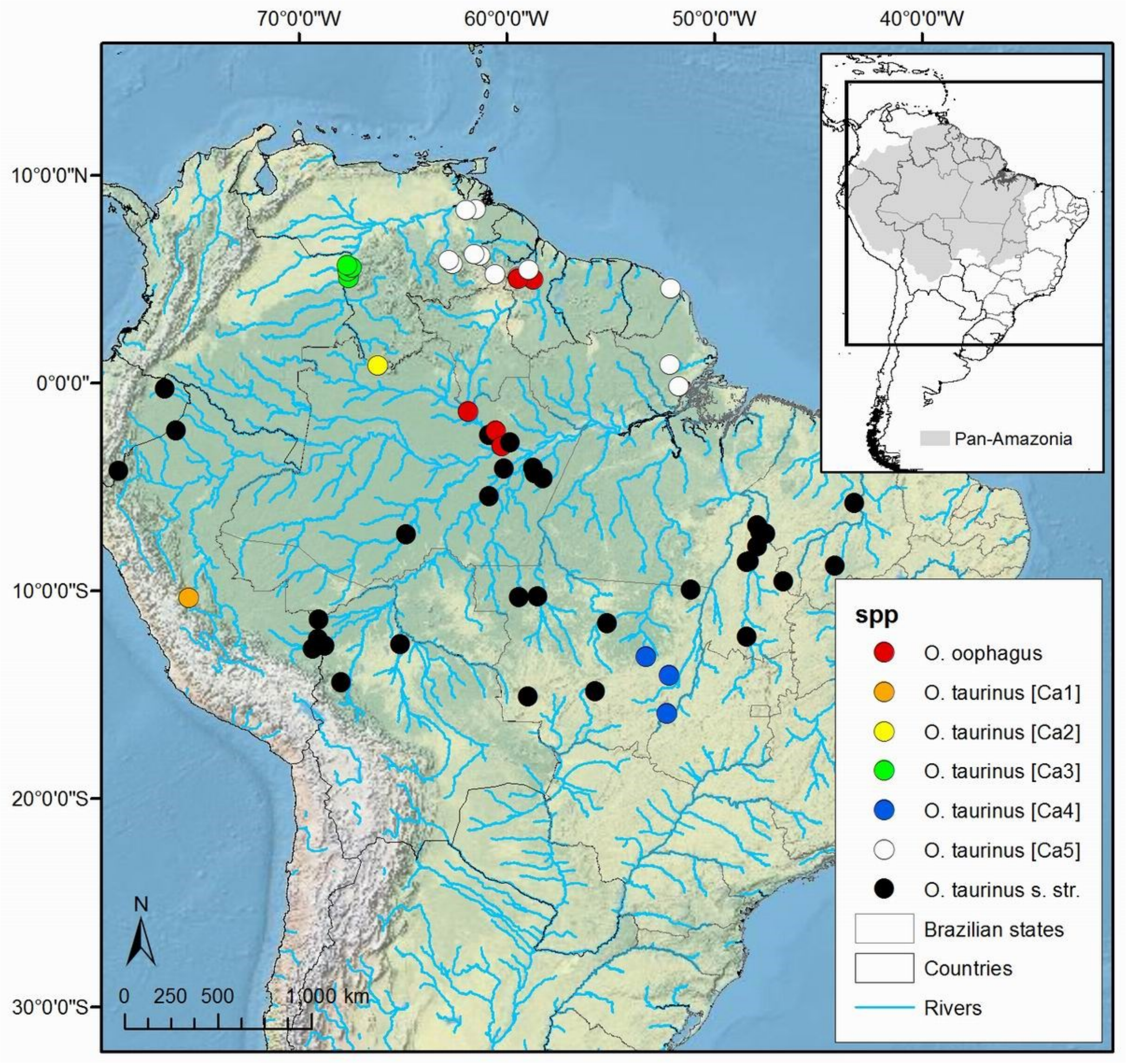
Appendix S8.5

Map of localities of sampled exemplars of the *Osteocephalus planiceps* Species Group.



