Zoologica Scripta

KUNGL. VETENSKAPS-AKADEMIEN
THE ROYAL SWEDISH ACADEMY OF SCIENCES

Systematics of spiny-backed treefrogs (Hylidae: *Osteocephalus*): an Amazonian puzzle

Karl-Heinz Jungfer, Julián Faivovich, José M. Padial, Santiago Castroviejo-Fisher, Mariana M. Lyra, Bianca V. M. Berneck, Patricia P. Iglesias, Philippe J. R. Kok, Ross D. MacCulloch, Miguel T. Rodrigues, Vanessa K. Verdade, Claudia P. Torres Gastello, Juan Carlos Chaparro, Paula H. Valdujo, Steffen Reichle, Jiří Moravec, Václav Gvoždík, Giuseppe Gagliardi-Urrutia, Raffael Ernst, Ignacio De la Riva, Donald Bruce Means, Albertina P. Lima, J. Celsa Señaris, Ward C. Wheeler & Célio F. B. Haddad

Submitted: 17 September 2012
Accepted: 5 April 2013
doi:10.1111/zsc.12015

Jungfer, K.-H., Faivovich, J., Padial, J. M., Castroviejo-Fisher, S., Lyra, M.M., Berneck, B.V.M., Iglesias, P.P., Kok, P. J. R., MacCulloch, R. D., Rodrigues, M. T., Verdade, V. K., Torres Gastello, C. P., Chaparro, J. C., Valdujo, P. H., Reichle, S., Moravec, J., Gvoždík, V., Gagliardi-Urrutia, G., Ernst, R., De la Riva, I., Means, D. B., Lima, A. P., Señaris, J. C., Wheeler, W. C., Haddad, C. F. B. (2013). Systematics of spiny-backed treefrogs (Hylidae: *Osteocephalus*): an Amazonian puzzle. —*Zoologica Scripta*, *42*, 351–380.

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 (i) the paraphyly of *Osteocephalus* with respect to *Tepuihyla*, (ii) the placement of '*Hyla*' *warreni* as sister to *Tepuihyla*, (iii) the non-monophyly of several currently recognized species within *Osteocephalus* and (iv) 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 and O. vilmae*) and three species of *Tepuihyla* (*T. celsae*, *T. galani and 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 phylogenetic hypothesis, and a novel type of amplexus (gular amplexus) is described.

Corresponding author: *Karl-Heinz Jungfer, Institute of Integrated Sciences, Department of Biology, University of Koblenz-Landau, Universitätsstr. 1, 56070 Koblenz, Germany. E-mail: khjungfer@aol.com*

Julián Faivovich, División Herpetología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'-CONICET, Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina and Departamento de Biodiversidad y Biologia Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina. E-mail: julian@macn.gov.ar

José M. Padial, Section of Amphibians and Reptiles, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA, 15213-4080, USA. E-mail: padialj@carnegiemnh.org

Santiago Castroviejo-Fisher, Department of Herpetology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024-5192, USA and Laboratorio de

Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil. E-mail: castroviejo.fisher@gmail.com

Mariana M. Lyra, and Bianca V. M. Berneck, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Av. 24A 1515, CEP 13506-900, Rio Claro, São Paulo, Brazil. E-mail: marillyra@gmail.com, bvmberneck@gmail.com

Patricia P. Iglesias, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Instituto de Ecología, Genética y Evolución de Buenos Aires, IEGEBA-CONICET, Universidad de Buenos Aires, Ciudad Universitaria Pab. II, C1428EHA, Buenos Aires, Argentina. E-mail: patricia.p.iglesias@gmail.com

Philippe J. R. Kok, Amphibian Evolution Lab, Department of Biology, Vrije Universiteit Brussel, Pleinlaan 2, B-1050, Brussels, Belgium and Department of Vertebrates, Royal Belgian Institute of Natural Sciences, rue Vautier 29, B-1000, Brussels, Belgium. E-mail: Philippe.Kok@naturalsciences.be

Ross D. MacCulloch, Department of Natural History, Royal Ontario Museum, 100 Queens Park, Toronto, ON, M5S 2C6, Canada. E-mail: rossm@rom.on.ca

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

Vanessa K. Verdade, Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Av. dos Estados, 5001, CEP 09210-971, Santo André, São Paulo, Brazil. E-mail: vverdade@gmail.com

Claudia P. Torres Gastello, Departamento de Herpetología, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Apto. 14-0434, Lima 14, Peru. E-mail: claprist@yahoo.com

Juan Carlos Chaparro, Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru. E-mail: jchaparroauza@yahoo.com

Paula H. Valdujo, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 05508-900, São Paulo, SP, Brazil. E-mail: paula.valdujo@gmail.com

Steffen Reichle, Fundación para la Conservación del Bosque Chiquitano, Av. Ejército Nacional No 160, Santa Cruz de la Sierra, Bolivia. E-mail: sreichle@cotas.net

Jiří Moravec, and Václav Gvoždík, Department of Zoology, National Museum, Prague 9, Czech Republic. E-mail: jiri.moravec@nm.cz, vgvozdik@email.cz

Giussepe Gagliardi-Urrutia, Programa de Investigación en Biodiversidad Amazónica del Instituto de Investigaciones de la Amazonia Peruana, Av. Quiñonez Km 2.5, Iquitos, Perú. E-mail: giussepe-gagliardi@yahoo.com

Raffael Ernst, Museum für Tierkunde, Senckenberg Natural History Collections Dresden, Königsbrücker Landstr. 159, D-01109, Dresden, Germany. E-mail: raffael.ernst@senckenberg.de

Ignacio De la Riva, Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales-CSIC, C/José Gutiérrez Abascal 2, 28006, Madrid, Spain. E-mail: iriva@mncn.csic.es

Donald Bruce Means, Coastal Plains Institute and Land Conservancy, 1313 Milton Street, Tallahassee, FL, 32303, USA. E-mail: means@bio.fsu.edu

Albertina P. Lima, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, CEP 69011-970, Manaus, Amazonas, Brazil. E-mail: lima@inpa.gov.br

J. Celsa Señaris, Laboratorio de Ecología y Genética de Poblaciones, Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas, 1020-A, Venezuela. E-mail: jsenaris@ivic.gob.ve

Ward C. Wheeler, Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024-5192, USA. E-mail: wheeler@amnh.org

Célio F. B. Haddad, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Av. 24A 1515, CEP 13506-900, Rio Claro, São Paulo, Brazil. E-mail: haddad1000@gmail.com

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 1999; Jungfer *et al.* 2000; Moravec *et al.* 2009; KHJ, personal observation). 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; KHJ, personal observation).

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 *Osteocephalus 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* and *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; *Tepuihyla 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, *Osteocephalus 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, for example 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 (SVL), appear to be insufficient to identify putative closely related species such as those of the *Osteocephalus 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. Köhler *et al.* 2010; Padial & De la Riva 2010; Brown *et al.* 2011; Castroviejo-Fisher *et al.* 2011).

The phylogenetic relationships within *Osteocephalus* 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 *Osteocephalus cabrerai*, *O. buckleyi*, *Osteocephalus mutabor* and *Osteocephalus verruciger*, a clade composed of *O. oophagus* + *O. taurinus* and a clade composed of *O. leprieurii* and *Osteocephalus planiceps*. An important point of their results was that '*Hyla*' *alboguttata*, a species considered *incertae sedis* by Faivovich *et al.* (2005), was embedded within *Osteocephalus*. 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 (i) test the monophyly of *Osteocephalus* and identify its sister group, (ii) explore relationships among its species, (iii) elucidate the potential number of unnamed species in the genus on the basis of molecular data, (iv) develop a monophyletic taxonomy and (v) 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 *Osteocephalus duellmani*, *Osteocephalus inframaculatus* and *Osteocephalus 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. and *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 Lophiohylini, 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), and terminating with the GenBank accession numbers of one of the sequences that revealed the putative species.

Character sampling and laboratory protocols

The mitochondrial gene sequences produced for this project include portions of cytochrome oxidase I (COI), cytochrome *b* (cyt*b*), 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 (ACHAAYCAYAAAGAYATYGG) - AnR1 (CCRAARAATCARAADARRTGTTG) for cytochrome oxidase I designed by MLL, 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), Salerno *et al.* (2012), and for outgroups, Faivovich *et al.* (2005, 2010), Wiens *et al.* (2005).

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, USA). Complete sequences were edited with BioEdit (Hall 1999).

Phylogenetic analyses

The phylogenetic analyses included treatment of sequences both as dynamic homologies (simultaneous tree searches and alignment) 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 analysed 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-h 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 CLUSTALW (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 performed 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 performed 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 analysed 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 parameter 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 551 characters 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; Hull 1976; Wiley 1978; 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), because 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, because 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 to determine whether 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 data set included 338 terminals and 6134 aligned characters (CLUSTALW 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 1–4, Appendices S5–S6). Maximum parsimony with direct optimization recovered four most parsimonious trees (length = 12 865), see Figs 1–4. For the static alignment, the MP new technology search hit 500 times the best length. It recovered 4232 MPT (length = 13 254), see Appendix S6. Further TBR revealed that there were more MPT (>10 000), 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 MPT (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. 1; see Appendices S5 and S6) differ from previous analyses (Faivovich *et al.* 2005; Wiens *et al.* 2006, 2010; Moen & Wiens 2009). 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 Lophiohylini, 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* as currently defined is paraphyletic. The most basal clade in the ingroup (Fig. 1) includes species of

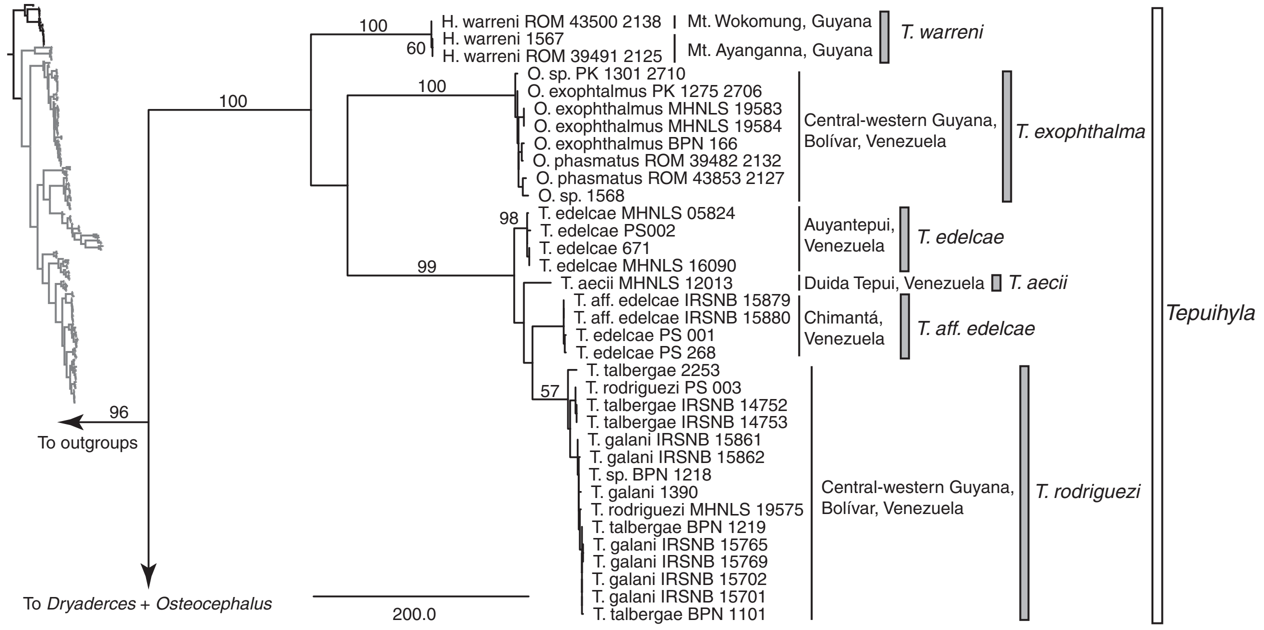


Fig. 1 Phylogenetic relationships of *Osteocephalus* and *Tepuihyla* inferred from maximum parsimony analysis under dynamic homology in the program POY4.1.1. This topology reflects one of the four most parsimonious trees (length 12 865 steps) with branch lengths proportional to the number of unambiguous 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 outgroups 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.

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 *Osteocephalus 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: (i) a clade including *O. taurinus*, *O. oophagus* and five candidate species that we call the *O. taurinus* Species Group (Fig. 2), (ii) a clade composed of *O. alboguttatus*, *O. heyeri*, and *O. subtilis* that we call the *O. alboguttatus* Species Group (Fig. 3), (iii) a clade composed of *O. leprieurii*, *O. yasuni* and two candidate species that we call the *O. leprieurii* Species Group (Fig. 3), (iv) a clade composed of *O. castaneicola*, *O. deridens*, *O. fuscifacies*, *O. leoniae*, *O. planiceps* and a candidate species that we call the *O. planiceps* Species Group (Fig. 3) and (v) 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. 4). Each of these five clades is in general well supported, but the relationships among most of them received poor support (Figs 1–4, Appendices S5 and S6). Furthermore, in both the static parsimony and ML analyses, the relationships 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 are 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 pathological 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

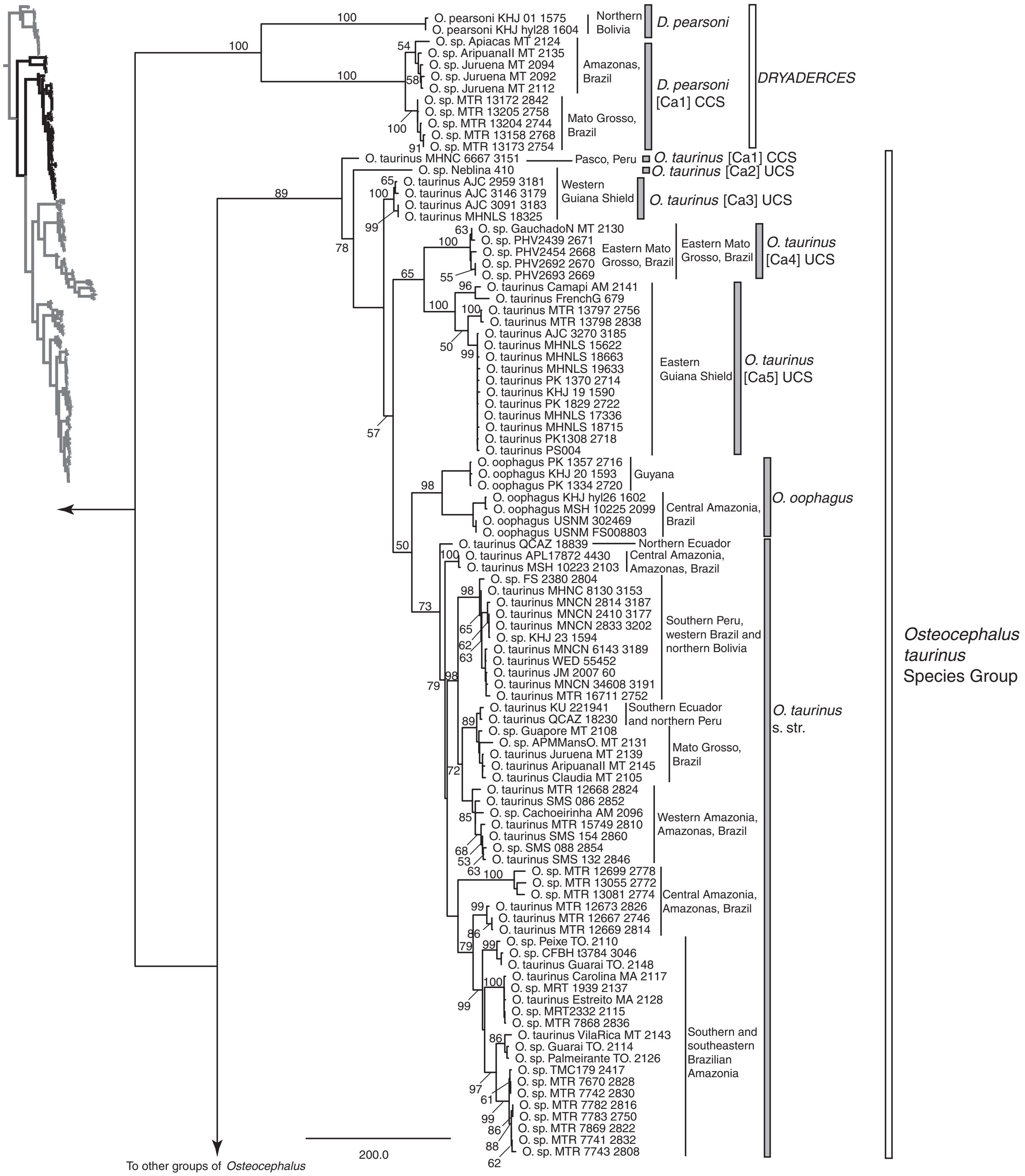


Fig. 2 Continuation of the phylogenetic tree of Fig. 1. Phylogenetic relationships of *Dryaderces* gen. n. and the *Osteocephalus taurinus* Species Group. For details, see Fig. 1.

likely for *O. mutabor* (Figs 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

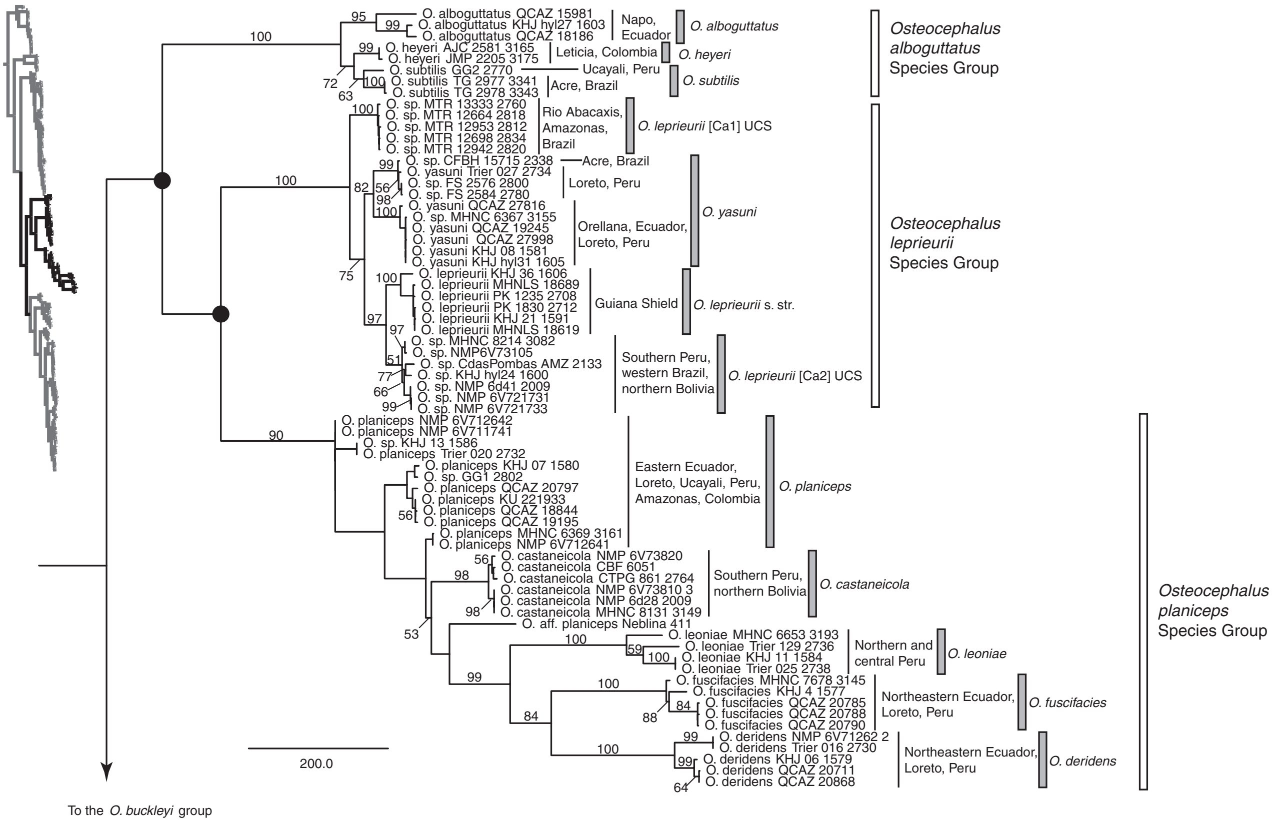


Fig. 3 Continuation of the phylogenetic tree of Fig. 1. Phylogenetic relationships of the *Osteocephalus alboguttatus*, *Osteocephalus leprieurii* and *Osteocephalus planiceps* Species Groups. For details, see Fig. 1.

(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, Appendix S6).

Within species placed in *Tepuihyla* (Fig. 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% to 0.2% between '*O. exophthalmus*' and '*O. phasmatus*', to 6.1–6.2% between '*Hyla warreni*' 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% to 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 *O. 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. 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 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. 2), *O. taurinus* is found paraphyletic with respect to *O. oophagus*.

