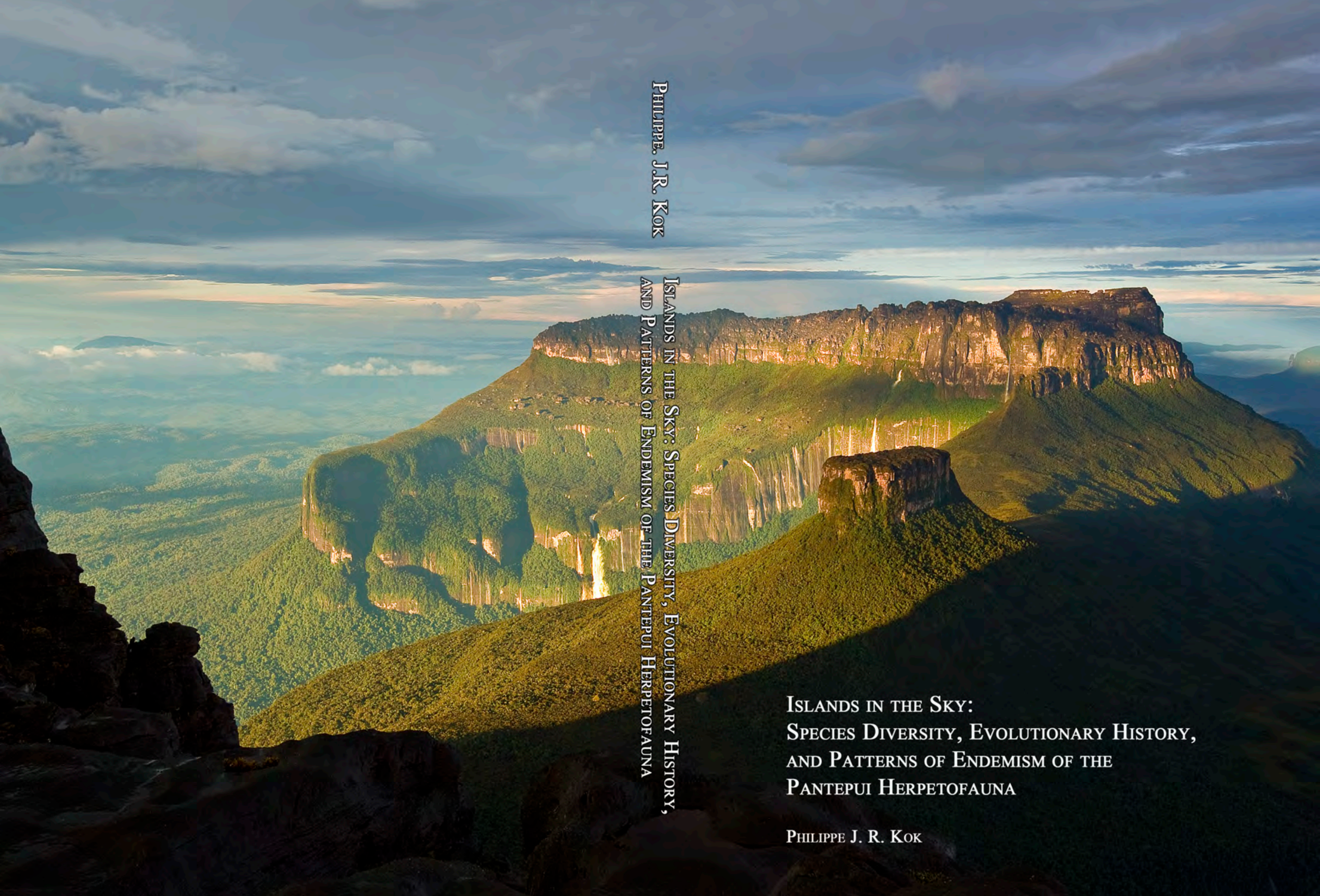

Philippe. J.R. Kok

Islands in the Sky: Species Diversity, Evolutionary History, and Patterns of Endemism of the Pantepui Herpetofauna

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OF THE PANTEPUI HERPETOFAUNA

PHILIPPE J. R. KOK

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Thesis Leiden University

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ISLANDS IN THE SKY: SPECIES DIVERSITY, EVOLUTIONARY HISTORY, AND PATTERNS OF ENDEMISM OF THE PANTEPUI HERPETOFAUNA

Proefschrift
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volgens besluit van het College voor Promoties
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door

Philippe Jacques Robert Kok

geboren te Watsa, Democratische Republiek Congo, in 1970

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Prof. Dr. M. Schilthuizen (Universiteit Leiden)

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Tepuihyla sp emerging from a small *Brocchinia tatei*, Abakapá-tepui, Venezuela. Photo by the author.

“I may not have gone where I intended to go, but I think I have ended up
where I intended to be”
D. Adams

“A scientific man ought to have no wishes, no affections, - a mere heart of stone”
C. Darwin

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Brussels, October 2012

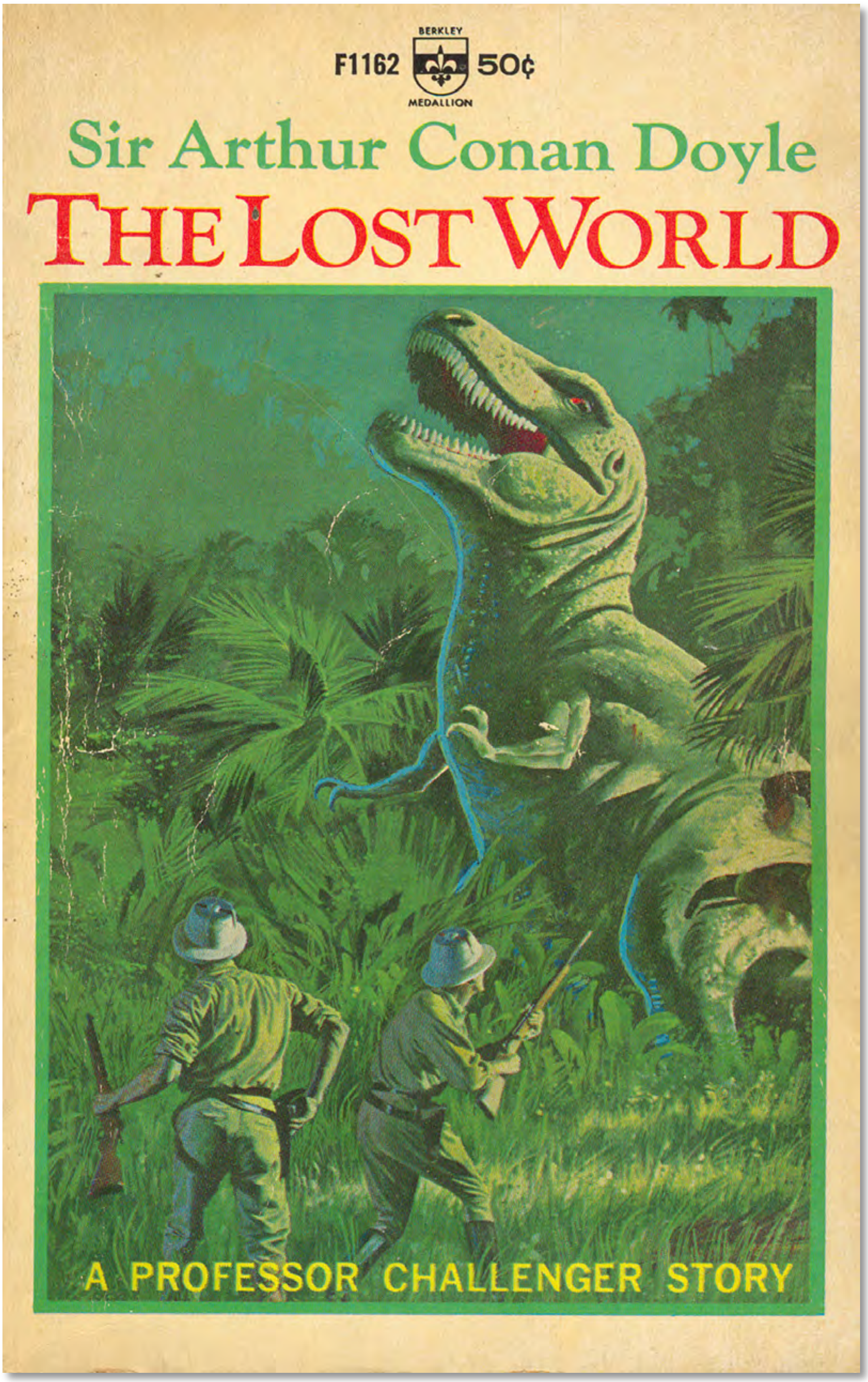
NEDERLANDSE INLEIDING EN SAMENVATTING

Sinds Darwins evolutietheorie zijn het ontstaan van bestaande soorten en de evolutionaire oorzaken daarvoor in de Neotropen van centraal belang gebleven. Aangezien historische gebeurtenissen zoals verspreiding en vicariantie, genetische sporen (“footprints”) op intraspecifiek niveau achterlaten, zijn moleculaire fylogenieën het ideale werktuig om de evolutionaire verwantschappen van organismen, en hoe en wanneer ze divergeerden, te reconstrueren en te begrijpen. Moleculaire fylogeniereconstructies en schattingen van de duur van divergentie geanalyseerd in de context van geologische gegevens kunnen helpen om sommige paleogeografische gebeurtenissen die anders moeilijk of onmogelijk gedateerd kunnen worden beter te begrijpen.

Zoals beschreven in Hoofdstuk 1 herbergt het noordwestelijke deel van Zuid-Amerika een gebied van spectaculaire en mysterieuze landschappen, Pantepui geheten. Traditioneel wordt Pantepui gezien als één van de belangrijkste centra van endemisme in de Neotropen, en het is beroemd om zijn typische tafelbergen met honderden meters verticale wanden en platte top, die boven de savannes en tropisch regenwoud uittorenen, voornamelijk in het Guayana gebied van zuidelijk Venezuela, in west-centraal Guyana en in het aangrenzende deel van noordelijk Brazilië. Deze tafelbergen, tepuis genaamd, hebben verticale wanden die tot aan 1000 m hoog kunnen zijn, waardoor zij in het horizontale vlak van elkaar gescheiden zijn, maar ook verticaal van hun directe omgeving. Een consequentie van deze isolatie is dat veel tepuis minder bezocht zijn dan de maan.

Tepuis zijn door erosie ontstane overblijfselen van Proterozoische (> 1,5 miljard jaar oud) zandsteensedimenten die gedurende 2 tot 6 miljoen jaar werden afgezet, ofwel in grote binnenmeren, ofwel in ondiepe zeeën. Deze enorme landmassa bleef begraven gedurende miljoenen jaren en werd vervolgens sporadisch, epirogenetisch opgeheven voordat ze door tektonische krachten, wind en verwering werd geërodeerd, waardoor geleidelijk het hedendaagse sterk ingesneden tepuilandschap ontstond. Alhoewel de Precambrische geschiedenis van het gebied en de meeste erosieprocessen die tot het ontstaan van de tepuis leidden geen onderwerp zijn van verschil in opvatting, zijn de leeftijd, snelheid en grootte van de opheffing(en), evenals de snelheid van erosie van de sedimentlagen onderwerp van controverse en op zijn minst speculatief.

Een eeuw geleden publiceerde Sir Arthur Conan Doyle, sterk geïnspireerd door de tepui geomorfologie, één van zijn bekendste boeken: “The Lost World”, dat de bron vormde voor veel science fiction films. In Doyle’s boek komen er op een tepuitop dinosauriërs voor en een vergeten beschaving die daar miljoenen jaren geïsoleerd geleefd had (Fig. 1). Net zoals Conan Doyle hebben een aantal wetenschappers geloofd dat de Neotropische tepuis voornamelijk oude endemische vormen herbergden, sommige wellicht gelijktijdig met de dinosauriërs en stammende van voor de scheiding van Afrika en Zuid-Amerika. Echter, het onderwerp van Doyle’s boek blijft een mysterie tot op de dag van vandaag: hoe en wanneer diversificeerde de fauna van de tepuitoppen zich?



Figuur **1.** Omslag van het boek “The Lost World” van Sir Arthur Conan Doyle, oorspronkelijk gepubliceerd in 1912. Het is fascinerend te zien hoe Doyle’s boek hypotheses betreffende de biogeografie van Pantepui heeft beïnvloed. Eén van de hypotheses is er zelfs naar genoemd: The Lost World Hypothesis.

Vanwege zijn ouderdom en sterk gefragmenteerde topografie werd aangenomen dat Pantepui een ideaal gebied zou zijn voor soortvorming, en tepuis zijn beschouwd als mogelijke vasteland tegenhangers van oceanische eilanden. Tepuis worden vaak “eilanden in de lucht” genoemd en hun toppen lijken inderdaad ideale plekken om relictsoorten te herbergen, geïsoleerd van de wereld gedurende miljoenen jaren. Echter, onze kennis betreffende het ontstaan en de diversificatie van de Pantepui biota is op zijn minst fragmentarisch, evenals de tepui fysiografie zelf. Dit heeft sommige auteurs ertoe gebracht het ontstaan van lokale biodiversiteit en endemisme te beschouwen als een nog niet opgelost vraagstuk.

Er zijn pogingen gedaan om dit mysterie op te lossen, maar onderzoek gebaseerd op moleculair fylogenetisch bewijs is buitengewoon zeldzaam en steunt op erg beperkte collecties. Alle hedendaagse hypotheses die het ontstaan en de diversificatie van de Pantepui biota proberen te verklaren, werden al geruime tijd geleden geformuleerd, en zijn grotendeels gebaseerd op “mobiele” organismen die zich door de lucht kunnen verspreiden (bv. vogels, vliegende insecten, planten). Vanwege hun verondersteld betere verspreidingsmogelijkheden, zijn deze organismen misschien niet de beste modellen om het raadsel van Pantepui op te lossen. Kleine terrestrische vertebraten met beperkte verticale verspreiding, zoals amfibieën en reptielen, zouden (tenzij anders kan worden aangetoond) veel betrouwbaarder modellen zijn voor fylogeografische studies in zo’n sterk ingesneden landschap. Amfibieën en reptielen zijn de opvallendste vertebraten op de tepuitoppen en 68,5% van de soorten amfibieën en reptielen op tepuis zijn gerapporteerd als voorkomend op slechts één tepui, zodoende voeding gevend aan de opvatting dat zij ideale modellen zijn om de speciatieprocessen in Pantepui op te lossen.

De belangrijkste doelen van dit werk zijn zodoende: (1) beter begrip van de soortenrijkdom, de evolutionaire geschiedenis, de dynamiek van biotische uitwisseling tussen toppen van tepuis, en de patronen van endemisme van de Pantepui fauna, gebruikmakend van morfologische analyses en de moleculaire fylogenie van zes herpetofauna taxa; (2) nieuwe inzichten verschaffen in de geomorfologische evolutie van de tepuis, in het licht van de diversificatie van soorten amfibieën en reptielen afgeleid van moleculair fylogenie reconstructies en schattingen van de diversificatietijd.

De isolatie van de tepuis en de daarmee gepaard gaande technische moeilijkheden (en daaraan gecorreleerde financiële aspecten) om veldwerk in het gebied te verrichten, hebben de verzameling van exemplaren en weefselmonsters voor gedetailleerde en diepgaande fylogenetische analyses van grote datasets ernstig belemmerd. Het meeste veldwerk in het gebied werd verricht voordat er standaard weefselmonsters werden verzameld. De taak was daarom moeilijk en uitdagend omdat de studie bijna met niets begon.

De afgelopen jaren slaagden Ross MacCulloch, Bruce Means en ik erin om in totaal 21 tepuitoppen/massieven en vele hoogland- en laaglandgebieden te bezoeken in het oostelijke Pantepui gebied en andere gebieden in Guiana (van het hoogland van de Gran Sabana in Venezuela tot het laagland van Frans Guiana). We verzamelden daar exemplaren en weefselmonsters van een aanzienlijk aantal tepuitaxa van bijna alle op de tepuitoppen vertegenwoordigde families. Dit veldwerk leidde tot de ontdekking van een nieuw hagedissengenus en verschillende nieuwe soorten amfibieën en reptielen, waarvan er verschillende in de taxonomische hoofdstukken van dit proefschrift beschreven worden.

In Hoofdstuk 2 wordt de hagedis *Arthrosaura hoogmoedi* (Gymnophthalmidae) beschreven en worden de soortengroepen van het genus *Arthrosaura*, wijd verspreid in Amazonisch Zuid-Amerika, behandeld op basis van morfologische kenmerken. Het hoofdstuk behandelt ook het zeldzame voorkomen van een ondoorzichtig, geheel gepigmenteerd onderste ooglid in Gymnophthalmidae.

In Hoofdstuk 3 wordt *Pantepuisaurus rodriguesi*, een nieuw genus en een nieuwe soort gymnophthalmide hagedis beschreven. Verwantschappen met twee andere gymnophthalmide genera die kennelijk ook tot Pantepui beperkt zijn (*Adercosaurus* Myers & Donnelly, 2001 en *Kaieteurosaurus* Kok, 2005) worden besproken, evenals de noodzaak om dit nieuwe genus op te richten voor deze nieuwe soort, om taxonomische verwarring te voorkomen.

In Hoofdstuk 4 wordt een nieuwe soort pad, *Oreophrynella* (Bufonidae) beschreven en het presenteert nieuwe inzichten over de verspreiding van het genus en over de verwantschappen tussen de soorten (allemaal beperkt tot het Pantepui gebied), op basis van morfologische gegevens.

In Hoofdstuk 5 wordt de kikker *Anomaloglossus megacephalus* (Aromobatidae) van Maringma-tepui, Guyana, beschreven. Deze soort werd tot dan verward met *A. tepuyensis*, een taxon beschreven van Auyantepui in Venezuela.

In Hoofdstuk 6 wordt de beschrijving van de kikker *Pristimantis aureoventris* (Strabomantidae) gepresenteerd. Behalve de morfologische beschrijving bevat het hoofdstuk de beschrijving van de paringsroep van de nieuwe soort en aanvullende morfologische gegevens van de slecht bekende *P. yuruaniensis* (inclusief de paringsroep), evenals nieuwe inzichten betreffende de verspreiding van dit genus in Pantepui.

In Hoofdstuk 7 wordt de gymnophthalmide hagedis *Anadia mcdiarmidi* van de top van Auyan-tepui in Venezuela beschreven. *Anadia* is één van de weinige genera die vertegenwoordigd zijn in zowel de Andes als in Pantepui en is daarom van buitengewoon belang in Pantepui studies omdat het licht kan werpen op verspreidingsmechanismes.

Veldwerk verschafte ook een beter begrip van de taxonomie en de verspreidingspatronen van slecht bekende tepuisoorten, en de resultaten van dit werk worden gepresenteerd in Hoofdstukken 8 en 9. In deze hoofdstukken worden soorten herbeschreven die voorheen slechts bekend waren van de oorspronkelijke beschrijving, en beschouwd werden als zijnde beperkt tot de bovenste hellingen van Mount Roraima. Behalve de herbeschrijving van de soorten bevatten de hoofdstukken beschrijvingen van kikkervissen en paringsroepen. Ook wordt het bekende verspreidingsgebied van de kikkers *Anomaloglossus praderioi* en *A. roraima* aanzienlijk vergroot.

Eén van de belangrijkste resultaten verkregen tijdens dit werk, is de eerste uitgebreide verzameling van weefselmonsters van verschillende geïsoleerde tepuitoppen. Dankzij deze verzameling kon voor het eerst de overall timing en de mate van biotische uitwisseling tussen tepuitoppen en de omringende hooglanden worden bestudeerd. In Hoofdstuk 10 wordt beschreven hoe fylogenetische analyse van twee mitochondriale genfragmenten die verschillend snel evolueerden (het relatief langzame 16S rDNA en het snel evoluerende ND1 mt1) onthulde dat er onverwacht lage genetische divergentie (zo laag als nul) was tussen soorten/populaties van vijf van de zes bestudeerde groepen die op verschillende tepuitoppen voorkwamen. Ook tussen sommige soorten/populaties van tepuitoppen en hoogland populaties die als verschillende soorten waren beschreven, bleek de genetische variatie laag te zijn. De resultaten suggereren dat er tot kort geleden (Laat-Pleistoceen-Holoceen) uitgebreide uitwisseling was van fauna tussen momenteel geïsoleerde tepuitoppen, evenals tussen tepuitoppen en de omringende hooglanden. Deze uitwisseling had ook invloed op taxa die leven in sommige van de meest tepuispecifieke habitats en op de meest ontoegankelijke toppen. Indien de tepuis zo oud zijn als vaak gesteld, dan kan de jonge leeftijd van de bestaande tepuitop fauna alleen verklaard worden door actieve verspreiding tussen toppen via de tussenliggende hooglanden, gevolgd door uitsterven (bijvoorbeeld tijdens de ijstijden) in die hooglanden, of door passieve verspreiding (bijvoorbeeld door vogels of stormen). De zeer specifieke ecologische niche voorkeur van sommige taxa die beperkt zijn tot tepuitoppen, gekoppeld aan de uitzonderlijke topografie van de tepuis hebben actieve verspreiding waarschijnlijk beperkt. Er moet echter opgemerkt worden dat tijdschattingen voor de isolatie van individuele tepuis ruwweg variëren van het Krijt tot het Quartair, en de jongste schattingen, alhoewel op grote schaal genegeerd in biologische studies, zouden compatibel zijn met de lage genetische diversiteit en daarom vicariantie als een mogelijk mechanisme voor soortvorming open laten. Onafhankelijk van het mechanisme toont dit hoofdstuk dat, zelfs in kleine vertebraten die beperkt zijn tot alleen op de tepuitoppen aanwezige habitat, er tot recent gene flow was, waardoor voorkomen op een enkele tepui waarschijnlijk eerder een uitzondering dan een regel is.

In Hoofdstuk 11 wordt een algehele conclusie gepresenteerd, gekoppeld aan een kritisch overzicht van de hypotheses die trachten de oorsprong en de diversificatie van de Pantepui biota te verklaren, gezien in het licht van moleculaire fylogeniereconstructie en schattingen van de divergentietijd. Er zijn verschillende theorieën gepresenteerd om de oorsprong en diversificatie van de Pantepui biota te verklaren, het merendeel gebaseerd op vogels, vervolgens uitgebreid tot planten en andere niet-vliegende organismen. De overheersende theorieën zijn in principe afgeleid van twee, vaak tegenstrijdige, mechanismes: organismen ontwikkelden zich *in situ* vanwege lange isolatie van tepuis (“oude” vicariantie), of taxa koloniseerden tepuitoppen gedurende glaciale-interglaciale perioden (“jonge” vicariantie). Dit laatste hoofdstuk probeert om een verklaring te geven voor het tijdsframe van geomorfologische evolutie van de tepuis en stelt daarbij een fylogenetisch gebaseerde hypothese voor diversificatie voor. Gegevens suggereren dat het ontstaan van Pantepui endemen geworteld is in het Paleogeen en dat de meeste herpetofaunistische diversiteitspatronen in Pantepui reeds ruim voor het Quartair waren uitgekristalliseerd. Fylogeniereconstructies gekoppeld aan schattingen van diversificatietijd suggereren dat soortdiversiteit aanzienlijk werd gereorganiseerd tijdens of kort na perioden van klimaatinstabiliteit die voorkwamen in de periode van het late Mioceen tot vandaag. De resultaten tonen voornamelijk dat: (1) herhaaldelijk non-exclusieve processen die vicariantie en verspreiding suggereren diversificatie in Pantepui bevorderden, (2) de veronderstelling dat tepuis al waren gevormd en geïsoleerd in het Krijt (70-90 miljoen jaar geleden) niet alleen slecht overeenkomt met de meeste geologische gegevens, maar ook niet overtuigend wordt gesteund door de fylogenetische data, en (3) een periode van versnelde opheffing en sterke fragmentatie zou kunnen hebben plaatsgevonden in het Eoceen/Oligoceen (25-45 miljoen jaar geleden), met een meer recente periode (laat Mioceen tot Holoceen) waarin complete isolatie van individuele tepuitoppen plaatsvond.

1

GENERAL INTRODUCTION AND SUMMARY

“Discovery consists of seeing what everybody has seen and thinking what nobody thought”

A. Szent-Gyorgyi

Yuruani-tepui photographed from the upper slope of Guadacapiapu-tepui, Venezuela. Photo by the author.

GENERAL INTRODUCTION AND SUMMARY

The tepuis

Few places on earth haunt the imagination more than the tepui region and its spectacular landscapes resting in the northeast corner of South America (Yates 2007).

The word *tepui* is derived from the local Pemón Amerindian idiom "*tepu'u*", which may translate to "sprouting rock" (McPherson 2008) or simply to "mountain" (Steyermark 1986). The meaning of *tepu'u* was occasionally embellished as "the House of Gods" without any apparent linguistic context, maybe to please the human need of dramatization.

The term tepui is now widely accepted in science and is used to characterize the impressive vertical-sided table mountains made of Proterozoic sandstone that rise above the savannah and tropical forest, mainly in the Guayana region of southern Venezuela, in west-central Guyana, and in extreme northern Brazil (states of Amazonas and Roraima).

Tepuis' vertical escarpments can be 1,000 m high, which makes most of these mountains isolated horizontally from one another, but also vertically from their surroundings (Figs. 1, 2). In addition to physiographic isolation, modern edaphic, climatic and ecological factors contribute to further isolate most tepui tops from the surrounding savannah and tropical forest. Indeed, tepui summits face harsh climatic condition (strong wind, extreme temperature variation), high ultraviolet radiation, and their characteristic vegetation grows on highly acidic, oligotrophic soils (Fig. 3).

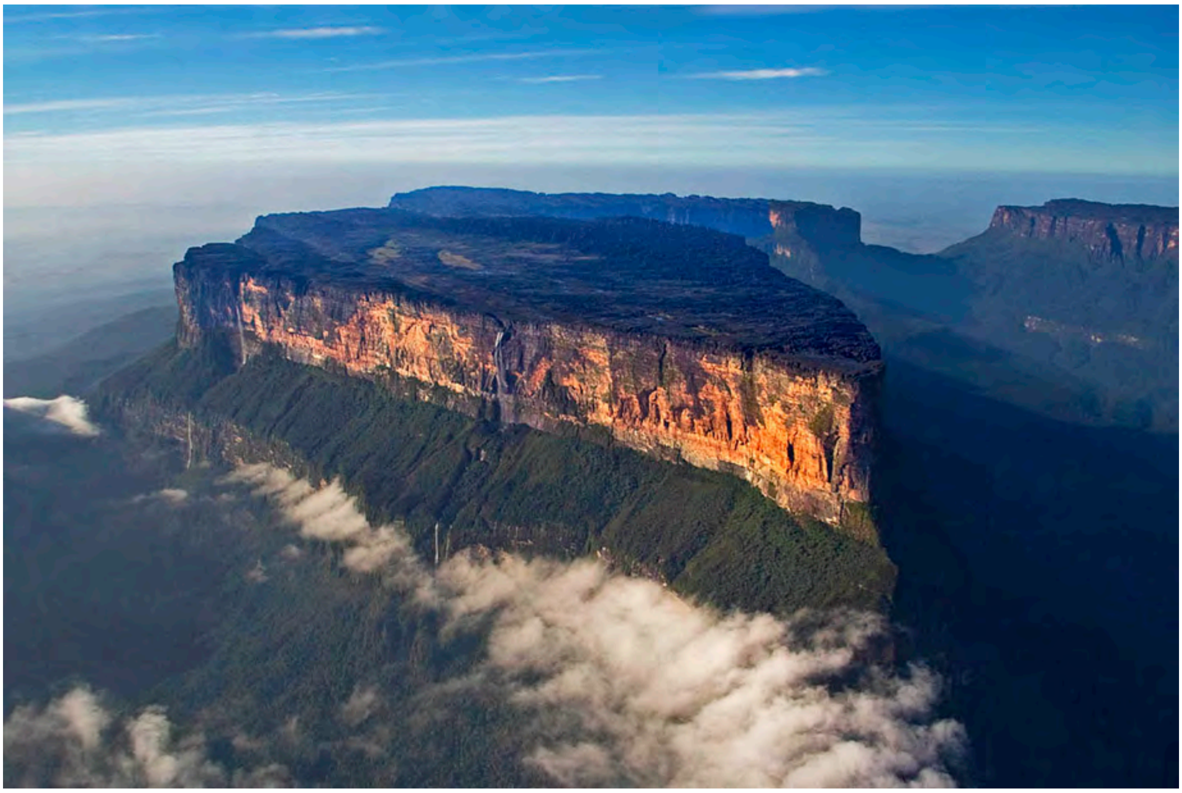


Figure **1.** Mount Roraima (Venezuela-Guyana-Brazil border, *ca.* 2,800 m elevation), an emblematic tepui showing the typical vertical sandstone escarpments and basal slopes. Photo courtesy of C. Brewer-Carías.

Figure **2.** Western cliffs of Abakapá-tepui, Venezuela. The summit of the tepui (*ca.* 2,300 m elevation) is not visible, lying above the clouds. Photo by the author.

Pantepui, the tepuis, and their geomorphological evolution

The remarkable biogeographic region where the tepuis—and the faunistically related granitic mountains—occur was named *Pantepui* by Mayr & Phelps (1967) in their seminal study on the origin of the bird fauna of the south Venezuelan Highlands. The occurrence of many monophyletic lineages (in plants and animals) coupled with the common geological history of the region and its spatio-temporal continuity justify considering Pantepui as a biogeographic unit. Pantepui is traditionally seen as one of the foremost centres of endemism in the Neotropics (Berry *et al.* 1995, Davis *et al.* 1997). Mayr & Phelps (1967) clearly restricted the term *Pantepui* to high-elevation, meso- or microthermic life zones, but did not offer any precise definition (Huber 1995). Pantepui is thus often limited to the area including all upper slopes and summits of the Guiana Shield Highlands, covering a total surface of *ca.* 5,000 km^2 with an altitudinal range of 1500–3014 m above sea level (Rull & Nogué 2007). It should be noted that the lower elevation of Pantepui—*i.e.* 1500 m—as suggested by Mayr & Phelps (1967) and adopted by several other authors (*e.g.* Rull 2005, Rull & Nogué 2007) is arbitrary and rarely reflects the lower limit of the tepui/highland life zone. As pointed out by McDiarmid & Donnelly (2005), this altitudinal range is nothing more than a workable limit. Consequently, the Pantepui bioregion has sometimes been considered in a less restrictive way and extended to include the intervening lowlands (roughly 200–500 m asl) and uplands (roughly between 500–1500 m asl) (*e.g.* Steyermark 1979, 1982, Kok 2010), which probably better reflects the biogeography and the past and current biotic interactions in the area.