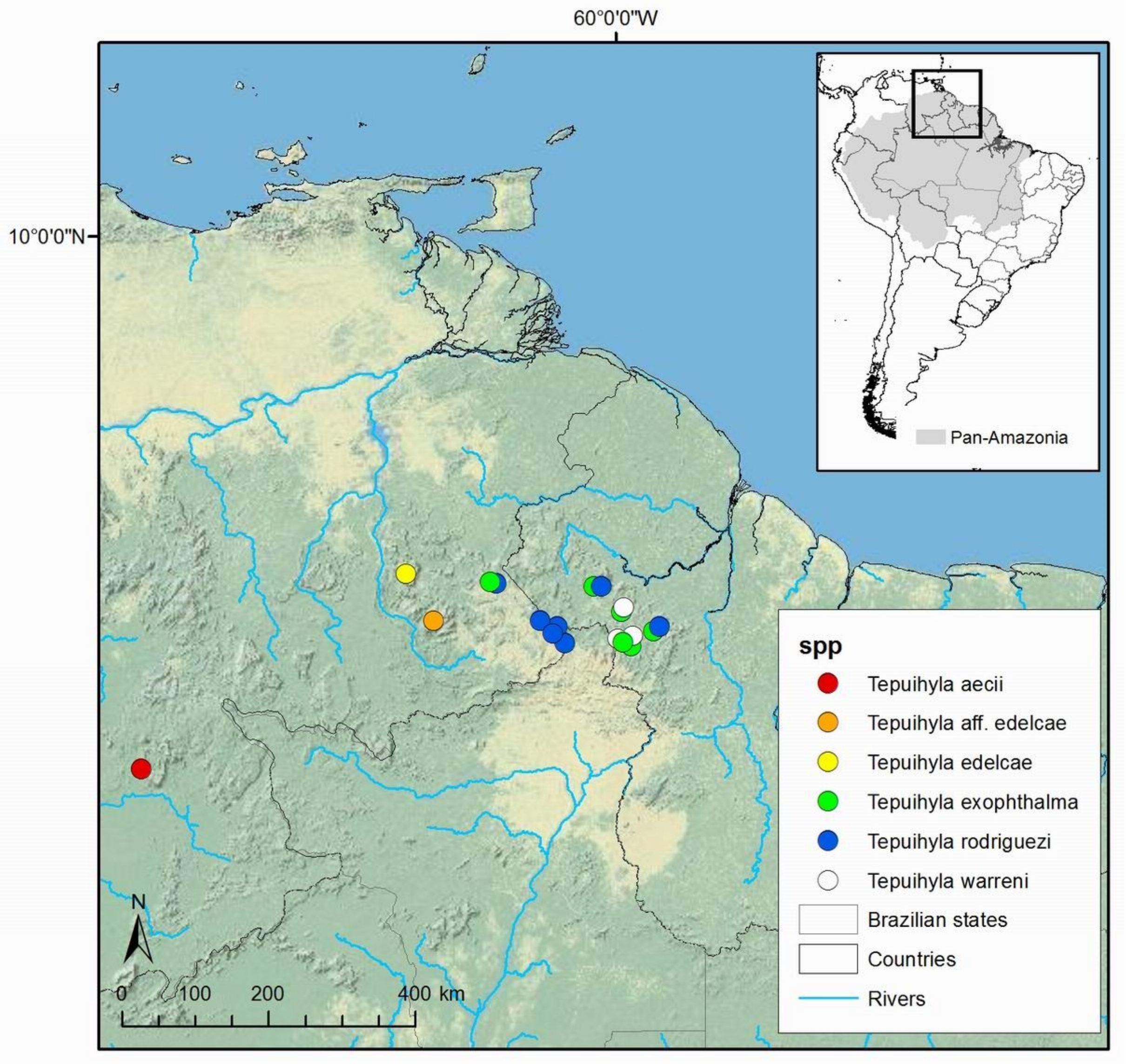
Appendix S8.6

Map of localities of sampled exemplars of the *Osteocephalus taurinus* Species Group.



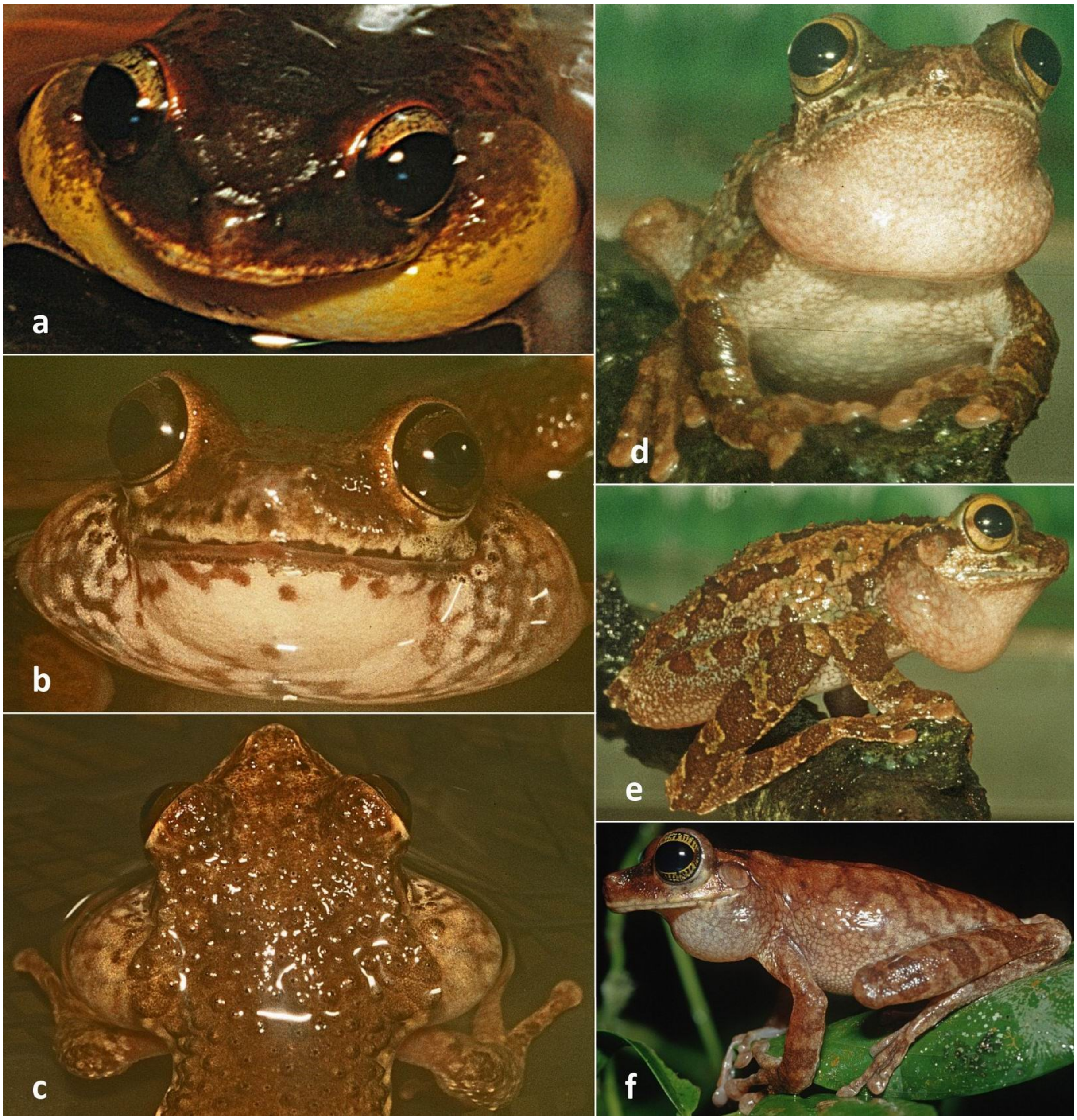
Appendix S8.7

Map of localities of sampled exemplars of *Tepuihyla* on the Guiana Shield.