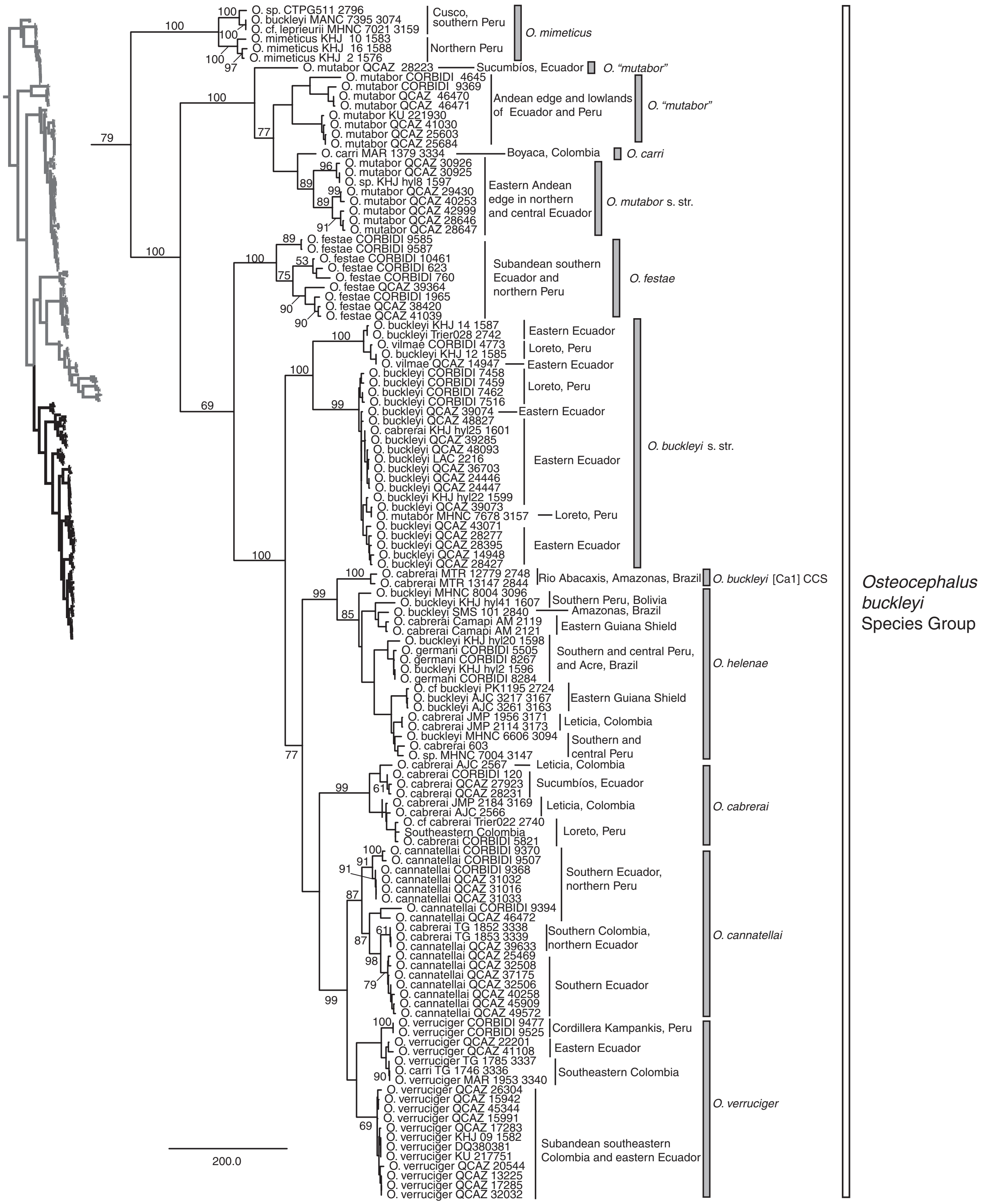


Fig. 4 Continuation of the phylogenetic tree of Fig. 1. Phylogenetic relationships of the *Osteocephalus buckleyi* Species Group. For details, see Fig. 1.

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 (Appendices S9 and 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% and 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, for example by Duellman & Lescure (1973) and Schlüter (1979) with *O. planiceps*. On the basis of phylogenetic position (Fig. 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 *O. 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 (KHJ, personal observation), 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 and 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. 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). *Osteocephalus planiceps* is retrieved as non-monophyletic in MP analyses, but as monophyletic in ML (Fig. 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% and 5.9%, while intraspecific genetic divergences within species of the group range between 0.0% and 4.0% (Appendix S4b).

Within the *O. leprieurii* Species Group, *O. leprieurii* is paraphyletic with respect to *O. yasuni* (Fig. 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% and 1.8%, while intraspecific divergences in the *O. leprieurii* Group range between 0.7% and 2.0%, taking into account the candidate species proposed below (Appendix S4c). Nonetheless, as *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 an 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% and 1.8%. Published morphological data are not available, and despite the large geographic 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*, *Osteocephalu festae*, *O. mimeticus* and *O. verruciger*, are monophyletic and well supported (Fig. 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 phenotypically 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. 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 *O. 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% and 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. 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 *O. 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. 4), and shows no genetic divergences. We consider this well-supported lineage as nominal *O. cabrerai*.

The type locality of *O. verruciger* is 'Ecuador'. Multiple samples from Ecuador assigned to this taxon cluster together in a well-supported clade (Fig. 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 *O. 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 (SR, personal observation), 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 *Dryaderces 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 SVLs 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 the study by 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, *O. 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. *verruciger* (Werner, 1901), *O. vilarsi* (Melin, 1941), *O. yasuni* Ron & Pramuk, 1999.

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 photograph, 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 Lophiohylini also lack an ontogenetic colour change, for example *Aparasphenodon brunoi* (CFBH, personal observation), *Argenteohyla siemersi* (D. Baldo, personal communication), *Itapotihyla langsdorffii* (Appendix S1), *Nyctimantis rugiceps*, *Osteopilus crucialis*, *O. wilderi* (KHJ, personal observation), *Phyllodytes luteolus* (MTR, personal observation), while in others juvenile patterns remain, but only slightly dissolve, as in *Trachycephalus hadroceps* (KHJ, personal observation) and *T. resinifictrix* (Jungfer & Proy 1998). Juvenile *T. typhonius* are as polymorphic in colouration and pattern as their adult phases (KHJ, personal observation). 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. *Osteocephalus alboguttatus* (Boulenger, 1882), *O. heyeri* Lynch, 2002, and *O. subtilis* Martins & Cardoso 1987.

Diagnosis. Males in this clade are small (<40 mm SVL) 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 1987; 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* (GGU, personal observation) and *O. mutabor* (KHJ, personal observation) 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 *Osteocephalus* 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, *O. 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, SVL, 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. *Osteocephalus 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, *O. 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 *O. 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 SVL, 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; KHJ, personal observation). 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 *et al.* 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 SVL, dorsal skin structure in breeding males, and call structure (Duellman & Lescure 1973 as *O. taurinus*; Schlüter 1979 as *O. leprieurii*; KHJ, personal observation). 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 *O. 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. 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. to the both 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 *et al*. 2010b).

Remarks. As currently defined, *O. taurinus* is an extremely polymorphic species. SVL of mature females ranges from 56.4 to 109.8 mm and from 50.3 to 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 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 *Tepuihyla rimarum* (Ptari-tepui, Venezuela) lack the juvenile coloration typical of *Osteocephalus* and usually have granular skin (PJRK, personal observation, 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), *Tepuihyla 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-Puppo & La Marca, 1999 a junior synonym of *T. luteolabris*, and *O. 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 Lophiohylini. The exposition of the frontoparietal fontanelle noted by Ayarzagüena et al. (1992) also is a putative synapomorphy overlooked by Faivovich *et al.* (2005), with several instances of homoplasy in the Lophiohylini 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. The phylogenetic relationships of *T. luteolabris* and *T. rimarum* remain unknown, as tissues of these species are still unavailable.

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, personal observation). Amplexus is axillary and eggs are laid as gelatinous masses (PJRK, personal observation). Tadpoles can tolerate acidic water (pH values *c.* 4). They are opportunistic feeders and have been seen feeding on dead animals including congeners (PJRK, personal observation). 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 *O. 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 (16%) 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: (i) 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 (ii) 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; Jansen *et al.* 2011; Funk *et al.* 2012) and in other tropical areas such as Madagascar (Vieites *et al.* 2009; Vences *et al.* 2010), Central America (Crawford *et al.* 2010) or South-East Asia (Stuart *et al.* 2006). Recent studies of other vertebrates confirm this pattern, for example, for birds (Milá *et al.* 2012), mammals (Pavan *et al.* 2012) or reptiles (Bergmann and Russell 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 either that *Osteocephalus* was 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 underestimated. Broad-scale taxonomic analyses as the one presented here are much needed for other groups of organisms 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 data). 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 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 SVL 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 with 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 Lophiohylini (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 5 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 (KHJ, personal observation).

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*, for example *S. elaeochroa* (Duellman 2001), *Dendropsophus*, for example *D. microps* (Kwet 2001), *D. minutus* (Marty & Gaucher 1999), *Trachycephalus mesophaeus* (MTR, personal observation) or *Triprion petasatus* (KHJ, personal observation). 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 (KHJ, personal observation), unlike those of lentic breeding *O. oophagus* (Jungfer & Weygoldt 1999), *O. taurinus* (KHJ, personal observation) 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 (KHJ, personal observation). 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 suggests that phytotelm breeding and tadpoles feeding on conspecific eggs have 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 data). 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, because 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

JF and KHJ designed the work. MTR, KHJ, JMP, SCF, VKV, JCC, CPTG, PHV, PJRK, SR, JM, CFBH, RDM, GGU, DBM, RE, IDR, APL and JCS contributed materials. JF, JMP and SCF analysed molecular data. JF, MLL, BvMB, PI, CFBH and WCW produced sequences. KHJ, JF, SCF and JMP wrote the paper. PHV prepared maps. All authors read, contributed and approved the final version of the manuscript.

Acknowledgements

We are indebted to the following persons and institutions: KHJ was funded by travel grants of GÖS and the Wilhelm Peters Funds of the Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT) and received logistic support in northern Peru from OFRA Spain. JF thanks ANPCyT PICT 2007-2202, 2011-1895, PME-2006-00490, UBACyT 2012-2015 20020110200213, NSF grant DEB-0407632, Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) procs. 05/56756-0, 06/52088-5, 08/50928-1 and 2012/10000-5, Consejo Nacional de Investigaciones Científicas y Tecnicas (CONICET), and the American Museum of Natural History. JMP's research was funded by a Gerstner Postdoctoral Fellowship through the Richard Gilder Graduate School of the American Museum of Natural History (New York) and by the projects CGL2010-21250 and CGL2011-30393 of the Ministerio de Educación, Cultura y Deportes (Spain). The work of SCF was financed by a Fulbright/Spanish Ministry of Education postdoctoral research contract. PPI thanks CONICET. Fieldwork by RDM was funded by the ROM Governors. MLL was funded by FAPESP (Postdoctoral fellowship 2010/50124-0). BVMB was funded by FAPESP (08/55235-4). PHV was funded by FAPESP (fellowship 2007/51956-6) and Fundação O Boticario de Proteção à Natureza (0798_20082). MTR thanks FAPESP, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Instituto Chico Mendes da Biodiversidade (ICMbio) and also the following persons for help in field or sending tissues: D. Pavan, F. F. Curcio, J. Cassimiro, J. M. Guellere, H. Zaher, G. Skuk, M. S. Hoogmoed, R. C. Amaro, R. Recoder, R. Vogt, S. M. Souza, V. Xavier, T. C. Ávila-Pires and also T. Grant, M. Rada, M. Rivera, I. Rey, B. Álvarez, F. J. M. Rojas-Runjaic and C. L. Barrio-Amorós. DBM received National Geographic Society Research and Exploration Council Grant #7498-03, Guyana EPA Biodiversity Research Permit #100703BR009, and export permit 030310SP001. CFBH thanks FAPESP and CNPq for financial support. The work of JM and VG was supported financially by the Ministry of Culture of the Czech Republic (DKRVO 2013/14). DBM was funded by National Geographic Society Research Grant # 7498-03 and grants from the Smithsonian Institution and Conservation International, and sanctioned under Guyana Environmental Protection Agency biodiversity research permit No. 100703 BR 009 and specimen export permit No.030319 SP 001. RE was supported by a research grant from the German Research Foundation (DFG ER 589/2–1) and permission to conduct biodiversity research in Guyana was provided by the Guyana EPA under research permit No. 180609 BR 112 and export permit No. 180909 SP 16. Field work by JCS (MHNLS samples from the Cucurital River Basin, and Auyán-tepui) was funded by grant No. 98003384 FONACIT with the permits for field work and collections of the Ministerio del Ambiente (No. 3644, 4110, 5179, 5182), INPARQUES (Providencia Administrativa No. PA-INP-026-2002) and the local communities of Kanaimö and Guayaraca. Permission to access to genetic resources, Guianan Hylidae No. 0076, dated 2 February 2011, was granted for the MHNLS.

Thanks to J.-M. Renjifo and J. Sommerhalder for the permission to use photos taken by them. For loans related to this study and/or the provision of working space at their respective institution, we are grateful to Ana Almendáriz (EPN), Franco Andreone (MZUT), Rafe Brown, Linda Trueb and William E. Duellman (KU), Barry T. Clarke and Colin McCarthy (BM), Jesús Córdova and César Aguilar (MUSM), Darrel R. Frost and David Kizirian (AMNH), Heinz Grillitsch and Richard Gemel (NMW), Alexander Haas and Jakob Hallermann (ZMH), W. Ronald Heyer (USNM), Gunther Köhler (SMF), John D. Lynch (ICN), Göran Nilson (GNM), Ronald Nussbaum, Arnold G. Kluge and Gregory Schneider (UMMZ), Dennis Rödder and Wolfgang Böhme (ZFMK), Andreas Schlüter (SMNS), Andreas Schmitz (MHNG), Harold K. Voris (FMNH), Hussam Zaher and Carolina Castro-Mello (MZUSP). We are indebted to two anonymous reviewers and U. Sinsch for helpful comments.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.

Almendáriz, A., Cisneros-Heredia, D., Jungfer, K.-H., Coloma, L. A. & Ron, S. (2004a). *Osteocephalus alboguttatus*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 5 August 2011.

Almendáriz, A., Cisneros-Heredia, D., Jungfer, K.-H., Coloma, L. A. & Ron, S. (2004b). *Osteocephalus deridens*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 5 October 2011.

AmphibiaWeb. (2012). Available via http://amphibiaweb.org/search/index.html. Accessed 15 December 2012.

Angulo, A., Coloma, L. A., Ron, S., Jungfer, K.-H., Cisneros-Heredia, D., Castro, F. & Rueda, J. V. (2004). *Osteocephalus verruciger*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 5 November 2011.

Antonelli, A., Quijada-Mascareñas, A., Crawford, A. J., Bates, J. M., Velazco, P. M. & Wüster, W. (2010). Molecular studies and phylogeography of Amazonian tetrapods and their relation to geological and climatic models. In C. Hoorn & F. P. Wesselingh (Eds) *Amazonia: Landscape and Species Evolution* (pp. 386–404). Chichester: Wiley-Blackwell.

Aubrecht, R., Barrio-Amorós, C. L., Breure, A. S. H., Brewer-Carías, C., Derka, T., Fuentes-Ramos, O. A., Gregor, M., Kodada, J., Kováčik, L'., Lánczos, T., Lee, N. M., Liščák, P., Schlögl, J., Šmída, B. & Vlček, L. (2012). *Venezuelan Tepuis: Their Caves and Biota*. Acta Geologica Slovaca Monograph, Bratislava: Comenius University.

Avise, J. C. (2000). *Phylogeography: The History and Formation of Species*. Cambridge: Harvard University Press.

Avise, J. C. & Ball, R. M. (1990). Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology*, 7, 45–67.

Ayarzagüena, J., Señaris, J. C. & Gorzula, S. (1992). El grupo *Osteocephalus rodriguezi* de las tierras altas de la Guayana venezolana: descripción de cinco nuevas especies. *Memoria Sociedad de Ciencias Naturales La Salle*, *52*, 113–142.

Ayarzagüena, J., Señaris, J. C. & Gorzula, S. ('1992' [1993]). Un nuevo genero para las especies del "grupo *Osteocephalus rodriguezi*" (Anura: Hylidae). *Memoria Sociedad de Ciencias Naturales La Salle*, *52*, 213–221.

Azevedo-Ramos, C. (2010). *Osteocephalus oophagus*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 4 November 2011.

Bergmann, P. J. & Russell, A. P. (2007). Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species. *Zoological Journal of the Linnean Society*, *149*, 339–370.

Blotto, B. L., Nuñez, J. J., Basso, N. G., Úbeda, C. A., Wheeler, W. C. & Faivovich, J. (2013). Phylogenetic relationships of a Patagonian frog radiation, the *Alsodes* + *Eupsophus* clade (Anura: Alsodidae), with comments on the supposed paraphyly of *Eupsophus*. *Cladistics*, *29*, 113–131.

Bokermann, W. C. A. (1964). Field observations on the hylid frog *Osteocephalus taurinus* Fitz. *Herpetologica*, *20*, 252–255.

Boulenger, G. A. (1882). *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum*. London: Trustees of the British Museum.

Brown, J. L. & Twomey, E. (2009). Complicated histories: three new species of poison frogs of the genus *Ameerega* (Anura: Dendrobatidae) from north-central Peru. *Zootaxa*, *2049*, 1–38.

Brown, J. L., Twomey, E., Amézquita, A., Barbosa de Souza, M., Caldwell, J. P., Lötters, S., von May, R., Melo-Sampaio, P. R., Mejía-Vargas, D., Perez-Peña, P., Pepper, M., Poelman, E. H., Sanchez-Rodriguez, M. & Summers, K. (2011). A taxonomic revision of the Neotropical poison frog genus *Ranitomeya* (Amphibia: Dendrobatidae). *Zootaxa*, *3083*, 1–120.

Castroviejo-Fisher, S., Vilà, C., Ayarzagüena, J., Blanc, M. & Ernst, R. (2011). Species diversity of *Hyalinobatrachium* glassfrogs (Amphibia: Centrolenidae) from the Guiana Shield, with the description of two new species. *Zootaxa*, *3132*, 1–55.

Chávez, G., Medina-Müller, M. & Pereyra, A. (2008). Amphibia, Anura, Hylidae, *Osteocephalus leoniae*: distribution extension. *Check List*, *4*, 401–403.

Cochran, D. & Goin, C. J. (1970). Frogs of Colombia. *United States National Museum Bulletin*, *288*, 1–655.

Cope, E. D. (1867). On the families of the raniform Anura. *Journal of the Academy of Natural Sciences*, *25*, 189–206.

Cope, E. D. (1874). On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. *Proceedings of the Academy of Natural Sciences*, *25*, 120–137.

Crawford, A. J., Lips, K. R. & Bermingham, E. (2010). Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 13777–13782.

De la Riva, I., Márquez, R. & Bosch, J. (1995). Advertisement calls of eight Bolivian hylids (Amphibia, Anura). *Journal of Herpetology*, *29*, 113–118.

De la Riva, I., Köhler, J., Lötters, S. & Reichle, S. (2000). Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetología*, *14*, 19–164.

De Laet, J. (2005). Parsimony and the problem of inapplicables in sequence data. In V. A. Albert (Ed.) *Parsimony, Phylogeny, and Genomics* (pp. 81–116). Oxford: Oxford University Press.

Deichmann, J. L. & Williamson, G. B. (2007). *Osteocephalus yasuni* (NCN) and *Osteocephalus planiceps* (NCN). Terrestrial behavior. *Herpetological Review*, *38*, 189.

Duellman, W. E. (1974). A reassessment of the taxonomic status of some Neotropical hylid frogs. *Occasional Papers of the Museum of Natural History, The University of Kansas*, *27*, 1–27.

Duellman, W. E. (1978). The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication University of Kansas Museum of Natural History*, *65*, 1–352.

Duellman, W. E. (2001). *Hylid Frogs of Middle America*. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Duellman, W. E. & Hoogmoed, M. S. (1992). Some hylid frogs from the Guiana Highlands, northeastern South America: new species, distributional records, and a generic reallocation. *Occasional Papers of the Museum of Natural History, The University of Kansas*, *147*, 1–21.

Duellman, W. E. & Lescure, J. (1973). Life history and ecology of the hylid frog *Osteocephalus taurinus*, with observations on larval behavior. *Occasional Papers of the Museum of Natural History, The University of Kansas*, *13*, 1–12.

Duellman, W. E. & Mendelson, J. R. (1995). Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. *University of Kansas Science Bulletin*, *55*, 329–376.

Duellman, W. E. & Trueb, L. (1986). *Biology of Amphibians*. New York, NY: McGraw-Hill.

Duellman, W. E. & Yoshpa, M. (1996). A new species of *Tepuihyla* (Anura: Hylidae) from Guyana. *Herpetologica*, *52*, 275–281.

Elmer, K. R., Dávila, J. A. & Lougheed, S. C. (2007). Cryptic diversity and deep divergence in an upper Amazonian leaflitter frog, *Eleutherodactylus ockendeni*. *BMC Evolutionary Biology*, 7, 247.

Ernst, R., Rödel, M.-O. & Arjoon, D. (2005). On the cutting edge – the anuran fauna of the Mabura Hill Forest Reserve, Central Guyana. *Salamandra*, *41*, 179–194.

Faivovich, J., Haddad, C. F. B., Garcia, P. C. A., Frost, D. R., Campbell, J. A. & Wheeler, W. C. (2005). Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, *294*, 1–240.

Faivovich, J., Haddad, C. F. B., Baêta, D., Jungfer, K.-H., Álvares, G.F.R., Brandão, R.A., Sheil, C., Barrientos, L.S., Barrio-Amorós, C. L., Cruz, C.A.G. & Wheeler, W. C. (2010). The phylogenetic relationships of the charismatic poster frogs, Phyllomedusinae (Anura, Hylidae). *Cladistics*, *26*, 227–261.

Farris, J. S. (1983). The logical basis of phylogenetic analysis. In N. I. Platnick & V. A. Funk (Eds) *Advances in Cladistics: Proceedings of the Third Meeting of the Willi Hennig Society 2* (pp. 7–36). New York, NY: Columbia University Press.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. (1996). Parsimony jackknifing outperforms neighbour-joining. *Cladistics*, *12*, 99–124.

Fitzinger, L. (1843). *Systema Reptilium*. Vienna: Braunmüller and Seidel.

Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M. & Gemmel, M. J. (2007a). Underestimation of species richness in Neotropical frogs revealed by mtDNa analyses. *PLoS ONE*, *2*, e1109.

Fouquet, A., Vences, M., Salducci, M.-D., Meyer, A., Marty, C., Blanc, M. & Gilles, A. (2007b). Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. *Molecular Phylogenetics and Evolution*, *43*, 567–582.