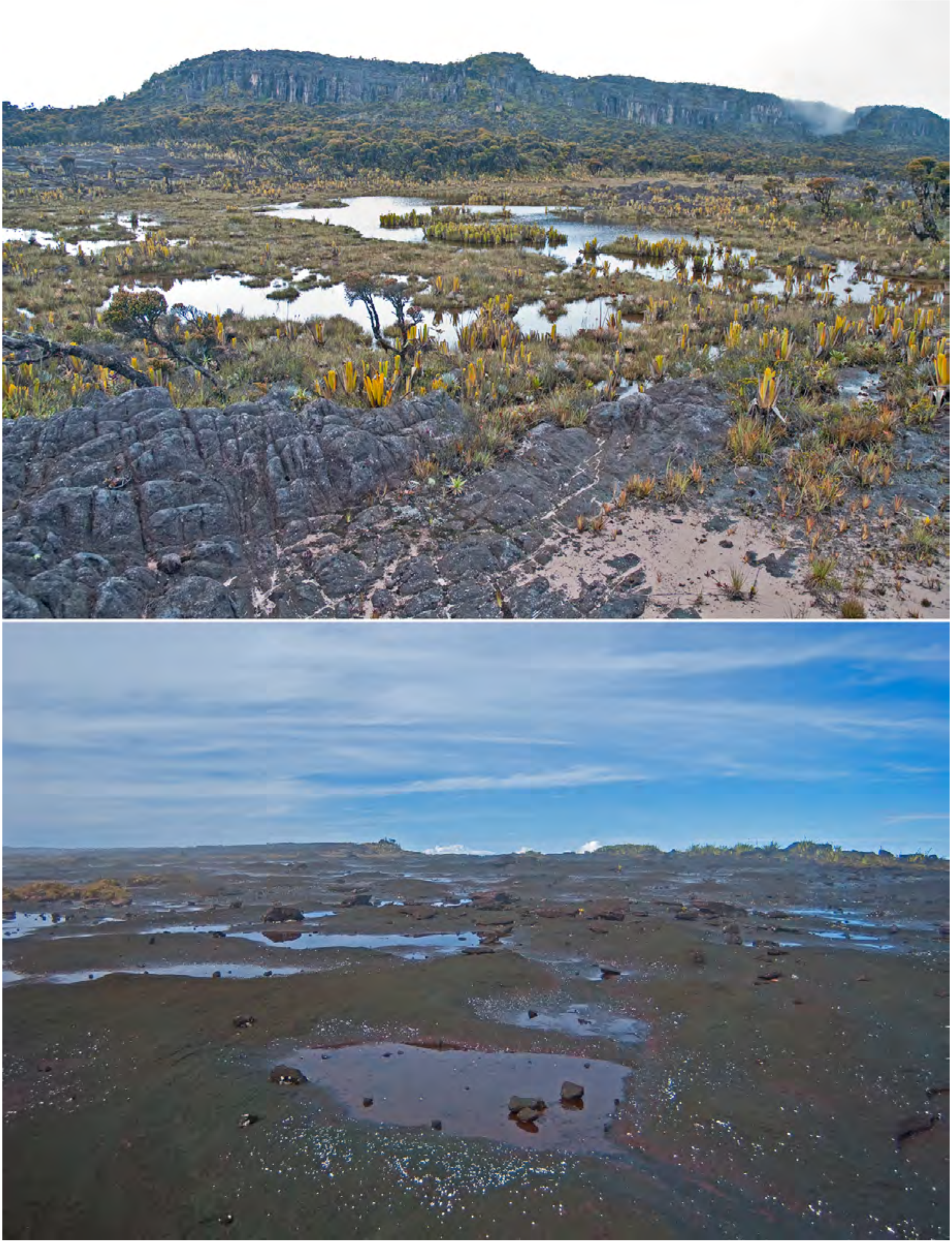


Figure **3.** Top: The summit of Aprada-tepui at *ca*. 2,540 m elevation, Venezuela. The typical tepui vegetation grows on soils mostly devoid of the nutrients essential for plant and animal life, making the summit environment drastically different from the surrounding forested highlands and uplands. Bottom: The small summit of Tramen-tepui at *ca*. 2,400 m elevation, Venezuela. The rocky summit harbours an even more impoverished flora, but still supports a few highly specialized vertebrates like the bufonid *Oreophrynella vasquezi*. Photos by the author (top) and courtesy of D. B. Means (bottom).

Pantepui *sensu lato* can be characterized by five main landscape types/life zones (Fig. 4), defined here as follows:

1. The **Pantepui lowlands** are the surface between *ca.* 200–400 m elevation;
2. The **Pantepui uplands** are the surface below tepui slopes, above *ca.* 400–500 m elevation, usually below 1,200 m elevation;
3. The **Tepui slopes** are the mostly inclined portion of ground separating tepui summits/cliffs from the uplands or the lowlands. In many cases the slopes are divided in upper and lower slopes by additional escarpments. Sometimes (*e.g.* Mount Ayanganna in Guyana) rather extensive intermediate planation surfaces of differential erosion occur between the escarpments and, when viewed in profile, these tepuis appear as a series of steps;
4. The **Tepui cliffs** are the vertical escarpments separating tepui summits from upper slopes, and upper slopes from lower slopes;
5. The **Tepui summits**, which are relatively flat, correspond to areas that (1) are higher than *ca.* 1,200 m above sea level *and* isolated from tepui slopes by vertical walls or (2) have an elevation of more than *ca.* 1,900 m, which usually favours different climate and vegetation than that from the slopes, even if there is no substantial demarcation between slopes and summit. Tepui summits as understood here are thus isolated topographically or ecologically, usually both. In this view, poorly differentiated summits of low elevation tepuis are similar to slopes. Defining tepui summits is an exercise that implies some arbitrariness because not all tepuis have exactly the same elevation and geomorphology (see Fig. 4).

Mayr & Phelps (1967) initially divided Pantepui into eastern and western biogeographic subregions separated by the Río Caroní (Braun *et al*. 2005). More recently, McDiarmid & Donnelly (2005), slightly modifying the proposition of Huber (1995), recognized four districts (western, central, eastern, and southern), each district being divided into several subdistricts. This new division was primarily based on floristic composition and major drainages.

Besides being divided into biogeographical subregions, Pantepui should also be divided into two altitudinal zones: the lower Pantepui (*ca.* 200-1,200 m elevation = lowlands/uplands of the Pantepui region) and the upper Pantepui (above *ca.* 1200 m elevation = tepui slopes/tepui summits). Although historically the lower and the upper Pantepui zones most probably formed a single more or less continuous area (see below), today Pantepui is found to be both biologically and geologically composite, and only the upper Pantepui zone should probably be seen as a “natural” biogeographic unit (*sensu* Michaux 2010).

Pantepui *sensu stricto* (*i.e.* upper Pantepui) is reported as one of the last three Old, Climatically Buffered, Infertile Landscapes (OCBIL) still prominent on earth (the two others being the Southwest Australian Floristic Region and the Greater Cape Floristic Region in South Africa). These ancient weathered infertile landscapes may have been more common globally prior Pleistocene glaciations, but are now extremely rare (Hopper 2009). OCBIL theory notably predicts that OCBIL organisms should exhibit reduced dispersability, increased local endemism, and common rarity (Hopper 2009).

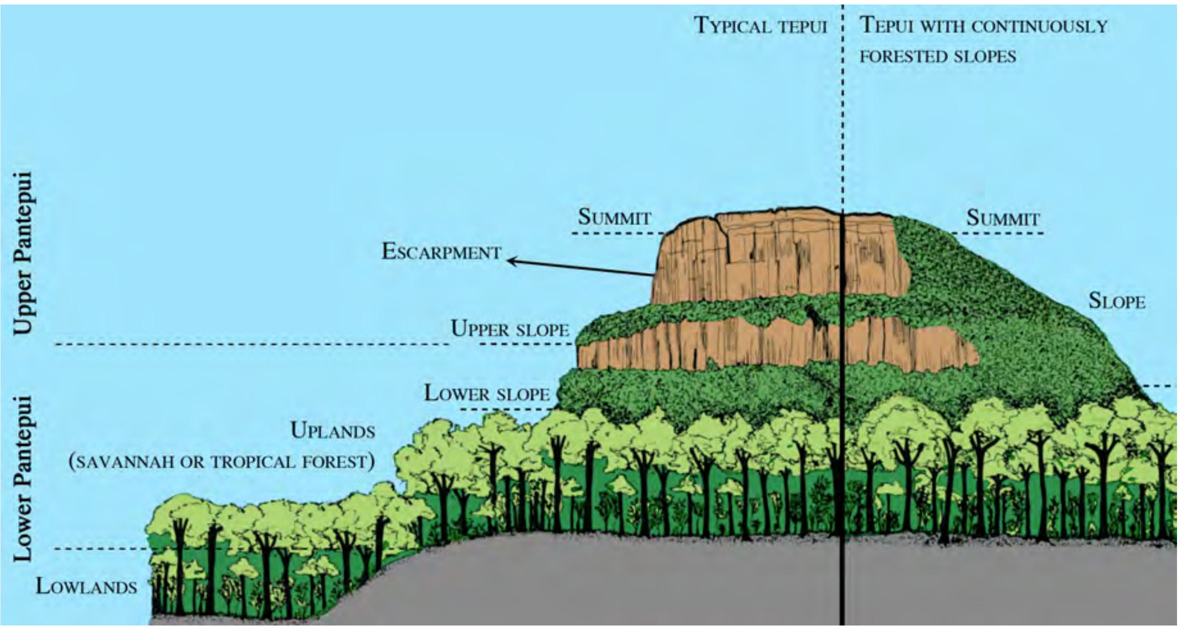


Figure **4.** Schematic illustration of two different tepui geomorphologies, and the main landscape types observed in the Pantepui region. A typical tepui (left) with well-marked vertical walls (escarpments) isolating its summit from the slopes, and a tepui lacking physiographic isolation (right). Modified from Steyermark (1986).

The Pantepui region lies in the northwestern part of the Guiana Shield and has an old and complex geological history. The igneous-metamorphic basement of the Guiana Shield—itself located in the northern part of the Amazon Craton—developed during different orogenetic phases that occurred during Archean and Proterozoic times when only the simplest forms of life existed. Four orogenetic phases are currently recognized, extending from *ca.* 3.6 to *ca.* 0.8 billion years ago (Huber 1995). These orogenetic phases resulted in the formation of several geologic provinces that have different ages and structural patterns.

During two to six hundred million years, parts of the resulting granitic nuclei were subsequently slowly overlain by multiple horizontal layers of sediments likely coming from the erosion of other upland landmasses located to the east and northeast of the western section of the ancient supercontinent of Gondwana (Huber 1995). This irregular process of sedimentation probably mainly took place in either large inner lakes, or in shallow seas and lagoons, as suggested by the frequent occurrence of cross-bedded sections and ripple marks on freshly exposed rocks of tepui summits (Huber 1995, see also Fig. 5). These ripple marks could also have been formed by wind in a continental setting; they are preserved by diagenetic processes and are very resistant to erosion (H. Briceño pers. comm.).

These horizontally layered strata of unfossiliferous sedimentary rocks were compacted and cemented together by silica during many successive thermal events until they reached thicknesses of more than three kilometres and formed what is known today as a geological unit called the Roraima Supergroup (also called Roraima Group, or Roraima Formation). The Roraima Supergroup is composed of eight stratigraphic units, namely the Arai, Uiramutã, Verde, Pauré, Cuquenán, Quinô, Uaimapué and Matauí Formations (from bottom to top, thus from oldest to youngest) (Reid 1972, Reis & Yánez 2001).

Some geologists (*e.g.* Gansser 1974, Ghosh 1985) have postulated that sedimentation possibly occurred during different periods and in separate basins instead of a single extensive contemporaneous continental sedimentation (Steyermark 1986). These authors further suggested that the different basins would have filled in first in the east, and later to the west and south, which implies that the eastern sediments are the oldest (Huber 1995). Huber (1995) highlighted that if that hypothesis is correct, the older granitic rocks of the Maigualida and Parima Mountains would have likely divided these different sedimentation basins. More recently, a study by Santos *et al.* (2003) confirmed that the sediments were actually deposited in two separate, but overlapping large foreland basins (*ca.* 1,200,000 km^2 each). Santos *et al.* (2003) suggested that the Roraima Supergroup represents fill in a foreland basin (named the Roraima Basin, with a northwestern limit corresponding to what is now known as the Maigualida and Parima Mountain ranges) that was derived from the Trans-Amazon orogenic belt to the north and northeast, which is *ca.* 300 myr older than the fill that is in the post-Roraima "Neblina Basin" that was derived from both the Trans-Amazon and Tapajós-Parima orogenic belts to the east and northeast (Santos *et al.* 2003). Metamorphic rock types (principally diabases) that appear today as large dikes and sills have more recently intruded into the sandstone shield (Huber 1988). The region has apparently been devoid of volcanic activity since the Mesozoic (Hammond 2005).

Erosion due to tectonic forces and wind, and particularly weathering (mechanical, *e.g.* by thermal stress, and chemical, *e.g.* due to the solution of quartzite by acidic water or by the chemical action of lichens and mosses) of the epeirogenically uplifted hard Proterozoic sandstone (Roraima Supergroup) that covered most of the base rock gradually led to the present-day landscape of the tepuis.

Tepuis are thus erosional remnants of these very ancient sedimentary masses, and developed mainly within the uppermost unit, the Mataui Formation, which has not been directly dated (Santos *et al.* 2003) (see Figs. 6–8). According to Santos *et al.* (2003), the best age estimated for all but the uppermost Roraima Supergroup is 1873 ± 3 my, determined by U-Pb analyses of zircons from a green ash-fall tuff of the Uaimapué Formation.

Figure **5.** Left: Ancient "ripple marks" that according to some authors (*i.a.* Huber 1995) corroborate fluvial/marine deposition of sediments. Right: Bizarre erosional formations possibly showing recemented sandstone sediments. Photos by the author, both taken on the summit of Yuruani-tepui, *ca.* 2,370 m elevation, Venezuela.

Most authors agree on the Precambrian history of Pantepui and the erosional processes that have produced the present-day tepui landscape. However, the geological timing, rate, and magnitude of uplifting, as well as the rate of erosion of the sediments and general lowering of the planation surface are controversial and speculative (*i.a.* Schubert *et al.* 1986, Briceño & Schubert 1990, Yanes & Briceño 1993, Piccini 1995). Knowledge of the timing of the uplift of the Roraima Formation sandstones, therefore, is critical to understanding the evolution of the flora and fauna of the area (Kubitzki 1989a, b).

Even though a complete review of the Pantepui geomorphology is beyond the scope of this work, the following assumptions gathered from the quite extensive and sometimes contradictory literature on the topic (mostly geological, and sometimes in grey literature such as conference reports and abstracts) are worthwhile to be underlined since they will be compared with molecular phylogenies and estimates of divergence time in Chapter 11:

Gansser (1954) suggested that the tepuis are remnants of a single sedimentary plain that would have originally covered over 1,200,000 km^2 of the Guiana Shield area. This implies that outlying isolated mountains (the Quasi-Roraima Formation *sensu* Gibbs & Barron 1993, *e.g.* the Tafelberg in Suriname) were at some point connected to the main Roraima Group (Hammond 2005). Erosion must have been extensive to remove at least 500,000 km^3 of sediments, and Gansser (1954) stated that erosion "*must have been active mainly during the later part of the Tertiary, subsequent to the regionally accepted Mio-Pliocene diastrophism*".

Simpson (1979) assumed a first initial uplift of what is now the Guiana Shield in the Proterozoic, *ca.* 2 billion years ago. According to Simpson three additional periods of uplift would have occurred: one in the Mesozoic, one in the Paleocene, and the last one later in the Tertiary. However, Simpson (1979) did not specify the extent of these uplifts and at which geological time exactly the region was first exposed to the earth's surface.

Hoogmoed (1979), citing Haffer (1974), mentioned that the area has not been submerged since Paleozoic times and that it was slightly uplifted during the Upper Cretaceous (said to be concomitant with the first signs of the Amazon Basin becoming visible), then further uplifted in the Tertiary.

Schubert *et al.* (1986), Schubert & Briceño (1987) and Briceño & Schubert (1990) underlined the difficulty of evaluating the influence of tectonism *versus* climate as the main driver of the elevational differences between erosional surfaces. However they argue that large differences in elevation between some surfaces must have been promoted by tectonic uplift. Citing Urbani *et al.* (1977), the same authors highlighted that "*at least several thousands of meters of rock existed on top of the present-day highest level of the Roraima Group*". According to Briceño *et al.* (pers. comm.), about 3,000 m of sediments have been removed from the top of the present-day tepuis. This is inferred from shale intervals on these summits that are made of pirophyllite from the reaction of kaolinite and quartz at pressures corresponding to a 3,000 m column (H. Briceño, pers. comm.).

Kubitzki, in two very similar papers (Kubitzki 1989a, b), argued that the major upheaval of the Roraima Supergroup could be more recent than generally accepted, postulating that it lasted until the Neogene or even the Pleistocene.

Briceño & Schubert (1990) stated that the exact age of initiation of the erosonial surface that currently forms the summits of most of the tepuis of the Roraima Supergroup—which they named Auyán-tepui Surface—is likely to date back to the Mesozoic, in the Triassic-Jurassic period.

Schubert & Huber (1990) assumed that the uppermost portions of the planation surface have been reduced by general surface lowering after uplift, which would imply that we are not seeing the original planation surface and that we might have wrong estimates of the amount of the uplift (Ollier & Pain 2000). Ollier & Pain (2000) considered general surface lowering by weathering as unlikely and suggested erosion as its main cause. The same authors mentioned that the bedrock and marine strata underwent "*a simple vertical uplift in post-Cretaceous time*".

Obviously based on a paper by Onstott *et al.* (1989), Sidder & Mendoza (1991) claimed that the uplift of the Imataca Complex "*and other rocks in the northern Guayana Shield of Venezuela*" (presumably the Roraima Supergroup) occurred just prior to or during the separation of South America from Africa. The same statement was later reported in Edmond *et al*. (1995) and Givnish *et al.* (2000, who reported it as "*widely assumed*"), both citing Sidder & Mendoza (1991) as their source. However my reading of Onstott *et al.* (1989), which deals with the Imataca Complex on the northern margin of the Amazonian Craton, never clearly points to such an assertion, but rather indicates a post-Trans-Amazonian Orogeny uplift and cooling of the Imataca Complex (Onstott *et al.* 1989).

Huber (1988) and Huber & García (2011), among others, reported the area to be a relatively stable and continuously emerged landmass since at least the Paleozoic (*ca.* 250 mya), a fact that they report to be "*unique in the otherwise so eventful geologic history of the tropical South American continent*" (Huber & García 2011). That relative tectonic stability would have been responsible for an undisturbed and continuous process of biological diversification on tepui summits during the last 60–100 myr (Huber 1988, Huber & García 2011).

According to Givnish *et al.* (2000), the dissection of individual tepuis likely proceeded for at least the past 90 myr. Givnish and colleagues hypothesize a rate of tepui margin erosion of 1.2 km per million year, or a "recession rate of adjacent tepuis" due to erosion/dissolution of ca. 2.5 km per million years.

Santos *et al.* (2003) assumed that the Roraima Supergroup and its "successor Mesoproterozoic Basin" remained buried until the Upper Jurassic, when they were block uplifted during the Takutu event [better known as the Tacutu or Takutu Graben (Crawford *et al.* 1985, Gibbs & Barron 1993)].

Rabassa (2010), citing Briceño *et al.* (1990) stated that the tepuis and their karst-like features appear to be the result of deep chemical weathering during at least 70 myr.

Lujan & Armbruster (2011), citing Schaefer & do Vale (1997), indicated that the region was exposed to subaerial erosion since at least the middle Paleozoic and that nondeformational, epeirogenic uplift occurred sporadically almost since its formation, the present topography resulting from cycles of uplift and stasis during which erosion occurred (Lujan & Armbruster 2011).

Very recently, Salerno *et al.* (2012) assumed a Cretaceous age of tepui isolation (70–90 mya), and reported that "*the Guiana Shield plateau underwent several periods of erosion and plateau uplift and fragmentation starting around 300 Ma*" (thus well before the Gondwana break-up), but none of the three references given by these authors to support their statements (*i.e.* Briceño & Schubert 1990, Briceño *et al.* 1990, and Gibbs & Barron 1993) contain such assertions.

A definitive conclusion about the age of the present-day elevations and topography of the tepuis, which is intuitively important for the understanding of the biotic diversification in the area, remains thus difficult to reach. What is striking and deserves to be mentioned is that the hypothesized time of uplift(s) of the tepui region (*i.a.* “Tertiary”, “post-Cretaceous”) covers geological time from *ca.* 2.6 mya up to more than 150 mya. Uplift(s) could thus have occurred anytime between these extremes.

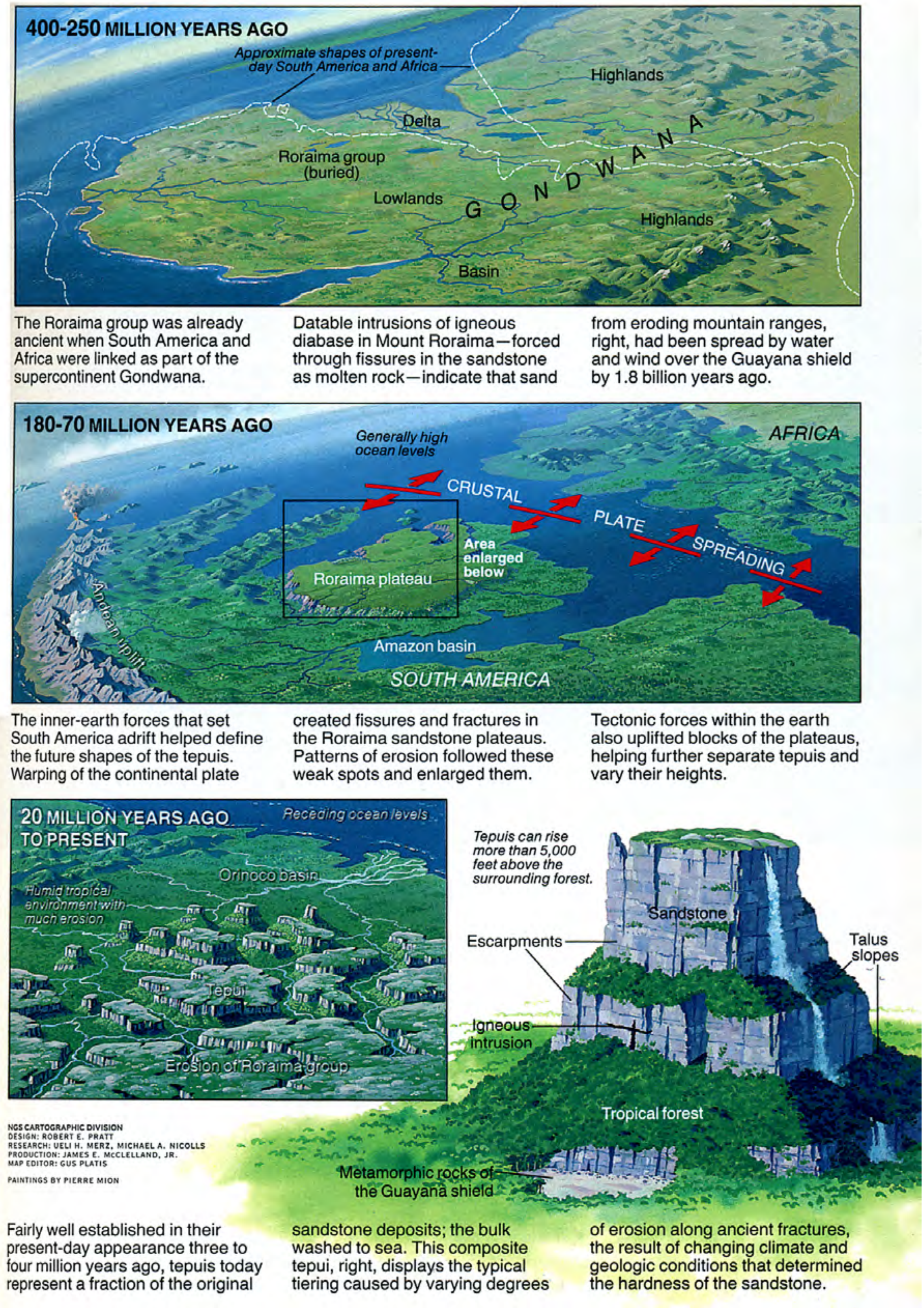
It does not seem incorrect to state that the last sedimentation events must have predated the first uplift of the area; therefore the age of the top sediments should not be much older than the age of the first uplift. However, because these last sediments were certainly removed by erosion after or during uplift (and are thus gone today, see above) their precise dating is impossible.

From the geological data and the most pertinent literature available on the subject (*i.a.* Gansser 1954, 1974, Urbani *et al.* 1977, Simpson 1979, Schubert *et al*. 1986, Schubert & Briceño 1987, Huber 1988, Briceño *et al.* 1990, Briceño & Schubert 1990, Schubert & Huber 1990, Gibbs & Barron 1993, Santos *et al*. 2003, Huber & García 2011) we can reasonably conceive that sedimentation occurred at least until the Paleozoic and that Pantepui experienced a first epeirogenic uplift during the Mesozoic, possibly contemporary with the Takutu Graben formation and the early break-up of Gondwana. This first upheaval could have been followed by a second one in the Upper Cretaceous/beginning of the Cenozoic when the first signs of the Amazon Basin became visible. A third uplift could have occurred more recently, during the Neogene or even the Quaternary, possibly concomitant with the emergence of the Central American Isthmus. There is apparently no reason to believe that the Roraima sandstone uplift was not a slow continuous event, with a few major (?) uplifts promoted by main tectonic/volcanic events.

The rate of erosion and denudation was definitely not constant and weathering, which was accelerated during the Cretaceous, was probably later reduced due to two main tectonic episodes: the emergence of the Central American Isthmus (final closure *ca.* 3 mya) and the Andean main uplift (starting *ca.* 25–30 mya, with a peak less than 10 mya). These two major regional mountain-building episodes drastically modified the hydrologic regime, but also the climate in South America; as a consequence the climate in the Guiana Shield region became less humid and more strongly seasonal (*i.a.* Hoorn 1993, Orme 2007, McPherson 2008).

Quaternary climate oscillations also played a significant role in the development of the tepui geomorphology by yet again accelerating weathering processes.

As observed today, some authors argue that tepuis could be separated recently since the end of the Pliocene (Schubert & Briceño 1987, Kubitzki 1989a, b). Unfortunately for biogeographers and ecologists, it is still uncertain when tepuis reached their present elevations and when their current summits have been topographically isolated from each other.



The Roraima group was already ancient when South America and Africa were linked as part of the supercontinent Gondwana. Datable intrusions of igneous diabase in Mount Roraima—forced through fissures in the sandstone as molten rock—indicate that sand from eroding mountain ranges, right, had been spread by water and wind over the Guayana shield by 1.8 billion years ago.

The inner-earth forces that set South America adrift helped define the future shapes of the tepuis. Warping of the continental plate created fissures and fractures in the Roraima sandstone plateaus. Patterns of erosion followed these weak spots and enlarged them. Tectonic forces within the earth also uplifted blocks of the plateaus, helping further separate tepuis and vary their heights.

Fairly well established in their present-day appearance three to four million years ago, tepuis today represent a fraction of the original sandstone deposits; the bulk washed to sea. This composite tepui, right, displays the typical tiering caused by varying degrees of erosion along ancient fractures, the result of changing climate and geologic conditions that determined the hardness of the sandstone.

NGS CARTOGRAPHIC DIVISION
DESIGN: ROBERT E. PRATT
RESEARCH: UELI H. MERZ, MICHAEL A. NICOLLS
PRODUCTION: JAMES E. MCCLELLAND, JR.
MAP EDITOR: GUS PLATIS

PAINTINGS BY PIERRE MION

Figure **6.** Artistic synoptic reconstruction of the geomorphological evolution of the tepuis. Note that this reconstruction accepts a Jurassic age for the summit surface. Copied with permission from George (1989, National Geographic Magazine).

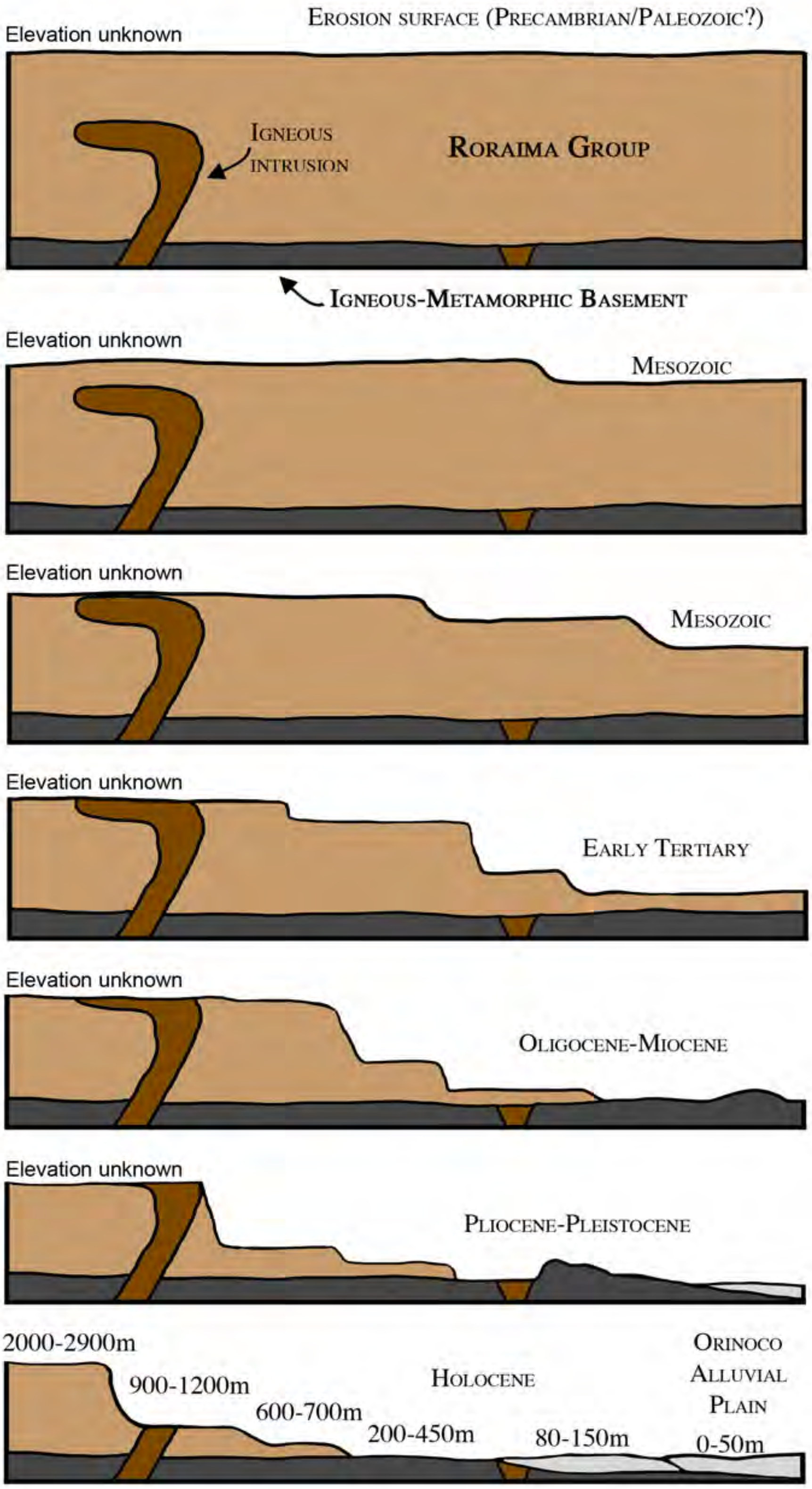


Figure **7.** Schematic model of the geomorphological evolution of the tepuis first proposed by Schubert & Briceño (modified with permission from Schubert & Briceño 1987), which assumes that the upper surfaces are reduced by general surface lowering.

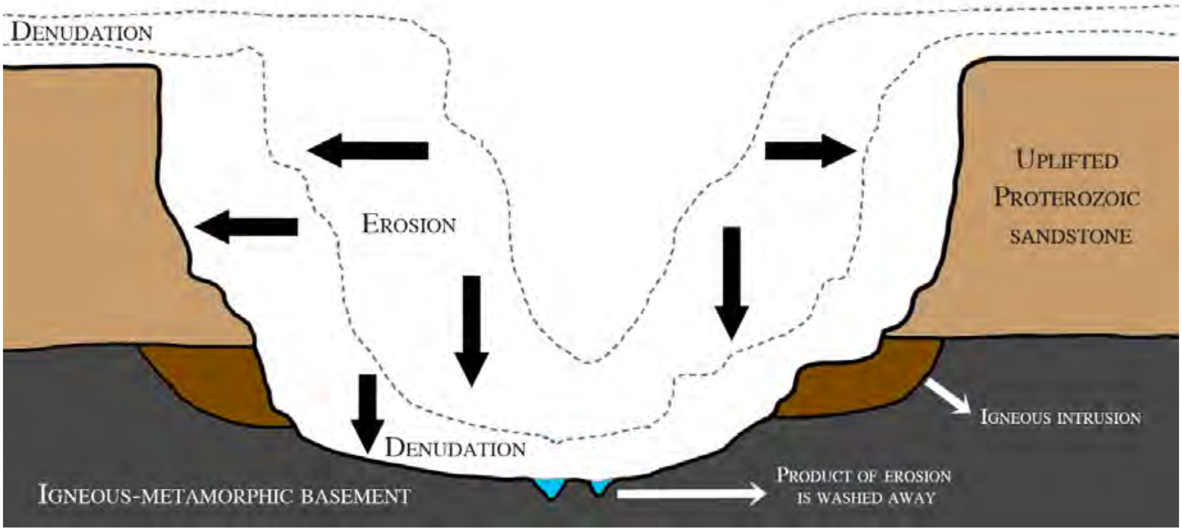


Figure **8.** Schematic model of the geomorphological evolution of the tepuis driven by erosion (modified with permission from McPherson 2008).