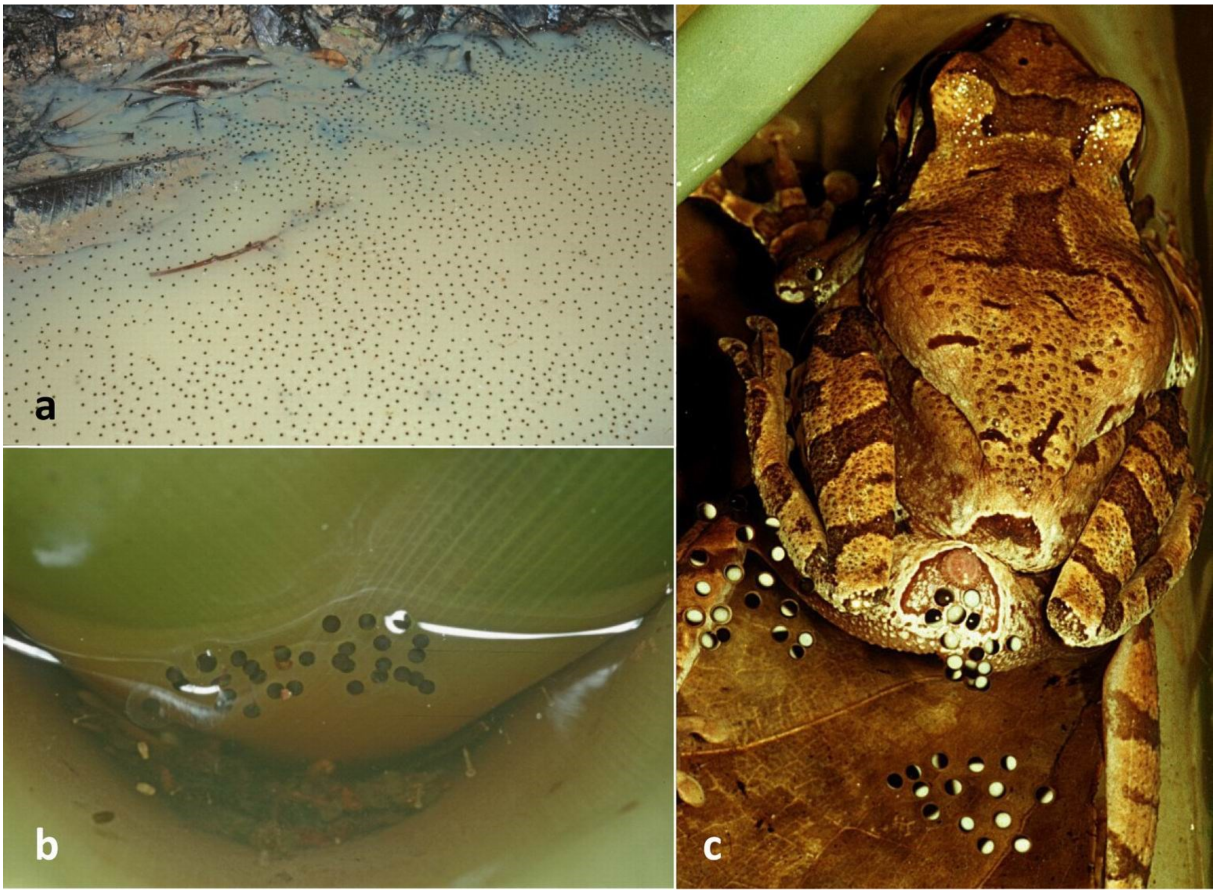
Appendix S9

Fully inflated vocal sacs in *Osteocephalus*: (**a**) paired, lateral with subgular expansion (*O. leprieurii*, pond breeder); (**b**) and (**c**) paired, lateral with subgular expansion (*O.verruciger*, stream breeder); (**d**) and (**e**) paired, lateral with subgular expansion (*O. buckleyi*, stream breeder); (**f**) single, subgular (*O. oophagus*, phytotelm breeder).