Fouquet, A., Loebmann, D., Castroviejo-Fisher, S., Padial, J. M., Orrico, V. G. D., Lyra, M. L., Roberto, I. J., Kok, P. J. R., Haddad, C. F. B. & Rodrigues, M. T. (2012). From Amazonia to the Atlantic forest: molecular phylogeny of Phyzelaphryninae frogs reveals unexpected diversity and a striking biogeographic pattern emphasizing conservation challenges. *Molecular Phylogenetics and Evolution*, *65*, 547–561.

Frost, D. R. (2013). Amphibian Species of the World: an Online Reference, Version 5.6. Available via http://research.amnh.org/vz/herpetology/amphibia/. Accessed 23 January 2013.

Frost, D. R. & Kluge, A. G. (1994). A consideration of epistemology in systematic biology, with special reference to species. *Cladistics*, *10*, 259–294.

Funk, W. C., Caminer, M. & Ron, S. R. (2012). High levels of cryptic species diversity uncovered in Amazonian frogs. *Proceedings of the Royal Society B*, *279*, 1806–1814.

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

Ghiselin, M. T. (1975). A radical solution to the species problem. *Systematic Zoology*, *23*, 536–544.

Gibson, R. C. & Buley, K. R. (2004). Maternal care and obligatory oophagy in *Leptodactylus fallax*: a new reproductive mode in frogs. *Copeia*, *2004*, 128–135.

Goin, C. J. (1961). Synopsis of the genera of hylid frogs. *Annals of the Carnegie Museum*, *36*, 5–18.

Goloboff, P. A. (1999). Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, *15*, 415–428.

Goloboff, P. A. (2003). Parsimony, likelihood, and simplicity. *Cladistics*, *19*, 91–103.

Goloboff, P. A. & Pol, D. (2005). Parsimony and Bayesian phylogenetics. In V. A. Albert (Ed.) *Parsimony, Phylogeny, and Genomics* (pp. 148–159). Oxford: Oxford University Press.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*, 774–786.

Gordo, M. & Neckel-Oliveira, S. (2004). *Osteocephalus planiceps*. *Herpetological Review*, *35*, 79.

Gorzula, S. & Señaris, J. C. ('1998' [1999]). Contribution to the herpetofauna of the Venezuelan Guayana I. A data base. *Scientia Guaianae*, *8*, 1–270.

Grant, T. & Kluge, A. G. (2009). Parsimony, explanatory power, and dynamic homology testing. *Systematics and Biodiversity*, 7, 357–363.

Hall, T. A. (1999). BoEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, *41*, 95–98.

Henle, K. (1981). *Hyla elkejungingerae*, ein neuer Hylide aus dem peruanischen Regenwald. *Amphibia-Reptilia*, *2*, 123–132.

Henle, K. (1992). Zur Amphibienfauna Perus nebst Beschreibung eines neuen *Eleutherodactylus* (Leptodactylidae). *Bonner zoologische Beiträge*, *43*, 79–129.

Hero, J.-M. (1990). An illustrated key to tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brazil. *Amazoniana*, *9*, 201–262.

Heyer, W. R. (2005). Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. *Arquivos de Zoologia*, *37*, 269–348.

Heyer, W. R. & de Sá, R. (2011). Variation, systematics, and relationships of the *Leptodactylus bolivianus* complex (Amphibia: Anura: Leptodactylidae). *Smithsonian Contributions to Zoology*, *635*, 1–58.

Hoogmoed, M. S. (1979). The herpetofauna of the Guianan region. *Monograph of the Museum of Natural History, The University of Kansas*, 7, 241–279.

Hoogmoed, M. S. & Avila-Pires, T. C. S. (1991). Annotated checklist of the herpetofauna of Petit Saut, Sinnamary River, French Guiana. *Zoologische Mededelingen*, *65*, 53–88.

Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, *330*, 927–931.

Hull, D. L. (1976). Are species really individuals? *Systematic Zoology*, *25*, 174–191.

IUCN. (2012). IUCN Red List of Threatened Species. Version 2012.2. Available via http://www.iucnredlist.org/amphibians. Accessed 15 December 2012.

Jansen, M., Bloch, R., Schulze, A. & Pfenniger, M. (2011). Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. *Zoologica Scripta*, *40*, 567–583.

Jungfer, K.-H. (1985). Beitrag zur Kenntnis von *Dendrobates speciosus* O. Schmidt, 1857 (Salientia: Dendrobatidae). *Salamandra*, *21*, 263–280.

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

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*, 247–253.

Jungfer, K.-H. & Hödl, W. (2002). A new species of *Osteocephalus* from Ecuador and a redescription of *O. leprieurii* (Duméril & Bibron, 1841) (Anura: Hylidae). *Amphibia-Reptilia*, *23*, 21–46.

Jungfer, K.-H. & Lehr, E. (2001). A new species of *Osteocephalus* with bicoloured iris from Pozuzo (Peru: Departamento de Pasco) (Amphibia: Anura: Hylidae). *Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden*, *51*, 321–329.

Jungfer, K.-H. & Proy, C. (1998). *Phrynohyas resinifictrix* (Goeldi, 1907), der Frosch, der seine Frau bei Vollmond ruft: Geschichte und Fortpflanzungsverhalten im Terrarium. *Herpetofauna*, *20*, 19–29.

Jungfer, K.-H., Ron, S., Seipp, R. & Almendáriz, A. (2000). Two new species of hylid frogs, genus *Osteocephalus*, from Amazonian Ecuador. *Amphibia-Reptilia*, *21*, 327–340.

Jungfer, K.-H. & Schiesari, L. C. (1995). Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura, Hylidae), with oophagous tadpoles. *Alytes*, *13*, 1–13.

Jungfer, K.-H. & Weygoldt, P. (1999). Biparental care in the tadpole-feeding Amazonian treefrog *Osteocephalus oophagus*. *Amphibia-Reptilia*, *20*, 235–249.

Kellog, R. (1932). Mexican tailless amphibians in the United States National Museum. *Smithsonian Institution United States National Museum Bulletin*, *160*, 1–224.

Kluge, A. G. (1981). The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscellaneous Publications*, *Museum of Zoology*, *University of Michigan*, *160*, 1–170.

Kluge, A. G. & Grant, T. (2006). From conviction to anti-superfluity: old and new justifications for parsimony in phylogenetic inference. *Cladistics*, *22*, 276–288.

Köhler, J., Koscinski, D., Padial, J. M., Chaparro, J. M., Handford, P., Lougheed, S. C. & De la Riva, I. (2010). Systematics of Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). *Zoologica Scripta*, *39*, 572–590.

Kok, P. J. R. & Kalamandeen, M. (2008). Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana. *ABC Taxa*, *5*, 1–278.

Kok, P. J. R., MacCulloch, R. D., Means, D. B., Roelants, K., Van Bocxlaer, I. & Bossuyt, F. (2012). Low genetic diversity in tepui summit vertebrates. *Current Biology*, *22*, R589–R590 and Supplemental Information available at http://dx.doi.org/10.1016/j.cub.2012.06.034.

Kwet, A. (2001). *Frösche im brasilianischen Araukarienwald*. Münster: Natur und Tier.

La Marca, E., Azevedo-Ramos, C., Coloma, L. A. & Ron, S. (2010a). *Osteocephalus buckleyi*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 2 October 2011.

La Marca, E., Azevedo-Ramos, C., Coloma, L. A. & Ron, S. (2010b). *Osteocephalus taurinus*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 25 September 2011.

La Marca, E., Reynolds, R., Azevedo-Ramos, C., Mijares, A. & Señaris, C. (2010c). *Osteocephalus leprieurii*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available via www.iucnredlist.org. Accessed 25 September 2011.

Lannoo, M. J., Townsend, D. S. & Wassersug, R. J. (1987). Larval life in the leaves: arboreal tadpole types, with special attention to the morphology, ecology, and behavior of the oophagous *Osteopilus brunneus* (Hylidae) larva. *Fieldiana: Zoology*, *38*, 1–31.

Lehr, E. (2001). New records for amphibians and reptiles from Departamentos Pasco and Ucayali, Peru. *Herpetological Review*, *32*, 130–132.

Lehtinen, R. M., Lannoo, M. J. & Wassersug, R. J. (2004). Phytotelm-breeding anurans: past, present and future research. *Miscellaneous Publications*, *Museum of Zoology*, *University of Michigan*, *193*, 1–9.

Lescure, J. & Marty, C. (2000). Atlas des Amphibiens de Guyane. *Patrimoines Naturels*, *45*, 388.

Lima, A. P., Magnusson, W. E., Menin, M., Erdtmann, L. K., Rodrigues, D. J., Keller, K. & Hödl, W. (2006). *Guia de sapos da Reserva Adolpho Ducke*, *Amazônia Central. Guide to the Frogs of Reserva Adolpho Ducke*, *Central Amazonia*. Manaus: Áttema Design Editorial.

Lovejoy, N. R., Willis, S. C. & Albert, J. S. (2010). Molecular signatures of Neogene biogeographical events in the Amazon fish fauna. In C. Hoorn & F. P. Wesselingh (Eds) *Amazonia: Landscape and Species Evolution* (pp. 405–417). Chichester: Wiley-Blackwell.

Lynch, J. D. (2002). A new species of the genus *Osteocephalus* (Hylidae: Anura) from the western Amazon. *Revista de la Academia Colombiana de Ciencias Exactas*, *Físicas y Naturales*, *26*, 289–292.

Lynch, J. D. (2005). Discovery of the richest frog fauna in the world—an exploration of the forests to the north of Leticia. *Revista de la Academia Colombiana de Ciencias Exactas*, *Físicas y Naturales*, *29*, 581–588.

Lynch, J. D. (2006). The amphibian fauna in the Villavicencio region of eastern Colombia. *Caldasia*, *28*, 135–155.

Lynch, J. D. (2008). *Osteocephalus planiceps* Cope (Amphibia: Hylidae): its distribution in Colombia and significance. *Revista de la Academia Colombiana de Ciencias Exactas*, *Físicas y Naturales*, *32*, 87–91.

Lynch, J. D. & Vargas-Ramírez, M. A. (2000). Lista preliminar de especies de anuros del Departamento del Guainía, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas*, *Físicas y Naturales*, *24*, 579–589.

MacCulloch, R. D. & Lathrop, A. (2005). Hylid frogs from Mount Ayanganna, Guyana: new species, redescriptions, and distributional records. *Phyllomedusa*, *4*, 17–37.

Martins, M. & Cardoso, A. J. (1987). Novas espécies de hilídos do Estado do Acre (Amphibia: Anura). *Revista Brasileira de Biologia*, *47*, 549–558.

Marty, C. & Gaucher, P. (1999). *Guide sonore des Amphibiens Anoures de Guyane. Sound Guide to the Tailless Amphibians of French Guiana*. Paris: Centre bioacoustique Alpin.

Menin, M., da Silva Melo, L. & Lima, A. P. (2011). The tadpole of *Osteocephalus cabrerai* from Central Amazonia, Brazil. *Phyllomedusa*, *10*, 137–142.

Mijares-Urrutia, A., Manzanilla-Puppo, J. & La Marca, E. (1999). Una nueva especie de *Tepuihyla* (Anura: Hylidae) del noroeste de Venezuela, con comentarios sobre su biogeografía. *Revista de Biología Tropical*, *47*, 1099–1110.

Milá, B., Tavares, E. S., Muñoz Saldanña, A., Karubian, J., Smith, T. B. & Baker, A. J. (2012). A trans-Amazonian screening of mtDNA reveals deep intraspecific divergence in forest birds and suggests a vast underestimation of species diversity. *PLoS ONE*, 7, e40541.

Moen, D. S. & Wiens, J. J. (2009). Phylogenetic evidence for competitively-driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). *Evolution*, *63*, 195–214.

Moravec, J., Aparicio, J., Guerrero-Reinhard, M., Calderón, G., Jungfer, K.-H. & Gvoždík, V. (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.

Moravec, J., Arista Tuanama, I. & Mármol Burgos, A. (2002). Amphibians recently recorded from the surroundings of Iquitos (Departamento Loreto, Peru). I. Hylidae. *Časopis Národního Muzea, Řada přírodovědná*, *171*, 29–44.

Myers, C. W. & Daly, J. W. (1976a). Preliminary evaluation of skin toxins and vocalizations in taxonomic and evolutionary studies of poison-dart frogs (Dendrobatidae). *Bulletin of the American Museum of Natural History New York*, *157*, 173–262.

Myers, C. W. & Daly, J. W. (1976b). A new species of poison frog (*Dendrobates*) from Andean Ecuador, including an analysis of its skin toxins. *Occasional Papers Natural History Museum University of Kansas*, *59*, 1–12.

Myers, C. W. & Daly, J. W. (1979). A name for the poison frog of the Cordillera Azul, eastern Peru, with notes on its biology and skin toxins (Dendrobatidae). *American Museum Novitates*, *2674*, 1–24.

Myers, C. W. & Daly, J. W. (1980). Taxonomy and ecology of *Dendrobates bombetes*, a new Andean poison frog with new skin toxins. *American Museum Novitates*, *2692*, 1–23.

Myers, C. W. & Donnelly, M. A. (2008). The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum–Terramar Expedition. *Bulletin of the American Museum of Natural History*, *308*, 1–147.

Nixon, K. C. (1999). The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics*, *15*, 407–414.

Nixon, K. C. (2002). *WinClada, vers. 1.00.8*. Ithaca, NY: Published by the author.

Padial, J. M., Bielskis, S. & Castroviejo, J. (2000). Sobre la fauna de anfibios del pie de monte del Departamento de La Paz (Bolivia). *Boletín de la Asociación Herpetológica Española*, *11*, 59–62.

Padial, J. M. & De la Riva, I. (2009). Integrative taxonomy reveals cryptic Amazonian species of *Pristimantis* (Anura). *Zoological Journal of the Linnaean Society*, *155*, 97–122.

Padial, J. M. & De la Riva, I. (2010). A response to recent proposals of integrative taxonomy. *Biological Journal of the Linnaean Society*, *101*, 747–756.

Padial, J. M., Castroviejo-Fisher, S., Köhler, J., Vilà, C., Chaparro, J. C. & De la Riva, I. (2009). Deciphering the products of evolution at the species level: the need for an integrative taxonomy. *Zoologica Scripta*, *38*, 431–447.

Padial, J. M., Miralles, A., De la Riva, I. & Vences, M. (2010). The integrative future of taxonomy. *Frontiers in Zoology*, 7, 1–14.

Padial, J. M., Chaparro, J. C., Castroviejo-Fisher, S., Guayasamín, J. M., Lehr, E., Delgado, A. J., Vaira, M., Teixeira, M. Jr, Aguayo, R. & De la Riva, I. (2012). A revision of species diversity in the Neotropical genus *Oreobates* (Anura: Strabomantidae), with the description of three new species from the Amazonian slopes of the Andes. *American Museum Novitates*, *3752*, 1–55.

Pavan, S. E., Rossi, R. V. & Schneider, H. (2012). Species diversity in the *Monodelphis brevicaudata* complex (Didelphimorphia: Didelphidae) inferred from molecular and morphological data, with the description of a new species. *Zoological Journal of the Linnaean Society*, *165*, 190–223.

Posada, D. (2008). jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, *25*, 1253–1256.

Pyron, R. A. & Wiens, J. J. (2011). A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, *61*, 543–583.

Ron, S. & Pramuk, J. B. (1999). A new species of *Osteocephalus* (Anura: Hylidae) from Amazonian Ecuador and Peru. *Herpetologica*, *55*, 433–446.

Ron, S. R., Santos, J. C. & Cannatella, D. C. (2006). Phylogeny of the túngara frog genus *Engystomops* (= *Physalaemus pustulosus* species group; Anura: Leptodactylidae). *Molecular Phylogenetics and Evolution*, *39*, 392–403.

Ron, S. R., Toral, E., Venegas, P. J. & Barnes, C. W. (2010). Taxonomic revision and phylogenetic position of *Osteocephalus festae* (Anura, Hylidae) with description of its larva. *ZooKeys*, *70*, 67–92.

Ron, S. R., Toral, E., Ortiz, D. & Almendáriz, A. (2011). Amphibia, Hylidae, *Osteocephalus cabrerai* Cochran and Goin, 1970: first confirmed records from Ecuador with distribution map. *Check List*, 7, 323–325.

Ron, S. R., Venegas, P. J., Toral, E., Read, M., Ortiz, D. A. & Manzano, A. L. (2012). Systematics of the *Osteocephalus buckleyi* species complex (Anura, Hylidae) from Ecuador and Peru. *ZooKeys*, *229*, 1–52.

Ruthven, A. G. (1919). The amphibians of the University of Michigan-Walker Expedition to British Guiana. *Occasional Papers of the Museum of Zoology, University of Michigan*, *69*, 1–14, plates I–III.

Salerno, P. E., Ron, S. R., Señaris, J. C., Rojas-Runjaic, F. J. M., Noonan, B. P. & Cannatella, D. C. (2012). Ancient Tepui summits harbor young rather than old lineages of endemic frogs. *Evolution*, *66*, 3000–3013.

Schiesari, L. C., Grillitsch, B. & Vogl, C. (1996). Comparative morphology of phytotelmonous and pond-dwelling larvae of four neotropical treefrog species (Anura, Hylidae, *Osteocephalus oophagus*, *Osteocephalus taurinus*, *Phrynohyas resinifictrix*, *Phrynohyas venulosa*. *Alytes*, *13*, 109–139.

Schlüter, A. (1979). Bio-akustische Untersuchungen an Hyliden in einem begrenzten Gebiet des tropischen Regenwaldes von Peru. *Salamandra*, *15*, 211–236.

Silva, J. M. C., Rylands, A. B. & da Fonseca, G. A. B. (2005). The fate of the Amazonian areas of endemism. *Conservation Biology*, *19*, 689–694.

Silverstone, P. A. (1975). A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Natural History Museum Los Angeles County Scientific Bulletin*, *21*, 1–55.

Simmons, M. P. (2012). Misleading results of likelihood-based phylogenetic analyses in the presence of missing data. *Cladistics*, *28*, 208–222.

Simmons, M. P. & Freudenstein, J. V. (2011). Spurious 99% bootstrap and jackknife support for unsupported clades. *Molecular Phylogenetics and Evolution*, *61*, 177–191.

Simmons, M. P. & Norton, A. P. (2013). Quantification and relative severity of inflated branch-support values generated by alternative methods: an empirical example. *Molecular Phylogenetics and Evolution*, *67*, 277–296.

Sites, J. W., Jr & Marshall, J. C. (2004). Operational criteria for delimiting species. *Annual Review of Ecology*, *Evolution and Systematics*, *35*, 199–227.

Smith, E. N. & Noonan, B. P. (2001). A new species of *Osteocephalus* (Anura: Hylidae) from Guyana. *Revista de Biologia Tropical*, *49*, 347–357.

Steindachner, F. (1862). Über zwei noch unbeschriebene Batrachier aus den Sammlungen des K. K. Museum zu Wien. *Archivio per la zoologia l'anatomia e la fisiologia*, *2*, 77–82 and Table VI.

Stuart, B. L., Inger, R. F. & Voris, H. K. (2006). High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters*, *2*, 470–474.

Swofford, D. L. (2002). *PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Ver. 4.b.10*. Sunderland, MA: Sinauer Associates.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, *25*, 4876–4882.

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

Trueb, L. & Duellman, W. E. (1970). The systematic status and life history of *Hyla verrucigera* Werner. *Copeia*, *1970*, 601–610.

Trueb, L. & Duellman, W. E. (1971). A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. *Occasional Papers of the Museum of Natural History*, *The University of Kansas*, *1*, 1–48.

Trueb, L. & Tyler, M. J. (1974). Systematics and evolution of the Greater Antillean hylid frogs. *Occasional Papers of the Museum of Natural History*, *The University of Kansas*, *24*, 1–60.

Ueda, H. (1986). Reproduction of *Chirixalus eiffingeri* (Boettger). *Scientific Report of the Laboratory of Amphibian Biology*, *Hiroshima University*, *8*, 109–116.

Valdujo, P. H., Silvano, D. L., Colli, G. & Martins, M. (2012). Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. *South American Journal of Herpetology*, 7, 63–78.

Varon, A., Vinh, V. S., Bomash, I. & Wheeler, W. C. (2009). POY 4.1.1. American Museum of Natural History. Available via http://research.amnh.org/scicomp/projects/poy.php

Vences, M. & Wake, D. (2007). Speciation, species boundaries and phylogeography of amphibians. In H. Heatwole (Ed.) *Amphibian Biology* (Vol. 7, pp. 2613–2669). Chipping Norton: Surrey Beatty & Sons.

Vences, M., Glaw, F., Köhler, J. & Wollenberg, K. C. (2010). Molecular phylogeny, morphology and bioacoustics reveal five additional species of arboreal microhylid frogs of the genus *Anodonthyla* from Madagascar. *Contributions to Zoology*, *79*, 1–32.

Vieites, D. R., Wollenberg, K. C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. (2009). Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Science of the United States of America*, *106*, 8267–8272.

Wells, K. D. (2007). *The Ecology and Behavior of Amphibians*. Chicago, London: University of Chicago Press.

Wesselingh, F. P., Hoorn, C., Kroonenberg, S. B., Antonelli, A., Lundberg, J. G., Vonhof, H. B. & Hooghiemstra, H. (2010). On the origin of Amazonian landscapes and biodiversity: a synthesis. In C. Hoorn & F. P. Wesselingh (Eds) *Amazonia: Landscape and Species Evolution* (pp. 421–431). Chichester: Wiley-Blackwell.

Wheeler, W. C. (1996). Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics*, *12*, 1–9.

Wheeler, W. C. (2002). Optimization alignment: down, up, error, and improvements. In R. De Salle, G. Giribet & W. C. Wheeler (Eds), *Techniques in Molecular Systematics and Evolution* (pp. 55–69). Basel: Birkhaüser Verlag.

Wheeler, W. C. (2003a). Iterative pass optimization of sequence data. *Cladistics*, *19*, 254–260.