The Lost World

One hundred years ago, in 1912, Sir Arthur Conan Doyle, largely inspired by the account of an expedition of the Royal Geographical Society of London to the summit of Mount Roraima (led in 1884 by Sir Everard im Thurn), coined the expression "The Lost World" in the title of his probably most famous novel. Doyle depicts an epic expedition to an isolated tepui in the middle of the tropical jungle of northern South America in search of dinosaur-like creatures and a forgotten civilisation (Doyle 1912). The extent to which Doyle’s novel has influenced hypotheses about the Pantepui biogeography is really fascinating, one of these hypotheses having even been named “The Lost World Hypothesis” (Rull 2004).

Due to its ancient age and complex topography, the “Lost World” has been thought for long to be a perfect nursery of cladogenesis, and even a potential inland counterpart to oceanic archipelagos (*e.g.* McCormack 2009). Each of these “islands in time” (as first coined by Brewer-Carías 1974) or “islands in the sky” (as first coined by Givnish *et al.* 2000) would indeed be an ideal candidate to harbour relict species, isolated from the rest of the world for millions of years. Taxonomic decisions were obviously affected by this preconception and sometimes led to erroneous conclusions (*e.g.* phenotypically divergent summit populations were assigned to new taxa without much questioning).

PhD objectives

Surrounded by myths and unconfirmed beliefs, the origin of the Pantepui biota (particularly the fauna) and the dynamics of biotic interchanges between tepuis, and especially tepui tops, are still an evolutionary enigma (Rull 2009). Likewise, exact timing of Pantepui fragmentation/vertical isolation, and of physiographic isolation in individual tepui summits remain unknown, even if geological data outlined how and when the tepuis formed.

Because genetic footprints are left at intraspecific levels by historical events such as dispersal and vicariance (Antonelli *et al.* 2010), molecular phylogenies are the ideal tool to examine these questions by helping to understand organisms' evolutionary relationships and how and when they diversified. Molecular phylogeny reconstructions and divergence time estimates compared with geological data should help to elucidate the "Lost World" conundrum.

The main goals of this work are thus (1) to better understand the species diversity, the evolutionary history, the dynamics of biotic interchanges between tepuis, and the patterns of endemism of the fauna in the Pantepui region, sorting facts from fiction through morphological analyses and molecular phylogenies, and (2) to provide new insights in the timing of the geomorphological evolution of the tepuis in the light of amphibian and reptile species diversification inferred from molecular phylogeny reconstructions and estimates of divergence time.

To solve these long-lasting mysteries and assess the impact of the tepuis' unique geomorphology on species diversification, several taxa of amphibians and reptiles were selected because, apart from being my favourite groups, they are the most conspicuous vertebrates on tepui summits (68.5% of amphibians and reptiles in the region are reported as single-tepui endemics by McDiarmid & Donnelly 2005), and thus models of choice for historical biogeographic studies. Furthermore, amphibians are assumed to be relatively poor dispersers, highly philopatric, with narrow elevational limits (Duellman & Trueb 1986, Blaustein *et al.* 1994).

Except the pioneering study by Duellman & Hoogmoed (1984) on the genus *Stefania* (morphology-based and including only the few specimens from the few species known by that time), no phylogenetic analysis (morphology- or molecular-based) of Pantepui amphibians or reptiles had been performed at the onset of the present study. The phylogenetic relationships among most Pantepui amphibian and reptile taxa (like any other Pantepui vertebrates) remained thus unknown or based on vague hypotheses at best. Whether taxa restricted to tepui summits are more related to each other or whether there is no difference in relationships among upland *versus* lowland taxa remains mostly undetermined, as well as the number of conspecific amphibian and reptile taxa that exclusively occur on separate tepui summits within the same massif. Very recently, Salerno *et al*. (2012) provided an incomplete phylogeny of the Pantepui frog genus *Tepuihyla* hypothesizing that *Tepuihyla* species recently invaded some tepui summits. Although their study is based on only four species (*T. aecii*, *T. edelcae*, *T. talbergae*, *T. rodriguezi*) from two upland localities and three tepui summits, Salerno *et al.* seemingly jumped to the conclusion that all tepui summits harbour young lineages. It should be highlighted that *Tepuihyla* species live in habitats extending from uplands to summits, and that—quite obviously—the study of four species within this single genus is not sufficient to fully understand the diversification processes in the region.

Because of the vastness of the area, the present study primarily focuses on the Eastern Pantepui District (*sensu* McDiarmid & Donnelly 2005), including all upland (*ca.* 500–1,500 m asl) and lowland (*ca.* 200–500 m asl) areas between tepuis. Figure 9 illustrates the Pantepui region as understood here; the Eastern Pantepui District (Fig. 10) is located east of the Río Caroní. We cannot explain distribution patterns while ignoring those lowland and upland areas that might have been decisive in the evolution of the Pantepui biota in harbouring both highland and lowland taxa (Rull 2005).

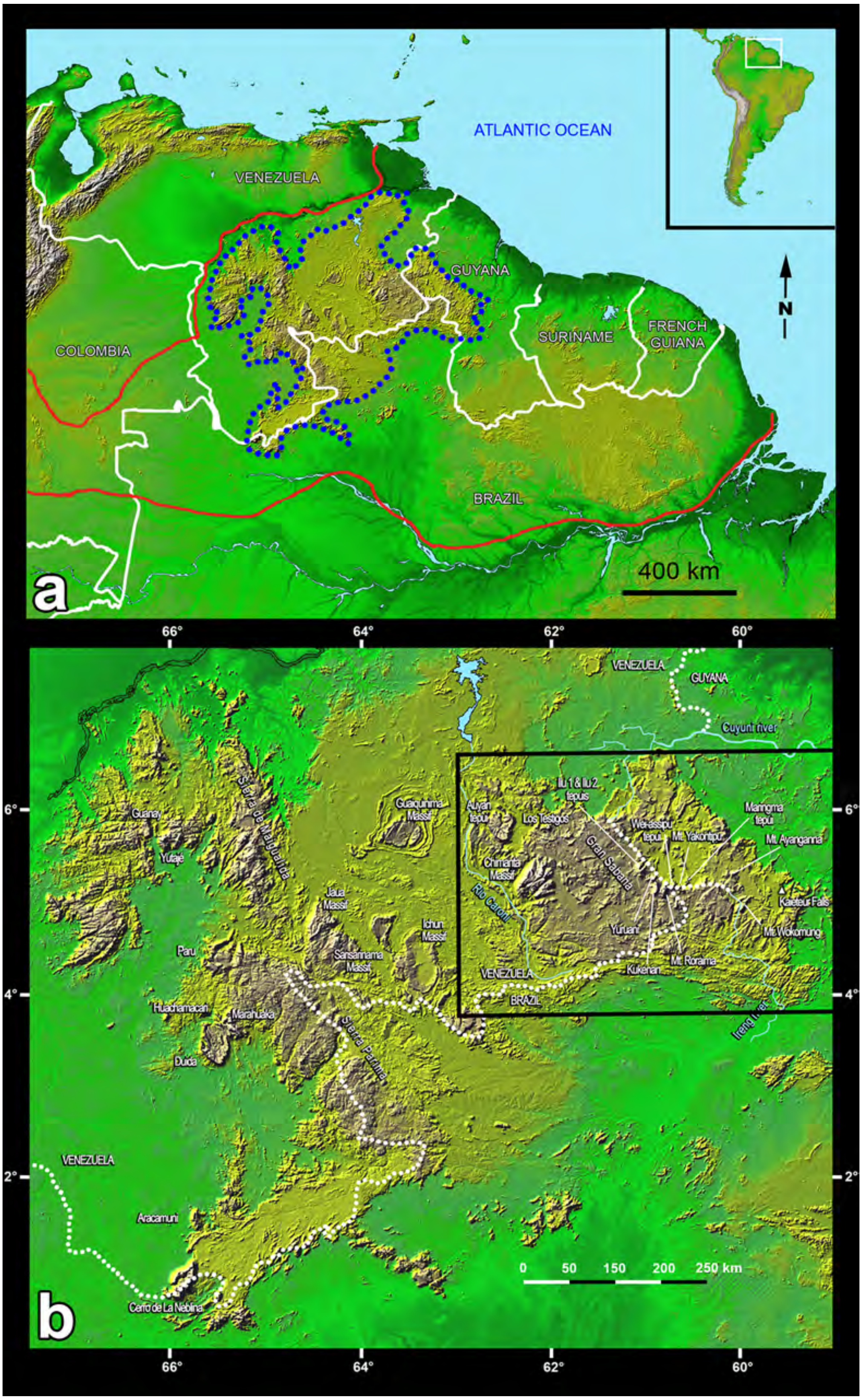


Figure **9.** Map of the Pantepui region as understood in the present study (blue dotted line in **a**), and its location in northern South America; red line indicates the Guiana Shield boundaries (*sensu* Señaris & MacCulloch 2005). The Eastern Pantepui District is indicated by a black rectangle in **b**.

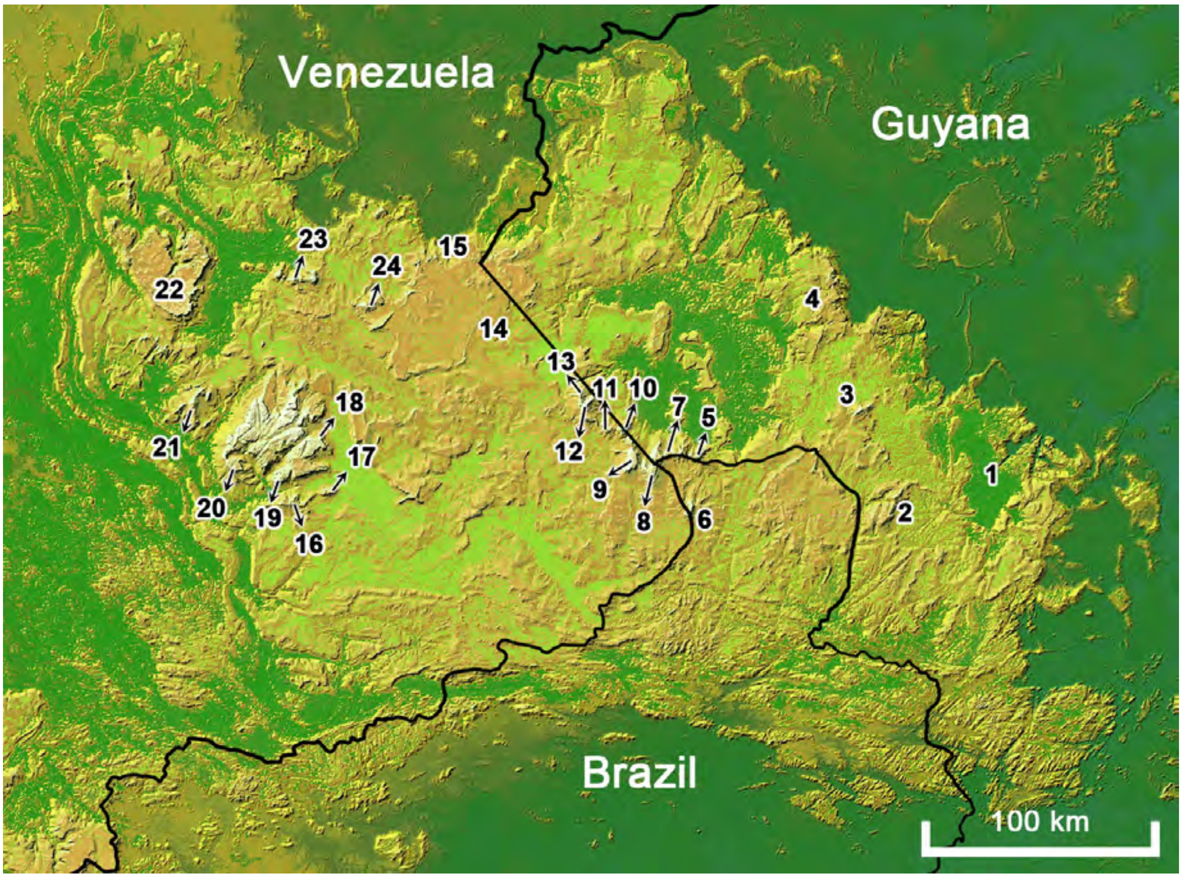


Figure **10.** Map of the Eastern Pantepui District (equivalent to the black rectangle in Fig. 9b), showing main sampled localities in the region (see Chapter 10 for additional localities sampled outside the Pantepui region). 1 = Kaieteur National Park, Guyana; 2 = Wokomung Massif, Guyana; 3 = Mount Ayanganna, Guyana; 4 = Merume Mountains, Guyana; 5 = Maringma-tepui, Guyana; 6 = Uei-tepui, Venezuela/Brazil border; 7 = Wei-Assipu-tepui, Guyana; 8 = Mount Roraima (Venezuela/Guyana/Brazil border); 9 = Kukenan-tepui, Venezuela; 10 = Yuruani-tepui, Venezuela/Guyana border; 11 = Guadacapiapu-tepui, Venezuela; 12 = Ilu-tepui, Venezuela; 13 = Tramen-tepui, Venezuela; 14 = northern Gran Sabana, Venezuela; 15 = La Escalera region, Venezuela; 16 = Angasima-tepui, Venezuela; 17 = Upuigma-tepui, Venezuela; 18 = Churi-tepui, Venezuela; 19 = Amuri-tepui, Venezuela; 20 = Abakapá-tepui, Venezuela; 21 = Aprada-tepui, Venezuela; 22 = Auyantepui, Venezuela; 23 = Murisipan-tepui, Venezuela; 24 = Ptari-tepui, Venezuela.

It may seem “trendy” to highlight it, but any study dealing with species diversity is crucial facing the growing concerns about climatic changes, especially in topographically isolated areas where biota are reported to be seriously threatened by global warming (*i.a.* Rull & Vegas-Vilarrúbia 2006, Hopper 2009). Unfortunately, environmental problems are of such a global nature that we probably can only anticipate the diversity loss, and any local conservation action seems rather illusory. We must “think locally, but act globally”, and hope that raising public awareness about the threats to the “relict fauna” of the table mountains that is often displayed in popular books on nature and documentary films may help to promote positive behaviour changes.

Brief introduction to the selected taxa

The genus *Anomaloglossus* (Amphibia, Anura, Aromobatidae), according to Frost (2011) includes 24 recognized species, 18 of which reported as endemic to Pantepui. The genus *Anomaloglossus* was proposed by Grant *et al.* (2006) to accommodate all the species formerly included in *Colostethus* that have a median lingual process, an unusual anatomic structure also known in some Asian and African ranoid frogs (Grant *et al*. 1997). According to Grant *et al.* (2006) *Anomaloglossus* is sister to *Rheobates*, a genus reported from the Cordillera Central and the Cordillera Oriental in Colombia. Molecular and morphology-based phylogenies of Grant *et al.* (2006) included only a very few *Anomaloglossus* from the Pantepui region, but indicated a sister species relationship between *A. beebei* and *A. roraima* (both species being terrestrial bromeliad specialists). The genus *Anomaloglossus* includes several species having very restricted distributions in the Pantepui region, sometimes reported from the summit of a single tepui only, whereas the genus seems to have some representatives in the Andes (including *cis*-Andean) and a single one in the Amazonian lowlands. Grant *et al.* (2006) pointed out that more taxon sampling is needed to clarify relationships between *cis*-Andean species and those occurring west of the Andes and that the *trans*-Andean species having a median lingual process must be included in phylogenetic analyses to corroborate their placement in *Anomaloglossus*. Very recently Grant *et al*. (2012) reported that Andean *Anomaloglossus* species belong in fact to the genus *Hyloxalus*, leaving *Anomaloglossus* with 21 species, all restricted to the Guiana Shield. *Anomaloglossus* species have a biphasic life cycle, eggs are usually laid on the ground, and the tadpoles are carried by the male to a suitable body of water (*e.g.* streams, puddles). In one species (*A. stepheni*) the tadpoles are nidicolous and endotrophic (= nonfeeding tadpoles), and in *A. degranvillei* the tadpoles are exoviviparous, completing their development while being transported by the male nurse frog (Grant *et al*. 2006). Phytotelm-breeding species have specific ecological niche preferences. In those species, eggs are laid on bromeliad leaves and tadpoles slide into the bromeliad tank.

Figure **11.** Examples of *Anomaloglossus* species. Left: *Anomaloglossus megacephalus* from the slopes of Maringma-tepui, Guyana. Right: *Anomaloglossus beebei* from Kaieteur National Park, Guyana. Photos by the author.

The genus *Oreophrynella* (Amphibia, Anura, Bufonidae) is endemic to the Eastern Pantepui District, and currently includes nine described species (Frost 2011). According to Graybeal & Cannatella (1995) *Oreophrynella* is monophyletic. The genus has been considered the sister taxon of *Atelopus* + *Dendrophryniscus*[1] + *Melanophryniscus* by McDiarmid (1971) and of *Dendrophryniscus* by Cannatella (1985). *Oreophrynella* was discussed by Señaris *et al.* (1994), who suggested relationships with *Metaphryniscus* and *Osornophryne*, the latter plus *Atelopus* considered as the sister taxon of remaining bufonids by Frost *et al.* (2006). Based on morphology, Graybeal (1997) presented a tree suggesting *Oreophrynella* most closely allied to African and Asian non-*Bufo* taxa (*Didynamipus* and *Pelophryne*, respectively). McDiarmid (1971) and McDiarmid & Donnelly (2005) suggested that *Oreophrynella* probably has arisen from a Gondwanan ancestor, an assumption in contradiction with the recent Pramuk *et al.*'s (2008) hypothesis of a strict South American origin of Bufonidae. Combining morphological and molecular data (obtained from *Oreophrynella dendronastes*), Pramuk (2006) presented a tree suggesting *Oreophrynella* most closely allied to *Atelopus* and *Dendrophryniscus*. More recently, Van Bocxlaer *et al*. (2010) showed a sister relationship with *Atelopus*, but did not confirm close relationship with *Dendrophryniscus*. Fouquet *et al*. (2012) provided similar results. Unfortunately, phylogenetic relationships with *Metaphryniscus* remain unknown owing to lack of material for molecular analyses. Most *Oreophrynella* species have very restricted distributions, nearly all of them being reported from a single tepui summit. *Oreophrynella* has never been the subject of any comprehensive phylogenetic analysis. *Oreophrynella* species are direct-developers, laying eggs in moist places where they develop into froglets, and most species have highly specific ecological preferences (*i.e.* exclusively occupying rocky habitats harbouring an extremely impoverished flora).

Figure **12.** Examples of *Oreophrynella* species. Left: the terrestrial *Oreophrynella nigra* from the summit of Yuruani-tepui, Venezuela. Right: the arboreal *Oreophrynella macconnelli* from the upper slopes of Maringma-tepui, Guyana. Photos by the author.

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[1] Fouquet *et al.* (2012a) recently allocated the Amazonian and Atlantic Forest clades of *Dendrophryniscus* to different genera, erecting the new genus *Amazophrynella* (Fouquet *et al.* 2012a, b) for the Amazonian clade.

The genus *Stefania* (Amphibia, Anura, Hemiphractidae) is endemic to Pantepui (two species present in extralimital lowlands) and currently includes 19 described species, 15 of which are found only on tepui slopes or summits (Frost 2011). The genus *Stefania* was erected by Rivero (1968) to accommodate *Cryptobatrachus evansi* and a few related new species all morphologically divergent from other *Cryptobatrachus* by having *i.a.* the first finger longer than the second, T-shaped terminal phalanges, inner margins of frontoparietals elevated, and large choanae. Rivero (1970) recognized two species-groups within *Stefania*: the *evansi* group including species having the head longer than broad and found in the lowlands and uplands, and the *goini* group including species having the head broader than long and found in the highlands; both groups are still recognized (*e.g.* MacCulloch & Lathrop 2002, 2006). Rivero (1970) extensively discussed the possible origin, endemism and distribution of the genus. Duellman & Hoogmoed (1984) revised the taxonomy of *Stefania* and investigated the phylogenetic relationships of the genus based on morphological and immunological comparisons; they suggested a sister relationship with *Cryptobatrachus*, a genus occurring in the northern Andes and Sierra de Santa Marta in Colombia, and in the Serranía de Perijá in Venezuela (Frost 2011). *Stefania* was later discussed by Señaris *et al.* (1997), who described five new species based on osteology, external morphology and ecology. Rivero (1968, 1970), suggested that *Stefania goini* and *S. ginesi* (at the time the only known representatives of the *goini* group) represent remnants of an ancestor that once occupied an extensive plateau subsequently dissected into the present-day tepuis, and doubted that species of the *goini* group could have originated independently from the "*evansi* stock" and acquired similar characteristics by convergence. By contrast, Señaris *et al.* (1997), who still recognized both species groups, assumed that species from the *goini* group (at that time six in number) evolved from the *evansi* group and that their common characteristics are due to convergence, instead of a common phylogenetic origin. Faivovich *et al.* (2005) and Frost *et al.* (2006) recovered *Stefania* as sister to *Cryptobatrachus*. Most recent molecular phylogenies indicate that *Stefania* is sister to *Gastrotheca* (Wiens 2007, Wiens *et al.* 2007, Pyron & Wiens 2011, all excluding *Cryptobatrachus*), a genus distributed from Costa Rica southward to northern Argentina, and also found in eastern and southeastern Brazil (Frost 2011), but the genus *Stefania* itself has never been the subject of molecular phylogenetic analyses. *Stefania* species are direct-developers, with eggs and juveniles carried on the back of the mother. They occupy various types of habitats, from lowland rainforest to tepui bogs.

Figure **13.** Examples of *Stefania* species. Left: *Stefania ginesi* ("*goini*" group) from the summit of Abakapá -tepui, Venezuela. Right: *Stefania evansi* ("*evansi*" group) from Kaieteur National Park, Guyana. Photos by the author.

The genus *Tepuihyla* (Amphibia, Anura, Hylidae) is endemic to Pantepui and currently includes seven described species, four of them reported from tepui tops only [an eighth species, *Tepuihyla celsae*, purportedly from Falcón, Venezuela (outside Pantepui) is most likely a junior synonym of *T. luteolabris* based on a specimen with incorrect labelling and locality data (C. Barrio-Amorós, pers. comm.)]. The genus *Tepuihyla* was proposed by Ayarzagüena *et al*. (1993) to accommodate six species previously included in the *Osteocephalus rodriguezi* group (all from the Guayana region in Venezuela), which were reported to differ from *Osteocephalus* sensu stricto mainly in osteological characters. *Tepuihyla* has been reported sister to *Osteocephalus* (Faivovich 2005, Pyron & Wiens 2011), a genus widely distributed in the Guiana Shield and in the Amazon Basin. At the onset of the present study, the genus *Tepuihyla* had never been the subject of any comprehensive phylogenetic analysis. Very recently, Salerno *et al*. (2012) provided an incomplete phylogeny of the genus, and indicated that *Tepuihyla* is nested within *Osteocephalus*, as *O. exophthalmus* is recovered as its sister taxon. Although their phylogenetic tree strongly suggests that *O. exophthalmus* should be transferred to the genus *Tepuihyla*, Salerno *et al.* did not take any taxonomic decision and took no further step to remedy the paraphyly of *Osteocephalus* and *Tepuihyla* with respect to each other. *Tepuihyla* species have a biphasic life cycle, eggs being laid in small pools and puddles. They occupy open herbaceous savannahs from the uplands to the summit of some tepuis.

Figure **14.** Examples of *Tepuihyla* species. Left: *Tepuihyla galani* from Wei-Assipu-tepui, Venezuela. Right: *Tepuihyla talbergae* from Kaieteur National Park, Guyana. Photos by the author.

The genus *Pristimantis* (Amphibia, Anura, Craugastoridae) is the most speciose vertebrate genus with more than 430 species currently recognized (Frost 2011). Twenty-two of these species are distributed in Pantepui, seven of them being restricted to tepui summits and upper slopes. These numbers do not include the many putative undescribed and highly restricted species (at least 16) reported from the region by McDiarmid & Donnelly (2005). Heinicke *et al.* (2007) removed *Pristimantis* from the synonymy of *Eleutherodactylus* on the basis of molecular data to accommodate a large "South American Clade" centred primarily in the Andes (Hedges *et al*. 2008). *Pristimantis* is sister to a clade including the genera *Oreobates*, *Lynchius*, and *Phrynopus* (Hedges *et al*. 2008, Pyron & Wiens 2011), all with primarily Andean distributions. Only a very few Pantepui taxa were included in the existing molecular phylogenies. Most Pantepui species are reported as having restricted distributions, several of them being reported from a single tepui summit and still awaiting description. *Pristimantis* species are direct-developers, laying eggs in moist places where they develop into froglets; they occupy various types of habitats, from lowland rainforest to tepui bogs.

Figure **15.** Examples of *Pristimantis* species. Left: *Pristimantis yuruaniensis* from the summit of Yuruani-tepui, Venezuela. Right: *Pristimantis jester* from the upper slopes of Maringma-tepui, Guyana. Photos by the author.

The family Gymnophthalmidae (Reptilia, Squamata) currently contains the largest number of reptile species represented on tepui summits (McDiarmid & Donnelly 2005), a few gymnophthalmid genera being endemic to tepui tops (*e.g. Riolama*). The taxonomic status of the family Gymnophthalmidae has a long history of controversy, but recent molecular evidence (*e.g.* Pellegrino *et al*. 2001, Castoe *et al*. 2004) strongly supports its validity. The family is sister to Teiidae. Gymnophthalmidae currently includes more than 45 genera widely distributed mostly in tropical, but also in temperate and subtropical areas of southern Mexico, Central America and South America. Approximately 18 gymnophthalmid genera are currently known to occur in the Guiana Shield region, 14 of them are found in Pantepui. None of the Pantepui genera has been the subject of any comprehensive phylogenetic analysis and relationships between tepui top species and upland/lowland species are mostly unknown. Some species like *Neusticurus rudis* (reported from the lowlands and tepui summits) are possible species complexes (*i.e.* Rivas *et al.* 2012). Hoogmoed (1979) suggested *Riolama* to be related to *Leposoma* and stated that the genus might have evolved from lowland gymnophthalmids "*by isolation on a sandstone tableland prior to the Oligocene, as was probably the case in* Stefania". Gymnophthalmid lizards occupy a wide range of habitats in the Guiana Shield, from lowland rainforest to tepui bogs.

Figure **16.** Examples of Gymnophthalmidae genera/species present in the Pantepui region. Left: *Riolama leucosticta* from Yuruani-tepui, Venezuela. Right: *Arthrosaura testigensis* from Murisipan-tepui, Venezuela. Photos by the author.

From a molecular perspective the objectives of this PhD study were unprecedented. As pointed out by McDiarmid & Donnelly (2005: 498):

“*Unfortunately, our knowledge of the phylogenetic relationships of tepui taxa is nonexistent; hence, we lack a basis for making historical arguments. Although several species from tepuis have been described, no phylogenetic treatment includes all known species for any Pantepui lineage*”.

Not really surprisingly (see below), almost no vertebrate taxa from this remote region were included in molecular phylogenies and most literature dealing with their systematics consists predominantly of alpha taxonomic descriptions. The scarcity of voucher specimens and tissue samples for molecular analyses of tepui taxa have clearly prevented any significant progress, therefore the first step was to conduct collecting expeditions in the area as well as seeking collaboration with the very few scientists who have been properly collecting tissue samples and voucher specimens in the tepui region, and especially on tepui tops.

It is worthwhile mentioning that the tepui summits are among the most inaccessible places on earth. Most of these flat-topped mountains are only reachable by helicopter and, as a consequence, the majority of these summits have been only very occasionally visited, if ever (several tepui summits remain unexplored). Technical and financial aspects have seriously hindered extensive tissue sampling for detailed and in-depth phylogenetic analyses of large datasets. Nevertheless, over the past years, Ross MacCulloch, Bruce Means and I managed to visit a total of 21 tepui summits/massifs and numerous uplands/lowlands localities in the Eastern Pantepui region and in other areas within the Guiana Shield (ranging from the uplands of the Gran Sabana in Venezuela, to the lowlands of French Guiana), and obtained specimens and tissue samples of a considerable number of tepui taxa of almost all families represented on tepui tops. These field trips led to the discovery of two new lizard genera and several new amphibian and reptile species, some of them being described in Chapters 2, 3, 4, 5, 6, and 7, and also allowed a better understanding of the morphology, taxonomy and the distribution patterns of poorly known tepui species, which is developed in Chapters 8 and 9.

In **CHAPTER 2** a new lizard of the genus *Arthrosaura* (Gymnophthalmidae) is described. The new species, named *A. hoogmoedi*, was discovered during herpetological investigations on the summit of Maringma-tepui at the border between Guyana and Brazil. Species groups in the genus *Arthrosaura* are briefly discussed based on morphological characters, as well as the rare occurrence of an opaque, completely pigmented, lower eyelid in gymnophthalmids.

In **CHAPTER 3** the description of *Pantepuisaurus rodriguesi*, a new genus and species of gymnophthalmid lizard, is presented. The new genus was also discovered during herpetological investigations on the summit of Maringma-tepui. Relationships with two other gymnophthalmid genera apparently restricted to the Pantepui region (*Adercosaurus* Myers & Donnelly, 2001 and *Kaieteurosaurus* Kok, 2005) are discussed, as well as the necessity of erecting a new genus to accommodate the new species in order to avoid taxonomic confusion. The hemipenis is described as well.

In **CHAPTER 4** a new species of *Oreophrynella* (Bufonidae) is described. The new species, named *O. seegobini*, is the third taxon discovered during herpetological investigations on the summit of Maringma-tepui. The chapter provides new insights on the distribution of the genus and investigates relationships among *Oreophrynella* species on the basis of morphological characters. It also reports new data on the poorly known *Oreophrynella macconnelli* (a species previously reported from the upper slopes of Mount Roraima only and the only *Oreophrynella* absent from tepui tops). The chapter further reports arboreality in *O. macconnelli* for the first time, discussing the occurrence of opposable toes, assumed to be plesiomorphic, and the extent of interdigital integument seen here as an adaptation to a more terrestrial way of life on tepui summits.

In **CHAPTER 5** the frog *Anomaloglossus megacephalus* (Aromobatidae) is described from the slopes of Maringma-tepui in Guyana. This species was previously confused with *A. tepuyensis*, a taxon described from Auyantepui in Venezuela.

In **CHAPTER 6** a new species of frog of the genus *Pristimantis* (Strabomantidae) from the summit of Wei-Assipu-tepui and the upper slopes of Mount Roraima is described and named *P. aureoventris*. In addition to the morphological description, the chapter also includes the description of the advertisement call of the new taxon, and additional morphological data on *P. yuruaniensis* (including advertisement call analysis), which was known from the three poorly preserved type specimens only. The chapter also provides new insights on the distribution of the genus in Pantepui and questions the occurrence of some species on more than one tepui, while others seem restricted to a single summit.