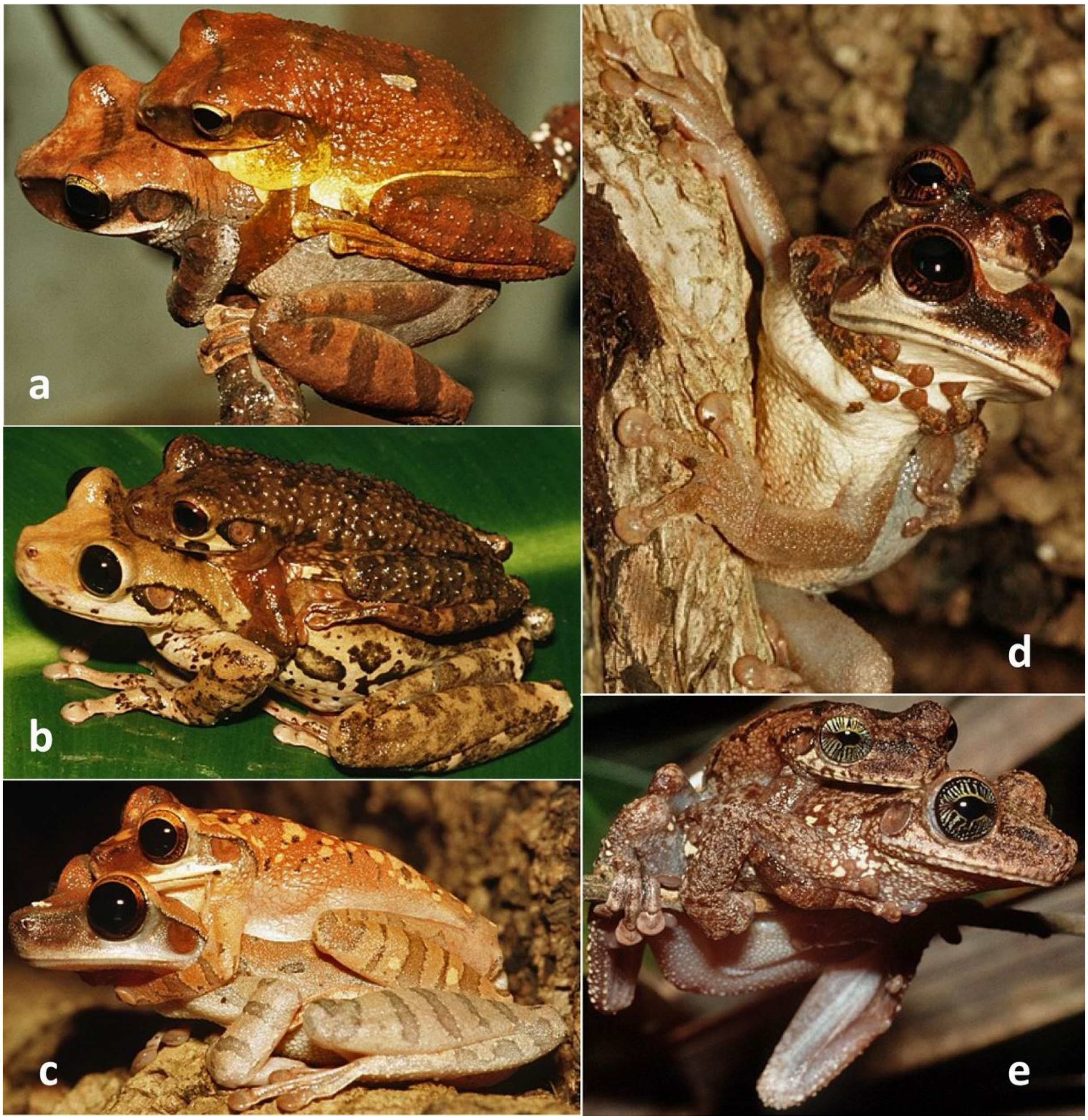
Appendix S10

Egg clutches of *Osteocephalus*: (**a**) surface film (*O. taurinus*, pond breeder); (**b**) clutch attached to a bromeliad leaf axil at surface level (*O. oophagus*, phytotelm breeder); (**c**) surface film of a phytotelm breeder at a spacious site (*O. planiceps*) forming during egg-laying.



Appendix S11

Types of amplexus in *Osteocephalus*: (**a**) axillary (*O. yasuni*, pond breeder); (**b**) axillary (*O. verruciger*, stream breeder); (**c**) gular (*O. leoniae*, phytotelm breeder); (**d**) gular (*O. deridens*, phytotelm breeder); (**e**) axillary *O. oophagus*, phytotelm breeder.



4. GENERAL DISCUSSION

With 23 currently recognized species (Table 4.1) plus at least nine genetically and in part morphologically distinct “candidate species”, the genus *Osteocephalus* is among the largest genera of hylid frogs in pan-Amazonia. It has posed numerous taxonomic and systematic problems. The reasons have been outlined in Chapter 1.2. The publications presented in Chapter 3 resolve many of them and have drastically changed our understanding of the species composition and relationships both on an intra- and intergeneric level.

In Chapter 3.1.1 a new species (*O. castaneicola*) is described from Amazonian Bolivia and adjacent southern Peru. It is peculiar for depositing eggs into opened fruit capsules of the Brazil nut (*Bertholletia excelsa*) and other phytotelmata where tadpoles feed on frog eggs, most likely provided by the parent mother. A preliminary molecular analysis demonstrates that the new species’ relationships are with other phytotelm-breeders, *O. planiceps* and *O. deridens*, but not with *O. oophagus*, another egg-eating and phytotelm-breeding species, indicating that breeding in phytotelmata and feeding on nutritive eggs have evolved twice independently within the genus.

Chapter 3.1.2 describes a new species, *O. duellmani*, from the Cordillera del Cóndor, an isolated mountain range east of the Andean main chain in the Ecuadorian-Peruvian border area. Morphologically, it can be assigned to the *O. buckleyi* species group. Its altitudinal distribution is unusually high (1910 m a.s.l.), only surpassed by one other species, *O. festae*.

Another new species, *O. camufatus* of the *O. buckleyi* species group, is described in Chapter 3.1.3. It is so far only known from two sites in lowland rain forest on the Rio Abacaxis, Brazilian Central Amazonia. This is the first formally described species of those that had been attributed the status of a “candidate species” by Jungfer *et al.* (2013).

Chapter 3.2 deals with the taxonomic status of several poorly known species assignable to *Osteocephalus*. One of them, *O. cabrerai*, had been placed in the synonymy of *O. buckleyi* by Trueb & Duellman (1971), but was resurrected by Duellman & Mendelson (1995). The specimen the latter used for that purpose was actually not *O. cabrerai*, but *O.* cf. *buckleyi*. I used own material from Peru to give a

Table 4.1. Currently recognized species of *Osteocephalus* and their respective groups.

Osteocephalus alboguttatus group	*O. alboguttatus*
	O. heyeri
	O. subtilis
Osteocephalus buckleyi group	*O. buckleyi*
	O. cabrerai
	O. cannatellai
	O. carri
	O. duellmani
	O. festae
	O. helenae
	O. mimeticus
	O. mutabor
	O. verruciger
Osteocephalus leprieurii group	*O. leprieurii*
	O. yasuni
Osteocephalus planiceps group	*O. castaneicola*
	O. deridens
	O. fuscifacies
	O. leoniae
	O. planiceps
Osteocephalus taurinus group	*O. oophagus*
	O. taurinus
	O. vilarsi

detailed description of *O. cabrerai*. *Hyla festae* had also been placed in the synonymy of *O. buckleyi* (Trueb & Duellman 1971). It is, however, well distinguishable from the latter and resurrected as *O. festae*.

When all Neotropical frogs in the catch-all genus *Hyla* were transferred to other genera (Faivovich *et al*. 2005), *Hyla inframaculata* from Central Amazonia was left there as *incertae sedis*. The only specimen known for more than 120 years and described by Boulenger in 1882, has characters typical of *Osteocephalus* and I consequently transferred it to that genus. Meanwhile, more specimens have been discovered. In describing them, Hoogmoed (2013) discussed the possibility that it was actually a species of *Dryaderces*, a genus split from *Osteocephalus* by Jungfer

Table 4.2. Species or subspecies described as or referred to *Osteocephalus* and their present status. An asterisk denotes that the taxonomic conclusion is based on this work.