Wheeler, W. C. (2003b). Implied alignment: a synapomorphy-based multiple-sequence alignment method and its use in cladogram search. *Cladistics*, *19*, 261–268.

Wheeler, W. C. (2012). Trivial minimization of extra-steps under dynamic homology. *Cladistics*, *28*, 188–189.

Wheeler, W. C., Aagesen, L., Arango, C. P., Faivovich, J., Grant, T., D'Haese, C., Janies, D., Smith, W. L., Varón, A. & Giribet, G. (2006). *Dynamic Homology and Phylogenetic Systematics: A Unified Approach Using POY*. New York: American Museum of Natural History.

Wiens, J. J., Fetzner, J. W., Jr, Parkinson, C. L. & Reeder, T. W. (2005). Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology*, *54*, 719–748.

Wiens, J. J., Graham, C. H., Moen, D. S., Smith, A. S. & Reeder, T. W. (2006). Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *American Naturalist*, *168*, 579–596.

Wiens, J. J., Kuczynski, C. A., Hua, X. & Moen, D. S. (2010). An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution*, *55*, 871–882.

Wiley, E. O. (1978). The evolutionary species concept reconsidered. *Systematic Zoology*, *27*, 17–26.

Wynn, A. & Heyer, W. R. (2001). Do geographically widespread species of tropical amphibians exist? An estimate of genetic relatedness within the neotropical frog *Leptodactylus fuscus* (Schneider, 1799) (Anura Leptodactylidae). *Tropical Zoology*, *14*, 255–285.

Zwickl, D. J. (2006). *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum like-*

lihood criterion. PhD dissertation. Austin: The University of Texas at Austin.

Appendix 1: 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. This species was considered as *incertae sedis* by Faivovich *et al.* (2005). However, its holotype (UMMZ 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 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 ¼ to ¾ of the flanks in '*O. vilmae*' and ⅓ 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 'cross-breed' (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 SVL, 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% to 0.2%), strongly suggests that a single species with a wider morphological and geographic 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 data). 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

Additional Supporting Information may be found in the online version of this article:

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. *Osteocephalus taurinus* Species Group: (a) *O. taurinus* (Reserva Ducke, Manaus, Amazonas, Brazil); (b) *O. oophagus* (Reserva Ducke, Manaus, Amazonas, Brazil). *Osteocephalus leprieurii* Species Group: (c) *O. leprieurii* (Arataï, French Guiana). *Osteocephalus planiceps* Species Group: (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). *Osteocephalus buckleyi* Species Group: (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).

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.

Appendix S3. Models of nucleotide substitution for the partitions used in the maximum likelihood phylogenetic analyses.

Appendix S4. (a) 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*. (b) 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. (c) 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*. (d) 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*.

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.

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 13 254 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 1–4 for current classification.

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.

Appendix S8. (1) Map of localities of sampled exemplars of *Dryaderces* gen. n. in central and southern Amazonia. (2) Map of localities of sampled exemplars of the *Osteocephalus alboguttatus* Species Group. (3a) Map of localities of sampled exemplars of the *Osteocephalus buckleyi* Species Group (part). (3b). Map of localities of sampled exemplars of the *O. buckleyi* Species Group (part). (4) Map of localities of sampled exemplars of the *Osteocephalus leprieurii* Species Group. (5) Map of localities of sampled exemplars of the *Osteocephalus planiceps* Species Group. (6) Map of localities of sampled exemplars of the *Osteocephalus taurinus* Species Group. (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.

Supplementary information

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. *Osteocephalus taurinus* Species Group: (**a**) *O. taurinus* (Reserva Ducke, Manaus, Amazonas, Brazil); (**b**) *O. oophagus* (Reserva Ducke, Manaus, Amazonas, Brazil). *Osteocephalus leprieurii* Species Group: (**c**) *O. leprieurii* (Arataï, French Guiana). *Osteocephalus planiceps* Species Group: (**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). *Osteocephalus buckleyi* Species Group: (**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).


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o

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	NMP6d28/2009	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_CPTG511_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_KHJhyl8_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**	---	---

	S04°35'49"W58°13'14"								
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_AJC3270_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, Corregimiento 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		IRSNB15879	JQ742232	---	JQ742399	---	---	---
Tepuihyla aff. *edelcae*	Venezuela: Bolívar: Chimantá		IRSNB15880	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*.

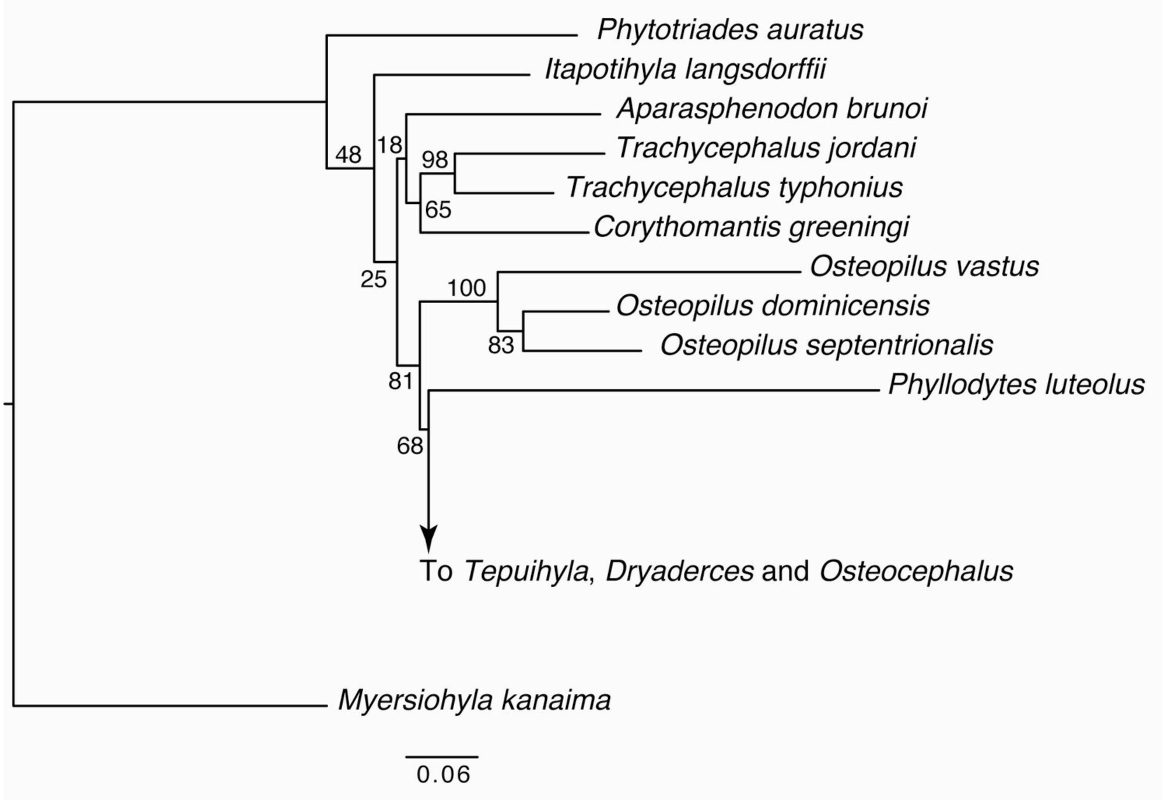
	O. leprieurii ss	*O. leprieurii* Ca1	*O. leprieurii* Ca2	*O. yasuni*
O. leprieurii ss (N=4)	0.0–1.1			
O. leprieurii Ca1 (N=4)	1.7–1.8	0.0		
O. leprieurii Ca2 (N=7)	0.9–1.8	1.5–2.0	0.0–0.6	
O. yasuni (N=7)	0.7–1.8	0.9–1.3	0.6–1.5	0.0–0.7

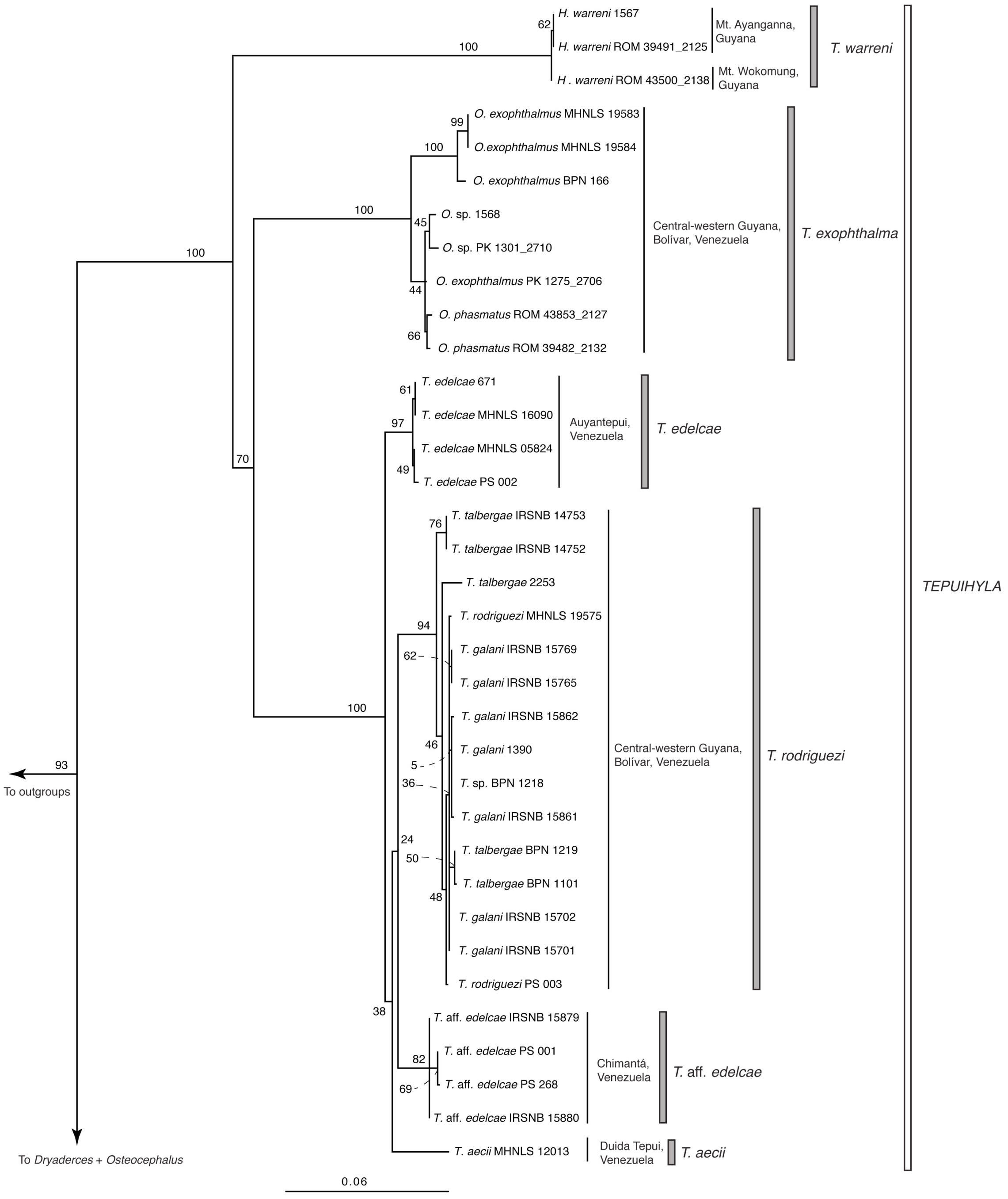
Appendix S4d. Inter- and intraspecific uncorrected genetic distances (diagonal and below the diagonal respectively) within members of the *Osteocephalus buckleyi* species group (sample size in parentheses) inferred from 551 aligned characters of a fragment of the mitochondrial 16S gene. ss = *sensu stricto*.

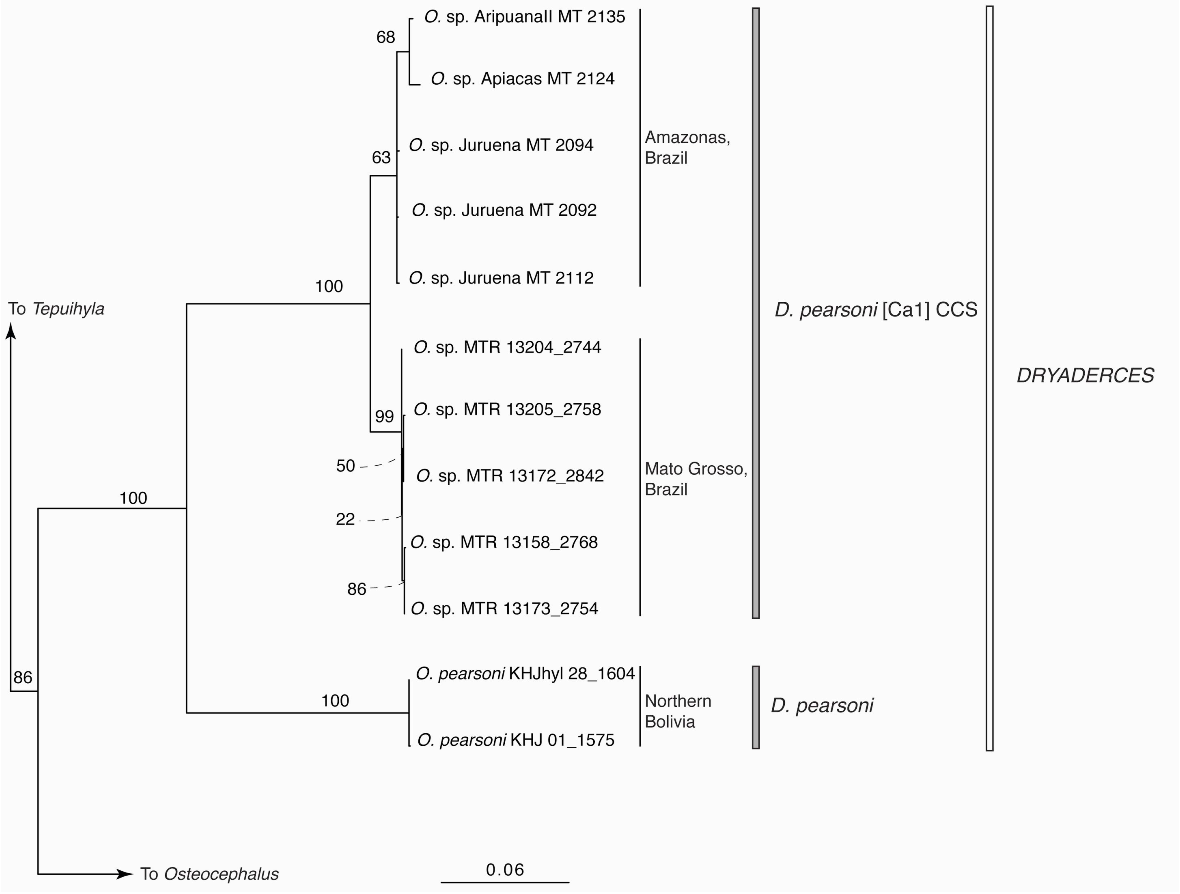
	O. buckleyi ss	*O. buckleyi* Ca1	*O. helenae*	*O. cabrerai*	*O. carri*	*O. mimeticus*	*O. mutabor*	*O. verruciger*
O. buckleyi ss (N=6)	0.0–1.5							
O. buckleyi Ca1 (N=2)	0.7–2.4	0.2						
O. helenae (N=15)	1.3–3.1	1.3–2.6	0.0–2.2					
O. cabrerai (N=2)	0.9–2.0	1.3–1.5	1.5–2.6	0.0				
O. carri (N=1)	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.

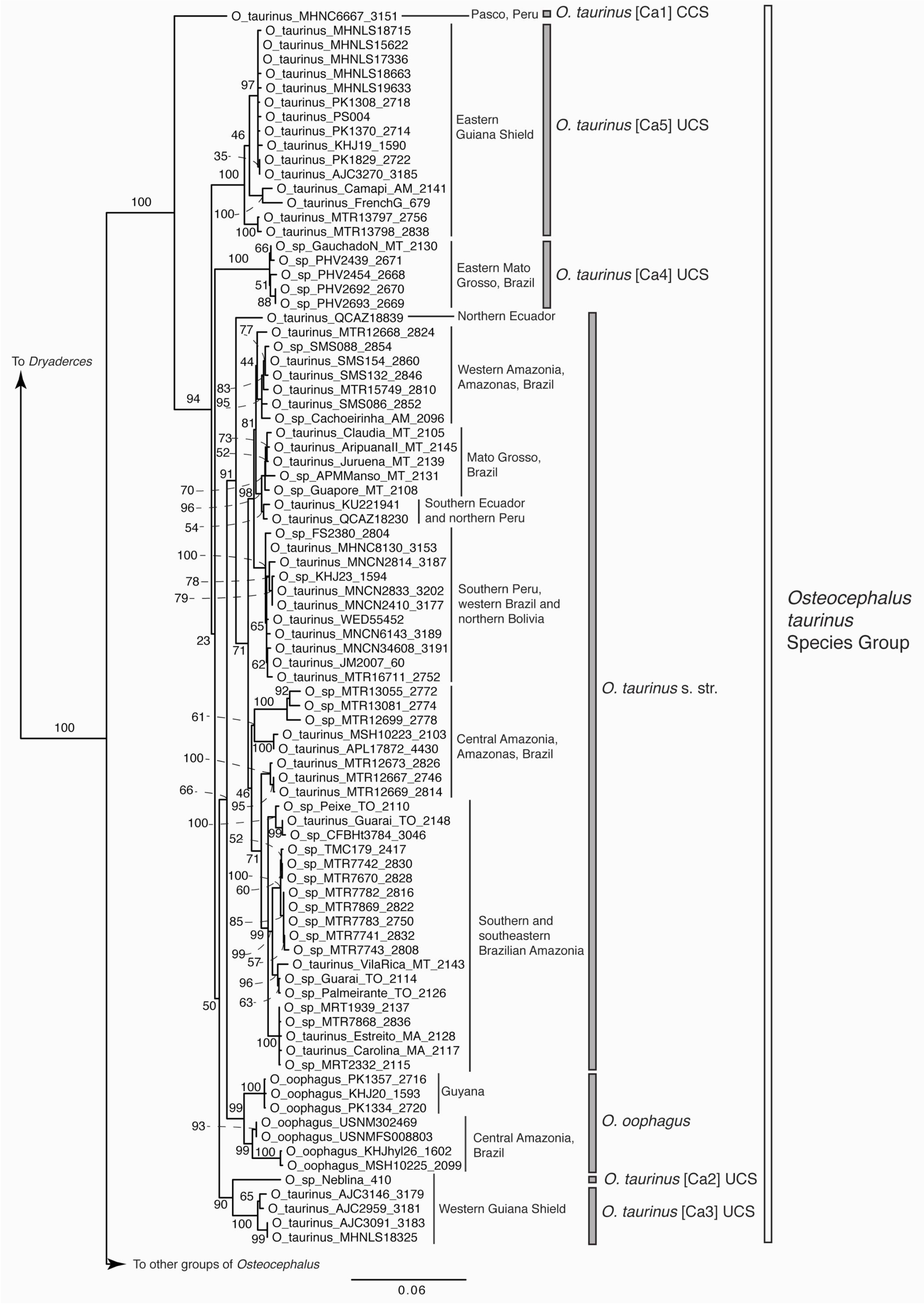
Phylogenetic relationships of *Dryaderces*, *Osteocephalus*, *Tepuihyla*, and outgroups inferred from a maximum likelihood analysis, executed in the program Garli 2.0, of a partitioned matrix of a static alignment (generated with a multiple sequence alignment in Clustal-W). Partitions and their respective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