In **CHAPTER 7** the gymnophthalmid lizard *Anadia mcdiarmidi* is described from the summit of Abakapá-tepui in Venezuela. *Anadia* is one of the very few genera having representatives both in the Andes and in Pantepui and therefore is of extreme interest in Pantepui studies, because it might shed light on distribution mechanisms. The hemipenis is described as well.

In **CHAPTER 8** *Anomaloglossus praderioi* (Aromobatidae), a species previously known from the original description only, and reported as restricted to the upper slopes of Mount Roraima in Venezuela and Guyana, is redescribed. The species was found on the slopes of Maringma-tepui in Guyana and an additional specimen is reported from the Sierra de Lema in Venezuela, thus considerably expanding its distribution. In addition to the species redescription, the chapter provides descriptions of the tadpole and advertisement call.

In **CHAPTER 9** the reassessment of the morphology of *Anomaloglossus roraima* (Aromobatidae), a species known from the subadult holotype only and thought to be restricted to the upper slopes of Mount Roraima in Venezuela is proposed. The species was found on the summit of two additional tepuis in Guyana (namely Maringma-tepui and Wei-Assipu-tepui) as well as on the Guyanese upper slopes of Mount Roraima. In addition to the species redescription, the chapter provides descriptions of the advertisement call and tadpole, and discusses phylogenetic relationships within *Anomaloglossus*.

In **CHAPTER 10** the overall timing and extent of biotic interchange between tepui summits and the surrounding uplands are investigated. Phylogenetic analyses of two mitochondrial gene fragments evolving at different rates (the relatively slow-evolving 16S rDNA and the fast-evolving ND1 mtDNA) revealed unexpectedly low genetic divergence—as low as zero—among multiple tepui summit species/populations in five of the six groups under study, as well as among some summit species/populations and uplands populations described as distinct species. Results suggest that recent (as recent as the late Pleistocene-Holocene) faunal interchange among currently isolated tepui summits, and among tepui summits and the surrounding uplands, has been extensive, and affected even taxa living in some of the most tepui-specific habitats and on the most inaccessible summits. If the tepuis are as ancient as often stated, the young age of extant summit fauna can only be explained by active dispersal among summits with subsequent extinction in the intervening uplands, but the highly specific ecological niche preferences of some taxa restricted to tepui summits coupled with the peculiar topography of the tepuis are likely to have limited active dispersal. However, the chapter highlights that time estimates for the isolation of individual tepuis range from the Cretaceous to the Quaternary, and the youngest estimates, although widely neglected in biological studies, could be compatible with the low genetic diversity and therefore leave vicariance as a possible mechanism for speciation. Regardless of the mechanism, this chapter shows that, even in small vertebrates restricted to summit-specific habitats, gene flow has been maintained until recently, making single-tepui endemism probably an exception instead of a rule.

In **CHAPTER 11** a general conclusion, coupled with a critical review of the hypotheses aiming at explaining the origin and diversification of the Pantepui biota that have been assumed so far, is proposed in the light of molecular phylogeny reconstructions and estimations of divergence time. Several theories have been suggested to explain the origin and diversification of the Pantepui biota, the majority of them based on the avifauna, then extended to floral elements and other non-flying organisms. Prevalent theories are essentially derived from two main, often conflicting, mechanisms: organisms evolved *in situ* through long isolation among tepuis (“old” vicariance), or organisms evolved from tepui-summit invaders (“recent” dispersal, *e.g.* during glacial-interglacial cycles), the latter hypothesis challenged by the unique geomorphology of the area and the apparent high rate of endemism on the highest tepui summits compared to the short time-scale involved (*e.g.* Willis & Niklas 2004). This last chapter aims to try to elucidate the timing of the geomorphological evolution of the tepuis proposing a phylogenetically supported diversification hypothesis. Data suggest that the origin of Pantepui endemics is rooted in the Paleogene and that most herpetofaunal diversity patterns in Pantepui were shaped well before the Quaternary. Phylogeny reconstructions coupled with divergence time estimates suggest that species diversity was substantially reorganized during or shortly after periods of climate instability that occurred in the area from the late Miocene until today. Results mainly tend to show that (1) multiple nonexclusive processes implying vicariance and dispersal promoted diversification in Pantepui, (2) the postulate of the tepuis being formed and already isolated in the Cretaceous (70–90 mya) is not only poorly consistent with most geological data, but is also not convincingly satisfied by the phylogenetic data, (3) a period of accelerated uplift and high fragmentation could have occurred during the Eocene/Oligocene (25–45 mya), with a more recent period for complete isolation of individual tepui summits (late Miocene to Holocene). The chapter additionally points out that several Pantepui taxa are characterized by surprisingly high phenotypic differentiations between tepui top populations (or between tepui top and upland populations) in the absence of (or very low) genetic divergence. Conversely, some species are morphologically undistinguishable while genetic divergence among these organisms is surprisingly high.

Finally, this study closes on a note about future perspectives.

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2

A New Highland Species of *Arthrosaura* Boulenger, 1885 (Squamata: Gymnophthalmidae) from Maringma Tepui on the Border of Guyana and Brazil

P. J. R. Kok

Abstract
A new species of *Arthrosaura* (Squamata: Gymnophthalmidae) is described based on a female specimen obtained at 2112 m above sea level on Mount Maringma, a poorly known sandstone flat-topped table mountain (tepui) located in the eastern Pakaraima Mountains, at the Guyana-Brazil border. *Arthrosaura hoogmoedi* **sp. nov.** is mainly distinguished from its known congeners by the following combination of characters: four supraoculars, prefrontals in contact with loreals, lower eyelid opaque, 32–33 smooth temporal scales, middorsal scales distinctly narrower than adjacent dorsal scales, and a dark brown dorsum with a black middorsal stripe from nape to tail, and a tan ill-defined dorsolateral line from nape to midbody.

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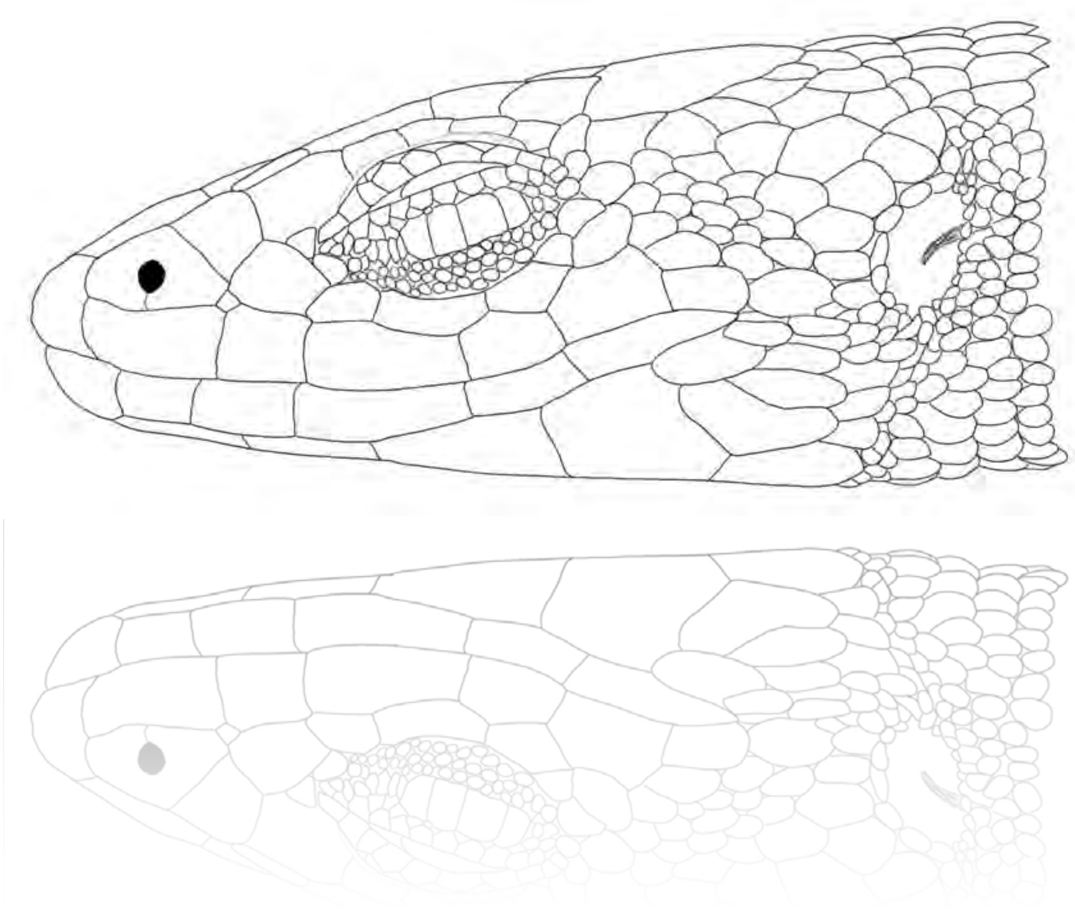
Text and figures remain unchanged, only the format was adapted to fit the thesis layout



INTRODUCTION

The phytogeographic province of Pantepui (Mayr & Phelps 1967) forms part of the biologically and geographically distinct unit called the Guiana Shield (GS) [see fig. 5 in Ávila-Pires (2005) for boundaries of the GS]. Pantepui includes all upper slopes and summits of the Guiana Shield highlands. The region, the well-known “Lost World” of Sir Arthur Conan Doyle (1912), probably still shelters many undiscovered species.

Although some of the characteristic flat-topped table mountains found in the area (the famous tepuis) received more attention and were repeatedly visited by scientists (see McDiarmid & Donnelly 2005, MacCulloch *et al.* 2007), many remain very poorly known and their fauna virtually undocumented. Arranging and conducting scientific expeditions in this mountainous region is very expensive and time-consuming due to the remoteness of the area, which partly explains that few tepuis have been extensively surveyed. A recent expedition to Mount Maringma (*ca.* 5° 13’ N, 60° 35’ W—Malaima tepui in local Akawaio language), a sandstone tepui located about 17 km (airline) east of Mount Roraima, resulted in the discovery of several new species of amphibians and reptiles (Kok, unpublished data). Mount Maringma (Fig. 1–2A) is one of the highest tepuis in Guyana (ca. 2147 m asl according to the GPS unit) and shares part of its southwest slope with Brazil.

Summit vegetation on Mount Maringma (Figs. 2B–4) is typical and similar to that of other tepuis in the area. It consists of a mixture of very dense low vegetation (the “tepui meadow”) with plants of the families Bonnetiaceae (*e.g. Bonnetia roraimae*, some of these small trees being much higher than the surrounding vegetation), Bromeliaceae (*e.g. Brocchinia tatei*), Clusiaceae (*e.g. Clusia* spp.), Orchidaceae, Rapateaceae (*e.g. Stegolepis guianensis*), Sarraceniaceae (*e.g. Heliamphora nutans*), Xyridaceae (*e.g. Orectanthe spectrum*), large areas of quaking peat bog, and patches of dwarf forests largely dominated by *Bonnetia roraimae*, which have their branches covered with a slimy mass of algae. Rocky outcrops are small and very limited in number.

Swampy pools—full of organic matter—are numerous, sometimes very deep, often covered by a mattress of thick vegetation. Only the very top of the tepui has solid “dry” ground. The tepui plateau is not completely flat but having different levels reminding of steps of a staircase; its total surface is roughly 170 ha. There is huge temperature fluctuation, and during our stay on the top of the tepui (25–30 November 2007) temperature varied from 13.5 to 37.5°C. Harsh cold winds, diluvian rains, and the usual dense, persistent mist (Fig. 3B)— sometimes cleared away by periods of intense sunshine—make the environment on Maringma tepui extreme, and make the place most of the time obviously inhospitable to humans.

The genus *Arthrosaura* Boulenger, 1885 currently comprises eight species distributed in northern South America. Historical reviews of the genus are provided in Hoogmoed & Ávila-Pires (1992) and in MacCulloch & Lathrop (2001).

The purpose of the present paper is to describe the new highland species of *Arthrosaura* collected on Maringma tepui.

MATERIAL AND METHODS

The specimen was collected by hand and photographed alive before euthanization by intracardiac injection of Xylocaine. Tissue (liver) was removed and preserved in 95% ethanol before fixation of the whole individual in 10% formalin. Both specimen and tissue were deposited at the Institut Royal des Sciences Naturelles de Belgique, where the animal was transferred to 70% ethanol for permanent storage.

Coordinates and elevations were acquired using a Garmin 60CSx GPS (Global Positioning System) unit and were referenced to map datum WGS84.

Scale counts were made using a stereo dissecting microscope. All measurements were taken on the preserved specimen to the nearest 0.1 mm with an electronic digital caliper or to the nearest 1.0 mm with a ruler. Snout-vent length (SVL) was measured from tip of snout to anterior border of cloaca; head length from tip of rostral to anterior edge of ear; trunk length is the distance between forelimbs and hindlimbs. Color characteristics were obtained from field notes and digital photographs. Sex was determined by the presence/absence of femoral pores. Scale terminology and character definitions mostly follow those of Harris (1994), Kizirian (1996), and Myers & Donnelly (2008); the term occipitals is used to name the distinct, enlarged, scales posterior to and bordering the parietals and the interparietal.

Diagnosis mostly follows the format of MacCulloch & Lathrop (2001), and Myers & Donnelly (2008) for ease of comparison.

The new species was compared to original descriptions of *Arthrosaura*, digital photographs of museum specimens, and museum material when available (additional material examined is in the Appendix 1). Intrageneric comparisons were mainly based on the work of Donnelly *et al.* (1992), Hoogmoed & Ávila-Pires (1992), Gorzula & Señaris (1998), MacCulloch & Lathrop (2001), and Myers & Donnelly (2008). Museum abbreviations are those used by Frost (2008).

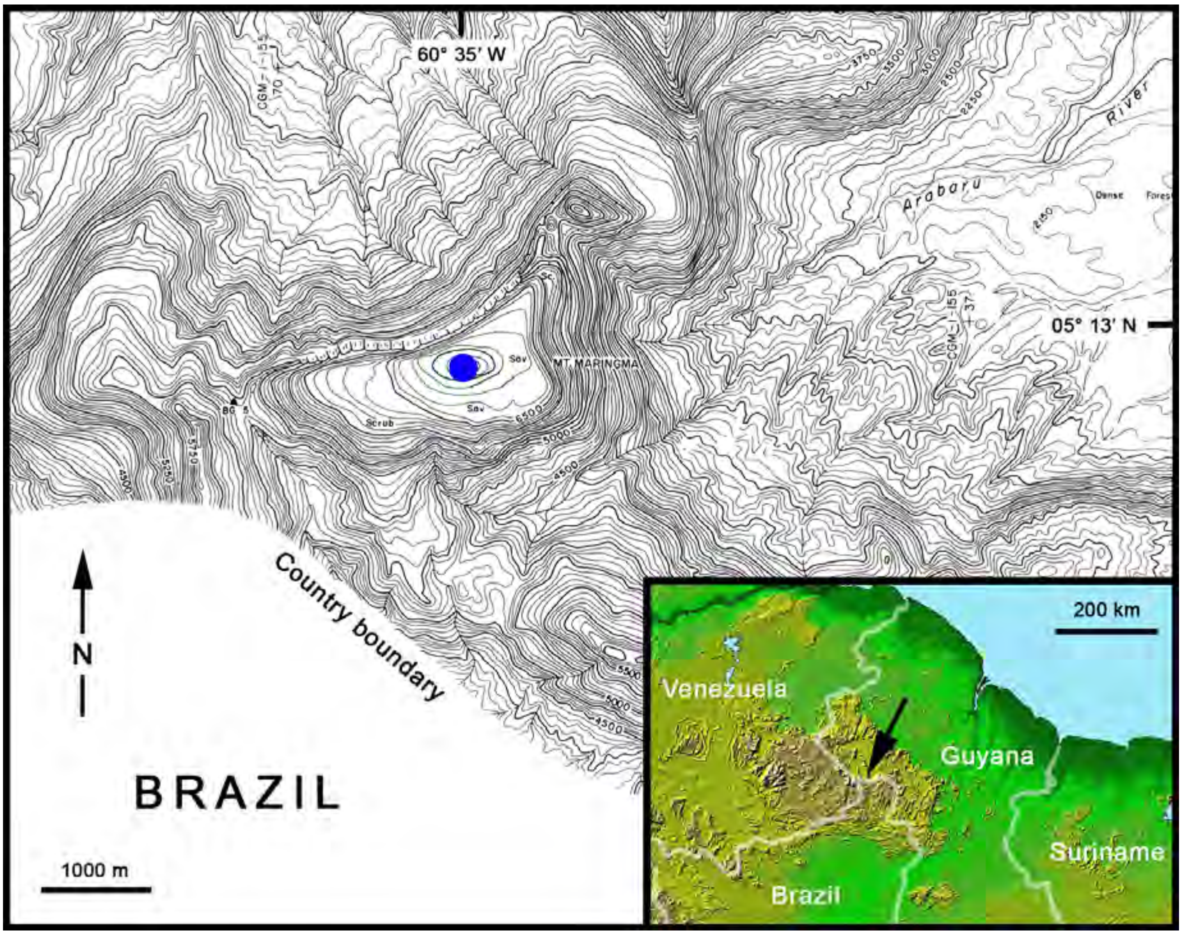


Figure **1.** Area map of Maringma tepui showing the type locality of *Arthrosaura hoogmoedi* sp. nov. (blue dot). Coordinates and boundary with Brazil are approximate and based on the available map (note that there is a substantial difference in the country boundary between this map and that shown in Google Earth). Maps elaborated after “Roraima Sheet 40 SE” published by the Survey Department of Guyana, 1972, and a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388.

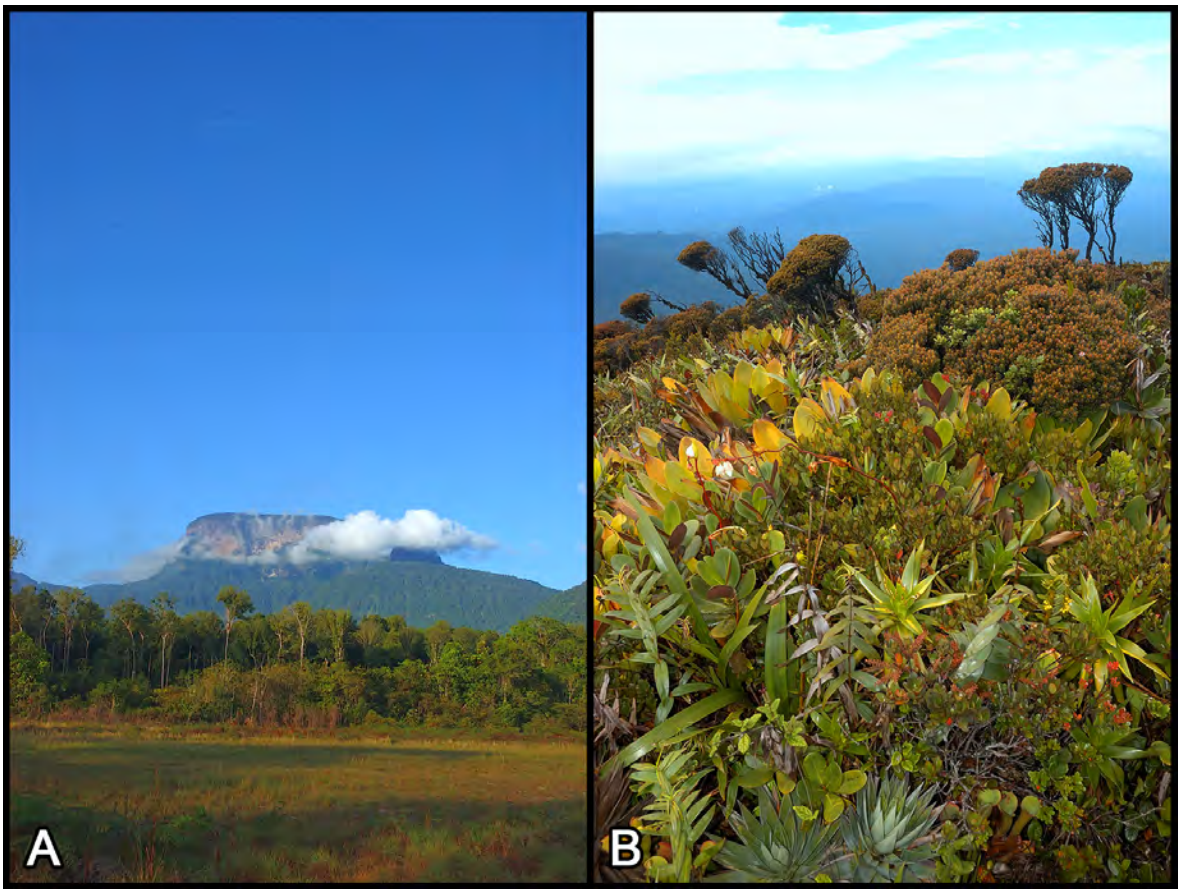


Figure **2.** Maringma tepui. A: Scenic view of the tepui from the east (20 November 2007). B: Dense vegetation on the summit plateau (28 November 2007).

RESULTS

Arthrosaura hoogmoedi species novum

Figs. 5–6, 7C, 8–9

Holotype. IRSNB 2653 (field number PK 2031), an adult female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 27 November 2007 at 11h00, summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (5° 12' 60" N, 60° 35' 06" W, 2112 m elevation).

Etymology. The specific epithet is a noun in the genitive case, honoring Dutch herpetologist Marinus Steven Hoogmoed. Marinus was curator of reptiles and amphibians at the National Museum of Natural History (Leiden, The Netherlands) for 38 years (1966–2004) before retiring as research associate at the Museu Paraense Emílio Goeldi in Belém, Brazil, where he is still very active. His contribution to the knowledge of the Guiana Shield herpetofauna is extensive, and most of his papers on the lizard fauna of the area are still authoritative.

Figure **3.** Maringma tepui. A: View from the summit plateau of the mountain, looking to the west; Yakontipu is visible on the right (28 November 2007). B: Dense mist on the summit plateau, the usual climatic condition during our stay on the top of the tepui (25 November 2007).

Figure **4.** Maringma tepui. Author's tent on the very top of the mountain; looking SWW, Mount Roraima is hidden by clouds (28 November 2007).

Diagnosis. The new species is assigned to the genus *Arthrosaura* because of the following combination of characters (modified from Ávila-Pires 1995, and MacCulloch & Lathrop 2001): (1) distinctive ear opening and moveable eyelids, (2) limbs pentadactyl with all digits clawed, (3) nasal scales separated by a single frontonasal, (4) prefrontals present (although absent in *Arthrosaura synaptolepis* Donnelly, McDiarmid & Myers, 1992), (5) frontoparietals, parietals and interparietal present, (6) parietals and interparietal longer than wide, (7) interparietal and parietals forming a straight posterior margin, (8) occipitals present, (9) second pair of enlarged genials in contact with two infralabials, (10) enlarged median pairs of gulars, (11) dorsal scales hexagonal, keeled, in transverse rows only, (12) ventral scales quadrangular, smooth, in both transverse and longitudinal rows, (13) tongue dorsally covered by scalelike papillae (although papillae are reported as interrupting oblique plicae in *Arthrosaura montigena* Myers & Donnelly, 2008).

In addition to the generic characteristics, the new species is characterized by the following features: four supraoculars; prefrontals in contact with loreals; palpebral disc completely opaque; 32–33 smooth temporal scales; scales around midbody 37; 3–4 middorsal scales distinctly narrower than adjacent dorsal scales; dorsal scales strongly keeled, in 29 transverse rows; trunk length 1.4x length of forelimb; overlap of limbs equivalent to seven lateral scales when they are adpressed along the body; dark brown dorsum with a black middorsal stripe from nape to tail, and a tan ill-defined dorsolateral line from nape to midbody; flanks black; ventrally cream with dark mottling.

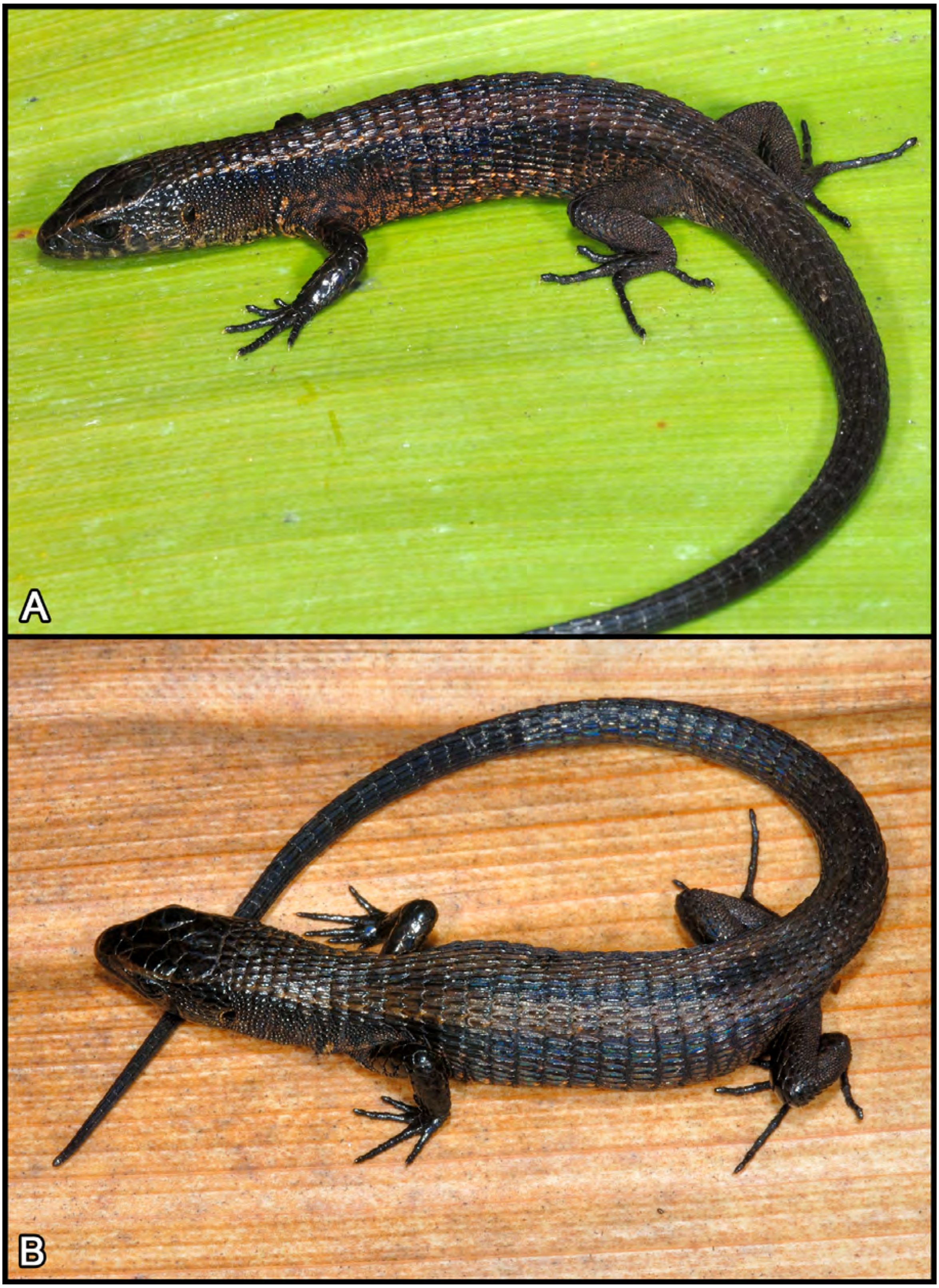


Figure **5.** *Arthrosaura hoogmoedi* **sp. nov.**, female holotype (IRSNB 2653), 59.3 mm SVL. A: Dorsolateral view. B: Dorsal view.

The new species is immediately distinguished from *Arthrosaura montigena*, *A. reticulata* (O'Shaughnessy, 1881), *A. synaptolepis*, *A. tyleri* (Burt & Burt, 1931), and *A. versteegii* Lidth de Jeude, 1904 in having four supraoculars (vs. three) and a black middorsal stripe from nape to tail (absent in the above-mentioned species). The new species agrees with *A. guianensis* MacCulloch & Lathrop, 2001, *A. kockii* (Lidth de Jeude, 1904), and *A. testigensis* Gorzula & Señaris, 1998 in having four supraoculars. *Arthrosaura guianensis* mainly differs (characters of *A. hoogmoedi* in parentheses) in having keeled parietals and interparietal (a feeble keel on interparietal only), unpigmented tympanum (pigmented), lower eyelid with semitransparent disc (disc opaque), 45 scales around midbody (37), 40–42 keeled temporals (32–33, smooth), and absence of a black middorsal stripe (present). *Arthrosaura kockii* mainly differs (characters of *A. hoogmoedi* in parentheses) in having broadly keeled temporals (smooth), unpigmented tympanum (pigmented), lower eyelid with semitransparent disc (disc opaque), a wide light vertebral stripe (black middorsal stripe), and in having an immaculate venter (dark mottled). *Arthrosaura testigensis* shares many characteristics with *A. hoogmoedi*, from which it mainly differs (characters of *A. hoogmoedi* in parentheses) in having less than 20 temporals (more than 30), lower eyelid with semitransparent disc (disc opaque), prefrontals separated from loreals by frontonasal-first supraocular contact (prefrontals in contact with loreals), weakly keeled dorsal scales (strongly keeled), middorsal scales not noticeably narrower than adjacent dorsal scales (3–4 middorsal scales distinctly narrower), and in having four narrow yellowish longitudinal stripes on dorsum (one middorsal black stripe and a tan ill-defined dorsolateral line).

Description of the Holotype. Adult female 59.3 mm SVL. Head length 21% SVL, 1.37x head width, head width 1.48x head height. Head slightly wider than neck, temporal region swollen, neck approximately as wide as anterior body. Snout blunt, rising gently posteriad. Body oval in transverse section, depressed, wider than high. Tail complete (regenerated distally), 97.0 mm, 1.63x SVL, circular in cross-section, tapering toward the tip. Limbs well-developed, moderately long, forelimbs 31% SVL, hindlimbs 48% SVL. Limbs pentadactyl, all fingers and toes with terminal claw. Overlap of limbs equivalent to seven lateral scales when they are adpressed along the body. Trunk length 25.7 mm, 43% SVL, 1.4x forelimbs (Fig. 5).

Tongue lanceolate, dorsally covered by oblique rows of small scalelike papillae; tip bifid, smooth; three well defined pairs of subequal infralingual plicae on the anterior part of the tongue, after fork. Anterior teeth conical, posterior teeth laterally compressed, tricuspid.

Rostral rectangular, twice as wide as high, visible from above, in broad contact with frontonasal. Frontonasal single, heptagonal, laterally in contact with nasal and in broad contact with loreal, not in contact with first supraocular. Prefrontals roughly pentagonal, as broad as long, with a long medial suture, laterally in broad contact with first supraocular, touching the loreal and the anterior point of the second supraocular. Frontal hexagonal, 2.1x as long as wide, slightly wider anteriorly, laterally markedly concave; laterally in contact over the entire length of second supraocular, separated from first supraocular by prefrontal-second supraocular contact, in point contact with third supraocular.

Frontoparietals roughly hexagonal, 1.5x as long as wide with relatively broad medial suture; frontoparietals in contact with frontal, distinctly separated from second supraocular by frontal-third supraocular contact, in broad contact with third and fourth supraoculars, one parietal and interparietal. Interparietal 1.6x as long as wide, roughly pentagonal with curved sides converging anteriad, distinctly longer and narrower than parietals. Parietals and interparietal form a relatively straight posterior margin; anteriorly each is angulate. Interparietal with a short median, feeble, longitudinal keel. A row of seven occipitals of various shapes, the central largest; all of them feebly keeled, except the first left one. Four supraoculars, first smallest, about half the size of the fourth; third distinctly larger, second largest. Six superciliaries, first much larger than the others, last two smallest, others subequal (Fig. 6).