Species or subspecies name	**Original name**	**Current opinion on status**
aecii	*Osteocephalus aecii* Ayarzagüena, Señaris & Gorzula, 1992	*Tepuihyla aecii*
alboguttata	*Hyla alboguttata* Boulenger, 1882	*Osteocephalus alboguttatus*
ayarzaguenai	*Osteocephalus ayarzaguenai* Señaris & Gorzula, 1996	*Osteocephalus leprieurii*
britti	Hyla *leprieurii britti* Melin, 1941	*Osteocephalus leprieurii*
buckleyi	*Hyla buckleyi* Boulenger, 1882	*Osteocephalus buckleyi*
cabrerai	*Hyla cabrerai* Cochran & Goin, 1970	*Osteocephalus cabrerai**
cannatellai	*Osteocephalus cannatellai* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012	*Osteocephalus cannatellai*
carri	*Hyla carri* Cochran & Goin, 1970	*Osteocephalus carri*
castaneicola	*Osteocephalus castaneicola* Moravec, Aparicio, Guerrero-Reinhard, Calderón, Jungfer & Gvoždík, 2009	*Osteocephalus castaneicola**
depressa	*Hyla depressa* Andersson, 1945	*Osteocephalus taurinus*
deridens	*Osteocephalus deridens* Jungfer, Ron, Seipp & Almendáriz, 2000	*Osteocephalus deridens*
duellmani	*Osteocephalus duellmani* Jungfer, 2011	*Osteocephalus duellmani**
edelcae	*Osteocephalus edelcae* Ayarzagüena, Señaris & Gorzula, 1992	*Tepuihyla edelcae*
elkejungingerae	*Hyla elkejungingerae* Henle, 1981	*Osteocephalus mimeticus**
exophthalmus	*Osteocephalus exophthalmus* Smith & Noonan, 2001	*Tepuihyla exophthalma**
festae	*Hyla festae* Peracca, 1904	*Osteocephalus festae**
flavolineatus	*Osteocephalus flavolineatus* Steindachner, 1862	*Osteocephalus taurinus*
fuscifacies	*Osteocephalus fuscifacies* Jungfer, Ron, Seipp & Almendáriz, 2000	*Osteocephalus fuscifacies*
galani	*Osteocephalus galani* Ayarzagüena, Señaris & Gorzula, 1992	*Tepuihyla rodriguezi**
germani	*Osteocephalus germani* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012	*Osteocephalus helenae**
helenae	*Hyla helenae* Ruthven, 1919	*Osteocephalus helenae**
heyeri	Osteocephalus *heyeri* Lynch, 2002	*Osteocephalus heyeri*
inframaculata	*Hyla inframaculata* Boulenger, 1882	*Dryaderces inframaculata*
langsdorffii	*Hyla langsdorffii* Duméril & Bibron, 1841	*Itapotihyla langsdorffii*
leoniae	*Osteocephalus leoniae* Jungfer & Lehr, 2001	*Osteocephalus leoniae*
leprieurii	*Hyla leprieurii* Duméril & Bibron, 1841	*Osteocephalus leprieurii*
luteolabris	*Osteocephalus luteolabris* Ayarzagüena, Señaris & Gorzula, 1992	*Tepuihyla luteolabris*
mimetica	*Hyla mimetica* Melin, 1941	*Osteocephalus mimeticus**
mutabor	*Osteocephalus mutabor* Jungfer & Hödl, 2002	*Osteocephalus mutabor*

Table 4.2. continued

oophagus	*Osteocephalus oophagus* Jungfer & Schiesari, 1995	*Osteocephalus oophagus*
orcesi	*Hyla orcesi* Funkhouser, 1956	*Osteocephalus verruciger*
pearsoni	*Hyla pearsoni* Gaige, 1929	*Dryaderces pearsoni**
phasmatus	*Osteocephalus phasmatus* MacCulloch & Lathrop, 2005	*Tepuihyla exophthalma**
planiceps	*Osteocephalus planiceps* Cope, 1874	*Osteocephalus planiceps*
rimarum	*Osteocephalus rimarum* Ayarzagüena, Señaris & Gorzula, 1992	*Tepuihyla rimarum*
riopastazae	*Hyla riopastazae* Andersson, 1945	*Osteocephalus verruciger*
rodriguezi	*Hyla rodriguezi* Rivero, 1968	*Tepuihyla rodriguezi*
subtilis	*Osteocephalus subtilis* Martins & Cardoso, 1987	*Osteocephalus subtilis*
taurinus	*Osteocephalus taurinus* Steindachner, 1862	*Osteocephalus taurinus*
verrucigera	*Hyla verrucigera* Werner, 1901	*Osteocephalus verruciger*
vilarsi	*Hyla vilarsi* Melin, 1941	*Osteocephalus vilarsi**
vilmae	*Osteocephalus vilmae* Ron, Venegas, Toral, Read, Ortiz & Manzano, 2012	*Osteocephalus buckleyi**
yasuni	*Osteocephalus yasuni* Ron & Pramuk, 1999	*Osteocephalus yasuni*

et al. (2013). In September 2013 I was able to inspect another fresh specimen and agree with Hoogmoed (2013) that *inframaculata* is a species of *Dryaderces*, morphologically very similar to an undescribed species of the same genus (Jungfer *et al*. 2013).

Two small frogs from the Peruvian eastern Andean edge were described as *Hyla mimetica* by Melin (1941) and *Hyla elkejunginerae* by Henle *et al*. (1983), respectively. While Henle later (1992) found that his specimens had been juveniles, the adults actually pertaining to *Osteocephalus*, *Hyla mimetica* was lost in the synonymy of another hylid (now *Dendropsophus*) (Duellman 1974). Both species could be shown to be conspecific, the valid name being *O. mimeticus*. Another species resurrected from various synonymies is *Hyla vilarsi*, also described by Melin (1941). It could be demonstrated that it was neither *O. leprieurii* (as stated by Cochran & Goin 1970), nor *O. taurinus* (Bokermann 1966, Trueb & Duellman 1971), but a valid species, *O. vilarsi*. There are a few more South American hylid frogs *incertae sedis* according to Faivovich *et al.* (2005), that are only known from the types and never encountered again. Some of them have proven to be nothing else but juvenile *Osteocephalus* (Jungfer, in prep.).

The distribution area of *Osteocephalus* covers roughly 7.5 million km^2 (Fig. 1.1 on p. 2) and includes parts of the territories of nine countries. This huge expanse alone reflects the problems that have to be tackled if one attempts to resolve the systematic relationships of the whole genus meaningfully. It would not have been possible without the help of numerous colleagues who contributed material, especially tissue samples, to the work presented in Chapter 3.3. It includes information on 328 specimens from 218 localities from eight countries. A molecular analysis resolved that the genus was paraphyletic with respect to *Tepuihyla*, a genus comprised of species restricted to the highlands of the Guiana Shield. Within *Osteocephalus*, five species groups are recognized and defined. Three species of *Osteocephalus* and three of *Tepuihyla* are placed in the synonymy of other species. Four species are reallocated ("*Hyla*" *helenae* to *Osteocephalus*, "*Hyla*" *warreni* and *O. exophthalmus* to *Tepuihyla*) and one new genus, *Dryaderces*, sister to *Osteocephalus*, is erected.