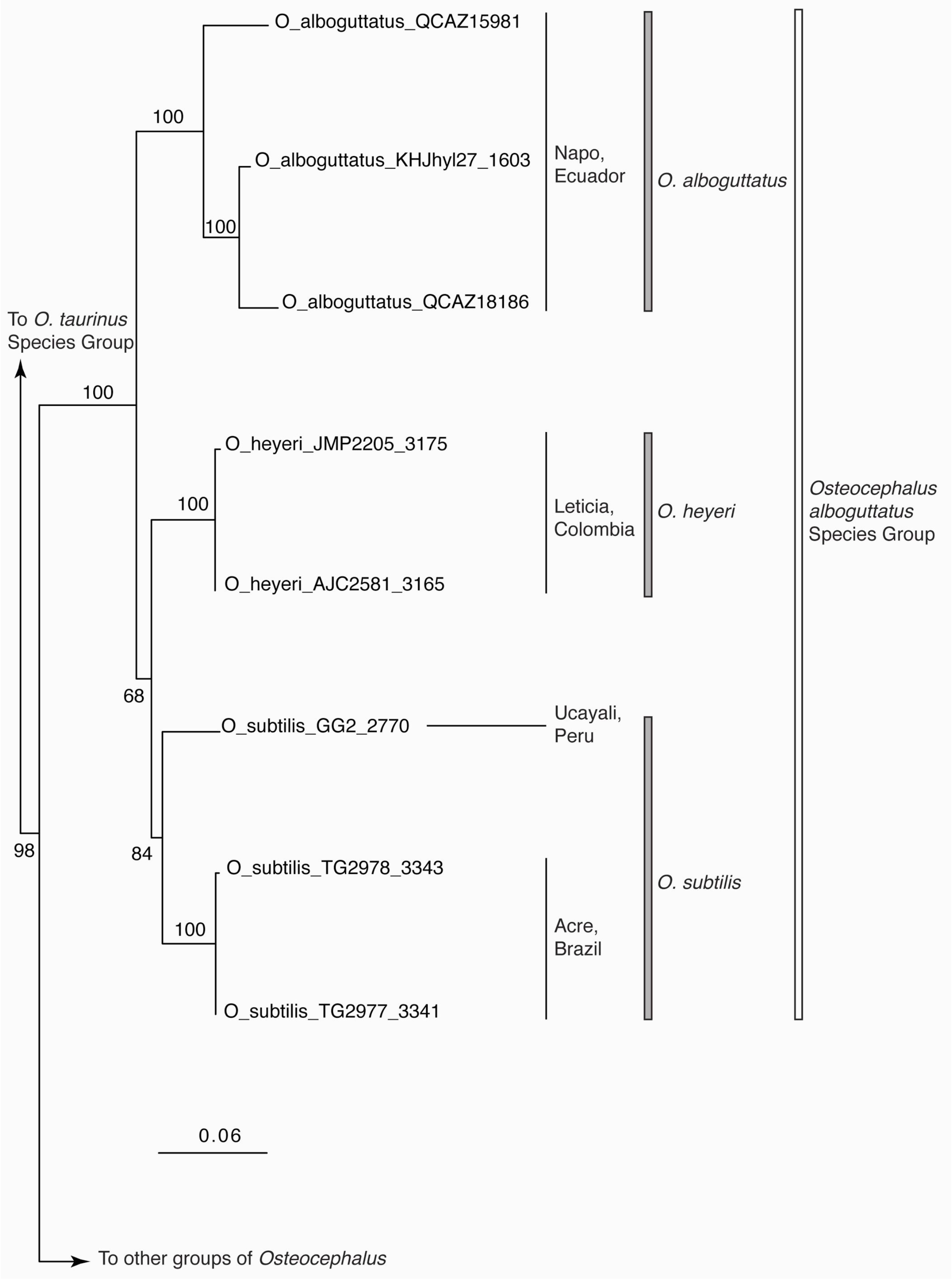



H. warreni 1567
H. warreni ROM 39491_2125
H . warreni ROM 43500_2138
Mt. Ayanganna, Guyana
Mt. Wokomung, Guyana
T. warreni
62
100
O. exophthalmus MHNLS 19583
O.exophthalmus MHNLS 19584
O. exophthalmus BPN 166
O. sp. 1568
O. sp. PK 1301_2710
O. exophthalmus PK 1275_2706
O. phasmatus ROM 43853_2127
O. phasmatus ROM 39482_2132
Central-western Guyana, Bolívar, Venezuela
T. exophthalma
99
100
100
45
44
66
100
T. edelcae 671
T. edelcae MHNLS 16090
T. edelcae MHNLS 05824
T. edelcae PS 002
Auyantepui, Venezuela
T. edelcae
61
97
49
70
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
76
94
62
100
46
5
36
24
50
48
38
93
To outgroups
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
82
69
T. aecii MHNLS 12013
Duida Tepui, Venezuela
T. aecii
TEPUIHYLA
To Dryaderces + Osteocephalus
0.06

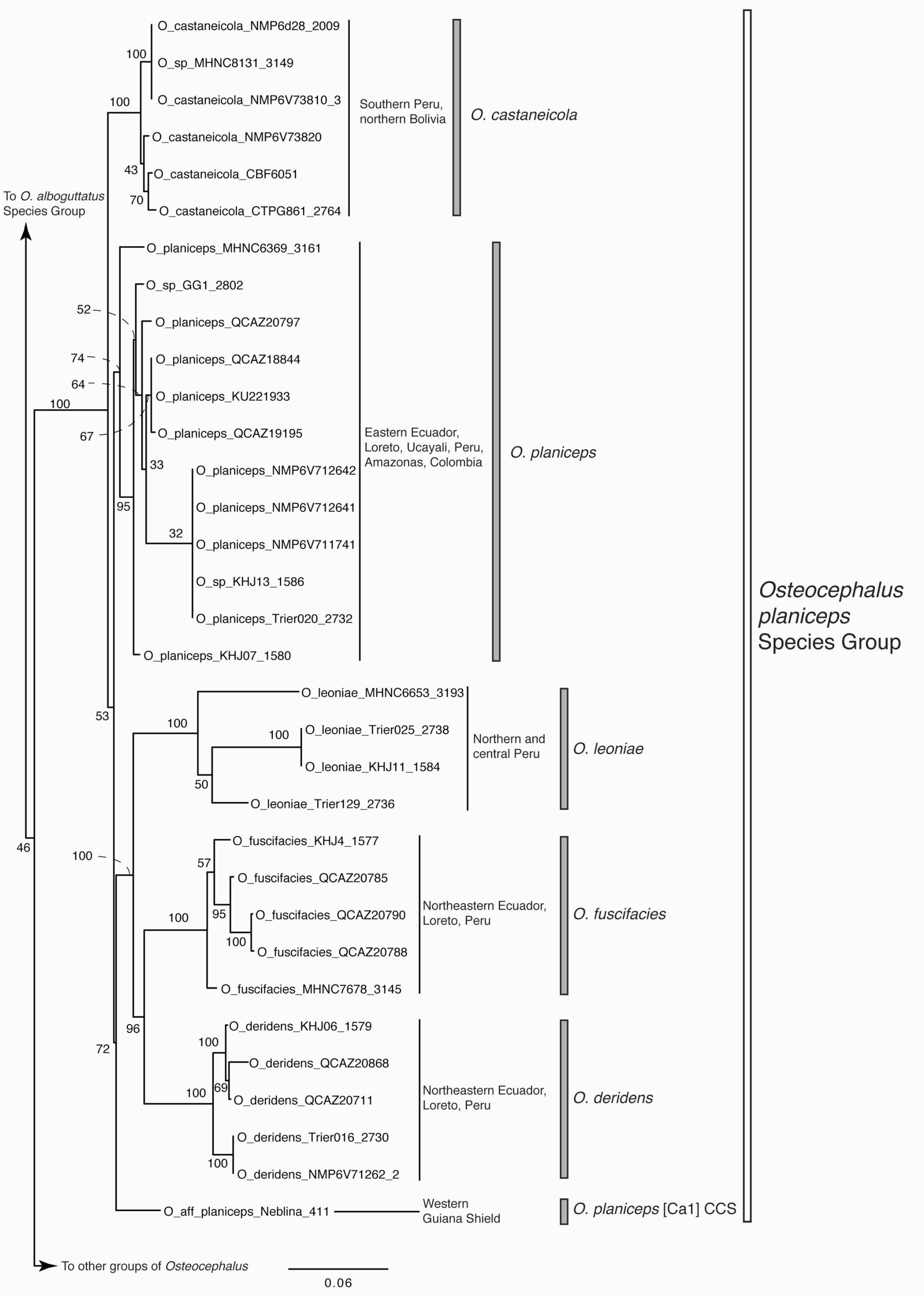


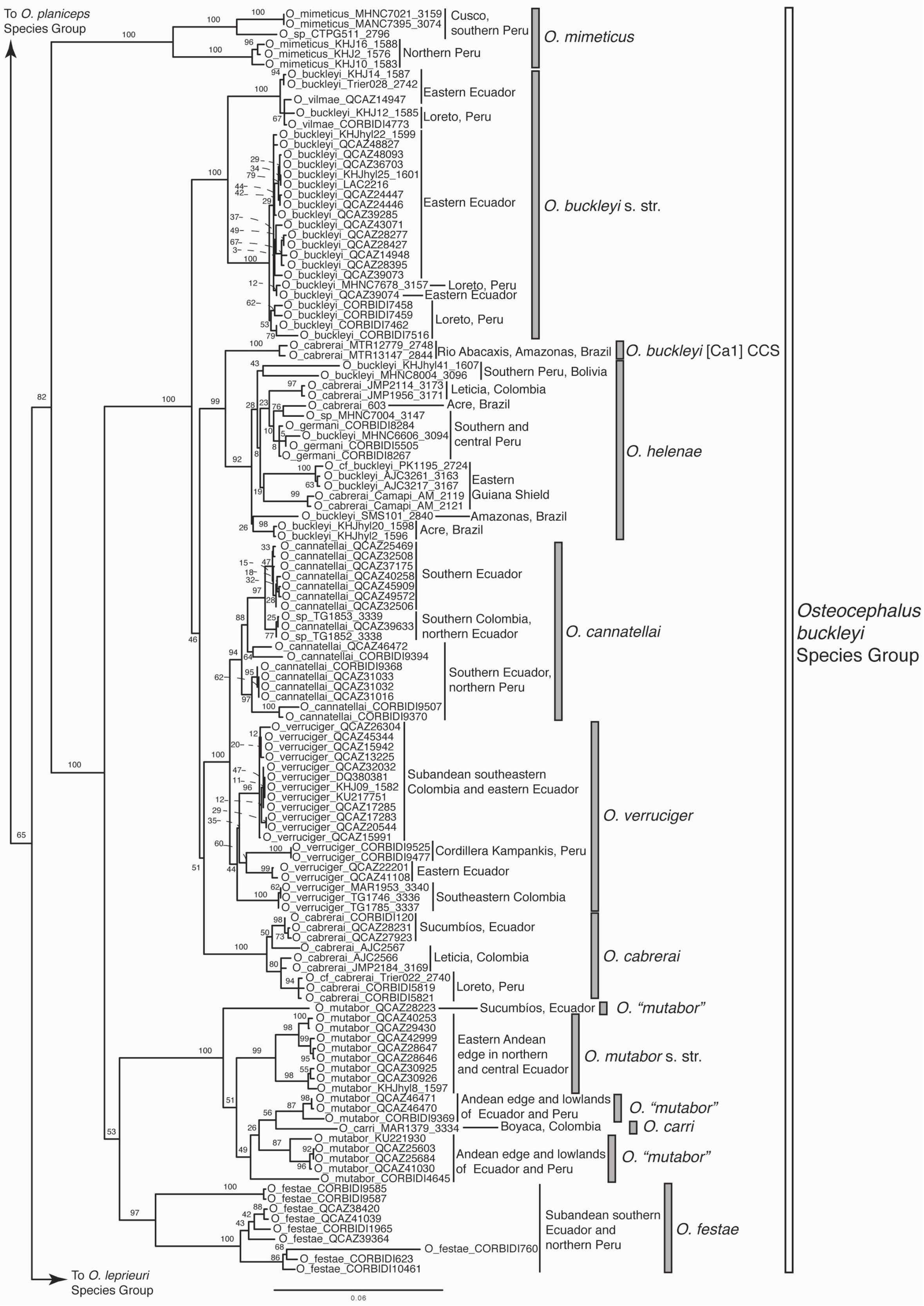
O. sp. AripuanaII MT 2135
O. sp. Apiacas MT 2124
O. sp. Juruena MT 2094
O. sp. Juruena MT 2092
O. sp. Juruena MT 2112
O. sp. MTR 13204_2744
O. sp. MTR 13205_2758
O. sp. MTR 13172_2842
O. sp. MTR 13158_2768
O. sp. MTR 13173_2754
O. pearsoni KHJhyl 28_1604
O. pearsoni KHJ 01_1575
Amazonas, Brazil
Mato Grosso, Brazil
Northern Bolivia
D. pearsoni [Ca1] CCS
D. pearsoni
DRYADERCES
To *Tepuihyla*
To *Osteocephalus*
68
63
100
99
50
22
86
100
100
86
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
O_oophagus_USNMFS008803
O_oophagus_KHJhyl26_1602
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
100
94
97
46
35
100
100
100
66
100
51
88
77
44
83
95
81
73
52
91
98
70
96
54
100
78
79
23
71
65
62
92
100
61
100
100
66
46
95
100
52
99
71
100
60
85
99
99
57
96
63
100
50
100
99
93
99
100
65
90
100
99

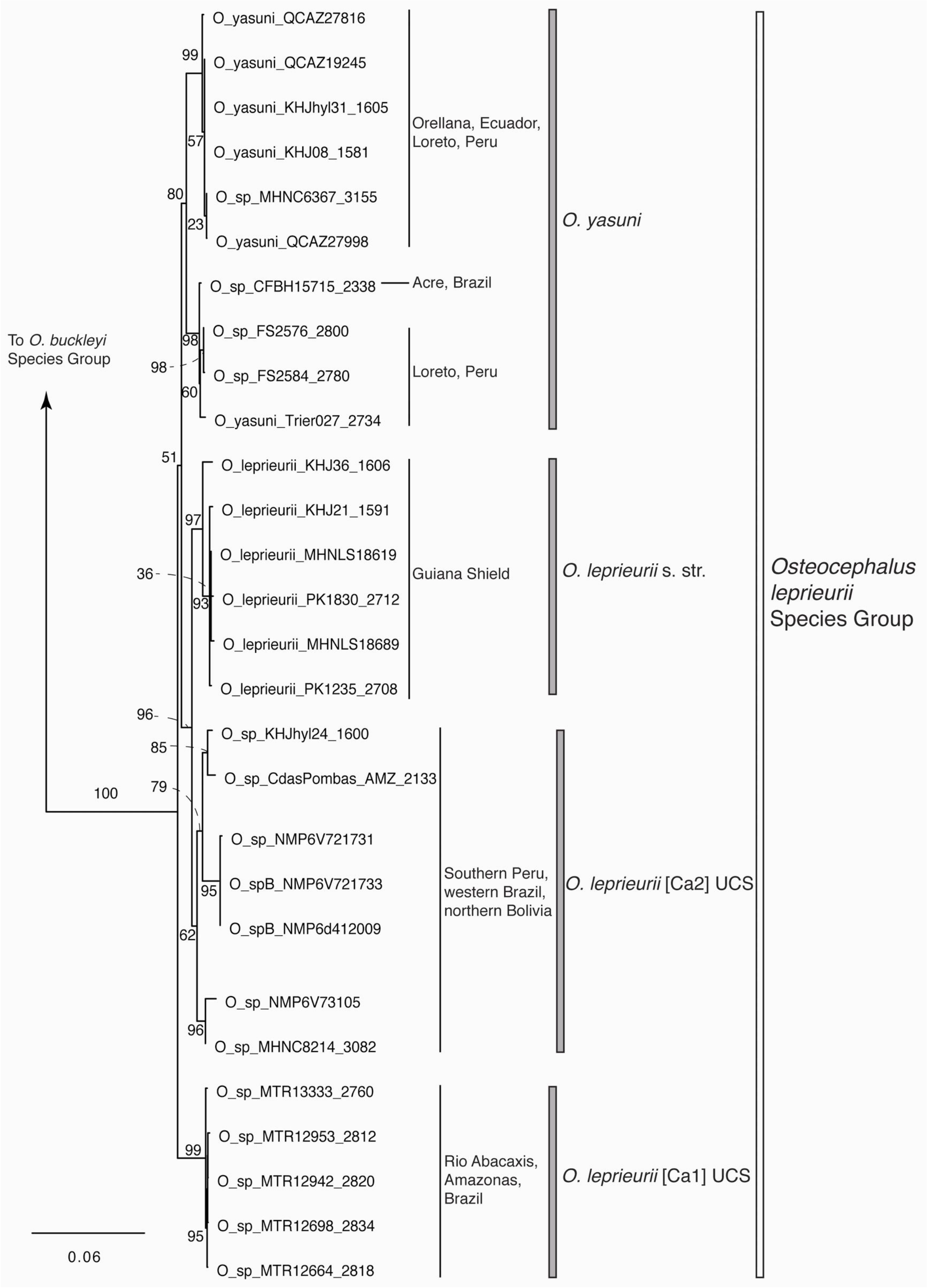


O_alboguttatus_QCAZ15981
100
O_alboguttatus_KHJhyl27_1603
100
O_alboguttatus_QCAZ18186
Napo, Ecuador
O. alboguttatus
To O. taurinus Species Group
100
O_heyeri_JMP2205_3175
100
O_heyeri_AJC2581_3165
Leticia, Colombia
O. heyeri
Osteocephalus alboguttatus Species Group
68
O_subtilis_GG2_2770
Ucayali, Peru
98
84
O_subtilis_TG2978_3343
100
O_subtilis_TG2977_3341
Acre, Brazil
O. subtilis
0.06
To other groups of Osteocephalus

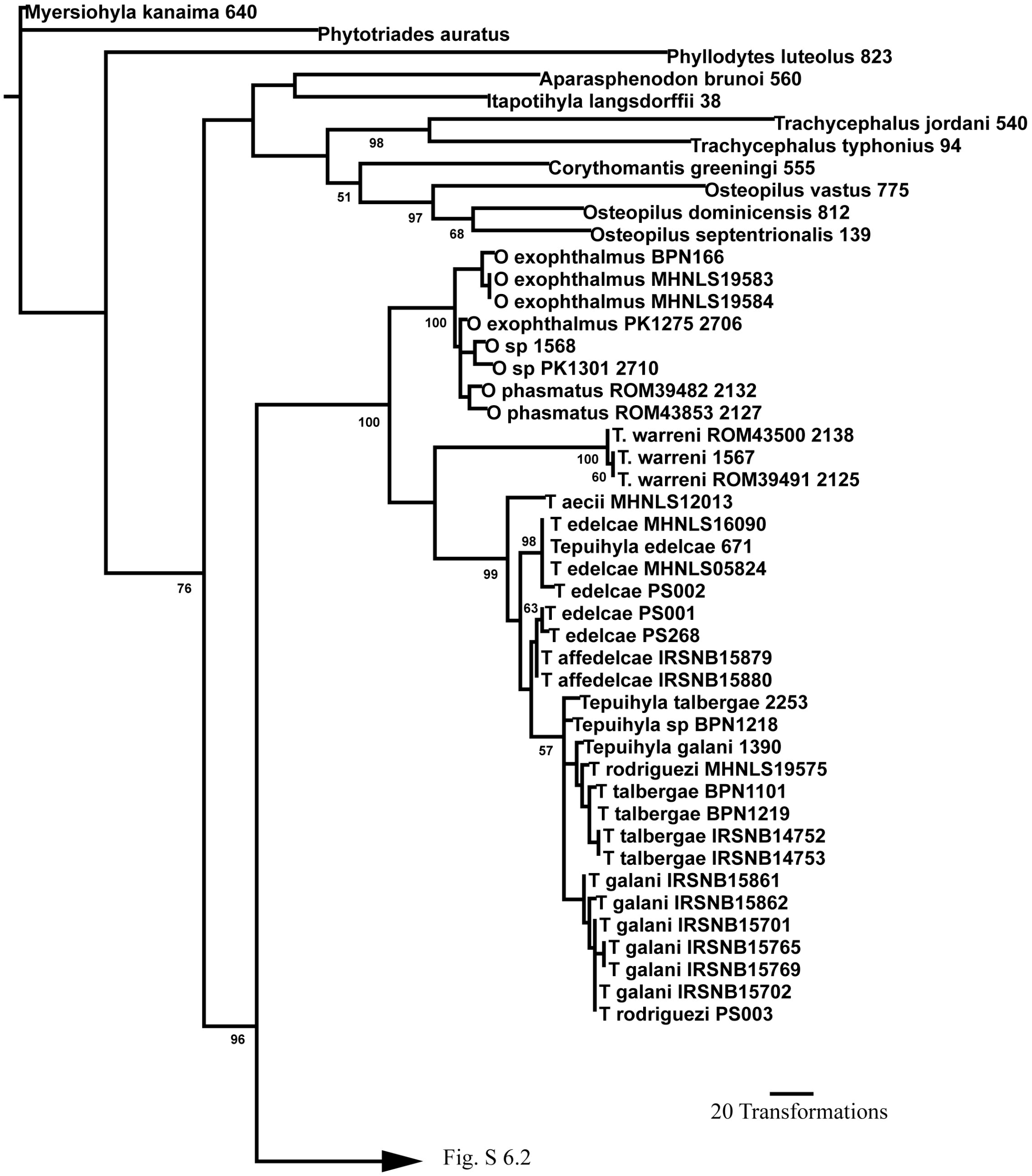

O_castaneicola_NMP6d28_2009
O_sp_MHNC8131_3149
O_castaneicola_NMP6V73810_3
O_castaneicola_NMP6V73820
O_castaneicola_CBF6051
O_castaneicola_CTPG861_2764
100
100
43
70
Southern Peru, northern Bolivia
O. castaneicola
To O. alboguttatus Species Group
O_planiceps_MHNC6369_3161
O_sp_GG1_2802
O_planiceps_QCAZ20797
O_planiceps_QCAZ18844
O_planiceps_KU221933
O_planiceps_QCAZ19195
O_planiceps_NMP6V712642
O_planiceps_NMP6V712641
O_planiceps_NMP6V711741
O_sp_KHJ13_1586
O_planiceps_Trier020_2732
O_planiceps_KHJ07_1580
52
74
64
67
100
33
95
32
Eastern Ecuador, Loreto, Ucayali, Peru, Amazonas, Colombia
O. planiceps
Osteocephalus planiceps Species Group
O_leoniae_MHNC6653_3193
O_leoniae_Trier025_2738
O_leoniae_KHJ11_1584
O_leoniae_Trier129_2736
53
100
100
50
Northern and central Peru
O. leoniae
O_fuscifacies_KHJ4_1577
O_fuscifacies_QCAZ20785
O_fuscifacies_QCAZ20790
O_fuscifacies_QCAZ20788
O_fuscifacies_MHNC7678_3145
46
100
57
100
95
100
Northeastern Ecuador, Loreto, Peru
O. fuscifacies
O_deridens_KHJ06_1579
O_deridens_QCAZ20868
O_deridens_QCAZ20711
O_deridens_Trier016_2730
O_deridens_NMP6V71262_2
96
100
72
100
69
100
Northeastern Ecuador, Loreto, Peru
O. deridens
O_aff_planiceps_Neblina_411
Western Guiana Shield
O. planiceps [Ca1] CCS
To other groups of Osteocephalus
0.06