Nasal entire, with a very short division running ventrad from naris to supralabial on the left side; naris just below centre; directed laterally. Loreal trapezoidal, anteriorly inclined, in contact with nasal, frenocular, first superciliary, first supraocular, and prefrontal and frontonasal, separated from supralabials by frenocular-nasal contact and an odd, very small, quadrangular, supernumerary scale located at the intersection of nasal, frenocular, and first and second supralabials, present on both sides. Three small preoculars on the right side, two on the left, between first superciliary and first subocular. Frenocular quadrangular, longer than wide, subequal to loreal, separated from the first supralabial by a small supernumerary scale. Four suboculars on the right side, five on the left. Two postoculars, the lower smallest. Seven supralabials on both sides, fifth highest, with suture between third and fourth below middle of the eye; suture between second and third supralabials in contact with first subocular, suture between first and second supralabials in contact with a small supernumerary scale on both sides (Fig. 6).

Upper eyelid with 10 ciliaries. Ocular recess with median row of five small scales separating median ciliaries from superciliaries. Lower eyelid with 12 ciliaries on the right side, 11 on the left side. Lower eyelid with a palpebral disc of four large, vertical, completely opaque (pigmented), palpebral scales (Figs. 6, 7C).

Temporal region with 32 irregularly shaped, juxtaposed, smooth scales on the right side, 33 on the left. Temporals arranged in six ill-defined oblique rows, much larger in the upper part [a distinct cluster of 16 (on the right) and 18 (on the left) smaller temporals in the lower part]. Ear opening moderately large, vertically oval, posteriorly bordered by many small, smooth, mostly granular scales; anteriorly bordered by four (on the right side) or six (on the left side) smooth, enlarged, juxtaposed scales. Auditory meatus moderately deep, tympanum pigmented (Fig. 6).

Mental trapezoidal, its posterior edge slightly concave. Postmental large, roughly heptagonal, laterally in contact with first and second infralabials. Three pairs of large genials, first two pairs in contact with each other medially, in lateral contact with infralabials, medial suture of second pair twice as long as that of first pair; third pair in contact with infralabials, but separated medially by small scales. A pair of enlarged postgenials separated medially by scales of varying sizes and widely separated from infralabials. Six infralabials on the right side, five on the left side. Six rows of two transversely enlarged gulars. Collar row with nine scales, decreasing in size laterally, forming a scalloped margin. Gular fold distinct, concealing three rows of very small scales (Figs. 6, 8B).

Head scales with numerous small pits, especially concentrated on rostral, frontonasal, supraoculars and lateral head scales, absent on ventral head scales and body scales. Scales on nape posterior to the row of occipitals longer than wide, keeled, mucronate, in transverse rows, grading posteriorly into dorsal body scales. Sides of neck with distinctly smaller granular scales, juxtaposed, not in rows, slightly decreasing in size posteriorly. Three (left side) or four rows (right side) of distinctly enlarged scales before arm insertion.

Dorsals imbricate, appearing hexagonal because of imbrication, elongate, strongly keeled, mucronate, in transverse rows only, 29 rows between the interparietal and posterior edge of hindlimbs (including row of occipitals). Three to four middorsal scales, between anterior margin of forelimbs and anterior margin of hindlimbs, distinctly narrower than adjacent dorsals and very similar to laterals (Fig. 9A), 37 scales around mid- body. A zone of small granular scales extending from anteriorly of forelimb insertion to above arm and becoming wider in the axilla. Small granular scales at hindlimb insertion. Flank scales similar to, but narrower than, most dorsal scales (except three to four middorsal ones, see above); no abrupt demarcation between dorsals and laterals. Lateral scales becoming smaller toward groin. Below the laterals, two rows of ventrolateral scales (see Myers & Donnelly 2008); some short, smaller scales intercalated between the transverse rows of laterals; no distinct demarcation between laterals and ventrolaterals.

Ventrals imbricate, smooth, longer than wide, with posterior margins slightly rounded, arranged in transverse and longitudinal rows (Fig. 8A). Eighteen transverse rows between collar and preanal plate, six longitudinal rows of ventrals at midbody (10 rows including the ventrolaterals). Preanal plate consisting of eight scales, three anterior scales, five posterior scales (four elongate large scales and a small distal medial triangular scale); lateral posterior preanal scales narrow, almost as long as adjacent scales. No preanal or femoral pores (Fig. 9B).

Scales on tail keeled, mucronate (except distally), imbricate, appearing hexagonal because of imbrication, similar to, but slightly shorter than, dorsal scales, in transverse rows only except two middorsal caudal scales that form an almost complete longitudinal row from the seventh dorsal caudal scale (from posterior margin of hindlimbs) to tip of tail. Regenerated portion of tail (distal 31.0 mm) with much shorter scales ventrally and dorsally. Pigmented subcaudal scales smooth, imbricate, with rounded ends, in both transverse and longitudinal rows, becoming keeled laterally, grading into laterals.

Dorsal surfaces of upper and lower arms with smooth, variably polygonal scales, ventral surface of upper arms with small, juxtaposed, granular scales, ventral surface of lower arms with scales similar to those on dorsal surface, except for a band on inner side with small juxtaposed granular scales. Thighs with a row of enlarged, smooth, hexagonal scales on anterior surface, bordered ventrally by two rows of slightly smaller, smooth, polygonal scales; bordered dorsally by 2–3 rows of keeled scales, diminishing in size dorsad, grading into small, granular, juxtaposed scales, which cover posterodorsal and posterior surfaces of thighs. Shanks ventrally and posteriorly with large, smooth, polygonal, imbricate scales; scales on anterior surface smaller, keeled, imbricate, grading into small, granular, juxtaposed scales, which cover distal portion of anterior side (near the ankle) and dorsal portion of shanks.

Dorsal surface of hands, feet, and digits with imbricate, smooth scales, except on the posterodorsal surface of feet where 2–3 scales are keeled; palms and soles covered with small roundish or elongate scales, juxtaposed, not projecting anteriorly. Two enlarged thenar scales on inner margin of palm below pollex, two enlarged hypothenar scales on outer margin of palm. Subdigital lamellae protuberant, slightly divided basally on some digits, single on distal halves of most digits; lamellae rounded laterally.

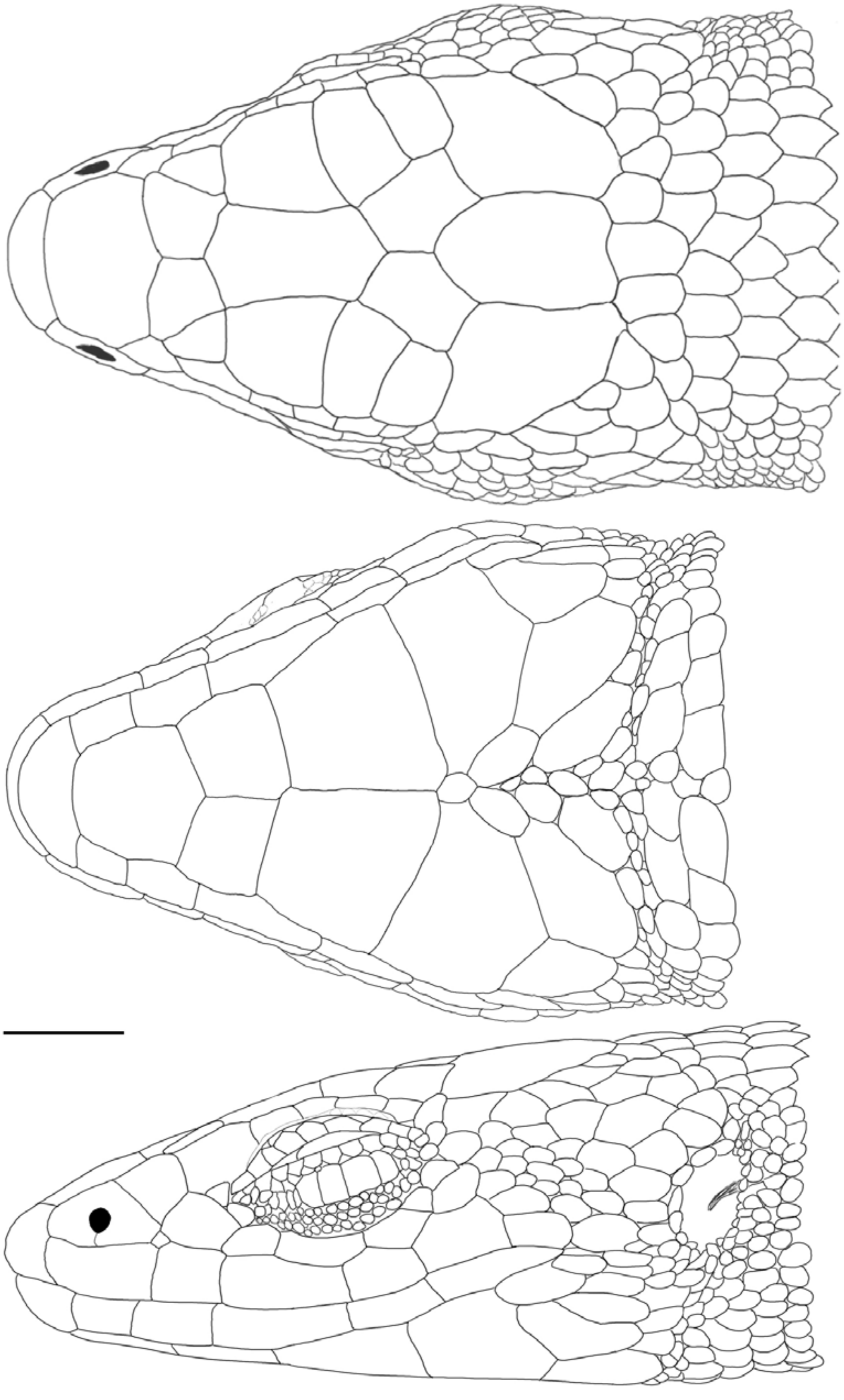


Figure **6.** *Arthrosaura hoogmoedi* **sp. nov.**, female holotype (IRSNB 2653), 59.3 mm SVL. Dorsal, ventral, and lateral views of head. Scale bar is 2 mm.

Figure **7.** Lower eyelid condition in *Arthrosaura hoogmoedi* **sp. nov.** and two related *Arthrosaura* species. A: Semi- transparent, unpigmented in *A. kockii* (IRSNB 15397). B: Semi-transparent, partly pigmented in *A. guianensis* (IRSNB 17343). C: Completely opaque, completely pigmented in *A. hoogmoedi* **sp. nov.** (IRSNB 2653, holotype).

Figure **8.** *Arthrosaura hoogmoedi* **sp. nov.**, female holotype (IRSNB 2653), 59.3 mm SVL. A: Ventral view in life. B: Detail of the gular region in life.

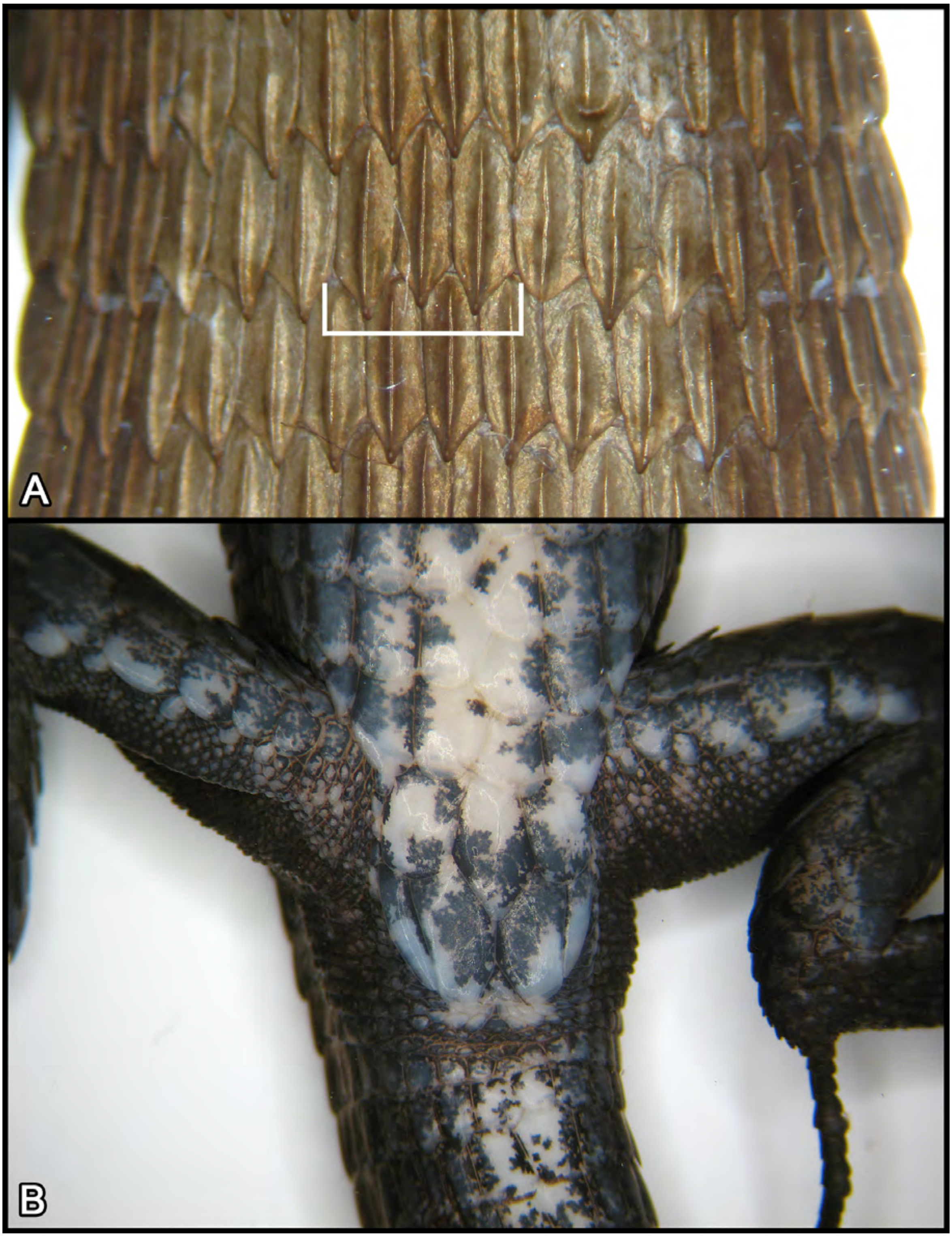


Figure **9.** *Arthrosaura hoogmoedi* **sp. nov.**, preserved female holotype (IRSNB 2653), 59.3 mm SVL. A: Detail of dorsal scales at midbody showing the 3–4 middorsal scales noticeably narrower than contiguous dorsal scales. B: Detail of perianal region.

Subdigital lamellae as follows (Roman numbers indicate digits, Arabic numbers indicate paired or single lamellae on left/right; lower ungual sheath scale is omitted from the counts): hands **I** 4/4, **II** 8/8, **III** 14/13, **IV** 15/14, **V** 8/8; feet **I** 6/6, **II** 9/19, **III** 14/14, **IV** 20/20, **V** 11/11.

Color of Holotype in life. Dorsum dark brown, with a black middorsal stripe (about two-three dorsal scales wide) extending from nape to tail, where it quickly becomes inconspicuous due to the dark coloration of the tail; subtle, irregular, tan dorsolateral line extending from nape to about midbody; flanks black, lower part of flanks peppered with reddish brown, and with some small pale brown spots ventrolaterally, forming an irregular ventrolateral line. Axilla region and underside of arms marbled with reddish brown and black. Head blackish brown with tan dorsolateral lines extending above eyes, from the anterior part of the loreals to the parietals. Tip of snout paler; diffuse paler blotches on lower part of lateral surface of head. Tympanum black, surrounded by some tan scales. Arms black, legs and tail blackish brown. Iris black (Fig. 5). Tongue dark gray. Palms and soles black. Chin, throat, chest, belly, and ventral surface of upper legs cream with dark mottling; lower legs ventrally reddish brown with dark mottling; tail ventrally black, except proximally where it is dirty white peppered with black (Fig. 8A).

Color of Holotype in preservative. After four months in 70% ethanol, color pattern is similar to that in life. The dorsolateral line became white and is more conspicuous, the cream coloration of the ventral surface also became white.

Distribution and ecology. The species is currently known only from the type locality, the summit of Maringma tepui in Guyana (Fig. 1). The only specimen available was collected in late morning (11h00), during a sunny spell, in a large bromeliad (*Brocchinia tatei*), about 60 cm above the ground (Fig. 10). Possibly the specimen was hunting for some insects and spiders that became numerous once the sun chased away the mist generally present all over the summit. One other specimen was observed on the same day (in the afternoon) in another patch of bromeliads, but that specimen escaped. Interestingly, Gorzula & Señaris (1998) and Fuentes & Rivas (2000) also reported collection of gymnophthalmids in *Brocchinia tatei*. This plant probably plays an important role as a refuge and food source for highland gymnophthalmids.

Discussion. *Arthrosaura hoogmoedi* shares many morphological characteristics with *A. testigensis* from Los Testigos (Estado Bolívar, Venezuela) a group of tepuis east of Auyán-tepui and situated about 180 km airline NWW from Maringma tepui. In having a black middorsal stripe, the new species resembles a putative new taxon ("*Arthrosaura* species a") reported by Gorzula & Señaris (1998: 124) from the Chimantá Massif (about 180 km airline W from Maringma tepui), unfortunately the absence of diagnostic characters and the poor quality of the photograph provided by Gorzula & Señaris (1998, photograph #89) does not allow further comparison.

Without formally naming them, MacCulloch & Lathrop (2001) postulated the existence of two species groups of *Arthrosaura*, one group containing the species having four supraoculars, a relatively short body with relatively long legs (which I propose to name the *kockii* group), the other group containing species with three supraoculars, gracile body and relatively short legs (which I propose to name the *reticulata* group). Among the *kockii* group, the presence of keeled temporals in *Arthrosaura kockii* (a lowland species) and *A. guianensis* (an upland and highland species) might indicate a close relationship between these two taxa, while the smooth temporals could indicate a close relationship between *A. hoogmoedi* and *A. testigensis*, both being highland species.

The completely opaque condition of the lower eyelid in *Arthrosaura hoogmoedi* is shared only with the recently described *A. montigena* from Auyantepui (Myers & Donnelly 2008) and is a rare trait within the family Gymnophthalmidae. It is unknown whether this is an adaptive character to high UV radiation and intense sunshine sometimes occurring on high elevation tepuis, or whether it is a plesiomorphic character state (secondarily lost in other species). Figure 7 shows a comparison of lower eyelid condition between *A. hoogmoedi* and two related *Arthrosaura* species (*A. kockii* and *A. guianensis*).

Figure **10.** A patch of *Brocchinia tatei* (Bromeliaceae), habitat on the summit plateau of Maringma tepui in which the holotype of *Arthrosaura hoogmoedi* **sp. nov.** was found.

Recently Myers & Donnelly (2008: 97) provided a key to the species of *Arthrosaura*. Unfortunately they inverted some characters of *A. testigensis* with those of *A. guianensis* and their key should be used with caution: interparietal and parietals are keeled in *A. guianensis*, but not in *A. testigensis*, and temporals are small in *A. guianensis*, but large in *A. testigensis*.

The only other lizard collected on the summit of Maringma tepui belongs to a possibly new gymnophthalmid genus, which will be treated in a separate publication.

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APPENDIX 1. COMPARATIVE MATERIAL EXAMINED

Arthrosaura guianensis.— Guyana: *Potaro-Siparuni*: Kaieteur National Park, Tukeit trail, *ca.* 420 m asl (05° 11'N, 059° 28'W) (IRSNB 17342–3); *Mazaruni-Potaro*: northern slope of Mount Roraima, 700 m asl (05° 17'N, 060° 45'W) [USNM 549323 (digital photographs)].

Arthrosaura kockii.— Brazil: *Pará*: Belém (01° 26'S, 048° 29'W) [USNM 15921 (digital photographs)]. French Guiana: *Régina*: Pic Matécho (03° 44' 53"N, 053° 02' 19"W) (IRSNB 15397); *Saül*: *ca.* 8 km from the village of Saül, near Montagne Belvédère (IRSNB 14574).

Arthrosaura synaptolepis.— Venezuela: *Amazonas*: Cerro de la Neblina, *ca.* 6.2 km NNE of Pico Phelps (= Pico da Neblina), Camp XI, 1400 m asl (00° 51' 45"N, 065° 58' 52"W) [USNM 317882 (digital photographs)].

Arthrosaura testigensis.— Venezuela: *Bolívar*: Altiplanicie sur Terekyurén-tepui, base de Los Testigos, 1800 m asl (05° 52'N, 062° 03'W) [MHNLS 10730, holotype (digital photographs)].

Arthrosaura tyleri.— Venezuela: *Bolívar*: Cerro Jaua, *ca.* 2 km from the central ridge, southern bank of the Marajano River, 1750 m asl [USNM 317880 (digital photographs)].

3

LIZARD IN THE CLOUDS: A NEW HIGHLAND GENUS AND SPECIES OF GYMNOPHTHALMIDAE (REPTILIA: SQUAMATA) FROM MARINGMA TEPUI, WESTERN GUYANA

P. J. R. KOK

Abstract

A new genus is erected for *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, collected at 2080 m elevation on Mount Maringma, a sandstone flat-topped table mountain (tepui) located in the eastern Pakaraima Mountains, at the Guyana- Brazil border. The new genus mainly differs from all other known gymnophthalmids by the following combination of characters: distinctive ear opening and moveable eyelids, limbs pentadactyl with all digits clawed, prefrontals present, interparietal and parietals forming a jagged, irregular posterior margin, three pairs of genials, second pair of genials in contact with only one infralabial, dorsal scales hexagonal, keeled, in transverse rows only, ventral scales imbricate, hexagonal, mucronate, broadly keeled, in transverse rows only, and hemipenis weakly bilobed with series of curved transverse plicae bearing mineralized spicules.

Article first published in *Zootaxa*, 1992, 53–57 (2009)
Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The first expedition to the summit of Maringma tepui (5°13’N, 60°35’W, Figs. 1–3), one of the highest tepuis of Guyana, located about 17 km (airline) east of Mount Roraima, was conducted in 2004 by botanist David Clarke (University of North Carolina at Asheville) and collaborators, who cut a trail from the base of the mountain to its summit. In February 2006 Bruce Means (Coastal Plains Institute and Land Conservancy, Florida) reached the summit of Maringma by helicopter and collected a few frog species at the top, apparently none of them being new to science (D. Bruce Means, pers. comm.).

At the end of 2007, our team (composed of the author, and two Guyanese counterparts; helped by several Amerindian porters) sampled the area along an altitudinal transect (see Means & Savage 2007) from the surrounding uplands around the village of Philipi (5°21’N, 60°22’W, *ca*. 510 m asl) to the highest summit of Mount Maringma (*ca*. 2147 m asl), which represents a walk of roughly 40 km. We mostly followed the trail pioneered by Clarke (although many parts of it became undetectable) from the base of Maringma to its summit.

Only the very top of Maringma tepui has solid “dry” ground, and rocky outcrops are small and very limited in number. The summit vegetation (Fig. 3) consists of a mixture of the typical “tepui meadow”, large areas of quaking peat bog, and patches of dwarf forests largely dominated by *Bonnetia roraimae* (Bonnetiaceae). Deep swampy pools are numerous and surround the tepui summit, its plateau being not completely flat but more or less stair-stepped, with a total surface of about 170ha. Climatic conditions on Maringma tepui are extreme, with great temperature fluctuation (we recorded temperature variation from 13.5 to 37.5°C during our stay on the summit between 25–30 November 2007). Freezing powerful winds, diluvian rains, and persistent mist were the usual weather conditions during our stay on the tepui.

Among the new species of amphibians and reptiles discovered during our field trip to Maringma tepui was one enigmatic lizard of the family Gymnophthalmidae from the summit of the mountain, which does not fit in any currently known gymnophthalmid genus and is described herein.

MATERIAL AND METHODS

The holotype was photographed alive before euthanization by intracardiac injection of Xylocaïne. Tissue (liver) was removed and preserved in 95% ethanol before fixation of the whole individual in 10% formalin. Both specimen and tissue were deposited at the Institut Royal des Sciences Naturelles de Belgique (IRSNB), where the specimen was transferred to 70% ethanol for permanent storage.

Coordinates and elevations were acquired using a Garmin 60CSx GPS (Global Positioning System) unit and were referenced to map datum WGS84.

Scale counts were made using a Leica stereo dissecting microscope. All measurements were taken on the preserved specimen to the nearest 0.1 mm with an electronic digital caliper or to the nearest 1.0 mm with a rule. Snout-vent length (SVL) was measured from tip of snout to anterior border of cloaca; head length from tip of rostral to anterior edge of ear; trunk length is the distance between the posterior margin of forelimbs and the anterior margin of hindlimbs. Color characteristics were obtained from field notes and color digital photographs. Sex was confirmed by the presence of hemipenes.

Taxonomy follows Pellegrino *et al.* (2001) and Rodrigues *et al.* (2005). Scale terminology and character definitions mostly follow those of Harris (1994), Kizirian (1996), and Myers & Donnelly (2008); the term *occipitals* is used to name the distinct, enlarged, scales posterior to and bordering the parietals and the interparietal.

Diagnosis mostly follows the format of Doan & Castoe (2005), Kok (2005), and Myers & Donnelly (2008) for ease of comparison.

The new genus was compared to original descriptions of gymnophthalmid genera, digital photographs of type specimens, and type museum material when available. Material studied is listed in Kok (2005); additional material examined is in the Appendix. Intergeneric comparisons were mainly based on the work of Uzzell (1969, 1973), Oftedal (1974), Hoogmoed & Avila-Pires (1992), Gorzula & Señaris (1998), MacCulloch & Lathrop (2001), Myers & Donnelly (2001, 2008), Rodrigues *et al.* (2002, 2005, 2007), and Kok (2005). Museum abbreviations are those of Frost (2008).

RESULTS

Pantepuisaurus genus novum

Type species. *Pantepuisaurus rodriguesi* **species novum**

Etymology. A noun in apposition, derived from “Pantepui” referring to the phytogeographic province where the type species was discovered, and the Greek *sauros* meaning “lizard”. Gender masculine.

Content. *Pantepuisaurus rodriguesi* **species novum**; monotypic.

Diagnosis. An elongate gymnophthalmid (known SVL in male 58.3 mm) with a long tail (1.6x SVL) and the unique following combination of characters: (1) distinctive ear opening and moveable eyelids, (2) limbs pentadactyl with all digits clawed, (3) nasal scales separated by a single frontonasal, (4) prefrontals present, (5) frontoparietals, parietals and interparietal present, (6) parietals and interparietal longer than wide, (7) interparietal and parietals forming a jagged, irregular posterior margin, (8) occipitals present, (9) three pairs of genials, second pair in contact with only one infralabial, (10) enlarged median pairs of gulars, (11) dorsal scales hexagonal, keeled, in transverse rows only, (12) ventral scales imbricate, hexagonal, mucronate, broadly keeled, in transverse rows only, (13) tongue anterodorsally covered by oblique, anteriorly converging plicae, posterodorsally covered by large scalelike papillae (14) hemipenis weakly bilobed with series of curved transverse plicae bearing mineralized spicules.

Pantepuisaurus differs from members of Alopoglossinae in having the tongue anterodorsally covered by oblique plicae and posterodorsally covered by large scalelike papillae (entirely covered by oblique plicae in Alopoglossinae), the interparietal and the parietals forming a jagged, irregular line (straight posterior margin), and in having ventral scales in transverse rows only (in transverse and longitudinal rows in Alopoglossinae);

from members of Gymnophthalminae in having hands pentadactyl with the first finger clawed (first finger absent, reduced and/or clawless in Gymnophthalminae); from Rhachisaurinae in having external ear openings (absent in Rhachisaurinae). Within Cercosaurinae (*sensu* Pellegrino *et al.* 2001 and Rodrigues *et al.* 2005), *Pantepuisaurus* differs from all genera except *Ecpleopus* and *Leposoma* of the *scincoides* group in having hexagonal, mucronate ventral scales arranged in transverse rows only. *Pantepuisaurus* is readily distinguished from *Ecpleopus* (characters of *Ecpleopus* in parentheses) notably by the presence of a broad keel on ventrals (absent), quadrangular gular scales (mucronate), complete superciliary series (incomplete), and the presence of femoral pores in males (absent). *Pantepuisaurus* is quickly separated from *Leposoma* of the *scincoides* group (characters of *Leposoma* in parentheses) in having quadrangular gular scales (mucronate), by the absence of distinct striations on head scales (present), the interparietal and the parietals forming a jagged, irregular line (round posterior margin), and the presence of occipitals (absent). Two additional gymnophthalmid genera, *Adercosaurus* and *Kaieteurosaurus*, have not been assigned to any subfamily yet, but might be related each other and with *Pantepuisaurus*. *Pantepuisaurus* is immediately distinguished from *Adercosaurus* (characters of *Adercosaurus* in parentheses) in having imbricate, hexagonal, mucronate, broadly keeled ventral scales in transverse rows only (smooth, in transverse and longitudinal rows), in having a highly reduced fourth infralabial (not reduced) and the second pair of genials partly separated from the infralabials and in contact with one infralabial only (not separated from the infralabials, in contact with two infralabials), in lacking oblique plicae at the rear of the tongue, which is posteriorly covered by large scalelike papillae (rear of tongue covered by oblique plicae), and in having mineralized spicules on hemipenes' plicae (absent). *Pantepuisaurus* is most similar to *Kaieteurosaurus* in having hexagonal, mucronate ventral scales arranged in transverse rows only, but it is readily distinguished from it (characters of *Kaieteurosaurus* in parentheses) by the presence of prefrontal scales (absent), three pairs of genials (two), in having a highly reduced fourth infralabial (not reduced) and the second pair of genials partly separated from the infralabials and in contact with one infralabial only (not separated from the infralabials, in contact with two infralabials), the common suture of the interparietal and parietals forming a jagged, irregular line (more or less straight posterior margin), an entire nasal (divided), and the aspect of the ventral scales that are much less lanceolate and mucronate than in *Kaieteurosaurus*. It should be emphasized here that *Kaieteurosaurus* also has broad "keels" on ventral scales (*i.e.* the central part of the scale is broadly elevated), a character that was only noticed while closely comparing the two genera. This character is not conspicuous in all *Kaieteurosaurus* specimens and is mostly noticeable on anteriormost and posteriormost ventral scales. In *Kaieteurosaurus* the significant lateral extension of the flat "keel" gives a lanceolate, smooth, "unkeeled" aspect to the ventral scales as described by Kok (2005), while the keel is more prominent and conspicuous in *Pantepuisaurus*. Figure 4 schematically illustrates the difference in the aspect of the broad keel on ventral scales between *Pantepuisaurus* and *Kaieteurosaurus*. A summary of main diagnostic characters for *Pantepuisaurus*, *Adercosaurus* and *Kaieteurosaurus* is in Table 1.

Distribution. The genus is currently known only from the type locality, the summit of Maringma tepui in Guyana (Fig. 1).

Taxonomic comments. No less than eight new gymnophthalmid genera have been described (Myers & Donnelly 2001, Doan & Castoe 2005, Kok 2005, Rodrigues *et al.* 2005, 2007, Rodrigues & Maranhão dos Santos 2008) since the molecular-based phylogenetic hypothesis of Pellegrino *et al.* (2001), who demonstrated the monophyly of Gymnophthalmidae. Some higher-level taxonomic changes are still in debate (see Castoe *et al.* 2004, Rodrigues *et al.* 2007) and refinement of higher-level taxonomy of gymnophthalmids is still necessary.

Morphologically, the new genus shows some similarities with *Adercosaurus* and *Kaieteurosaurus*. Giving the low number of specimens available, any speculation on the relationships between *Adercosaurus* (known only from the holotype), *Kaieteurosaurus* (known only from three specimens), and *Pantepuisaurus* (known only from the holotype) seems premature. More specimens of these three genera are clearly needed to elucidate relationships between them. However, preliminary molecular analysis and comparisons do indicate affinities between *Pantepuisaurus* and *Kaieteurosaurus* (unfortunately, molecular data on *Adercosaurus* are not available), but reveal significant genetic divergences between these two genera that give further support to the erection of a new genus. Molecular analysis also suggests assignment of *Pantepuisaurus* and *Kaieteurosaurus* to the tribe Ecpleopini (Cercosaurinae) (M. T. Rodrigues, pers. comm.).