Four widespread species, three of them distributed almost throughout Amazonia and the lowlands of the Guianan region, each contain several lineages with genetic distances sufficient to consider them species. In other words, these nominal species are supposed to constitute assemblages of cryptic and yet unrecognized species. By applying the term "candidate species" (Vieites *et al.* 2009), we flag nine putative new species indicating a high component of hidden diversity among *Osteocephalus*. Counting the candidate species as true species would mean that there was an increase of species of up to 37.5%. In the paper we rely heavily on the uncorrected pairwise genetic divergences in the 16S rRNA gene. Vieites *et al.* (2009) found distances among species of Madagascan frogs to be >3% in general. No such absolute thresholds are detectable in *Osteocephalus*. The distance between *O. oophagus*, a morphologically and behaviourally well-distinguishable species, and *O. taurinus* sensu stricto is 0.9-2.2% (Fig. 1.6 on p. 14 and S4a on p. 189). The fact that the former is embedded in the different lineages of what is presently called *O. taurinus* (sensu lato), renders *O. taurinus* paraphyletic. Establishing a threshold of, e.g., 3% would just implement an artificial limit into the continuum of evolutionary processes. Vieites *et al.* (2009) distinguish between "Confirmed Candidate Species" (CCS) and "Unconfirmed Candidate Species" (UCS). The former is characterized by some genetic differentiation, but also by at least one character either indicating a premating reproductive barrier, a diagnostic morphological character important for the group, or sympatric occurrence without mixture in combination with at least one, albeit perhaps subtle, phenotypic character state difference. One of the CCS in the *O. buckleyi* group is now being described as a new species, *O. camufatus*, in Chapter 3.1.3. In contrast, despite having inspected hundreds of preserved *O. taurinus* sensu lato, none of those CCS characters is obvious to me for a whole lineage among them (except *O. oophagus*). Unfortunately, important characters, such as vocalizations and other behavioural traits, are unavailable yet and the knowledge of distributions is rudimentary in most cases. Those lineages with genetic differentiation, but data deficiency in morphology, ecology or distribution are termed UCS and apply to most of those currently lumped under "*O. taurinus*". With the acquisition of more data in the future, the status of several candidate species will likely to be resolved.

However, there may be undetected species even among those lineages not clearly demarcated by high genetic distances (and hence not termed candidate species here). An example is *O. helenae*, a polymorphic species until recently considered conspecific with *O. buckleyi*, resurrected by Jungfer *et al.* 2013 (Chapter 3.3). We took a conservative position then, leaving together several morphs with low genetic differentiation under one species name. New data gathered since then indicate that two well-distinguishable morphs occur sympatrically in French Guiana and appear to be specifically distinct (unpublished data).

The species of *Osteocephalus* (including, for comparative reasons, candidate species that, whether true species or not, exhibit their own evolutionary history) are not evenly distributed over pan-Amazonia. One of the most generalized species groups from a reproductive biological point of view is the *O. taurinus* group (8 spp.) that is distributed over almost the entire area of the genus, but is most speciose in the Guianan region north of the Amazon (6 spp.). It is the only group that has entered the drier Cerrado in the south-eastern Amazon. The fact that one species from the north-east (the eastern Guiana Shield) has an allopatric sister species in the south-west (Mato Grosso) indicates a complex history of the two lineages that yet has to be resolved. The *O. leprieurii* group is similarly generalized with respect to reproduction. One species each occurs in the NW, NE, SE and SW part of Amazonia, apparently without overlap. The *O. buckleyi* group with a derived reproductive mode of breeding in lotic water is equally wide-ranging. But while relatively few species occur in the lowlands of the eastern half of Amazonia (2 spp.), they are speciose in the western Andean foothills and adjacent lowlands (10 spp.). At least five species of them occupy eastern Andean versants between 500 and 2200 m asl. from Colombia to southern Peru. Since they occur in allopatry or at least nearly so, their history appears to be connected with the uplift of the Andean chain especially in the Late Miocene (ca. 7-11 Ma) (Hoorn *et al.* 2010, Wesselingh *et al.* 2010) and vicariance is likely to be the origin of speciation. The two remaining groups are from the western part of the Amazon Basin. The *O. alboguttatus* group (3 spp.), for which no information on reproduction is available, is exclusively north-western, while the phytotelm-breeding *O. planiceps* group (6 spp.) encompasses one relatively unspecialized species (with omnivorous larvae) occurring in western Amazonia from southern Colombia to southern Peru. Four other species with higher specialization (oophagous larvae) together occupy about the same area (slightly beyond it in the south to northern Bolivia), but the four of them appear to occur in allopatry, replacing each other from north to south. A closely related undescribed species (not included in Jungfer *et al.* 2013) occurs allopatrically from the other four species in the Brazilian-Peruvian border area of the Sierra del Divisor (unpublished). One apparently isolated and data-deficient species is known from the base of Pico de Neblina, an outcrop of the Guiana Shield, on the Venezuelan-Brazilian border.

Adaptations to different breeding sites is one of the reasons that had led taxonomists such as Lynch (2002) to doubt whether *Osteocephalus* formed a biological unit at all. It is apparent from the phylogenetic tree that morphological reductions play an important role in the diversification of the genus. The spiny dorsa typical of all lentic and many lotic breeding species is lost in almost all phytotelm-breeding species. If one assumes that the adaptive significance of a spiny dorsum is quick sex recognition in a breeding congregation (see p. 9), the lack of it in males breeding in phytotelmata scattered throughout the forest is not surprising. A similar scenario may explain the small sizes of all but one phytotelm-breeding species, since phytotelmata usually offer limited space to reproducing adults. The cavernous bilobed vocal sacs of lentic and lotic breeding males are replaced by small single, subgular ones. Reductions can be noted in tadpoles as well. Duellman (1970) stated that two anterior and three posterior tooth rows are the generalized hylid formula. In *Osteocephalus*, they are found only in the two clades of highly specialized