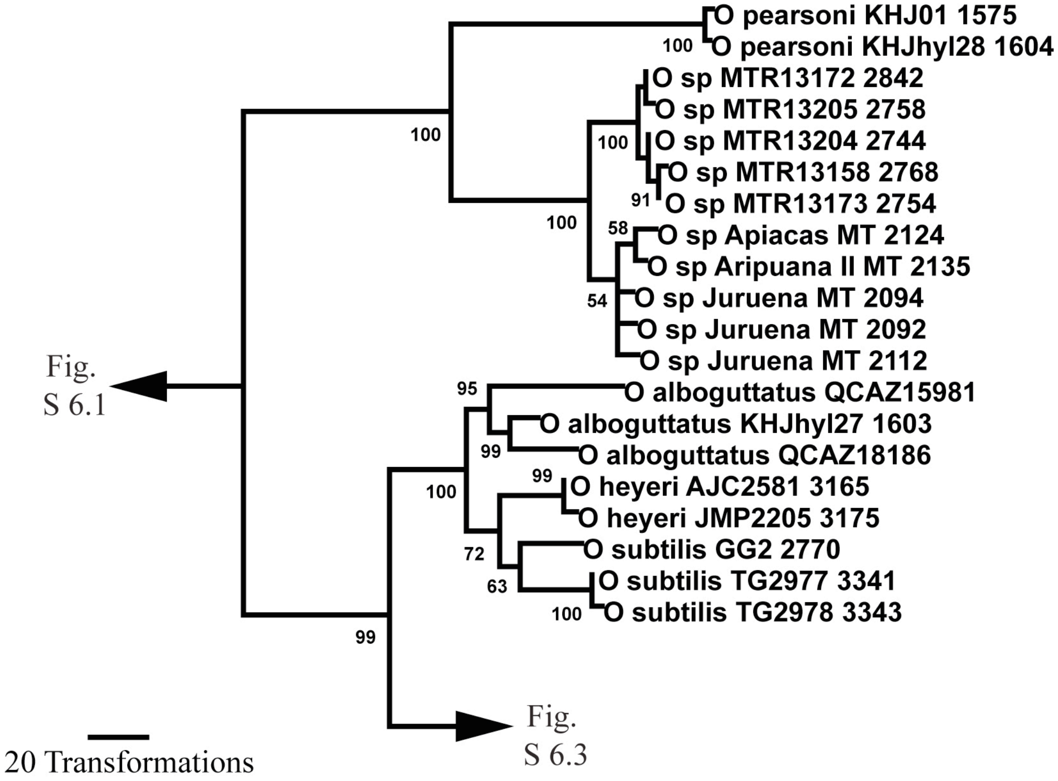


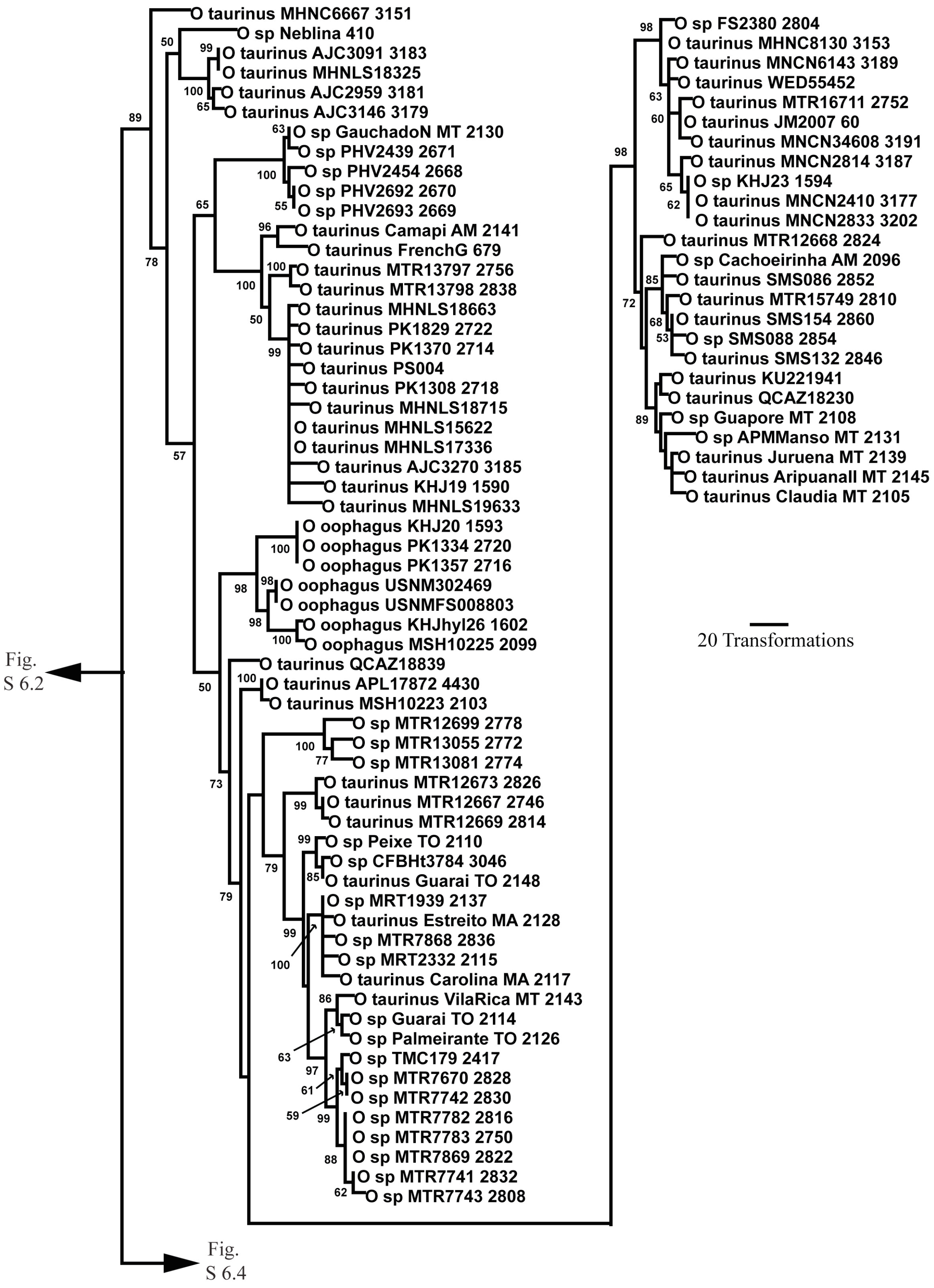
To O. planiceps Species Group
100
100
100
O_mimeticus_MHNC7021_3159
O_mimeticus_MANC7395_3074
O_sp_CTPG511_2796
Cusco, southern Peru
100
96
O_mimeticus_KHJ16_1588
O_mimeticus_KHJ2_1576
O_mimeticus_KHJ10_1583
Northern Peru
O. mimeticus
94
O_buckleyi_KHJ14_1587
O_buckleyi_Trier028_2742
100
O_vilmae_QCAZ14947
Eastern Ecuador
67
O_buckleyi_KHJ12_1585
O_vilmae_CORBIDI4773
Loreto, Peru
100
O_buckleyi_KHJhyl22_1599
O_buckleyi_QCAZ48827
29
34
79
44
42
29
O_buckleyi_QCAZ48093
O_buckleyi_QCAZ36703
O_buckleyi_KHJhyl25_1601
O_buckleyi_LAC2216
O_buckleyi_QCAZ24447
O_buckleyi_QCAZ24446
O_buckleyi_QCAZ39285
37
49
67
3
100
O_buckleyi_QCAZ43071
O_buckleyi_QCAZ28277
O_buckleyi_QCAZ28427
O_buckleyi_QCAZ14948
O_buckleyi_QCAZ28395
O_buckleyi_QCAZ39073
Eastern Ecuador
O. buckleyi s. str.
12
O_buckleyi_MHNC7678_3157
Loreto, Peru
O_buckleyi_QCAZ39074
Eastern Ecuador
62
53
79
O_buckleyi_CORBIDI7458
O_buckleyi_CORBIDI7459
O_buckleyi_CORBIDI7462
O_buckleyi_CORBIDI7516
Loreto, Peru
82
100
O_cabrerai_MTR12779_2748
O_cabrerai_MTR13147_2844
Rio Abacaxis, Amazonas, Brazil
O. buckleyi [Ca1] CCS
100
99
43
O_buckleyi_KHJhyl41_1607
O_buckleyi_MHNC8004_3096
Southern Peru, Bolivia
97
O_cabrerai_JMP2114_3173
O_cabrerai_JMP1956_3171
Leticia, Colombia
28
23
76
O_cabrerai_603
Acre, Brazil
O_sp_MHNC7004_3147
10
5
8
8
O_germani_CORBIDI8284
O_buckleyi_MHNC6606_3094
O_germani_CORBIDI5505
O_germani_CORBIDI8267
Southern and central Peru
O. helenae
92
100
63
O_cf_buckleyi_PK1195_2724
O_buckleyi_AJC3261_3163
O_buckleyi_AJC3217_3167
19
99
O_cabrerai_Camapi_AM_2119
O_cabrerai_Camapi_AM_2121
Eastern Guiana Shield
O_buckleyi_SMS101_2840
Amazonas, Brazil
26
98
O_buckleyi_KHJhyl20_1598
O_buckleyi_KHJhyl2_1596
Acre, Brazil
33
15
47
18
32
97
28
O_cannatellai_QCAZ25469
O_cannatellai_QCAZ32508
O_cannatellai_QCAZ37175
O_cannatellai_QCAZ40258
O_cannatellai_QCAZ45909
O_cannatellai_QCAZ49572
O_cannatellai_QCAZ32506
Southern Ecuador
88
25
77
O_sp_TG1853_3339
O_cannatellai_QCAZ39633
O_sp_TG1852_3338
Southern Colombia, northern Ecuador
O. cannatellai
46
94
64
O_cannatellai_QCAZ46472
O_cannatellai_CORBIDI9394
62
95
97
O_cannatellai_CORBIDI9368
O_cannatellai_QCAZ31033
O_cannatellai_QCAZ31032
O_cannatellai_QCAZ31016
100
O_cannatellai_CORBIDI9507
O_cannatellai_CORBIDI9370
Southern Ecuador, northern Peru
Osteocephalus buckleyi Species Group
12
20
O_verruciger_QCAZ26304
O_verruciger_QCAZ45344
O_verruciger_QCAZ15942
O_verruciger_QCAZ13225
100
47
11
96
12
29
35
O_verruciger_QCAZ32032
O_verruciger_DQ380381
O_verruciger_KHJ09_1582
O_verruciger_KU217751
O_verruciger_QCAZ17285
O_verruciger_QCAZ17283
O_verruciger_QCAZ20544
O_verruciger_QCAZ15991
Subandean southeastern Colombia and eastern Ecuador
O. verruciger
100
60
100
O_verruciger_CORBIDI9525
O_verruciger_CORBIDI9477
Cordillera Kampankis, Peru
51
44
99
O_verruciger_QCAZ22201
O_verruciger_QCAZ41108
Eastern Ecuador
100
62
O_verruciger_MAR1953_3340
O_verruciger_TG1746_3336
O_verruciger_TG1785_3337
Southeastern Colombia
98
50
73
O_cabrerai_CORBIDI120
O_cabrerai_QCAZ28231
O_cabrerai_QCAZ27923
Sucumbíos, Ecuador
100
O_cabrerai_AJC2567
80
O_cabrerai_AJC2566
O_cabrerai_JMP2184_3169
Leticia, Colombia
O. cabrerai
94
O_cf_cabrerai_Trier022_2740
O_cabrerai_CORBIDI5819
O_cabrerai_CORBIDI5821
Loreto, Peru
O_mutabor_QCAZ28223
Sucumbíos, Ecuador
O. “mutabor”
100
O_mutabor_QCAZ40253
O_mutabor_QCAZ29430
99
98
99
95
O_mutabor_QCAZ42999
O_mutabor_QCAZ28647
O_mutabor_QCAZ28646
100
55
98
O_mutabor_QCAZ30925
O_mutabor_QCAZ30926
O_mutabor_KHJhyl8_1597
Eastern Andean edge in northern and central Ecuador
O. mutabor s. str.
65
53
51
98
87
56
O_mutabor_QCAZ46471
O_mutabor_QCAZ46470
O_mutabor_CORBIDI9369
Andean edge and lowlands of Ecuador and Peru
O. “mutabor”
26
O_carri_MAR1379_3334
Boyaca, Colombia
O. carri
87
49
92
96
O_mutabor_KU221930
O_mutabor_QCAZ25603
O_mutabor_QCAZ25684
O_mutabor_QCAZ41030
O_mutabor_CORBIDI4645
Andean edge and lowlands of Ecuador and Peru
O. “mutabor”
100
O_festae_CORBIDI9585
O_festae_CORBIDI9587
97
88
42
43
O_festae_QCAZ38420
O_festae_QCAZ41039
O_festae_CORBIDI1965
O_festae_QCAZ39364
100
68
86
O_festae_CORBIDI760
O_festae_CORBIDI623
O_festae_CORBIDI10461
Subandean southern Ecuador and northern Peru
O. festae
To O. leprieuri Species Group
0.06


O_yasuni_QCAZ27816
99
O_yasuni_QCAZ19245
O_yasuni_KHJhyl31_1605
57
O_yasuni_KHJ08_1581
80
O_sp_MHNC6367_3155
23
O_yasuni_QCAZ27998
Orellana, Ecuador,
Loreto, Peru
O. yasuni
O_sp_CFBH15715_2338
Acre, Brazil
O_sp_FS2576_2800
To O. buckleyi
Species Group
98
98
O_sp_FS2584_2780
60
Loreto, Peru
O_yasuni_Trier027_2734
51
O_leprieurii_KHJ36_1606
O_leprieurii_KHJ21_1591
97
O_leprieurii_MHNLS18619
36
Guiana Shield
O. leprieurii s. str.
Osteocephalus
leprieurii
Species Group
O_leprieurii_PK1830_2712
93
O_leprieurii_MHNLS18689
O_leprieurii_PK1235_2708
96
O_sp_KHJhyl24_1600
85
O_sp_CdasPombas_AMZ_2133
79
100
O_sp_NMP6V721731
O_spB_NMP6V721733
95
Southern Peru,
western Brazil,
northern Bolivia
O. leprieurii [Ca2] UCS
O_spB_NMP6d412009
62
O_sp_NMP6V73105
96
O_sp_MHNC8214_3082
O_sp_MTR13333_2760
O_sp_MTR12953_2812
99
Rio Abacaxis,
Amazonas,
Brazil
O. leprieurii [Ca1] UCS
O_sp_MTR12942_2820
O_sp_MTR12698_2834
95
0.06
O_sp_MTR12664_2818

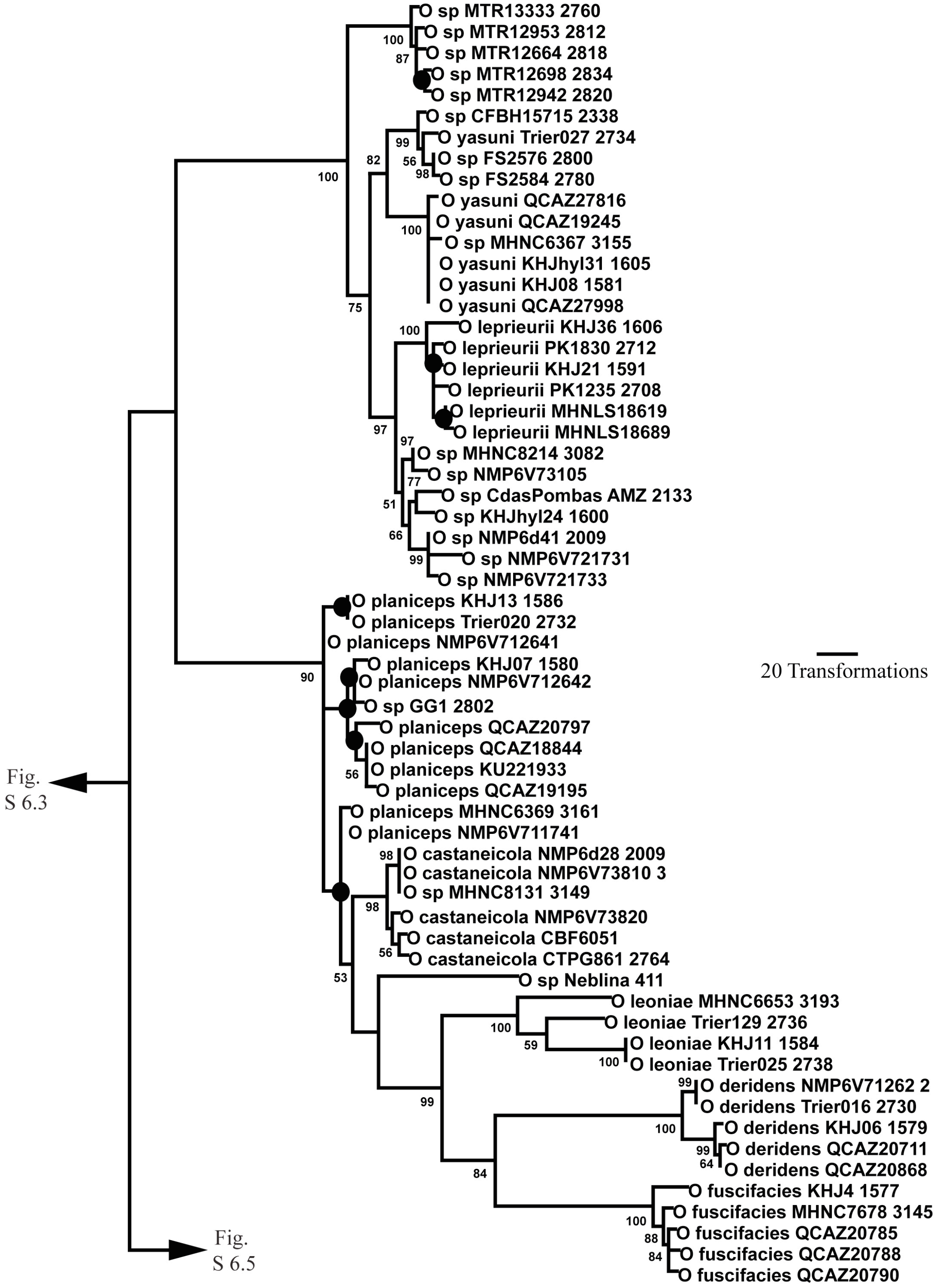
Appendix S6.1-6. Phylogenetic relationships of *Dryaderces*, *Osteocephalus*, *Tepuihyla*, and outgroups inferred from maximum parsimony analysis under a static alignment (generated with a multiple sequence alignment in Clustal-W) in the program T.N.T., Willi Hennig Society Edition. This topology reflects 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 1–4 for current classification.

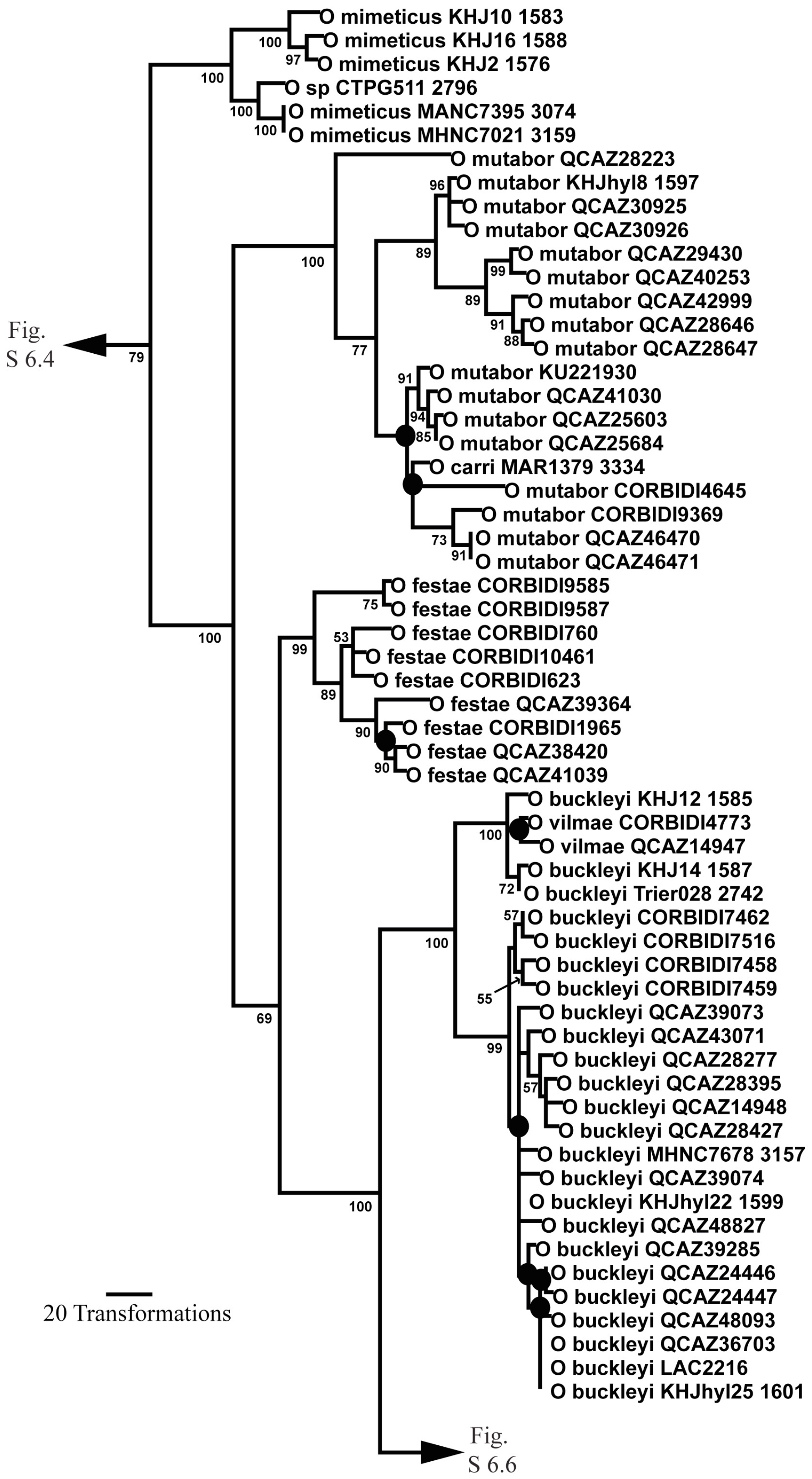

Myersiohyla kanaima 640
Phytotriades auratus
Phyllodytes luteolus 823
Aparasphenodon brunoi 560
Itapotihyla langsdorffii 38
Trachycephalus jordani 540
98
Trachycephalus typhonius 94
Corythomantis greeningi 555
51
Osteopilus vastus 775
97
Osteopilus dominicensis 812
68
Osteopilus septentrionalis 139
O exophthalmus BPN166
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
60
T. warreni ROM39491 2125
T aecii MHNLS12013
T edelcae MHNLS16090
98
Tepuihyla edelcae 671
T edelcae MHNLS05824
99
T edelcae PS002
63
T edelcae PS001
T edelcae PS268
T affedelcae IRSNB15879
T affedelcae IRSNB15880
Tepuihyla talbergae 2253
Tepuihyla sp BPN1218
76
57
Tepuihyla galani 1390
T rodriguezi MHNLS19575
T talbergae BPN1101
T talbergae BPN1219
T talbergae IRSNB14752
T talbergae IRSNB14753
T galani IRSNB15861
T galani IRSNB15862
T galani IRSNB15701
T galani IRSNB15765
T galani IRSNB15769
T galani IRSNB15702
T rodriguezi PS003
96
20 Transformations
Fig. S 6.2