A more “conservative” attitude would have been to accommodate the new species in an already known monotypic genus sharing some morphological similarities (*i.e.* *Adercosaurus* or *Kaieteurosaurus*). However this would have given rise to two important problems: (1) assignment of the new species to either of these two genera would have been arbitrary and poorly supported because the new species differs from both of them in a combination of important characteristics currently used to diagnose gymnophthalmid genera (*e.g.* condition of the posterior margin of the interparietal and parietals, condition of ventral scales, number of genials, presence of prefrontals, hemipenial morphology, tongue morphology) (2) because the new species differs from these two genera in morphological characteristics used to separate other genera (especially in the tribe Ecpleopini), placing the new species in one of them would have rendered the taxonomic status of these and other genera dubious by suggesting that these characters are variable intragenerically (thus making taxonomy of the group more complicated instead of simplifying it). One could suggest that *Kaieteurosaurus* is a synonym of *Adercosaurus*, however this is not supported by any evidence, these two genera being differentiated on the basis of many important diagnostic characters (see Kok 2005).

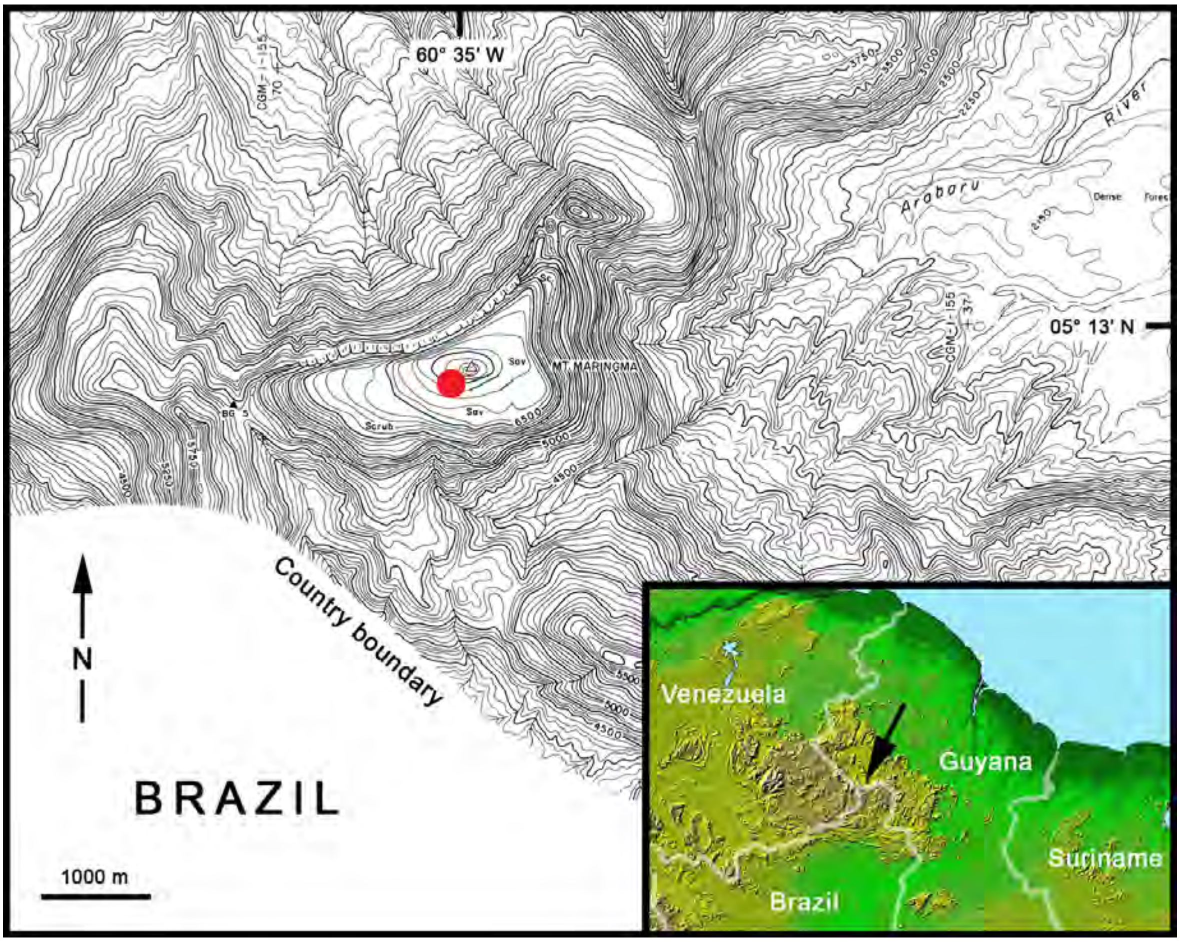

Figure **1.** Area map of Mount Maringma showing the type locality of *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.** (red dot). Coordinates and boundary with Brazil are approximate and based on the available map (note that there is a substantial difference in the country boundary between this map and that shown in Google Earth). Maps elaborated after "Roraima Sheet 40 SE" published by the Survey Department of Guyana, 1972, and a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388.

Pantepuisaurus rodriguesi species novum
Figs. 5–9

Holotype. IRSNB 2650 (field number PK 2044), an adult male collected by Paul Benjamin, Philippe J. R. Kok and Claudius Perry, 28 November 2007 at 14h55, summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05° 12' 57"N, 060° 35' 07"W, 2080 m).

Etymology. The specific epithet is a noun in the genitive case, honoring Brazilian herpetologist Miguel Trefaut Rodrigues (Universidade de São Paulo, São Paulo, Brazil) for his huge contribution to the knowledge of the family Gymnophthalmidae using both morphological and molecular approaches.

Diagnosis. In addition to the generic characteristics, the new species is also characterized by the following features: four supraoculars; 15 smooth temporal scales; scales around midbody 32; dorsal scales sharply keeled, in 33 transverse rows; ventral scales in 20 transverse rows; trunk length 2.6x length of forelimb; dorsum and flanks completely black, iris red.

Description of the Holotype. An adult male 58.3 mm SVL. Head length 19% SVL, 1.38x head width, head width 1.45x head height. Head slightly wider than neck, temporal region not distinctly swollen, neck approximately as wide as anterior body. Snout blunt. Body oval in transverse section, slightly depressed, slightly wider than high. Tail complete, 93.3 mm, 1.60x SVL, circular in cross-section, tapering toward the tip. Limbs well-developed, forelimbs 19% SVL, hindlimbs 29% SVL. Limbs pentadactyl, all fingers and toes with terminal claw. Limbs short, not overlapping when adpressed along the body. Distance between forelimbs and hindlimbs (trunk length) = 29.2 mm, 50% SVL, 2.6x forelimbs (Fig. 5).

Tongue lanceolate, anterodorsally covered by oblique (chevron-shaped), anteriorly converging plicae, posterodorsally covered by large scalelike papillae; tip bifid, smooth; one pair of infralingual plicae after fork. Anterior teeth conical, most of posterior ones bicuspid, a few of them tricuspid.

Rostral roughly hexagonal, twice as wide as high, visible from above, in broad contact with frontonasal. Frontonasal single, heptagonal, laterally in contact with nasal and loreal, not in contact with first supraocular. Prefrontals roughly pentagonal, as broad as long, with a moderately long medial suture, laterally in broad contact with first supraocular and the loreal, touching the anterior point of the second supraocular on the right, separated from it by first supraocular-frontal contact on the left. Frontal hexagonal, 1.4x as long as wide, anteriorly as wide as posteriorly, laterally markedly concave; frontal laterally in contact over the entire length of second supraocular, touching the first supraocular on the left, separated from it by prefrontal-second supraocular contact on the right, in contact with third supraocular. Frontoparietals pentagonal, 1.3x as long as wide with moderately long medial suture; each frontoparietal in contact with frontal, distinctly separated from second supraocular by frontal-third supraocular contact, in broad contact with third supraocular, parietal and interparietal, and narrow contact with the fourth supraocular. Interparietal heptagonal, posteriorly projecting, 1.7x as long as wide, with parallel sides, distinctly longer than parietals. Interparietal and parietals form a jagged, irregular, posterior margin. A row of five smooth occipitals of various shapes, shorter and wider than dorsal neck scales, the central smallest. Four supraoculars, first smallest, about 3/4 of the fourth; second and third larger, subequal. Five superciliaries, first much larger than the others, with a short incomplete suture running dorsad from ciliaries on the right side and a similar very short suture on the left side; second and third smallest, subequal, fourth distinctly larger, about twice the size of the fifth (Fig. 6).

	Adercosaurus	*Kaieteurosaurus*	*Pantepuisaurus* **gen. nov.**
Condition of the posterior margin of the interparietal and parietals	Interparietal distinctly projecting beyond parietals, posterior margin of parietals and interparietal forming a jagged irregular line	Interparietal and parietals of approximately similar length, forming a more or less straight posterior margin	Interparietal distinctly projecting beyond parietals, posterior margin of parietals and interparietal forming a jagged irregular line
Condition of the ventral scales	Quadrangular, smooth, slightly imbricate, in transverse and longitudinal rows	Lanceolate, broadly keeled (keel most conspicuous on anteriormost and posteriormost ventrals), strongly imbricate, in transverse rows only	Mucronate, broadly keeled, strongly imbricate, in transverse rows only
Presence of prefrontals	Yes	No	Yes
Number of pairs of genials	3	2	3
Second pair of genials in contact with two	Yes	Yes	No
Tongue morphology	Covered by oblique, anteriorly converging plicae, interrupted by a midsection of imbricate scalelike papillae (rear of tongue covered by plicae)	Anterodorsally covered by oblique, anteriorly converging plicae, posterodorsally covered by large imbricate scalelike papillae (rear of tongue covered by plicae)	Anterodorsally covered by oblique, anteriorly converging plicae, posterodorsally covered by large imbricate scalelike papillae (rear of tongue covered by papillae)
Hemipenial morphology	Bilobed with series of curved transverse plicae lacking mineralized spicules	Unknown	Bilobed with series of curved transverse plicae bearing mineralized spicules

Table **1.** Summary of main diagnostic characters for *Pantepuisaurus* **gen. nov.** and two possibly related genera (*Adercosaurus* and *Kaieteurosaurus*). The diagnostic characters are those currently used to separate genera in the tribe Ecpleopini [*sensu* Pellegrino *et al.* (2001); Ecpleopinae *sensu* Castoe *et al.* (2004)]. Based on Myers & Donnelly (2001), Kok (2005) and the present paper.

Figure **2.** Maringma tepui, view of the mountain from the east (20 November 2007).

Nasal entire, with two short divisions running ventrad from naris to supralabial on the left side, these two short divisions are incomplete, running from the first supralabial, on the right side; naris just below centre, directed laterally. Loreal quadrangular, slightly anteriorly inclined, in contact with nasal, frenocular, one preocular, first superciliary, first supraocular, prefrontal and frontonasal, separated from supralabials by frenocular-nasal contact. Two small preoculars between first superciliary and first subocular. Frenocular roughly quadrangular, longer than wide, about half-size the loreal, in contact with first supralabial. Four suboculars. Two postoculars, the lower smallest. Seven supralabials on both sides, fifth highest, fourth below middle of the eye; a very short, inconspicuous division on the first supralabial on the right side (running ventrad from nasal); suture between second and third supralabials in contact with first subocular, suture between first and second supralabials in contact with frenocular (Fig. 6).

Upper eyelid with three ciliaries on both sides, second very large, apparently resulting from the fusion of several smaller scales. Ocular recess with median row of three scales separating median ciliary from superciliaries. Lower eyelid with a semi-transparent, slightly pigmented, palpebral disc of two long vertical palpebral scales (Fig. 6).

Temporal region with 15 irregularly shaped, juxtaposed, smooth scales on both sides. Temporals arranged in four oblique rows. Ear opening moderately large, vertically semi-circular with a straight posterior margin, bordered by a few small, juxtaposed, smooth scales. Auditory meatus moderately deep, tympanum mostly transparent, slightly pigmented (Fig. 6).

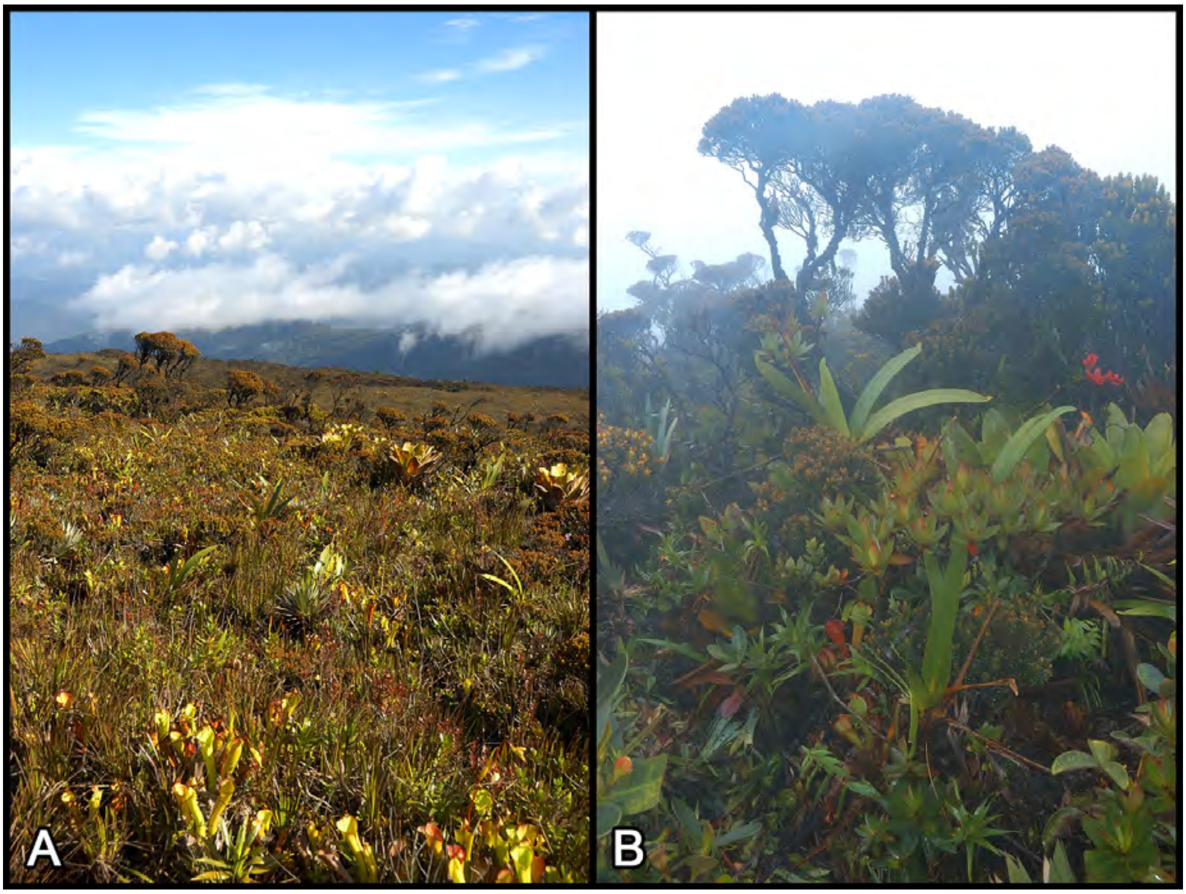

Figure **3.** Vegetation on the summit plateau of Maringma tepui. A: Habitat of *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, the typical tepui meadow, consisting of very dense low vegetation with plants mainly in the families Bonnetiaceae, Bromeliaceae, Clusiaceae, Orchidaceae, Rapateaceae, Sarraceniaceae and Xyridaceae; view from the summit plateau of the mountain, looking to the south (25 November 2007). B: Dense vegetation and *Bonnetia roraimae* (Bonnetiaceae) in the mist on the very top of the tepui (26 November 2007).

Mental trapezoidal, its posterior edge almost straight, slightly concave. Postmental large, heptagonal, laterally in contact with first and second infralabials. Three pairs of large genials, first two pairs in contact with each other medially. First pair in lateral contact with second and third infralabials; second pair in lateral contact with third infralabial only, separated from fourth and fifth infralabials by a large sublabial scale, medial suture of second pair slightly longer than that of first pair; third pair in lateral contact with fifth infralabial, separated medially by two small scales. A pair of enlarged postgenials separated medially by scales of varying sizes and widely separated from infralabials. Seven infralabials on the right side, six on the left side, fourth scale highly reduced on both sides. One row of imbricate, smooth pregulars with rounded posterior margins. Five rows of gulars, four of them with two transversely enlarged scales. Collar row with seven scales, central one distinctly larger, others decreasing in size laterally, forming a slightly scalloped margin. Gular fold distinct, concealing one row of very small scales (Figs. 6, 7B).

Head scales with numerous small pits, especially concentrated on rostral, frontonasal, supraoculars, and lateral head scales, also present on ventral head scales, and body and limbs scales. Scales on nape posterior to occipitals longer than wide, with a broad, flat keel, mucronate, in transverse rows, grading posteriorly into dorsal body scales. Sides of neck with medium-sized, roughly subequal, smooth, juxtaposed scales in about eight oblique rows, not distinctly decreasing in size posteriorly but interrupted by a row of smaller scales 2/3 the way before arm insertion, which weakly form annuli with nape and gular scales.

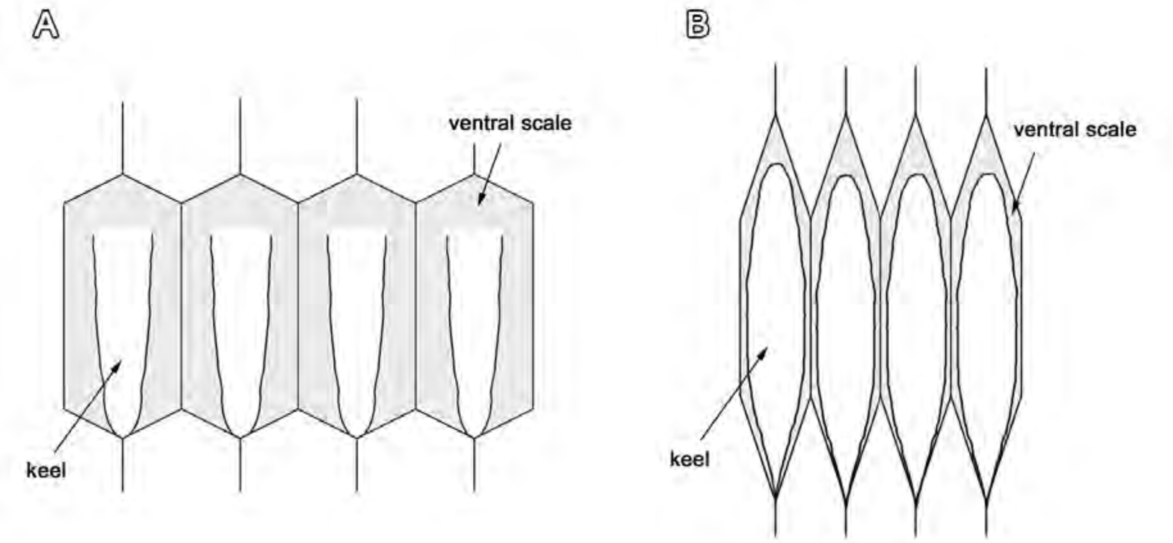

Figure **4.** Schematic illustration of the ventral scale condition in *Pantepuisaurus* **gen. nov.** and *Kaieteurosaurus*. A: Four posterior ventral scales of *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.** showing the broad keel (in white). B: Four posterior ventral scales of *Kaieteurosaurus hindsi* showing the broad keel (in white) that significantly extends laterally giving an aspect of smooth unkeeled lanceolate ventrals. Drawings are not at scale.

Dorsals imbricate, pentagonal, some appearing hexagonal because of imbrication, elongate, sharply keeled, mucronate, except very few isolated scales. Dorsal scales in transverse rows only, 33 rows between the interparietal and the posterior edge of hindlimbs (including row of occipitals). Middorsal scales not distinctly narrower than adjacent dorsals. A zone of small juxtaposed scales before arm insertion. Flank scales similar to, but slightly narrower than, dorsal scales, most of flank scales are not mucronate but have a straight or slightly rounded posterior margin; no abrupt demarcation between dorsals and laterals. Lateral scales becoming slightly smaller just before leg insertion. No row of ventrolateral scales (see Myers & Donnelly 2008) can be detected; some very small, longitudinally oval or rounded scales intercalated in the interstitial skin between the transverse rows of lateral; these small scales are more conspicuous along the first anterior third of flank and before leg insertion. All transverse rows of dorsals correspond to one row of laterals, except at midbody on the right side where one transverse row of dorsals corresponds to two rows of laterals, and before leg insertion and after arm insertion.

Ventrals imbricate, broadly keeled, longer than wide, mucronate except very few isolated scales, in transverse rows only (Fig. 7A). Most transverse rows of ventrals correspond to a transverse row of laterals and of dorsals (exceptions occur at midbody). Twenty transverse rows between collar and preanal plate, 32 scales around midbody. Preanal plate consisting of six scales, one anterior, five posterior scales, most lateral posterior scales narrow, distinctly smaller than adjacent scales (Fig. 8). Four preanal pores. Four femoral pores on the right side, three on the left side, each femoral pore between three scales.

Scales on tail keeled, not mucronate (except proximally), slightly imbricate, roughly rectangular, as long as dorsal scales, in transverse rows only, in uninterrupted annuli. Pigmented subcaudal scales keeled, slightly imbricate, slightly mucronate, roughly rectangular, in transverse rows only.

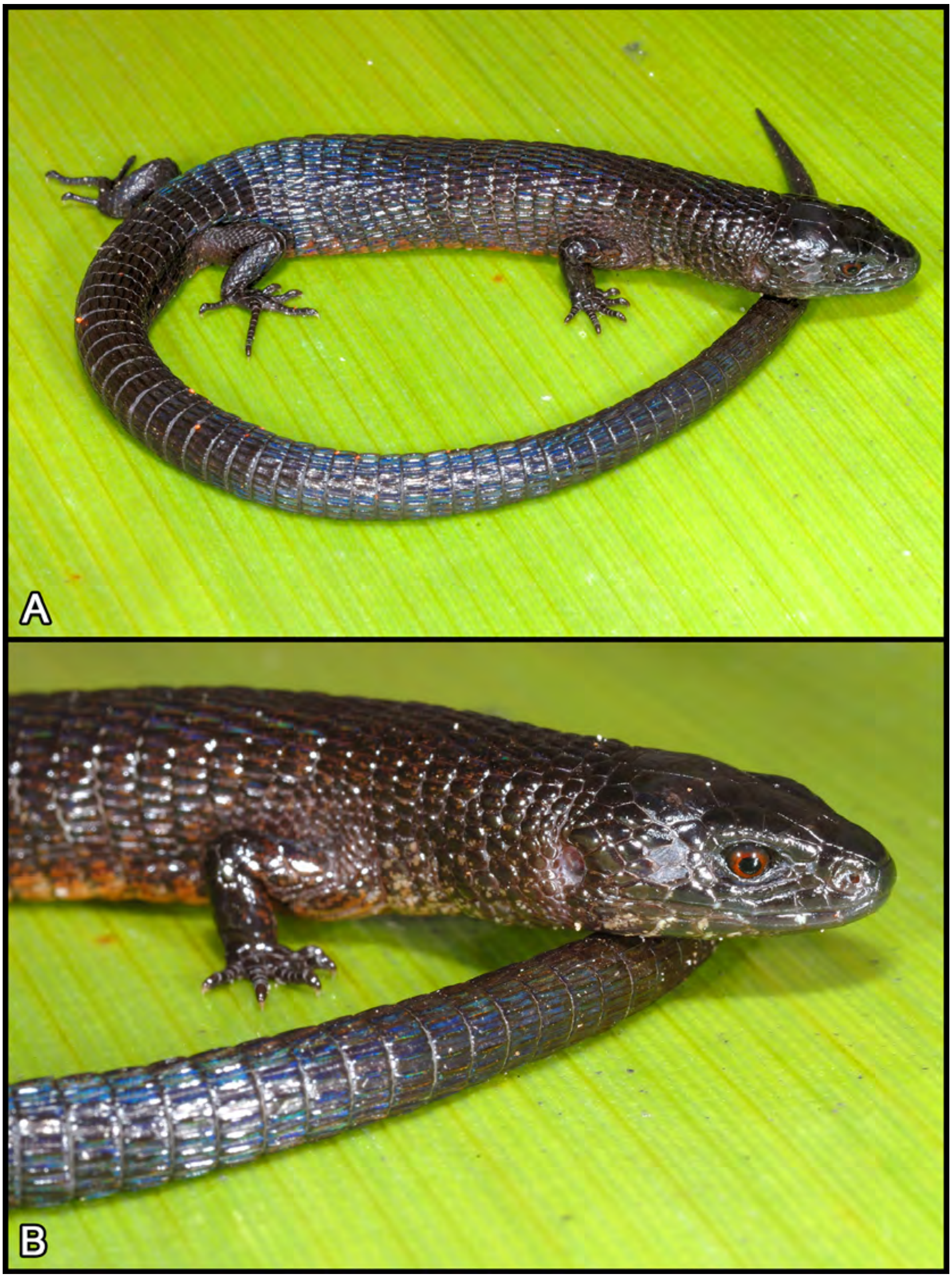

Figure **5.** *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, male holotype (IRSNB 2650), 58.3 mm SVL. A: Dorsolateral view. B: Detail of head and neck region.

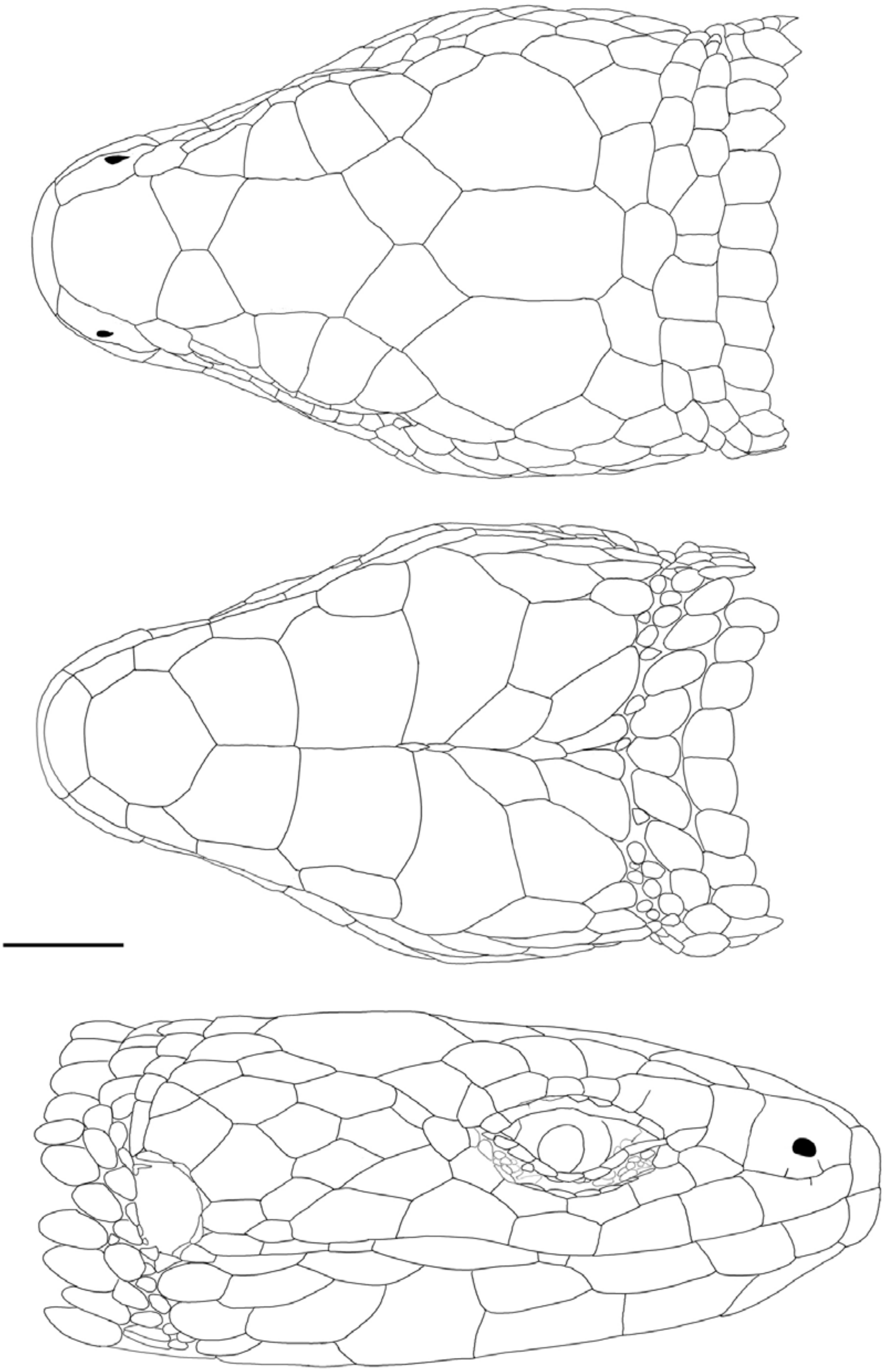

Figure **6.** *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, male holotype (IRSNB 2650), 58.3 mm SVL. Dorsal, ventral, and lateral views of head. Scale bar is 2 mm.

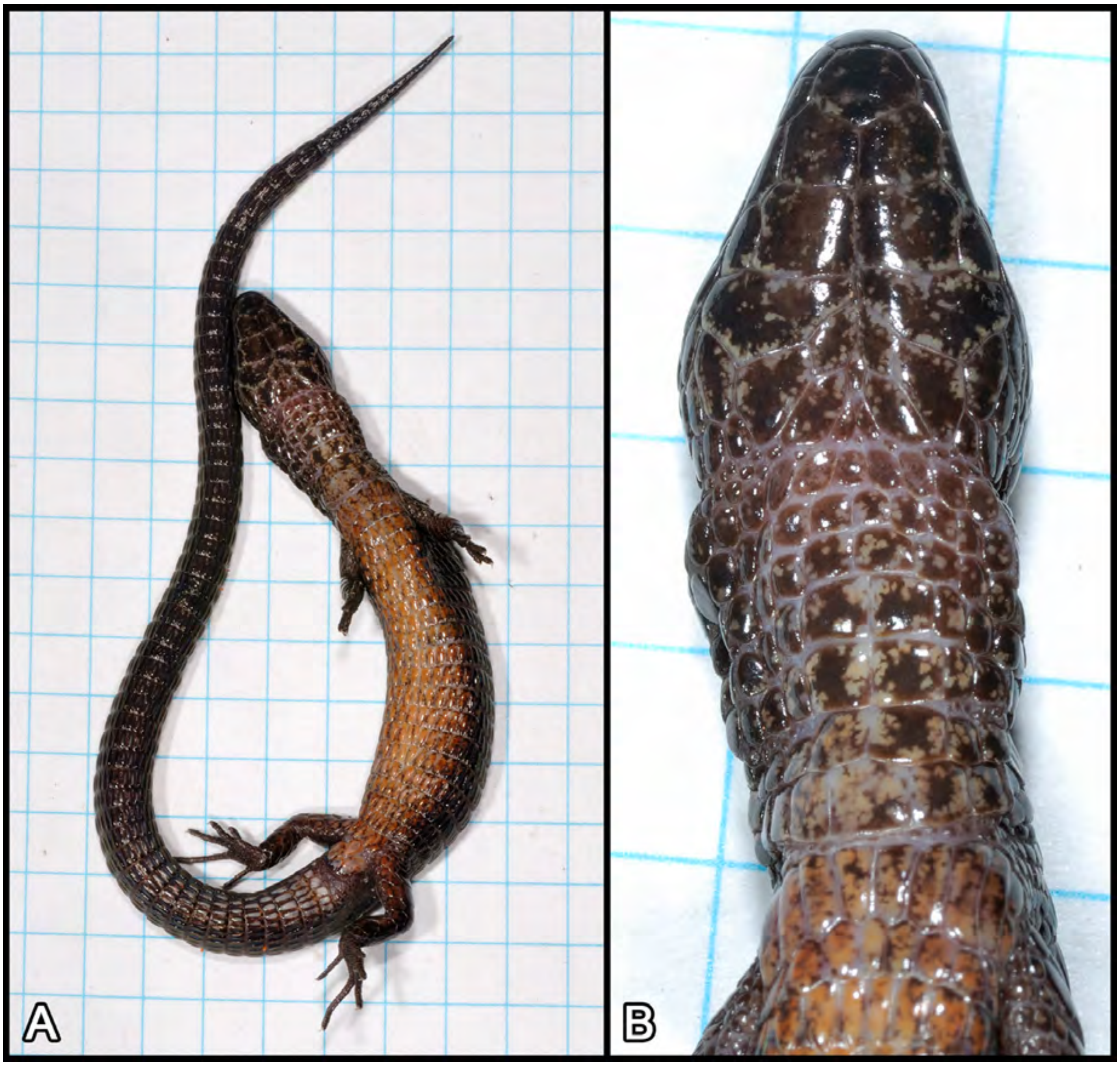

Figure **7.** *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, male holotype (IRSNB 2650), 58.3 mm SVL. A: Ventral view. B: Detail of the gular region.