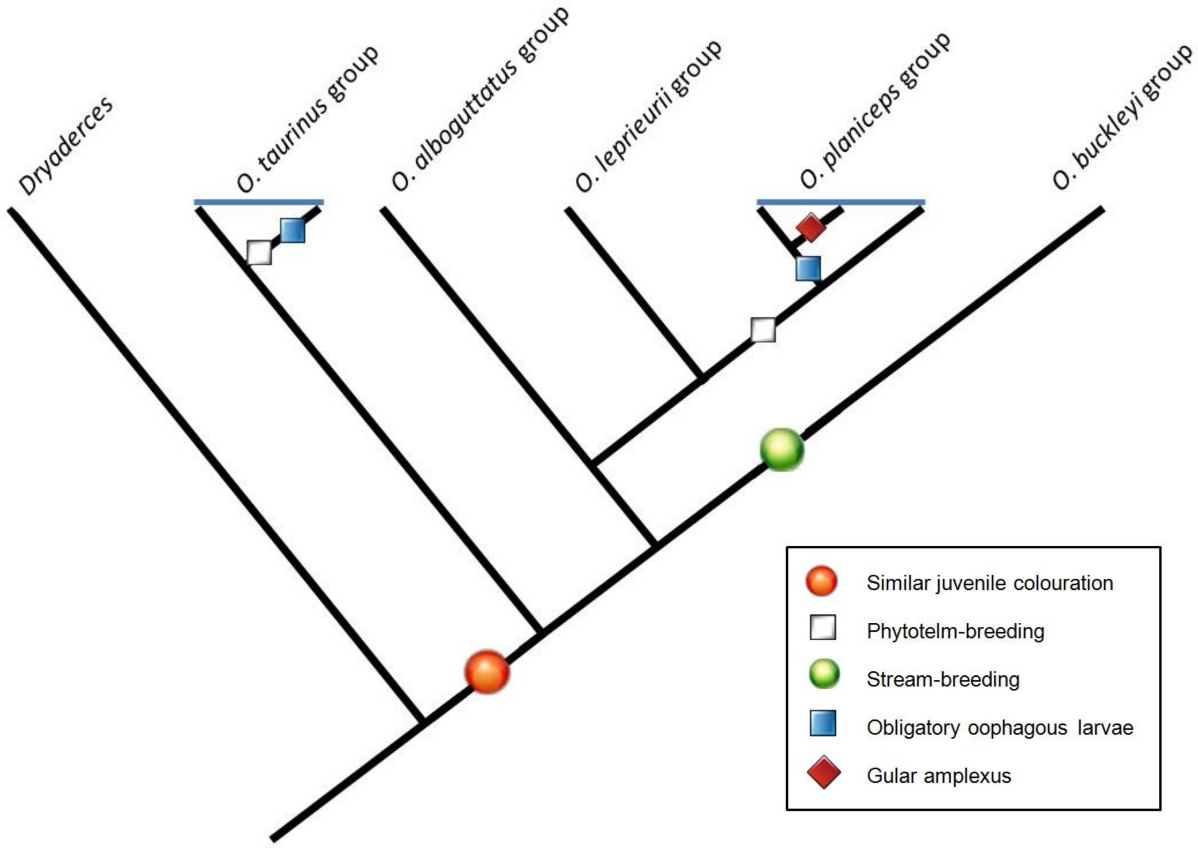


Fig. 4.3. Diagrammatic view of the relationships among *Osteocephalus* and its sister genus *Dryaderces* and the appearance of some derived characters.

oophagous phytotelm-dwelling species. The lentic and lotic *Osteocephalus* larvae all have higher labial tooth row numbers. So in *Osteocephalus* the "generalized" formula actually is the derived one. It may be interesting to note that there is a remarkable convergence in species of *Trachycephalus*, in which one phytotelm-dwelling species with oophagous larvae, *T. hadroceps*, has developed the same reductions in adult size and larval tooth rows and has a subgular vocal sac, while other species share the characters found in generalized *Osteocephalus* (pers. obs.).

Among anurans, there are only a few amplectic positions, namely the lumbar amplexus in basal groups, the axillary amplexus among higher groups such as hylids and a few positions derived from them (Duellman & Trueb 1986). A unique feature is the gular amplexus found only in two species of phytotelm-breeding species (see Chapter 3.3 and Fig. S11 on p. 219). The shift from axillary in all other species to gular amplexus may have its adaptive significance in more mobility of the female while climbing to a suitable breeding site.

With so many features separating different clades among *Osteocephalus*, there are also a few found to be present in all species (although only one restricted to the genus). A putative synapomorphy of *Osteocephalus* is the juvenile colouration of newly metamorphosed individuals exhibiting a red iris and light spots on the limbs (Fig. S1 on p. 154). In fact, most juveniles resemble each other much more interspecifically than conspecific adults of different sexes. One exception is "*O.*" *pearsoni*, which was one important reason to lead us to assign one distinct clade without ontogenetic colour change, formerly in *Osteocephalus*, to a new genus, *Dryaderces* (Chapter 3.3).

Although reproducing either in lentic water (the *O. leprieurii* group), in lentic water on the ground or in phytotelmata (the *O. taurinus* group), in lotic water (the *O. buckleyi* group) or exclusively in phytotelmata (the *O. planiceps* group), the four species groups deposit their eggs as films on the water's surface. The reproduction site and eggs are unknown in the *O. alboguttatus* group. With their direct contact to air, surface films are supposed to facilitate oxygen uptake in warm, stagnant water (e.g. Wells 2007) and may also be advantageous in phytotelmata often containing decomposing plant and animal matter. It seems, however, to be of limited value in the usually well aeriated lotic water in which the members of the *O. buckleyi* group breed, indicating the group's ancestry from pool breeders. This is also obvious in the phytotelm-breeding species which have retained the surface film clutch type in both groups where phytotelm-breeding occurs.