O pearsoni KHJ01 1575
100
O pearsoni KHJhyl28 1604
O sp MTR13172 2842
O sp MTR13205 2758
100
100
O sp MTR13204 2744
O sp MTR13158 2768
91
O sp MTR13173 2754
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
72
O subtilis GG2 2770
63
O subtilis TG2977 3341
100
O subtilis TG2978 3343
99
Fig.
S 6.3
20 Transformations


O taurinus MHNC6667 3151
O sp Neblina 410
O taurinus AJC3091 3183
O taurinus MHNLS18325
O taurinus AJC2959 3181
O taurinus AJC3146 3179
O sp GauchadoN MT 2130
O sp PHV2439 2671
O sp PHV2454 2668
O sp PHV2692 2670
O sp PHV2693 2669
O taurinus Camapi AM 2141
O taurinus FrenchG 679
O taurinus MTR13797 2756
O taurinus MTR13798 2838
O taurinus MHNLS18663
O taurinus PK1829 2722
O taurinus PK1370 2714
O taurinus PS004
O taurinus PK1308 2718
O taurinus MHNLS18715
O taurinus MHNLS15622
O taurinus MHNLS17336
O taurinus AJC3270 3185
O taurinus KHJ19 1590
O taurinus MHNLS19633
O oophagus KHJ20 1593
O oophagus PK1334 2720
O oophagus PK1357 2716
O oophagus USNM302469
O oophagus USNMFS008803
O oophagus KHJhyl26 1602
O oophagus MSH10225 2099
O taurinus QCAZ18839
O taurinus APL17872 4430
O taurinus MSH10223 2103
O sp MTR12699 2778
O sp MTR13055 2772
O sp MTR13081 2774
O taurinus MTR12673 2826
O taurinus MTR12667 2746
O taurinus MTR12669 2814
O sp Peixe TO 2110
O sp CFBHt3784 3046
O taurinus Guarai TO 2148
O sp MRT1939 2137
O taurinus Estreito MA 2128
O sp MTR7868 2836
O sp MRT2332 2115
O taurinus Carolina MA 2117
O taurinus VilaRica MT 2143
O sp Guarai TO 2114
O sp Palmeirante TO 2126
O sp TMC179 2417
O sp MTR7670 2828
O sp MTR7742 2830
O sp MTR7782 2816
O sp MTR7783 2750
O sp MTR7869 2822
O sp MTR7741 2832
O sp MTR7743 2808
O sp FS2380 2804
O taurinus MHNC8130 3153
O taurinus MNCN6143 3189
O taurinus WED55452
O taurinus MTR16711 2752
O taurinus JM2007 60
O taurinus MNCN34608 3191
O taurinus MNCN2814 3187
O sp KHJ23 1594
O taurinus MNCN2410 3177
O taurinus MNCN2833 3202
O taurinus MTR12668 2824
O sp Cachoeirinha AM 2096
O taurinus SMS086 2852
O taurinus MTR15749 2810
O taurinus SMS154 2860
O sp SMS088 2854
O taurinus SMS132 2846
O taurinus KU221941
O taurinus QCAZ18230
O sp Guapore MT 2108
O sp APMManso MT 2131
O taurinus Juruena MT 2139
O taurinus AripuanaII MT 2145
O taurinus Claudia MT 2105
20 Transformations
Fig.
S 6.2
Fig.
S 6.4

S6.4


O sp MTR13333 2760
O sp MTR12953 2812
O sp MTR12664 2818
O sp MTR12698 2834
O sp MTR12942 2820
O sp CFBH15715 2338
O yasuni Trier027 2734
O sp FS2576 2800
O sp FS2584 2780
O yasuni QCAZ27816
O yasuni QCAZ19245
O sp MHNC6367 3155
O yasuni KHJhyl31 1605
O yasuni KHJ08 1581
O yasuni QCAZ27998
O leprieurii KHJ36 1606
O leprieurii PK1830 2712
O leprieurii KHJ21 1591
O leprieurii PK1235 2708
O leprieurii MHNLS18619
O leprieurii MHNLS18689
O sp MHNC8214 3082
O sp NMP6V73105
O sp CdasPombas AMZ 2133
O sp KHJhyl24 1600
O sp NMP6d41 2009
O sp NMP6V721731
O sp NMP6V721733
O planiceps KHJ13 1586
O planiceps Trier020 2732
O planiceps NMP6V712641
O planiceps KHJ07 1580
O planiceps NMP6V712642
O sp GG1 2802
O planiceps QCAZ20797
O planiceps QCAZ18844
O planiceps KU221933
O planiceps QCAZ19195
O planiceps MHNC6369 3161
O planiceps NMP6V711741
O castaneicola NMP6d28 2009
O castaneicola NMP6V73810 3
O sp MHNC8131 3149
O castaneicola NMP6V73820
O castaneicola CBF6051
O castaneicola CTPG861 2764
O sp Neblina 411
O leoniae MHNC6653 3193
O leoniae Trier129 2736
O leoniae KHJ11 1584
O leoniae Trier025 2738
O deridens NMP6V71262 2
O deridens Trier016 2730
O deridens KHJ06 1579
O deridens QCAZ20711
O deridens QCAZ20868
O fuscifacies KHJ4 1577
O fuscifacies MHNC7678 3145
O fuscifacies QCAZ20785
O fuscifacies QCAZ20788
O fuscifacies QCAZ20790
100
87
100
82
99
56
98
100
75
100
97
97
77
51
66
99
90
56
98
98
56
53
100
59
100
99
99
100
99
64
84
100
88
84
20 Transformations
Fig.
S 6.3
Fig.
S 6.5


O mimeticus KHJ10 1583
100
O mimeticus KHJ16 1588
97
O mimeticus KHJ2 1576
100
O sp CTPG511 2796
100
O mimeticus MANC7395 3074
100
O mimeticus MHNC7021 3159
O mutabor QCAZ28223
96
O mutabor KHJhyl8 1597
O mutabor QCAZ30925
O mutabor QCAZ30926
100
89
O mutabor QCAZ29430
99
O mutabor QCAZ40253
89
O mutabor QCAZ42999
91
O mutabor QCAZ28646
88
O mutabor QCAZ28647
Fig.
S 6.4
79
77
91
O mutabor KU221930
O mutabor QCAZ41030
94
O mutabor QCAZ25603
85
O mutabor QCAZ25684
O carri MAR1379 3334
O mutabor CORBIDI4645
O mutabor CORBIDI9369
73
O mutabor QCAZ46470
91
O mutabor QCAZ46471
O festae CORBIDI9585
75
O festae CORBIDI9587
100
99
53
O festae CORBIDI760
O festae CORBIDI10461
O festae CORBIDI623
89
O festae QCAZ39364
90
O festae CORBIDI1965
O festae QCAZ38420
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
O buckleyi CORBIDI7516
100
O buckleyi CORBIDI7458
55
O buckleyi CORBIDI7459
69
O buckleyi QCAZ39073
O buckleyi QCAZ43071
99
O buckleyi QCAZ28277
57
O buckleyi QCAZ28395
O buckleyi QCAZ14948
O buckleyi QCAZ28427
O buckleyi MHNC7678 3157
O buckleyi QCAZ39074
100
O buckleyi KHJhyl22 1599
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


O aff. cabrerai MTR12779 2748
100
O aff. cabrerai MTR13147 2844
99
O buckleyi MHNC8004 3096
O buckleyi KHJhyl41 1607
O buckleyi SMS101 2840
85
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
O buckleyi MHNC6606 3094
77
O cabrerai 603
65
O sp MHNC7004 3147
O cabrerai AJC2567
O cabrerai CORBIDI120
O cabrerai QCAZ27923
61
99
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
100
O verruciger CORBIDI9525
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
O verruciger QCAZ20544
99
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

<u>Appendix S7.</u> 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

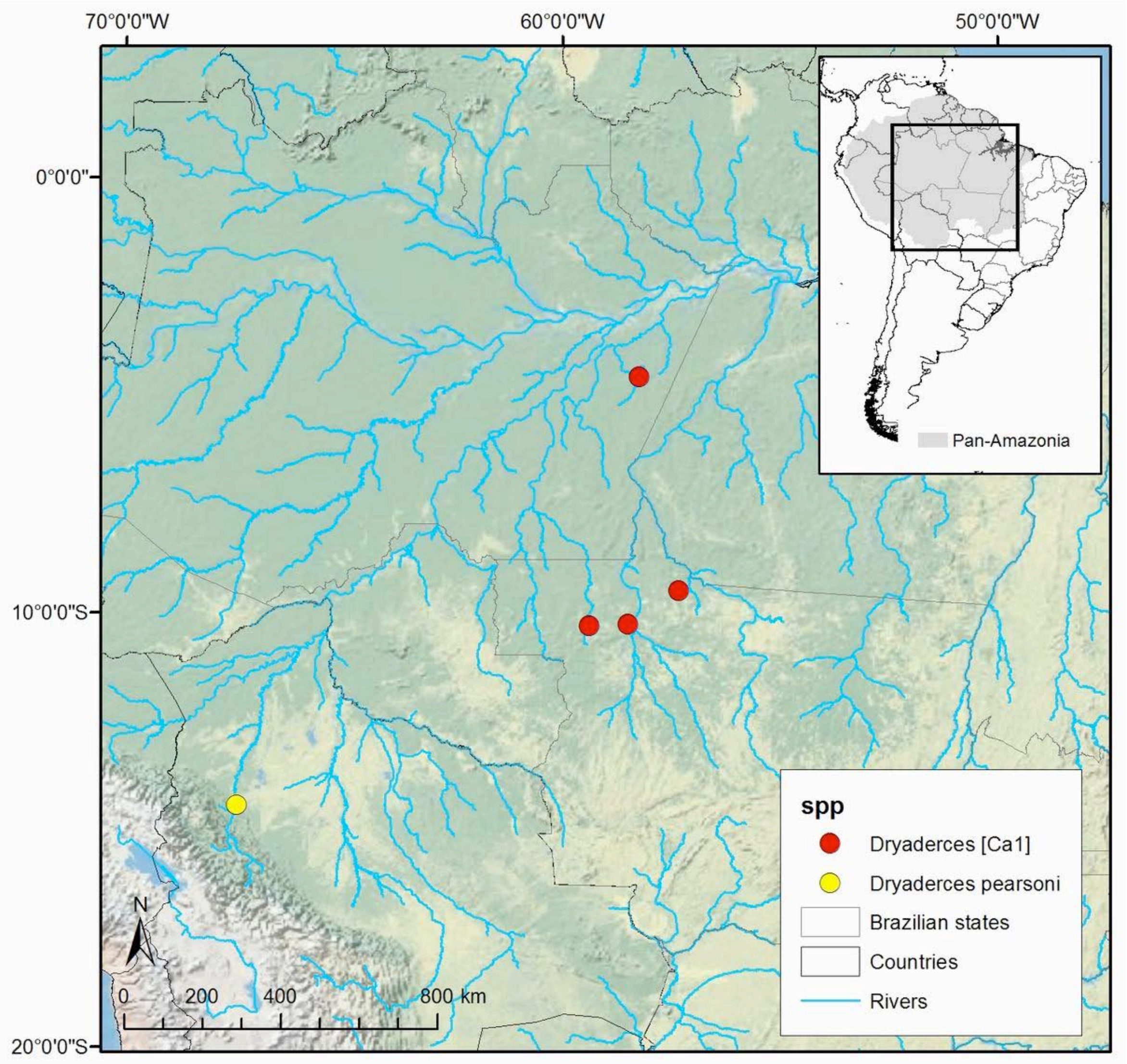
Osteocephalus

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

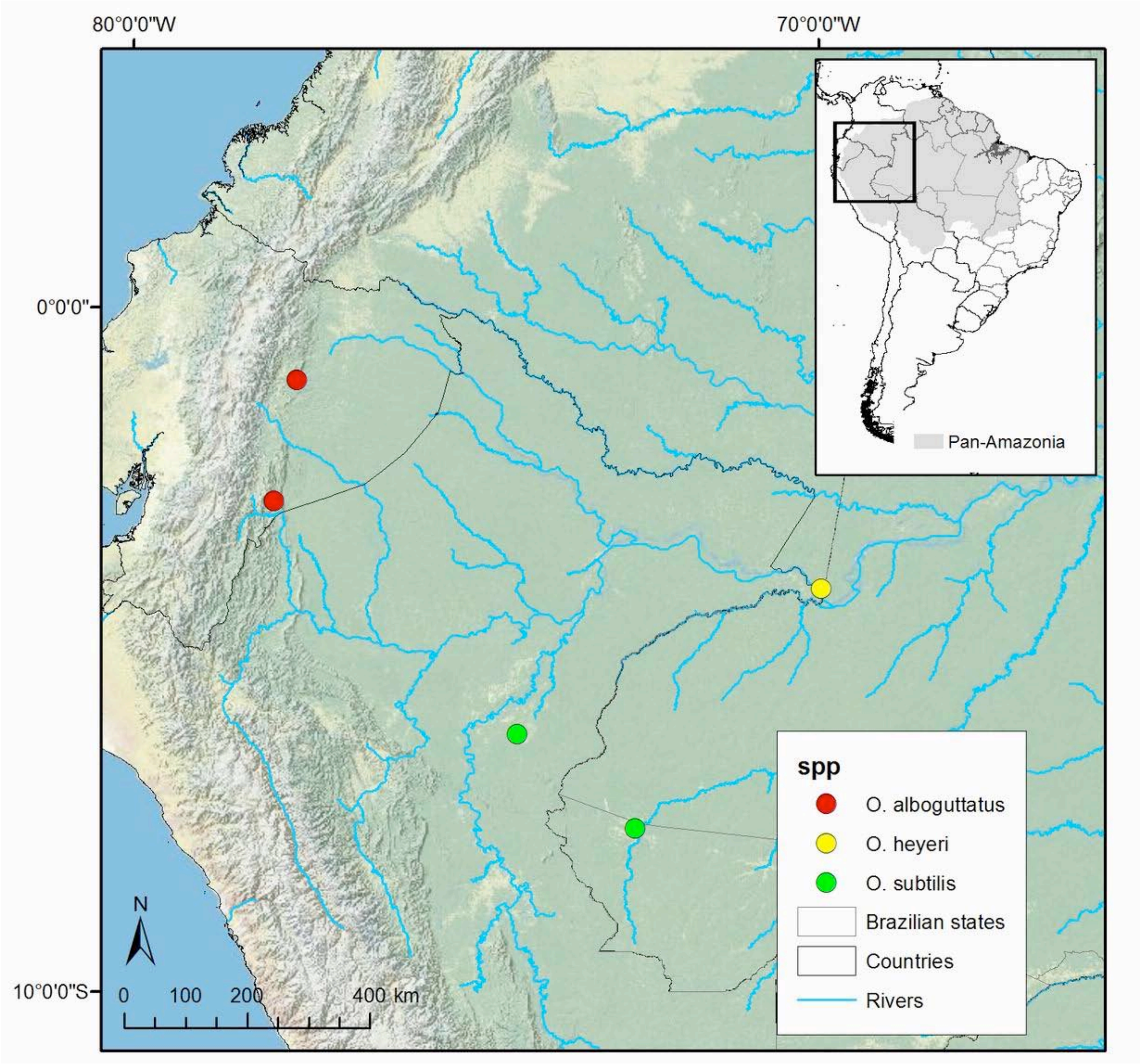
Tepuihyla

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

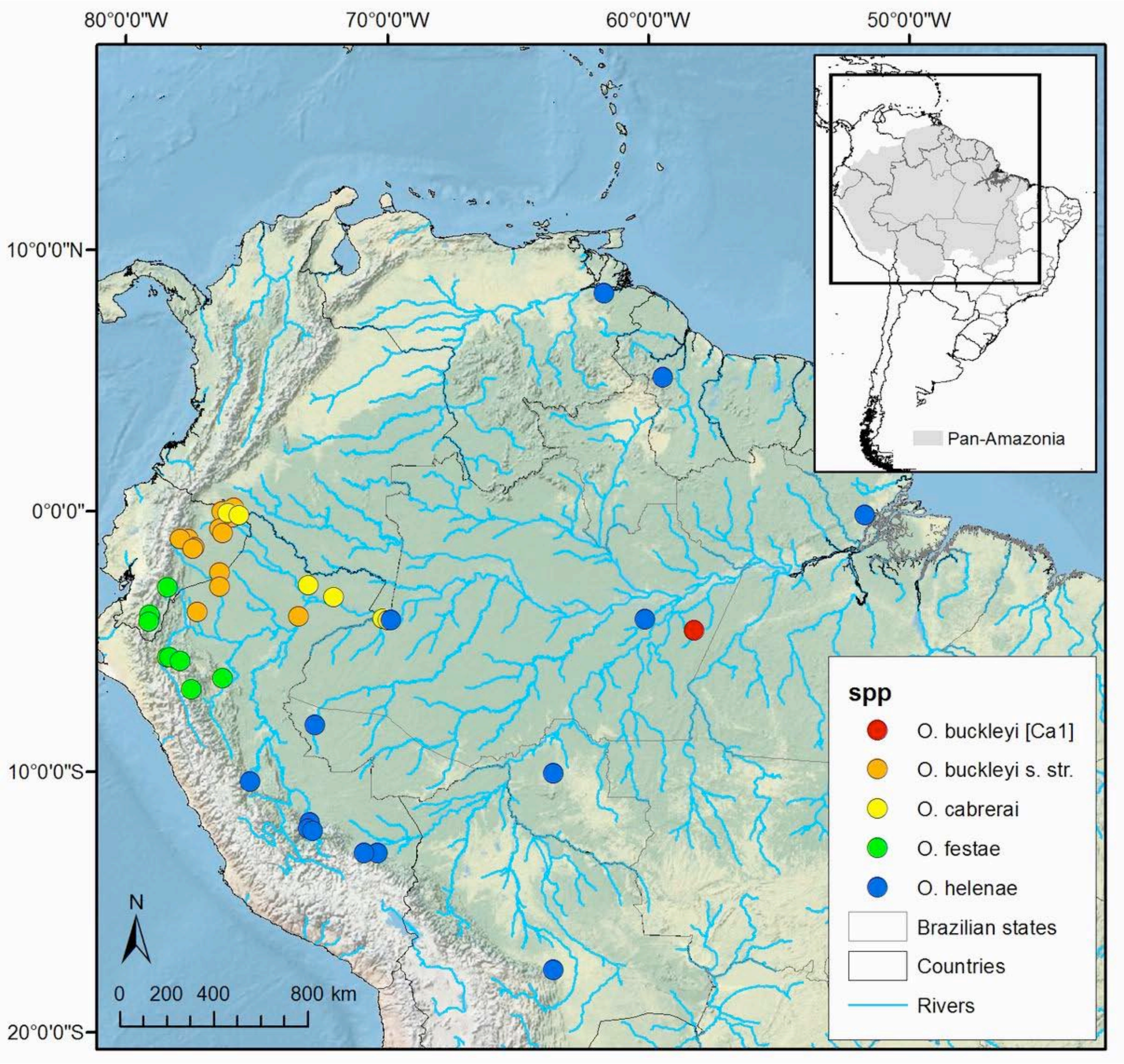
<u>Appendix S8.1.</u> Map of localities of sampled exemplars of *Dryaderces* gen. n. in central and southern Amazonia.