Dorsal surfaces of upper and lower arms with smooth, variably polygonal scales, ventral surface of upper arms with small, juxtaposed scales, ventral surface of lower arms with scales similar to those on dorsal surface, except at the base of hands where scales are juxtaposed and distinctly smaller. Thighs with a row of enlarged, smooth, roughly hexagonal scales on anterior surface, bordered ventrally by two rows of smaller polygonal scales diminishing in size ventrad (scales of first row smooth, scales of second row broadly keeled); bordered dorsally by 2–3 rows of keeled scales diminishing in size dorsad, grading into small, smooth (but with many very small asperities and pits that give a rugose aspect), slightly granular, juxtaposed scales, which cover posterodorsal and posterior surfaces of thighs; these scales increase in size ventrally. Shanks ventrally and posteriorly with large, smooth, polygonal, imbricate scales. Scales on upper and anterior surfaces of shanks slightly smaller, imbricate, rugose (see above), and strongly keeled.

Dorsal surface of hands and digits with imbricate, smooth scales, dorsal surface of feet with imbricate, broadly keeled scales, except a few anterodorsally; palm and soles covered with small, smooth, slightly protuberant, juxtaposed, polygonal scales. Two enlarged, subequal, thenar scales on inner margin of palm below pollex, each with produced inner edge, similar scales occur at the base of Toes I and III–IV; two slightly enlarged hypothenar scales on outer margin of palm. Subdigital lamellae divided basally and single on distal halves on most digits.

Figure **8.** *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, male holotype (IRSNB 2650), 58.3 mm SVL. Detail of perianal region.

Subdigital lamellae as follows (Roman numbers indicate digits, Arabic numbers indicate paired or single lamellae on left/right; lower ungual sheath scale is omitted from the counts): hands **I** 4/4, **II** 7/7, **III** 9/9, **IV** 10/11, **V** 6/7; feet **I** 5/5, **II** 8/8, **III** 11/10, **IV** 16/16, **V** 9/8.

Color of Holotype in life. Dorsal and lateral surfaces completely black; closer examination shows that black scales on body and neck are peppered with brown or reddish brown. Upper surface of head black. Tympanum light pink. Arms, legs and tail black. Iris red (Fig. 5). Tongue dark gray in its anterior two-thirds, whitish with gray flecks on its posterior third. Palms and soles black. Underside of head and throat black with irregular light gray markings; venter orangish brown, ventral scales peppered with black; underside of upper legs black; underside of lower legs black with irregular orangish brown markings; underside of tail black, except proximally where some scales are white (Figs. 7–8).

Color of Holotype in preservative. After four months in 70% ethanol, the holotype became very dark brown, the light gray markings on the underside of head and chest are white; venter is whitish peppered with dark gray; tympanum is transparent, no other noticeable change.

Hemipenis. The hemipenes of the holotype were everted in the field. The left organ was subsequently removed, sent to and prepared by Pedro Nunes (Universidade de São Paulo, São Paulo, Brazil), currently working on a PhD thesis on the hemipenial morphology in the family Gymnophthalmidae. The hemipenis was inflated with blue petroleum jelly and the spicules were stained with Alizarin Red (Fig. 9). The left hemipenis is 6.9 mm long, with a greatest width of 4.5 mm. The organ is weakly bilobed, with each of the short divisions terminating in 2–3 protuberances. Sulcus spermaticus medial, broad, poorly defined. Asulcate surface with a conspicuous series of 15–18 curved transverse plicae (tissue ridges) encircling the side of the organ and terminating laterally on the sulcate surface, most plicae being laterally shortly interrupted by a narrow nude space. A wide nude space between the *ca.* 8–9 distal plicae on the asulcate surface. All plicae bear mineralized spicules; plicae located on the proximal part of the hemipenis bear a single spicule, the number of spicules is increasing from the proximal part towards the tip resulting in plicae bearing a series of several uniform spicules interrupted by a larger central one (Fig. 9).

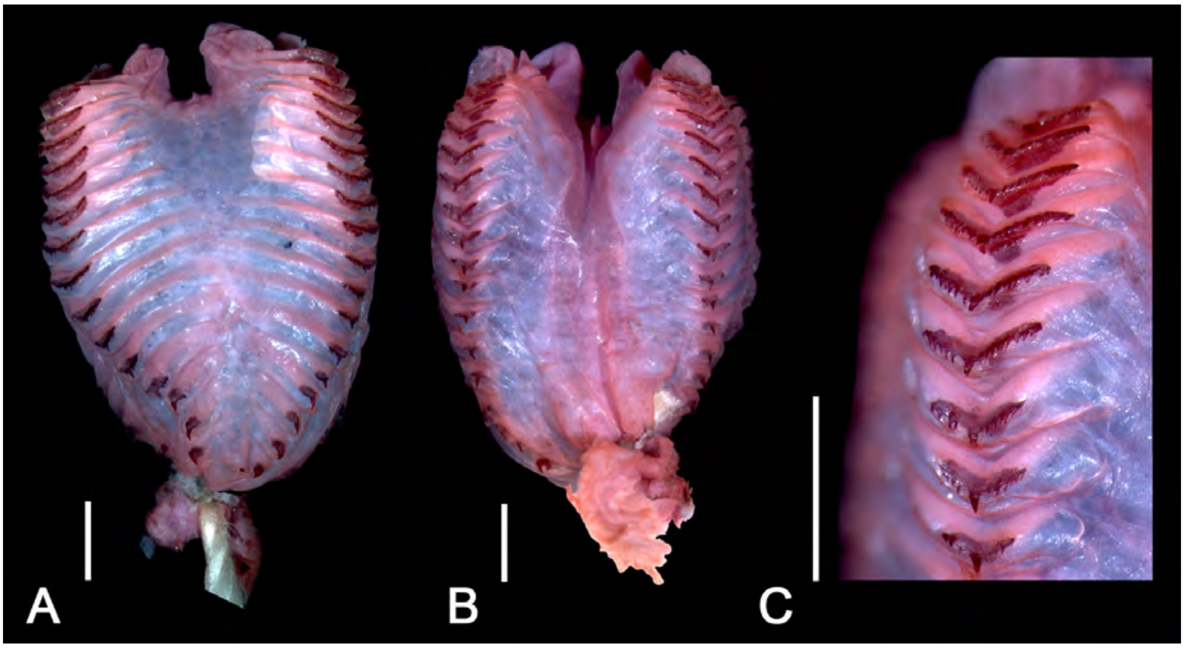

Figure **9.** Everted hemipenis of the holotype of *Pantepuisaurus rodriguesi* **gen. nov. sp. nov.**, (IRSNB 2650, left organ). A: Asulcate view. B: Sulcate view. C. Detail of mineralized spicules showing series of similar spicules interrupted by one enlarged central spicule. Scale bar is 1 mm. Photographs by Pedro Nunes.

Distribution and ecology. The species is currently known only from the type locality, the summit of Maringma tepui in Guyana (Fig. 1). The only specimen available was collected in the afternoon (14h55), during a sunny spell, in a sunny spot, on the ground, among dense vegetation (Fig. 3). No other specimen was observed. The only other lizard species recorded from the summit of Mount Maringma is *Arthrosaura hoogmoedi* Kok, 2008.

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APPENDIX. ADDITIONAL COMPARATIVE MATERIAL EXAMINED

Arthrosaura guianensis.— Guyana: *Potaro-Siparuni*: Kaieteur National Park, Tukeit trail, *ca.* 420 m asl (05° 11'N, 059° 28'W) (IRSNB 17342-3).

Arthrosaura testigensis.— Venezuela: *Bolívar*: Altiplanicie sur Terekyurén-tepui, base de Los Testigos, 1800 m asl (05° 52'N, 062° 03'W) [MHNLS 10730, holotype (digital photographs)].

Kaieteurosaurus hindsi.— Guyana: *Potaro-Siparuni*: Kaieteur National Park, Tukeit trail, *ca.* 420 m asl (05° 11'N, 059° 28'W) [IRSNB 2628 (holotype), IRSNB 17322-3].

Riolama leucosticta.— Venezuela: *Bolívar*: Ilu-tepui, 2500 m asl (05° 25'N, 061° 02'W) [USNM 284483 (digital photographs)]; Mt. Roraima, 8600ft [BM 1946.8.2.8 (holotype, formerly 1899.3.25.4)]; summit of Mount Roraima, near boundary marker for Venezuela, Guyana and Brazil, *ca.* 2600 m asl (05° 25' 08"N, 060° 44' 07"W) [USNM 284484-5 (digital photographs)].

Riolama luridiventris.— Venezuela: *Amazonas*: Municipio Atabapo, Cumbre del Cerro Marahuaca, Parque Nacional Duida-Marahuaca, 2480 m asl [ULABG 4584, holotype (digital photographs)].

Riolama uzzelli.— Venezuela: *Amazonas*: Cumbre del Cerro Marahuaca, 1850 m asl [MHNLS 12855, paratype (digital photographs)].

4

A New Species of *Oreophrynella* (Anura: Bufonidae) from the Pantepui Region of Guyana, with Notes on *O. macconnelli* Boulenger, 1900

P. J. R. Kok

Abstract

Oreophrynella seegobini **sp. nov.** is described from 2088 m elevation on Maringma tepui in the Pakaraima Mountains of Guyana, at the Guyana-Brazil border. The new species is mainly distinguished from known congeners by small size, indistinct frontoparietal crests, prominent postorbital crests, prominent suborbital crests, well-developed webbing on hand and foot, dorsal skin minutely spiculate with scattered medium to large elevated tubercles, ventral skin anteriorly rugose with few flat granules, posteriorly tuberculate, blackish brown dorsal colour, and dark brownish orange ventral colour. Data on four specimens of *O. macconnelli* collected on the southeast slope of the tepui are provided.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The upland and highland genus *Oreophrynella* currently contains eight species endemic to tepuis and tepui slopes in the Guiana Shield highlands (see Lathrop & MacCulloch 2007 for an updated distribution map of the species of *Oreophrynella*). The type species for the genus, *O. quelchii*, was originally described in the preoccupied genus *Oreophryne* Boettger, 1895 by Boulenger (1895a) and subsequently assigned to the genus *Oreophrynella* (Boulenger 1895b). *Oreophrynella* species occur between *ca.* 1067–2600 m elevation and are readily distinguished from all other bufonids by their small size, thick skin between digits, and opposable toes.

According to Graybeal & Cannatella (1995), the genus is monophyletic; it has been considered the sister taxon of *Atelopus* + *Dendrophryniscus* + *Melanophryniscus* by McDiarmid (1971) and of *Dendrophryniscus* by Cannatella (1985). The genus was discussed by Señaris *et al.* (1994), who suggested relationships with *Metaphryniscus* and *Osornophryne*, the latter plus *Atelopus* considered as the sister taxon of remaining bufonids by Frost *et al.* (2006). Ruiz-Carranza & Hernández-Camacho (1976) discussed striking phenetic similarities with *Osornophryne*, which according to them are due to evolutionary convergence. Based on morphology, Graybeal (1997) presented a tree suggesting *Oreophrynella* most closely allied with African and Asian non-*Bufo* taxa (*Didynamipus* and *Pelophryne*, respectively). Combining morphological and molecular data [obtained from *O. dendronastes* (as *Oreophrynella sp*)], Pramuk (2006) presented a tree suggesting *Oreophrynella* most closely allied to *Atelopus* and *Dendrophryniscus*.

Most *Oreophrynella* species were described subsequent to 1990 and our knowledge of these interesting creatures is slowly, but surely increasing as a result of recent collecting efforts in the Pakaraima Mountains of Guyana and Venezuela (Lathrop & MacCulloch 2007, Señaris *et al*. 1994, 2005).

A recent expedition to Maringma tepui, a sandstone flat-topped table mountain located at the Guyana-Brazil border, has uncovered an additional *Oreophrynella* species from the tepui summit that is described below. Four specimens of *O. macconnelli* Boulenger, 1900 were collected on the southeast slope of the tepui and supplementary data on this poorly known taxon are provided.

MATERIAL AND METHODS

Specimens were collected by hand, photographed alive and euthanized by immersion in Xylocaine. Tissue (a piece of liver) was removed from each specimen and preserved in 95% ethanol. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens and tissues have been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB).

Coordinates and elevations were acquired using a Garmin 60Csx Global Positioning System unit and referenced to map datum WGS84.

All measurements were taken on the preserved specimens, to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital caliper. Measurements were taken and abbreviated as follows: SVL = snout vent length, from the tip of the snout to the posterior margin of the vent; HL = head length, from the tip of the snout to just behind the jaw articulation; HW = greatest width of the head; SL = snout length, from the tip of the snout to anterior margin of the eye; EN = eye-nostril distance, from the posterior margin of the nostril to the anterior margin of the eye; EYE = horizontal diameter of the eye; IND = internarial distance, the distance between the median margins of the nostrils; IOD = interorbital distance, the distance between the median margins of the orbits; HAND = hand length, from the proximal edge of the palmar tubercle to the tip of Finger III; FEM = femur length, from the vent to the outer edge of the flexed knee; TIB = tibia length, from the outer edge of the flexed knee to the tip of the heel; FOOT = foot length, from the proximal edge of the inner metatarsal tubercle to the tip of Toe IV. Sex was determined by the presence/absence of vocal slit(s) or by dissection.

Although authors have used the terms “absent” or “present” to characterize the cephalic crests condition in *Oreophrynella*, I prefer to use the terms “indistinct” (crest not visible), “barely distinct” (crest barely visible), or “prominent” (crest well-developed), because most cephalic crests are present in all *Oreophrynella* species, even if not externally visible.

The term “webbing” is used to refer to the thick interdigital integument, which as pointed out by Señaris *et al*. (2005) considerably differs in *Oreophrynella* compared to the webbing in other anurans.

The new species was compared to original descriptions of *Oreophrynella* and museum specimens when available (additional material examined is listed in Appendix 1). Intrageneric comparisons were mainly based on the work of Boulenger (1895a, 1900), Diego-Aransay & Gorzula (1990), Lathrop & MacCulloch (2007), Myers & Donnelly (2008), Señaris (1995), and Señaris *et al*. (1994, 2005). Diagnosis mostly follows the format of Lathrop & MacCulloch (2007) and Señaris *et al*. (2005) for ease of comparison. Museum acronyms are those of Frost (2008).

RESULTS

***Oreophrynella seegobini* sp. nov.**

Figs. 1–3

Holotype. IRSNB 1979 (field number PK 2052), an adult male collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 29 November 2007 at 16h45, summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05° 12’ 59”N, 060° 35’ 05”W, 2088 m elevation).

Paratype. IRSNB 1980 (field number PK 2053), an adult male with same data as holotype.

Etymology. It is my pleasure to name this species in honour of my friend Giuliano “Kinky” Seegobin to acknowledge him for his friendship, hospitality, and always enthusiastic help during field work in Kaieteur National Park, Guyana. Kinky (as nicknamed by his friends and diamond miner colleagues) developed a keen interest in amphibians and reptiles and is continuously ready for a collecting trip, even in the middle of the night. He unfortunately cancelled the Maringma expedition due to a health issue.

Diagnosis. The new species is assigned to the genus *Oreophrynella* because of the following suite of characters: habitus bufoniform, parotoid glands absent, adult size less than 38 mm, Toes I–II opposed to III–V, thick skin between digits, skin tuberculate, tympanum absent. No other anuran in northern South America shares this combination of characters.

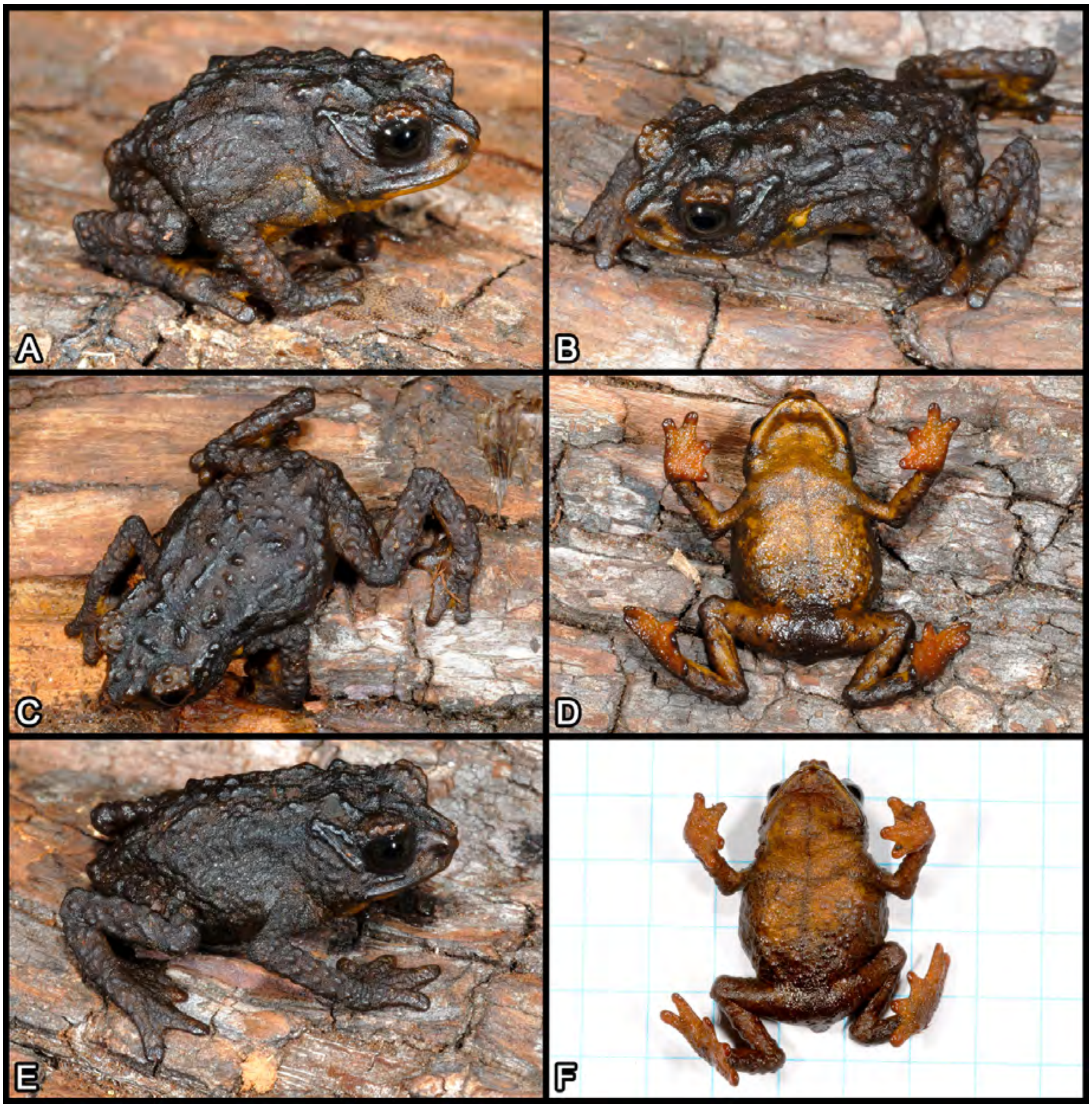

Figure **1.** *Oreophrynella seegobini* **sp. nov.** A–C: Dorsolateral and dorsal views of the holotype in life (IRSNB 1979, 20.0 mm SVL). D: Ventral view of the holotype in life. E: Dorsolateral view of the paratype in life (IRSNB 1980, 20.6 mm SVL). F: Ventral view of the paratype in life.

In addition to the aforementioned diagnostic characters, the following features characterize the new species: (1) small size (up to 20.6 mm SVL in male, female unknown); (2) frontoparietal crests indistinct; (3) postorbital crests prominent; (4) prominent short suborbital crests; (5) dorsal skin minutely spiculate with scattered medium to large, elevated, oval and round tubercles; (6) ventral skin anteriorly rugose with few large, flat, round granules, posteriorly tuberculate; (7) webbing on hand and foot well-developed; (8) adult dorsal colour in life blackish brown; (9) adult ventral colour in life dark brownish orange; (10) one vocal slit present on the left or on the right side of the floor of the buccal cavity.

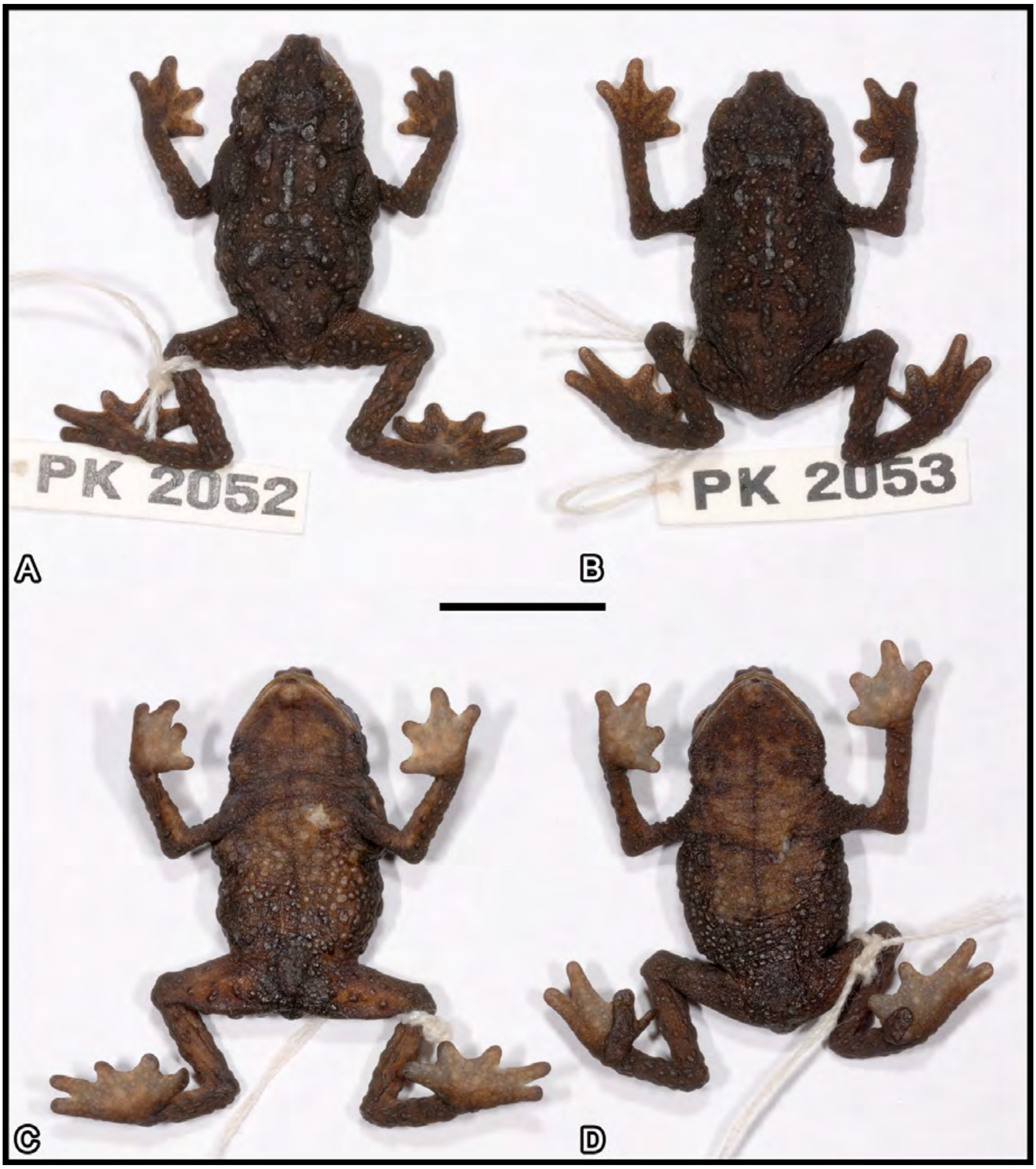

Figure **2.** *Oreophrynella seegobini* **sp. nov.** A: Dorsal view of the holotype (IRSNB 1979, 20.0 mm SVL) in preservative. B: Dorsal view of the paratype (IRSNB 1980, 20.6 mm SVL) in preservative. C: Ventral view of the holotype in preservative. D: Ventral view of the paratype in preservative. Scale bar is 10 mm.

Oreophrynella seegobini is immediately distinguished from all its known congeners, except *O. weiassipuensis* Señaris, DoNascimiento and Villarreal, 2005 by indistinct frontoparietal crests and prominent postorbital crests.

In addition to the cephalic crests condition, *Oreophrynella seegobini* further differs from *O. dendronastes* Lathrop and MacCulloch, 2007 and *O. macconnelli* by well-developed webbing (basal in *O. dendronastes* and *O. macconnelli*), blackish brown dorsal colour in life (light brownish orange to olive brown in *O. dendronastes* and *O. macconnelli*) and dark ventral colour in preservative (creamy yellow in *O. dendronastes* and *O. macconnelli*); from *O. nigra* Señaris, Ayarzagüena and Gorzula, 1994 by well-developed webbing (moderate in *O. nigra*), low density of large tubercles (high density of small closely-set tubercles in *O. nigra*) and dark brownish orange belly in life (blackish brown in *O. nigra*); from *O. quelchii* by well-developed webbing (moderate in *O. quelchii*), low density of large tubercles (high density of tubercles in *O. quelchii*) and dark brownish orange belly in life (bright orange with black mottling in *O. quelchii*); from *O. vasquezi* Señaris, Ayarzagüena and Gorzula, 1994 by well-developed webbing (moderate in *O. vasquezi*), low density of large tubercles (high density of closely-set tubercles in *O. vasquezi*) and dark flanks in life and in preservative (distinctly lighter than dorsum in *O. vasquezi*); from *O. cryptica* Señaris, 1995 by well-developed webbing (basal to moderate in *O. cryptica*), blackish brown dorsal colour in life (dark reddish brown in *O. cryptica*), and dark ventral colour in preservative (creamy white, often with a dark patch in the centre of the belly in *O. cryptica*); and from *O. huberi* Diego-Aransay and Gorzula, 1990 by well-developed webbing (basal to moderate in *O. huberi*), blackish brown dorsal colour in life (rufous-orange in *O. huberi*), and dark ventral colour in preservative (creamy white in *O. huberi*).

The new species is distinguished from *Oreophrynella weiassipuensis* by [characters of *O. weiassipuensis* according to Señaris *et al.* (2005) are in parentheses] having more prominent postorbital crests that are straight or slightly anteriorly concave (less developed, posteriorly concave), short prominent suborbital crest (indistinct), prominent canthal ridge extending roughly from tip of snout to halfway between nostril and upper eyelid (low), eye-nostril distance 79–86% of eye diameter (59%), larger and more prominent dorsal tubercles, ventral skin anteriorly rugose with large, flat, round granules, posteriorly tuberculate (granular with few small tubercles), a blackish brown dorsal colour without mid-dorsal line (reddish brown with darker marks and a thin dark brown mid-dorsal line), a dark brownish orange ventral colour with a black mid-ventral line (light reddish brown without black mid-ventral line), and orange palm and sole (light brown).

Description of the Holotype. Adult male (Figs. 1A–D, 2A, C), head slightly wider than long, HL 34% SVL, EN 86% EYE. Snout with a small fleshy conical projection on the tip, acuminate in profile, projecting beyond the level of the lower jaw, SL 1.4x EYE; loreal region smooth, vertical, slightly concave; canthus rostralis distinct, angular, with a prominent canthal ridge extending roughly from tip of snout to halfway between nostril and upper eyelid; nostrils protuberant directed laterally; internarial area highly concave; IND 117% EN; IOD 0.8x SL, 31% HW, with a few medium-sized tubercles; frontoparietal crests indistinct. Temporal region vertical, postorbital crest well-developed, prominent, very sharp, anteriorly inclined, almost straight, slightly concave anteriorly; tympanum absent; sharp subocular crest well visible, shorter than eye length, not connecting with postorbital crest; tongue lanceolate, wider posteriorly, 35% longer than wide, attached anteriorly, posterior quarter free. One vocal slit on the left side (absent on the right side), short, lateral. Premaxillary and maxillary teeth absent; choanae small, round; odontophores and vomerine teeth absent.

Forelimbs long, slender; axillary membrane absent; hands moderately large, relative finger lengths III>II=IV>I, fingers flattened, tips not expanded; palm, fingers and webbing covered by numerous small, round, supernumerary tubercles; subarticular tubercles larger than surrounding supernumerary tubercles; thenar and palmar tubercles conspicuous, prominent, thenar tubercle at base of first finger, ovoid, subequal to round palmar tubercle; webbing well-developed (Fig. 3A).

Hindlimbs long, slender, TIB 39% SVL, femur slightly longer than tibia (FEM 104% TIB), tibiotarsal articulation extending to jaw articulation when hindlimbs adpressed along body; feet moderately large; FOOT 84% TIB; Toes I–II opposed to III–V, relative toe length IV>I>V>II=III, toes flattened, tips not expanded; sole, toes and webbing covered by numerous small, round, supernumerary tubercles; subarticular tubercles larger than surrounding supernumerary tubercles; inner and outer metatarsal tubercles small, of size similar to subarticular tubercles at the base of Toes II–V, inner metatarsal tubercle slightly larger than outer one; webbing well-developed (Fig. 3B).

Cloacal opening directed ventrally at mid-level of thighs, covered by a fleshy sheath.

Dorsal skin minutely spiculate with scattered medium to large oval and round, conspicuously elevated tubercles; top of head with a few medium-sized to large tubercles, upper eyelid covered with smaller tubercles, those close to the external margin aligned in a more or less distinct row; limbs densely covered by medium-sized to large round tubercles (Fig. 1A–C). Ventral skin anteriorly rugose with few scattered large, flat, round granules, posteriorly tuberculate (Fig. 1D).

Measurements of the Holotype (mm). SVL 20.0; HL 6.8; HW 7.8; SL 3.0; EN 1.8; EYE 2.1; IND 2.1; IOD 2.4; HAND 4.7; FEM 8.1; TIB 7.8; FOOT 6.6.