With respect to threat and vulnerability caused by anthropogenic activity, for the time being all described species are either of least concern or data deficient according to the IUCN (2014) Red List of Threatened Species categories. However, this situation may change in the near future for some populations when "candidate species" among the wide-ranging *O. leprieurii sensu lato*, *O. taurinus sensu lato* and frogs in the *O. buckleyi* group (especially *O. helenae*) have been found to represent distinct species. Hoogmoed (2014) assumed high pressure and possible threats to populations of *Dryaderces* (a genus split from *Osteocephalus*, see Chapter 3.3) *inframaculata* due to dam constructions. Agricultural activities may especially be a threat to species occurring on the south-western edge of Amazonia. At the moment distributional data are too spotty especially in that area and the status of several “candidate species” needs to be verified to give meaningful statements. But the fact that almost all species are inhabitants of primary or old secondary forests indicates the potential vulnerability of species in the genus.

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ABSTRACT

The pan-Amazonian treefrog genus *Ostecephalus* is poorly understood both on a taxonomic and phylogenetic level. The status of several frogs already or not yet referred to the genus is unclear and the relationships among the genus and with respect to related genera is not understood. In this work, *O. cabrerai* (Cochran and Goin, 1970) from Colombia and Peru is redescribed and *O. festae* (Peracca, 1904) from the foothills of the Andes in Ecuador is revalidated. *Hyla inframaculata* Boulenger, 1882, from the lower Amazon in Brazil, is reallocated to *Osteocephalus* and *O. elkejungingerae* (Henle, 1981) from the Andean foothills in Peru is shown to be a synonym of *Hyla mimetica* (Melin, 1941), the valid name being *O. mimeticus*. *Hyla vilarsi* Melin, 1941 is considered a valid species in the genus *Osteocephalus* and revalidated from the synonymies of several other frogs.

Three new species, *O. castaneicola* from northern Bolivia and southern Peru, *O. duellmani* from a sub-Andean mountain range in southern Ecuador, and *O. camufatus* from central Amazonian Brazil, are described.

A phylogenetic analysis based on up to nine mitochondrial genes and one nuclear one reveals the paraphyly of the genus as previously understood with respect to the genus *Tepuihyla*. A new taxonomy is proposed, securing the monophyly of *Osteocephalus* and *Tepuihyla* by rearranging and redefining the content of both genera. A new genus, *Dryaderces*, is erected for the sister group of *Osteocephalus*. The colouration of newly metamorphosed individuals is proposed as a morphological synapomorphy for *Osteocephalus*. Five monophyletic species groups within *Osteocephalus* are recognized, three species of *Osteocephalus* (*O. germani, O. phasmatus, O. vilmae*) and three species of *Tepuihyla* (*T. celsae, T. galani, T. talbergae*) synonymized and three species (*Hyla helenae* to *Osteocephalus*, *O. exophthalmus* to *Tepuihyla* and *O. pearsoni* to *Dryaderces* gen. n.) reallocated. Furthermore, nine putative new species are flagged (an increase to 138% of the current diversity), an indication that species numbers are largely underestimated, with most hidden diversity centred on widespread and polymorphic nominal species. The evolutionary origin of breeding strategies within *Osteocephalus* is discussed in the light of this new phylogeny and pond-breeding identified as the ancestral state from which breeding in lotic water and phytotelmata is derived. A novel type of amplexus (gular amplexus) is described.

ZUSAMMENFASSUNG

Die pan-amazonische Baumfrosch-Gattung *Osteocephalus* ist unzureichend bearbeitet sowohl bezüglich ihrer Taxonomie als auch ihrer Phylogenie. Der Status einer Reihe von Arten, die bereits oder noch nicht zu dieser Gattung gezählt werden, ist unklar und die Verwandtschaftsbeziehungen innerhalb der Gattung und zu verwandten Gattungen nicht geklärt. In dieser Arbeit wird *O. cabrerai* (Cochran and Goin, 1970) aus Kolumbien und Peru nochmals detailliert beschrieben und *O. festae* (Peracca, 1904) aus einem Anden-Vorgebirge in Ecuador revalidiert. *Hyla inframaculata* Boulenger, 1882, vom Unterlauf des Amazonas in Brasilien, wird in die Gattung *Osteocephalus* gestellt und *Osteocephalus elkejungingerae* (Henle, 1981) vom östlichen Andenrand in Peru wird mit *Hyla mimetica* (Melin, 1941) als *O. mimeticus* synonymisiert. Das Taxon *Hyla vilarsi* Melin,1941, bisher als Synonym unterschiedlicher Arten betrachtet, wird als valide angesehen und in die Gattung *Osteocephalus* gestellt.

Drei neue Arten werden beschrieben: *Osteocephalus castaneicola* aus Nord-Bolivien und Süd-Peru, *O. duellmani* von einer subandinen Bergkette in Süd-Ecuador und *O. camufatus* aus dem zentralamazonischen Teil Brasiliens.

Eine phylogenetische Analyse auf Basis von bis zu neun mitochondrialen und einem Kern-Gen zeigt, dass *Osteocephalus* bezüglich der Gattung *Tepuihyla* paraphyletisch ist. Deshalb wird hier eine neue Taxonomie vorgeschlagen, die die Monophylie von *Osteocephalus* und *Tepuihyla* sichert. Eine neue Gattung, *Dryaderces*, wird für die Schwestergruppe von *Osteocephalus* aufgestellt. Die Färbung frisch metamorphosierter Jungfrösche wird als morphologische Synapomorphie von *Osteocephalus* angesehen. Fünf monophyletische Artengruppen werden innerhalb der Gattung aufgestellt, drei Arten der Gattung *Osteocephalus* (*O. germani, O. phasmatus, O. vilmae*) und drei der Gattung *Tepuihyla* (*T. celsae, T. galani, T. talbergae*) synonymisiert, außerdem drei Arten anderen Gattungen zugerechnet (*Hyla helenae* zu *Osteocephalus*, *O. exophthalmus* zu *Tepuihyla* und *O. pearsoni* zu *Dryaderces* gen. n.). Außerdem werden neun potentiell neue Arten identifiziert, was einer Artenzunahme von 138% im Vergleich zur derzeit bekannten Diversität entspräche. Daraus ist zu schließen, dass die tatsächliche Artenzahl weit

unterschätzt wird. Unbeschriebene Arten verbergen sich vor allem unter den weit verbreiteten, polymorphen Nominatarten. Die Evolution der Fortpflanzungsstrategien innerhalb der Gattung wird im Licht der neuen Phylogenie diskutiert, wobei die Eiablage in lenitischen Gewässern als ursprünglich angesehen wird. Ein neuer Amplexustyp (Kehlamplexus) wird beschrieben.

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