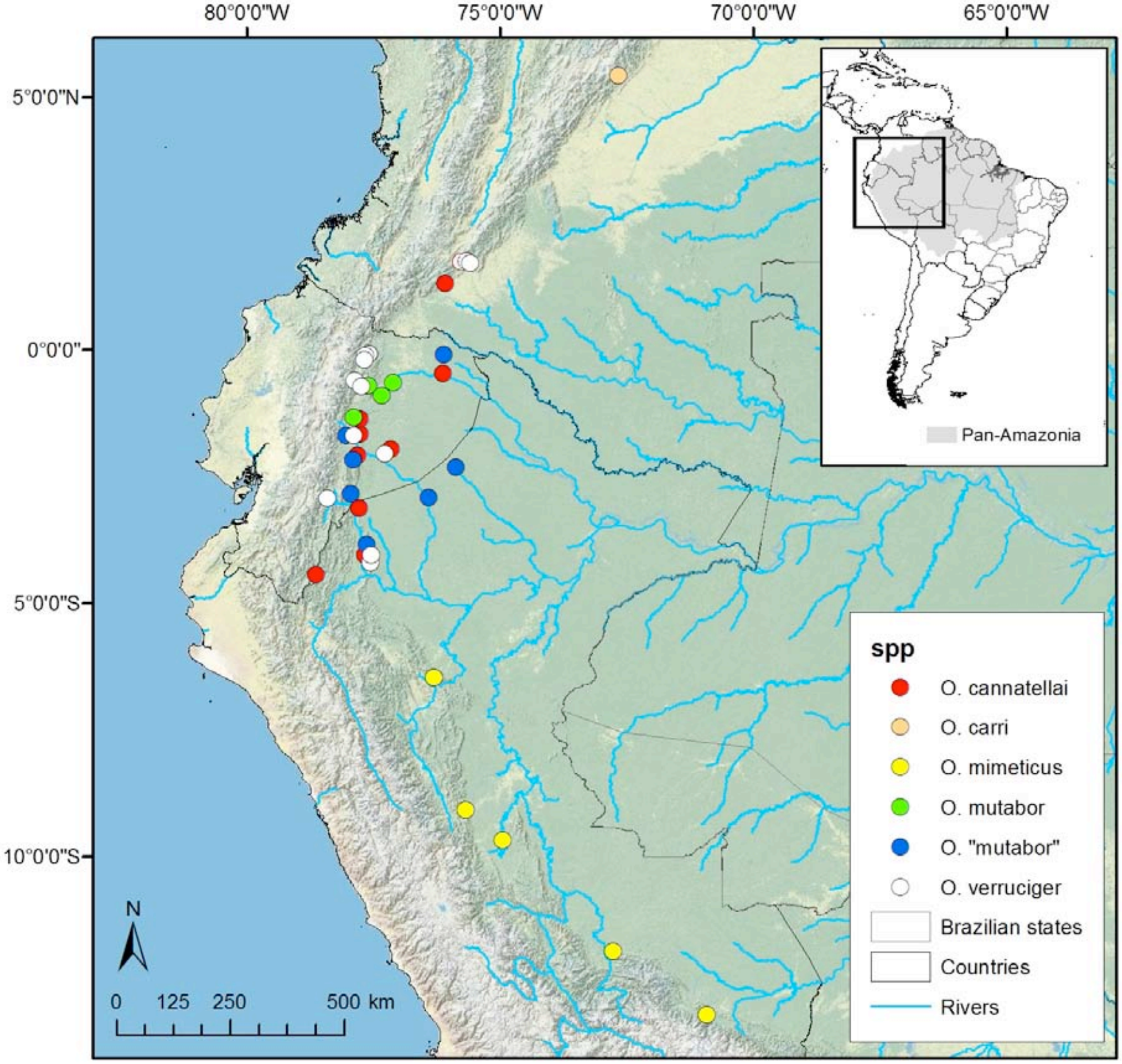
Appendix S8.2. Map of localities of sampled exemplars of the *Osteocephalus alboguttatus* Species Group.



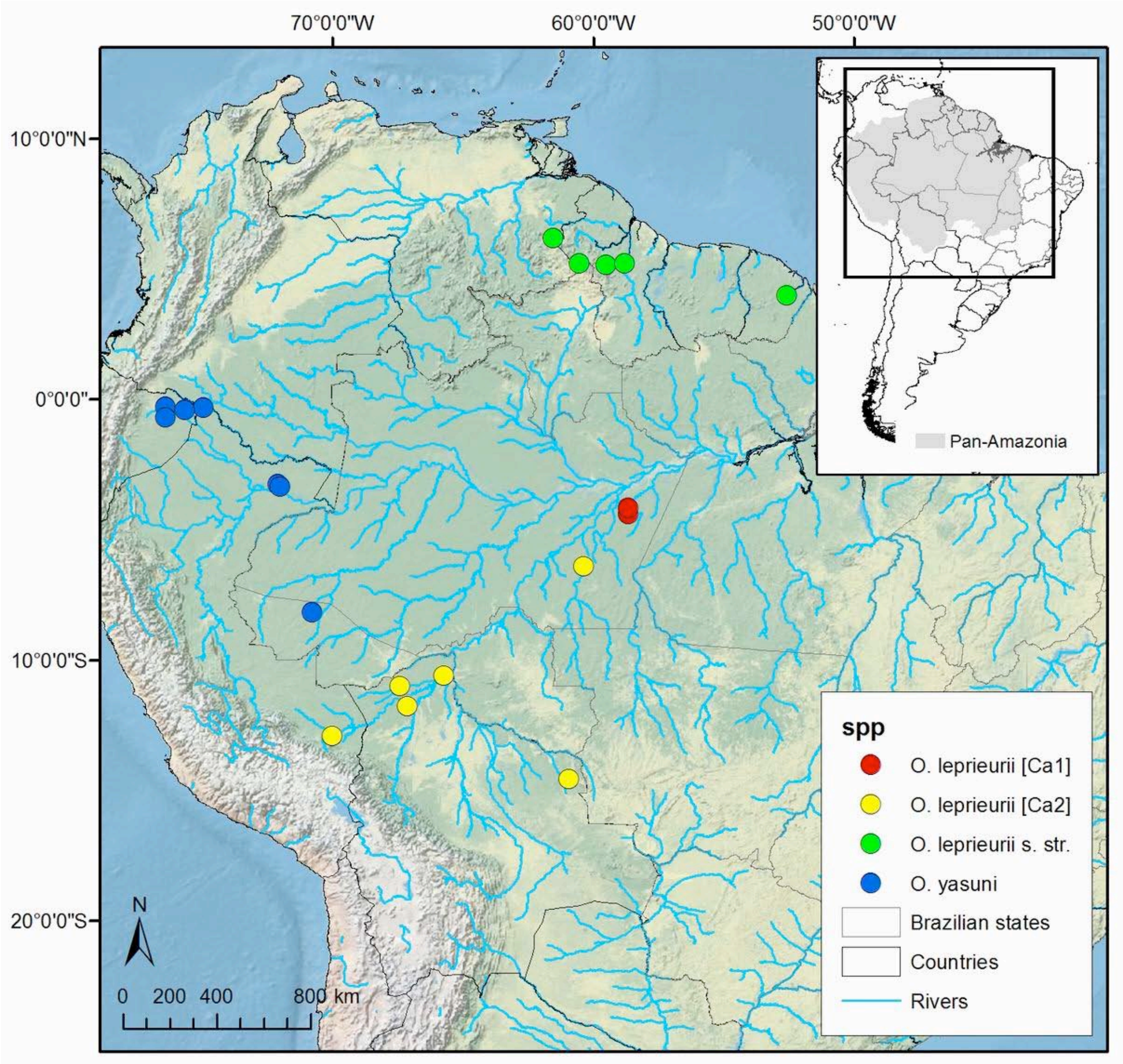
<u>Appendix S8.3a.</u> Map of localities of sampled exemplars of the *Osteocephalus buckleyi* Species Group (part).



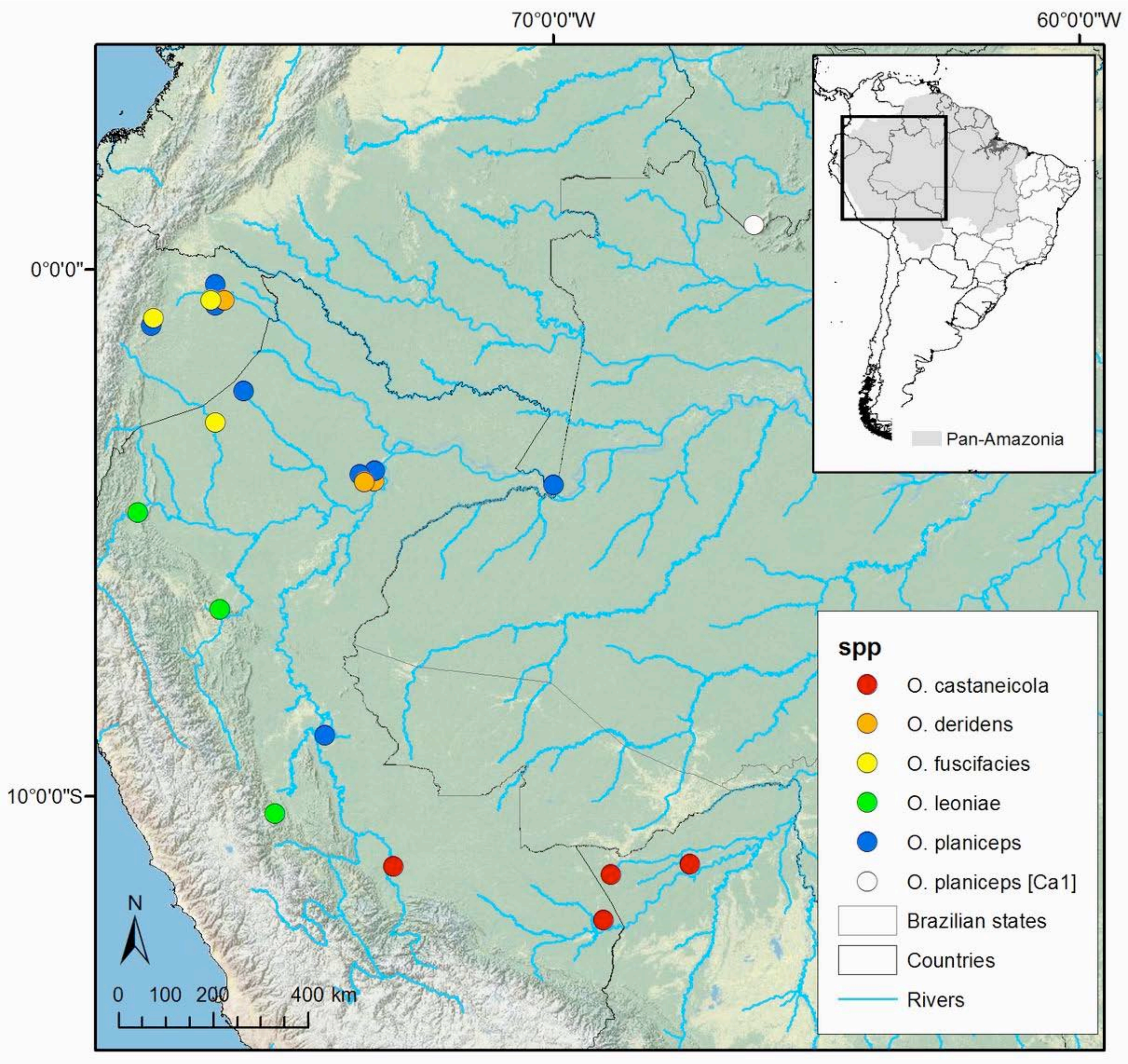
Appendix S8.3b. Map of localities of sampled exemplars of the *Osteocephalus buckleyi* Species Group (part).



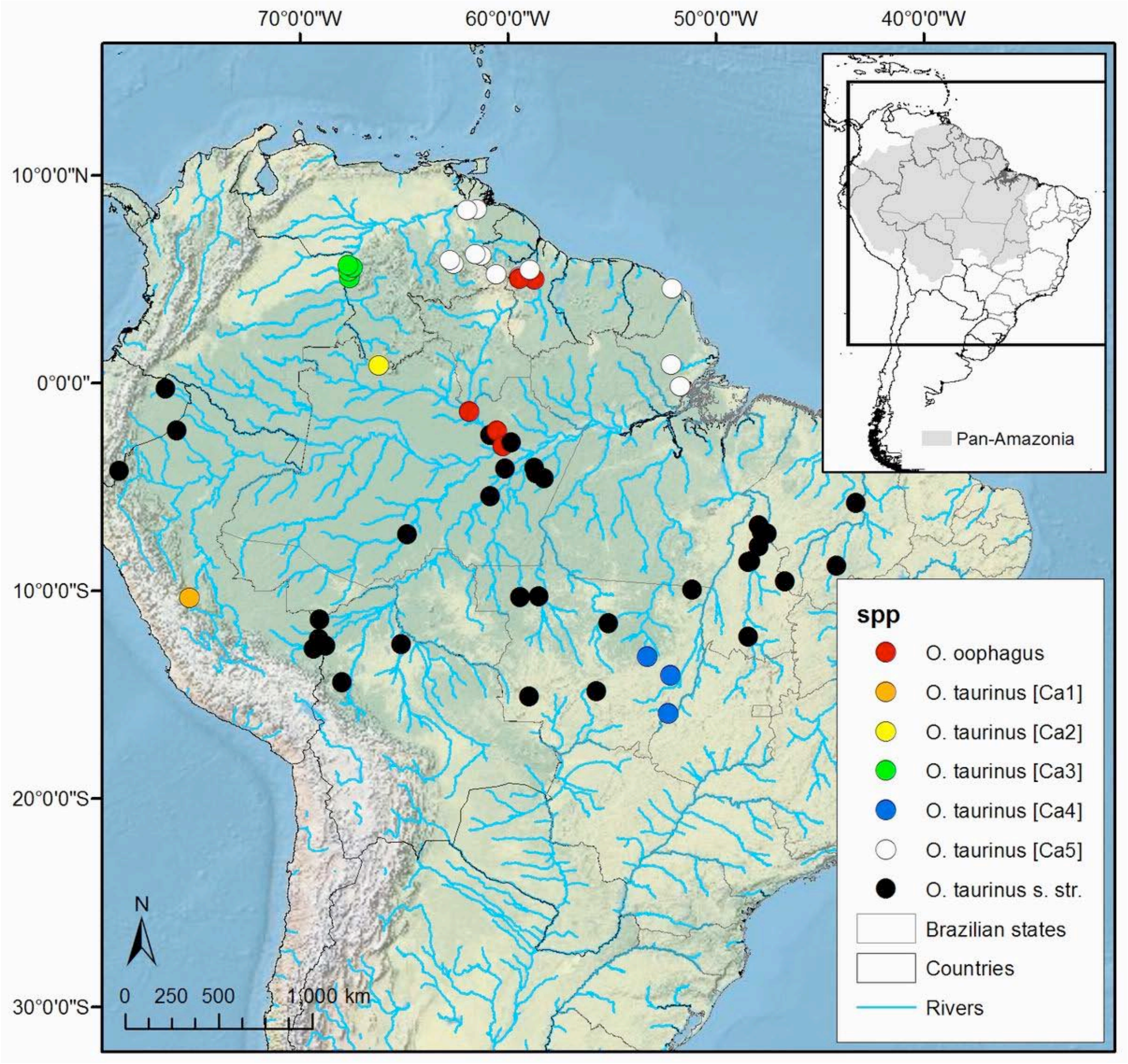
Appendix S8.4. Map of localities of sampled exemplars of the *Osteocephalus leprieurii* Species Group.



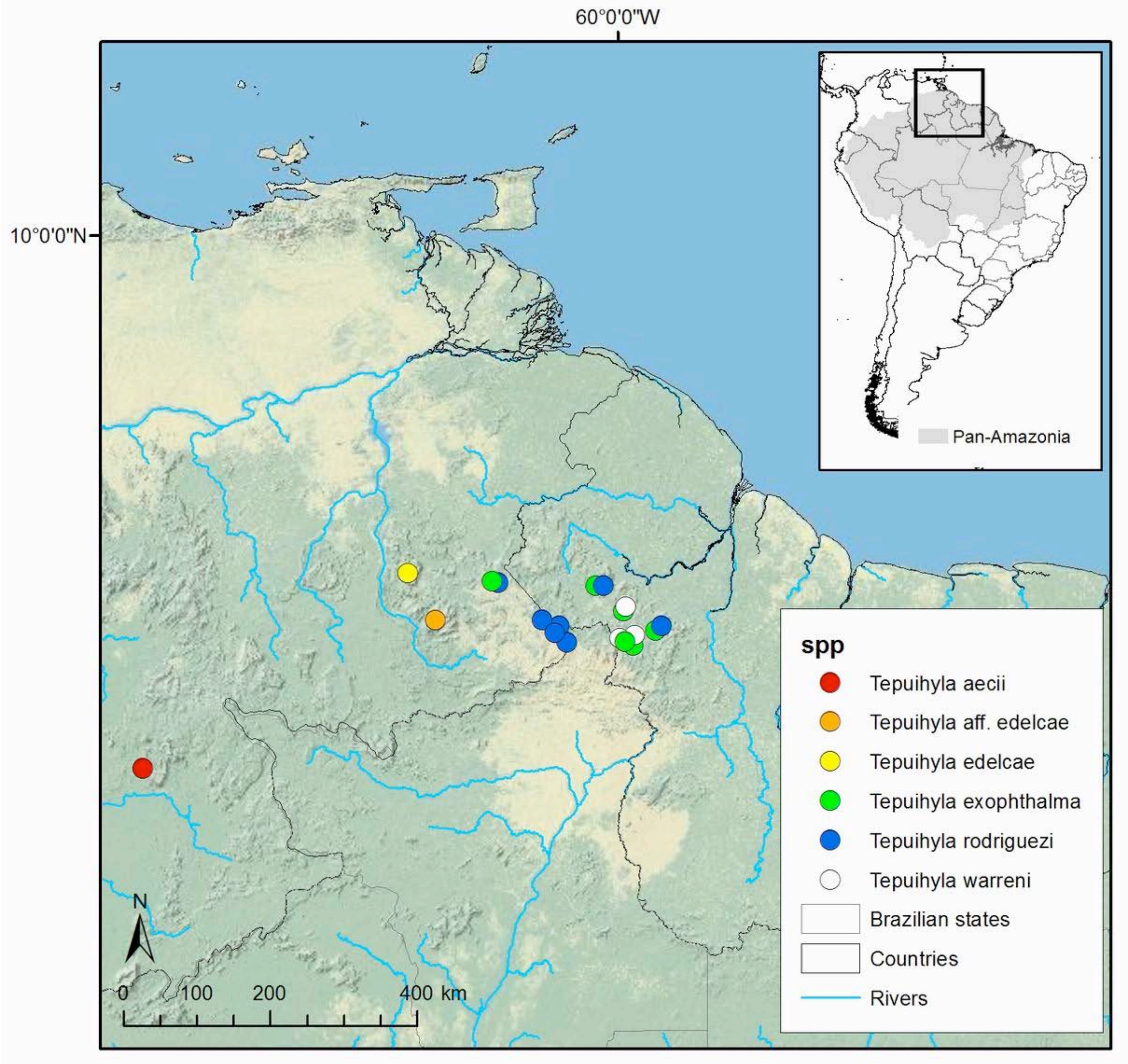
Appendix S8.5. Map of localities of sampled exemplars of the *Osteocephalus planiceps* Species Group.



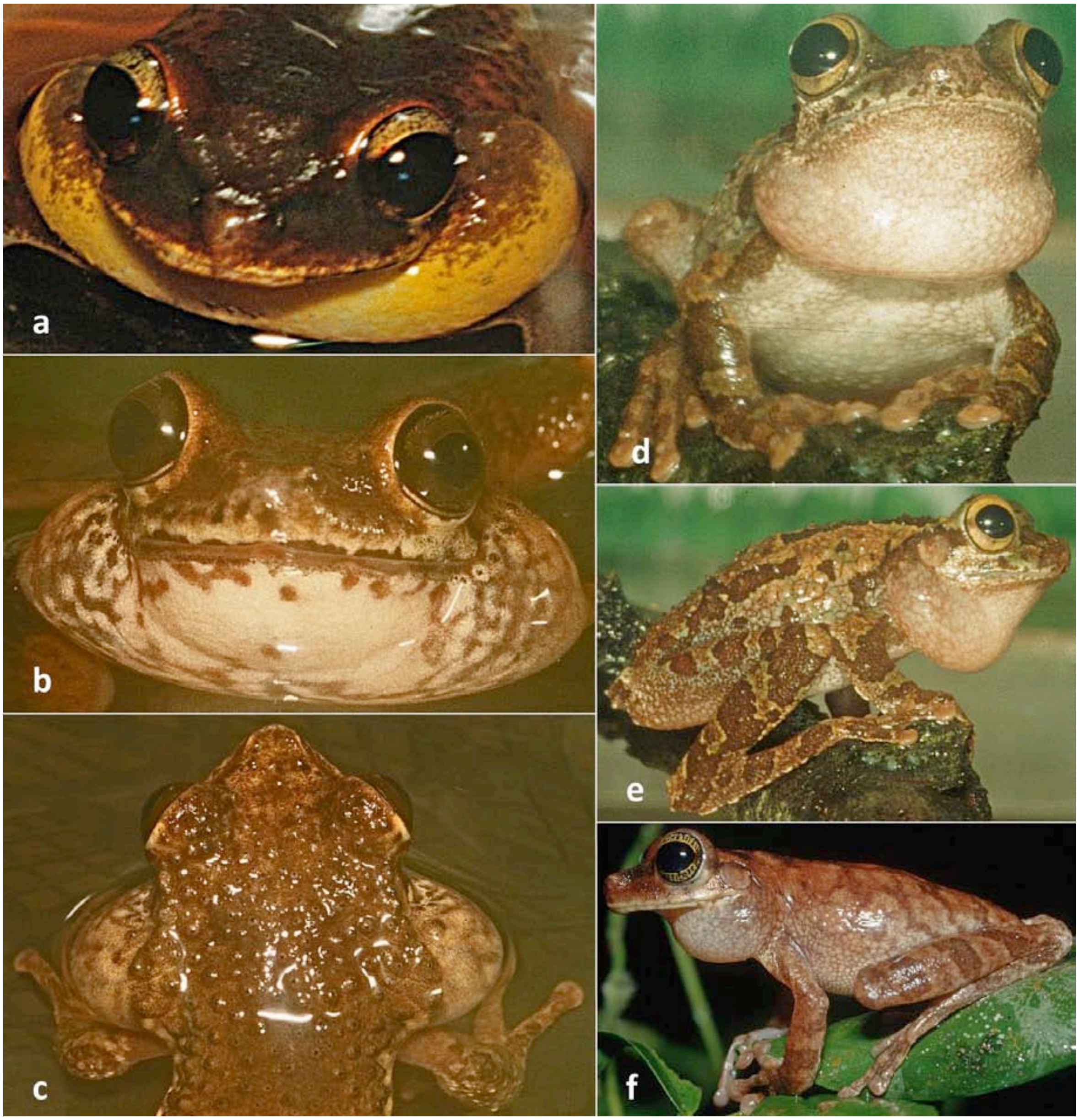
<u>Appendix S8.6.</u> Map of localities of sampled exemplars of the *Osteocephalus taurinus* Species Group.



Appendix S8.7. Map of localities of sampled exemplars of *Tepuihyla* on the Guiana Shield.



<u>Appendix S9.</u> 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).



<u>Appendix S10.</u> 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.

<u>Appendix S11.</u>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.