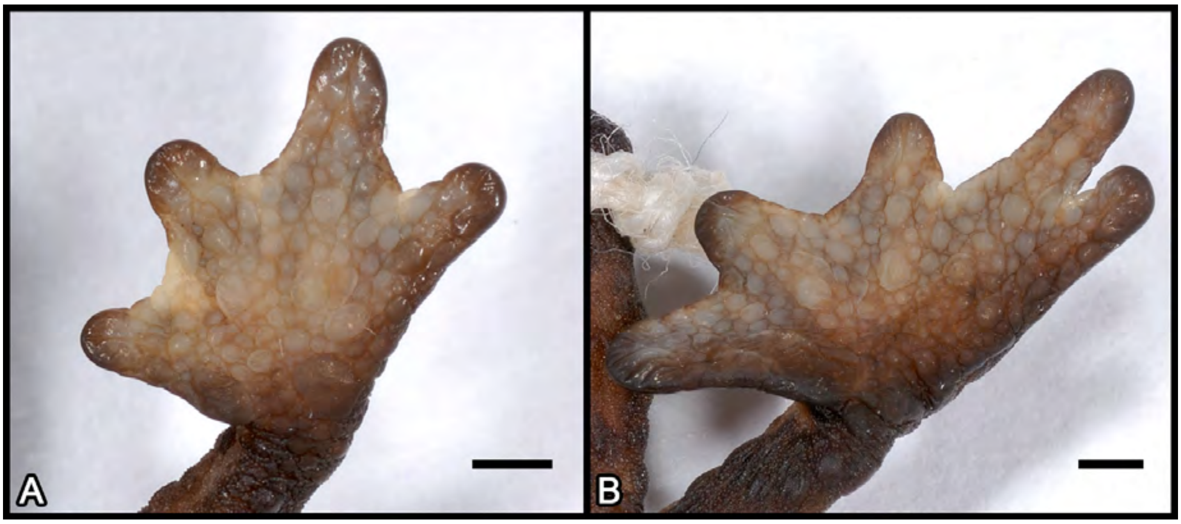

Figure **3.** *Oreophrynella seegobini* **sp. nov.**, preserved holotype (IRSNB 1979, 20.0 mm SVL, ventral view). A: Left hand. B: Left foot. Scale bars are 1 mm.

Colour in life. Dorsum, top of head and flanks blackish brown, lower arm, hindlimbs and top of hands and feet slightly lighter than dorsum. A bright yellowish orange spot at arm insertion on the left side, lacking on the right side where the area is dark brownish orange. Upper eyelids and lateral surfaces of snout dark brownish orange (Fig. 1A–C). Throat, chest and anterior part of belly dark brownish orange, posterior part of belly and area below vent blackish brown. A black mid-ventral line running from tip of lower jaw to posterior part of belly, slightly curved sinistrally. Ventral surface of limbs brownish orange. Palms and soles orange (Fig. 1D). Iris dark greenish brown with inconspicuous dark grey streaks.

Colour in preservative. Dorsal surfaces very dark brown, dorsal surfaces of hands and foot slightly lighter (Fig. 2A). Ventral surfaces dark greyish brown, with a black patch below vent. Black mid-ventral line running from tip of lower jaw to posterior part of belly more conspicuous than in life. Palms and soles light grey (Fig. 2C).

Variation. The paratype is very similar to the holotype, except as follows: EN 79% EYE; SL 0.8x EYE; IND 105% EN; IOD 1.3x SL, 29% HW; TIB 38% SVL; FEM 108% TIB; FOOT 86% TIB; inner metatarsal tubercle proportionally larger and more conspicuous, outer indistinct; subocular crest longer and more conspicuous; tongue proportionally wider posteriorly; one vocal slit on the right side (vs. on the left side in the holotype); dorsal colour slightly darker, absence of yellowish orange spot at arm insertion (Figs. 1E, 2B); ventral surface of hindlimbs dark brown (instead of brownish orange); mid-ventral line slightly curved dextrally (Figs. 1F, 2D).

Measurements of the Paratype (mm). SVL 20.6; HL 7.0; HW 7.9; SL 3.0; EN 1.9; EYE 2.4; IND 2.0; IOD 2.3; HAND 4.6; FEM 8.4; TIB 7.8; FOOT 6.7.

Distribution and ecology. *Oreophrynella seegobini* is currently known only from the type locality, the summit of Maringma tepui in Guyana (Figs. 4A–B).

Both specimens were collected on the same day at the same time (16h45), *ca.* 1.0 m from each other. The holotype was walking slowly on the muddy ground, while the paratype was found hidden under a rotting bromeliad leaf. Habitat consists of tepui scrub (Fig. 5, see Kok 2008 for details on the vegetation of the summit of Maringma tepui). Both specimens emitted a soft “peep” when handled, a similar sound that was heard around the camp in early morning and before sunset. It is thus probable that the call of the species is a soft “peep-peep-peep” similar to the call of other high elevation *Oreophrynella* species (McDiarmid & Gorzula 1989, D. B. Means, pers. comm.). The species might be more abundant than expected, but difficult to find due to minute size and cryptic colouration. More colour photographs of the habitat of the species are in Kok (2008). The only other amphibian species collected during our stay on the summit of Maringma tepui (25–30 November 2007) are *Anomaloglossus* cf. *roraima, A.* sp, and *Hypsiboas sibleszi*.

Oreophrynella macconnelli Boulenger, 1900

Oreophrynella Macconnelli [sic] Boulenger, 1900: 55
Oreophrynella quelchii macconnelli Rivero, 1961: 175
Oreophrynella macconnelli McDiarmid, 1971: 41

Oreophrynella macconnelli was described by Boulenger (1900) on the basis of a single specimen (a male, although not stated in the description) collected at *ca.* 1067 m elevation on Mount Roraima, Guyana.

Four specimens (three males, one juvenile) of this poorly known species with characteristic basal webbing on hand and foot (Fig. 6A–B) were collected on the southeast slope of Maringma tepui and conform to the holotype and to two topotypic specimens examined. Variation of measurements of the Maringma specimens is given in Table 1. I refrain from redescribing *Oreophrynella macconnelli* since a formal redescription of the species is in progress by Means (D. B. Means, pers. comm.).

The following features characterize the Maringma specimens: (1) small size (up to 22.7 mm SVL in male, female unknown); (2) frontoparietal crests indistinct; (3) postorbital crests barely distinct; (4) suborbital crest indistinct; (5) dorsal skin minutely spiculate with scattered small to medium, low, round tubercles; (6) ventral skin coarsely granular; (7) webbing on hand and foot basal; (8) adult dorsal colour in life variable, from light brownish orange to olive brown, with a series of yellow spots forming a dorsolateral line, and series of yellow spots on upper arm and thigh forming short longitudinal lines; (9) adult ventral colour in life creamy yellow with brown marbling; (10) one vocal slit present on the left side of the floor of the buccal cavity.

Colour in life. Adult dorsal colour is variable (Fig. 7A–B), ranging from light brownish orange (IRSNB 14333, adult male) to olive brown with darker spotting (IRSNB 14334–5). Olive brown specimens have distinct white spots on the lower flank, while in the orange specimen these spots are yellowish and less conspicuous. All adult specimens with a series of yellow (IRSNB 14333) to brownish orange (IRSNB 14334–5) spots forming a dorsolateral line, and series of similar spots on axilla, upper arm, groin and thigh forming short longitudinal stripes on limbs. All adult specimens have a white to yellow spot below the eye, although this spot is inconspicuous in IRSNB 14333. Adult ventral colour is creamy yellow with brown marbling; palm and sole are orange (Fig. 7D). IRSNB 14336, a juvenile, is much darker than adults in having a kaki dorsum with a few yellow spots, and dark brown flanks with a few whitish spots. A few white spots form a less conspicuous dorsolateral line than in adults, and a large longitudinal whitish spot is present on the upper arm and thigh. An anteriorly inclined whitish stripe extends from before the eye to upper lip; white spot below eye smaller than in adults (Fig. 7C). Ventral colour similar to adults, but much darker.

Character	Males (*n*=3)	Juvenile (*n*=1)
SVL	22.4 ± 0.27 (22.2–22.7)	12.3
HL	7.7 ± 0.23 (7.4–7.8)	4.5
HW	8.27 ± 0.35 (7.9–8.6)	4.8
SL	3.5 ± 0.10 (3.4–3.6)	2.0
EN	2.1 ± 0.10 (2.0–2.2)	1.1
EYE	2.6 ± 0.06 (2.5–2.6)	1.7
IND	2.33 ± 0.15 (2.2–2.5)	1.4
IOD	3.13 ± 0.12 (3.0–3.2)	2.1
HAND	5.5 ± 0.10 (5.4–5.6)	3.0
FEM	9.03 ± 0.23 (8.9–9.3)	5.4
TIB	8.53 ± 0.23 (8.4–8.8)	5.0
FOOT	6.83 ± 0.41 (6.4–7.2)	3.6

Table **1.** Morphometric measurements (in mm) of *Oreophrynella macconnelli* specimens from Maringma tepui. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

Colour in preservative. Dorsal colour ranges from light brown (IRSNB 14333) to dark grey, almost black (IRSNB 14334–6). All spots and stripes are creamy white (Fig. 8A). Ventral colour is creamy yellow in adults, dark grey with white spots in the juvenile. Palm and sole are light grey (Fig. 8B).

Distribution and ecology. According to Señaris & MacCulloch (2005) and MacCulloch *et al*. (2007), *Oreophrynella macconnelli* is reported only from the slopes of Mount Roraima in Guyana and Venezuela, between 1067–1800 m elevation. MacCulloch *et al*. (2007) considered *O. macconnelli* a highland species (*i.e.* typically occurring over 1500 m elevation) with highly restricted distribution.

Specimens from Maringma tepui were collected at 1376 m elevation and expand the known geographic range of the species to the west (roughly 17 km airline, Fig. 4A–B) suggesting a wider distribution than expected. Instead of being a highland species, *O. macconnelli* appears rather to be an upland species occasionally invading higher elevation areas.

Habitat consists of montane medium-canopy forest with abundant epiphytes and mosses, and rich undergrowth (Fig. 9A). All the Maringma specimens were found active by night, walking on the apex of epiphytic ferns (*Campyloneurum* sp., Polypodiaceae, Fig 9B) about 1.0–3.0 m above the ground, except IRSNB 14333 (adult male), which was collected on the ground at 17h00.

When handled specimens exhibited a defensive posture consisting of arching the back and flexing the head downward towards the handler (Fig. 7B).

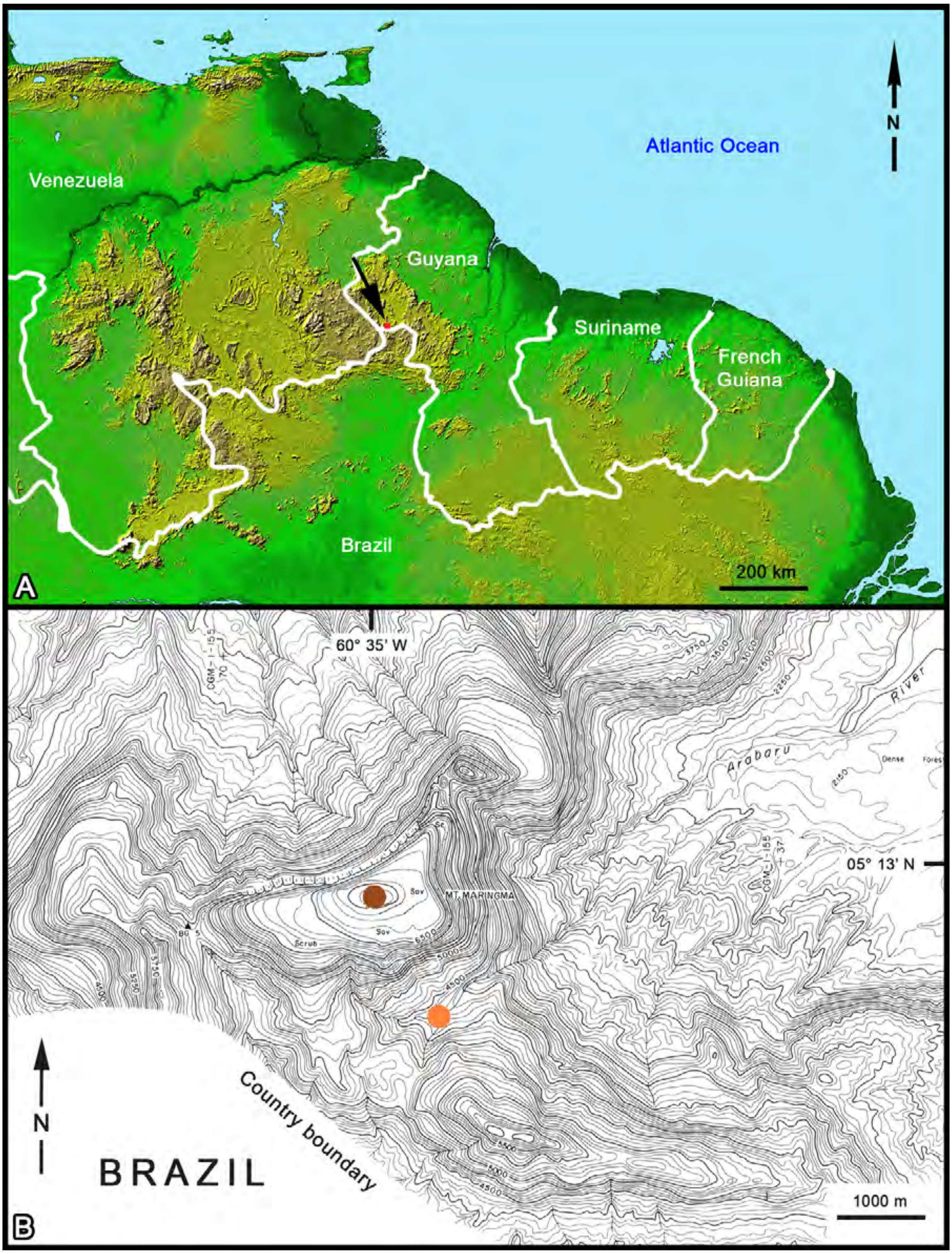

Figure **4.** A: Map of the Guiana Shield, dark arrow indicates location of Maringma tepui (in red). B: Area map of Maringma tepui showing the type locality of *Oreophrynella seegobini* **sp. nov.** (brown dot) and the collecting locality of *O. macconnelli* (orange dot). Coordinates and boundary with Brazil are approximate and based on the available map (note that there is a substantial difference in the country boundary between this map and that shown in Google Earth). Maps elaborated after "Roraima Sheet 40 SE" published by the Survey Department of Guyana, 1972, and a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388.

Figure **5.** The summit of Maringma tepui, habitat of *Oreophrynella seegobini* **sp. nov.** (29 November 2007).

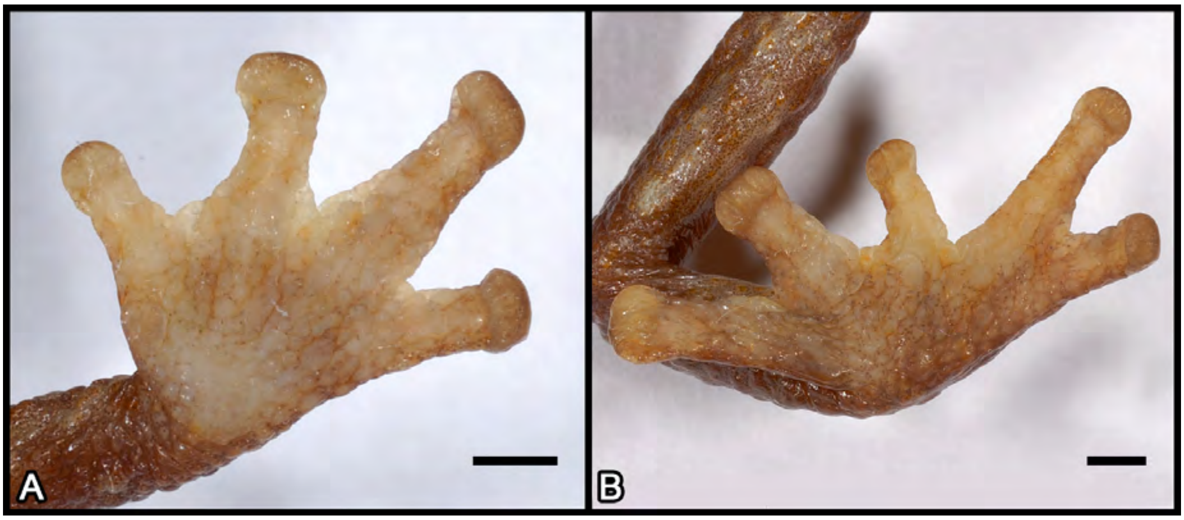

Figure **6.** *Oreophrynella macconnelli*, preserved specimen (IRSNB 14335, 22.3 mm SVL, ventral view). A: Left hand. B: Left foot. Scale bars are 1 mm.

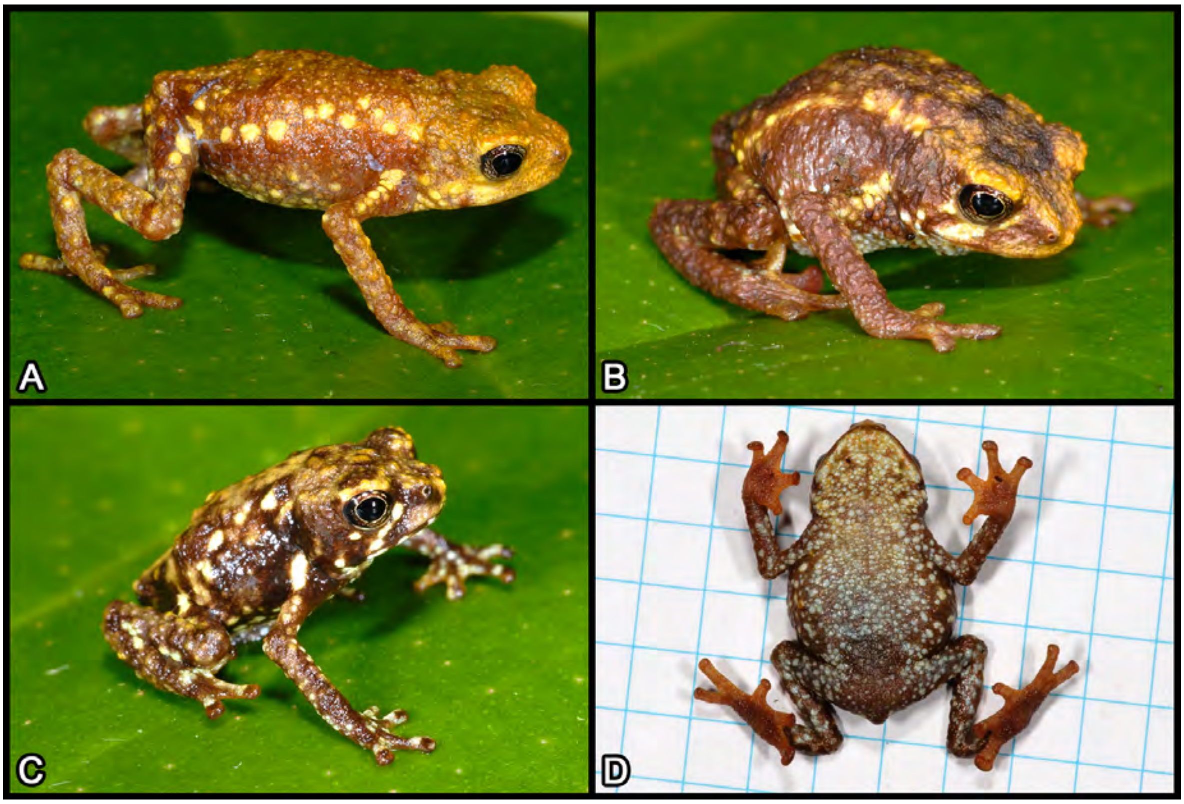

Figure **7.** *Oreophrynella macconnelli*. A: Dorsolateral view of IRSNB 14333 (adult male, 22.7 mm SVL) in life. B: Dorsolateral view of IRSNB 14334 (adult male, 22.2 mm SVL) in life. C: Dorsolateral view of IRSNB 14336 (juvenile, 12.3 mm SVL) in life. D: Ventral view of IRSNB 14334 (adult male, 22.2 mm SVL) in life.

Discussion. Since the Museo de la Estación Biológica de Rancho Grande (EBRG) and the Museo La Salle de Ciencias Naturales (MHNLS) refused to lend type material (F. Bisbal in *e-litt*., 8 January 2007, and J. C. Señaris in *e-litt*., 5 May 2008, respectively), I unfortunately have not seen specimens of *Oreophrynella huberi* and *O. weiassipuensis* and have relied on the original descriptions in Diego-Aransay & Gorzula (1990) and Señaris *et al*. (2005), respectively.

Morphologically, the new species is most similar to *Oreophrynella weiassipuensis*, with which it notably shares well-developed postorbital crests and indistinct frontoparietal crests; the two species mainly differ in colour pattern and shape of postorbital crests.

According to Señaris *et al.* (2005: 65), only two *Oreophrynella* species are known to occur on more than one tepui, which in both cases are in close proximity (max. 3–4 km airline apart) and connected by upland ridges (above 1500 m): *O. nigra* (Kukenán and Yuruaní tepuis) and *O. quelchii* (Mt. Roraima and Wei Assipu tepui). Although relatively close to Wei Assipu tepui (*ca.* 15 km airline) and Mt. Roraima (*ca.* 17 km airline), Maringma tepui is currently not connected to those mountains by upland ridges. It remains unknown if Maringma tepui was connected to Mt. Roraima and Wei Assipu tepui by upland ridges that might have served as faunal interchange in the past (see comments by Myers & Donnelly 2001, and Señaris *et al.* 2005).

McDiarmid (1971: 31) is apparently the first and only to mention the absence of vocal slits in *Oreophrynella* (based on the material available to him at the time, which is not listed in his text). In their revision of the genus, Señaris *et al.* (1994) make no mention of the absence/presence of vocal slits in *Oreophrynella*, and I could not find any reference to vocal slits in subsequent new *Oreophrynella* species descriptions (Diego-Aransay & Gorzula 1990, Lathrop & MacCulloch 2007, Señaris 1995, and Señaris *et al*. 2005) although most of them included male specimens. Interestingly, a single vocal slit is present in *O. macconnelli* (on the left side of the tongue in all males examined [n = 6], except the holotype in which it is undetectable, possibly because of the bad condition of the specimen) and *O. seegobini* (on the left side of the tongue in the holotype, on the right side in the paratype). The male paratype of *O. dendronastes* I examined (ROM 39652) has bilateral vocal slits, the left one being almost undetectable. The presence of a unilateral vocal slit in adult males is observed in some species of other bufonid genera (*e.g. Anaxyrus*, *Ansonia*, *Ingerophrynus*, *Melanophryniscus*).

There appear to be four *Oreophrynella* species groups: a first group containing upland species with indistinct frontoparietal crests, barely distinct postorbital crests, basal webbing, and arboreal habits (*O. dendronastes* and *O. macconnelli*); a second group containing highland species with indistinct frontoparietal crests, indistinct to barely distinct postorbital crest, moderate webbing, and terrestrial habits (*O. nigra*, *O. quelchii*, and *O. vasquezi*); a third group containing highland species with prominent frontoparietal and postorbital crests, basal to moderate webbing, and terrestrial habits (*O. cryptica* and *O. huberi*); and a fourth group containing highland species with indistinct frontoparietal crests, prominent postorbital crests, well-developed webbing, and terrestrial habits (*O. seegobini* and *O. weiassipuensis*).

McDiarmid (1971) predicted that opposable toes in *Oreophrynella* could reflect a partially arboreal existence, which was later refuted by McDiarmid & Gorzula (1989). However we now know that at least two upland species (*O. dendronastes* and *O. macconnelli*) have arboreal habits. Even in the absence of a phylogeny it seems likely that (1) opposable toes are a plesiomorphic character for the genus, and (2) extension of the interdigital integument is apomorphic and might be an adaptation to a more terrestrial way of life. These hypotheses should be tested by thorough morphological and molecular studies (Kok, in progress).

The recently described *Oreophrynella dendronastes* (Lathrop & MacCulloch 2007) from Mount Ayanganna, Guyana is very similar to *O. macconnelli*. Lathrop & MacCulloch (2007) differentiated between the species on the basis of a single character, the shape of the snout in profile (reported as truncate in *O. dendronastes* vs. projecting beyond mouth in *O. macconnelli*). This character is variable among the preserved specimens of *O. macconnelli* that I have examined (including the holotype and two topotypic specimens) and probably subject to post-mortem and preservation artefacts. Therefore *O. dendronastes* might be conspecific with *O. macconnelli*. Additionally, as observed in the Maringma specimens and as reported on the label of a topotypic specimen of *O. macconnelli* (BM 1976.702) collected 12 feet (*ca*. 3.6 m) above ground level, both species share arboreal habits, an apparently unique trait in the genus *Oreophrynella*. The fact that *O. macconnelli* is an upland rather than a highland-restricted species might explain a wider distribution than other *Oreophrynella* taxa. The larger size of *O. dendronastes* might prove to be adequate to separate the species (see comments by Lathrop & MacCulloch 2007), but our knowledge of relations between body size and age in the genus is nonexistent. Additional data and material (especially from the upland areas between Mt. Roraima and Mt. Ayanganna) should be examined to test the validity of *O. dendronastes*.

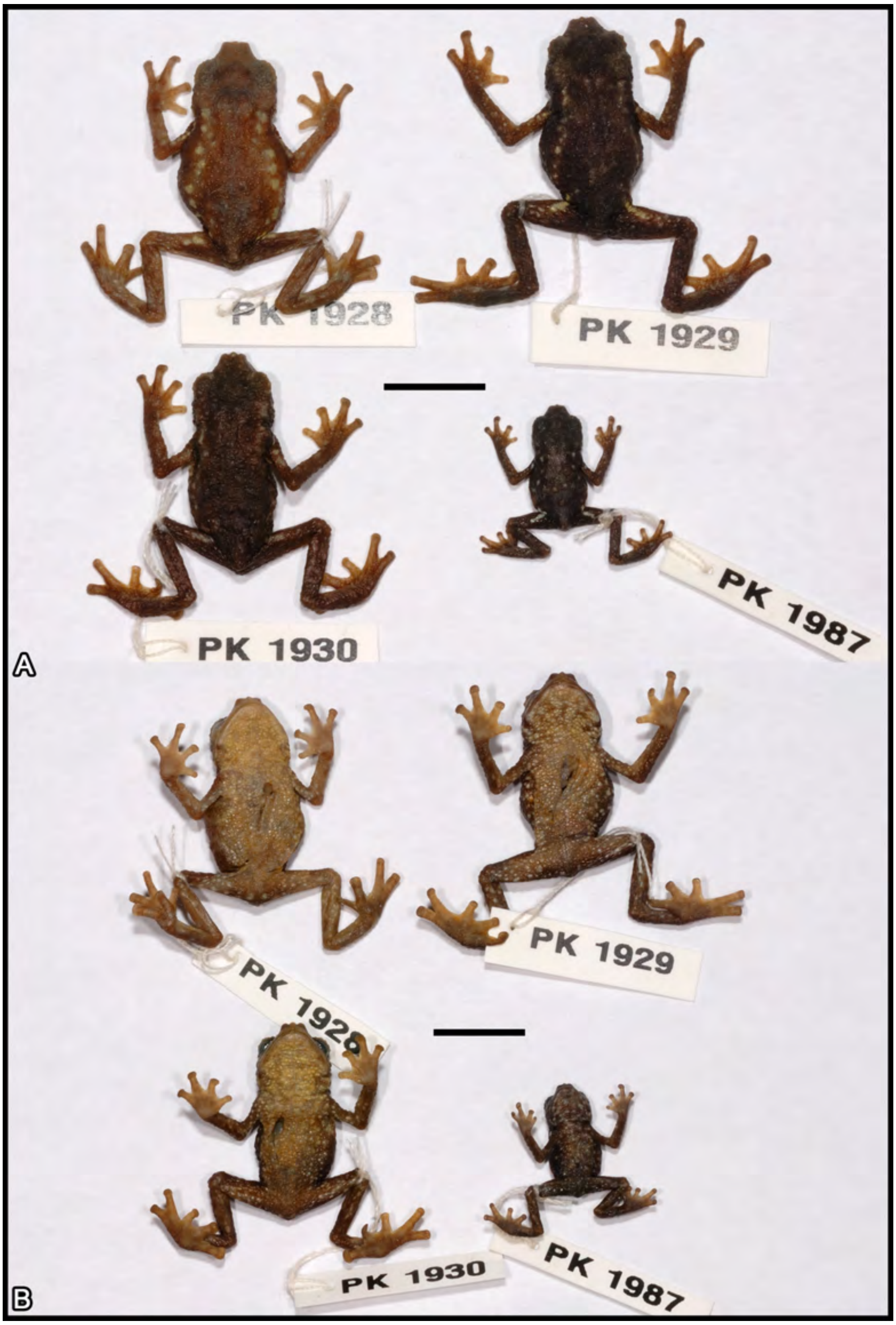

Figure **8.** *Oreophrynella macconnelli*, preserved specimens. A: Upper row, from left to right, dorsal view of IRSNB 14333 (adult male, 22.7 mm SVL) and IRSNB 14334 (adult male, 22.2 mm SVL); lower row, from left to right, dorsal view of IRSNB 14335 (adult male, 22.3 mm SVL) and IRSNB 14336 (juvenile, 12.3 mm SVL). B: Ventral views of the same specimens as above, respectively.

Figure **9.** Habitat of *Oreophrynella macconnelli* on the southeast slope of Maringma tepui. A: Montane medium-canopy forest with abundant epiphytes and mosses, and rich undergrowth. B: *Campyloneurum* sp., Polypodiaceae, an epiphytic fern species on which most specimens of *O. macconnelli* specimens were collected (white arrow indicates typical location of a specimen).

McDiarmid (1971) and McDiarmid & Donnelly (2005) suggested that *Oreophrynella* probably has arisen from a Gondwanan ancestor, but this hypothesis is in contradiction with Roelants *et al.* (2007), who suggested that the family Bufonidae originated in the Paleogene (thus well after Africa-South America separation), and the recent hypothesis of Pramuk *et al.* (2008) of a strict South American origin of Bufonidae.

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APPENDIX 1. ADDITIONAL MATERIAL EXAMINED

Oreophrynella dendronastes.— Guyana: *Mazaruni-Potaro*: northeast slope of Mount Ayanganna, 1490 m asl [IRSNB 1981 (paratype, formerly ROM 39647), ROM 39652 (paratype)].

Oreophrynella cryptica.— Venezuela: Auyantepui summit, 7750 ft (approx. 2400 m) (BM 1976.1116, 1976.169–170, 1976.172).

Oreophrynella macconnelli.— British Guiana [Guyana]: Mt. Roraima, 3500 feet [BM 1947.2.14.40 (holotype, formerly 1899.3.25.17)]; Mt. Roraima, northern slopes, camp VIII, 4800 feet (BM 1976.702); Mt. Roraima, northern slopes, camps IX–VIII trail, 5800 feet (BM 1976.703); Maringma tepui, southeast slope, 1376 m asl (05° 12’ 16”N, 060° 34’ 39”W) (IRSNB 14333-6).

Oreophrynella nigra.— Venezuela: *Estado Bolívar*: Kukenan-tepui, 2550–2600 m [IRSNB 1969 (paratype, formerly MHNLS 10485)]; Cerro Cuquenan, 2550–2600 m (BM 1982.1377–78).

Oreophrynella quelchii.—Venezuela: Roraima summit, 8600 feet [BM 1899.3.25.7–13 (syntypes), BM 1976.174–202, 1976.1115].

Oreophrynella vasquezi.—Venezuela: *Estado Bolívar*: Ilu-tepui, *ca.* 2500 m (BM 1982.1379–80).

5

A New Species of *Anomaloglossus* (Anura: Aromobatidae) from the Pakaraima Mountains of Guyana

P. J. R. Kok, R. D. MacCulloch, A. Lathrop,
B. Willaert & F. Bossuyt

Abstract

We describe a new species of *Anomaloglossus* from the Pakaraima Mountains of Guyana. *Anomaloglossus megacephalus* **sp. nov.** is currently known from Maringma Tepui at 1060 m elevation and from Mt. Ayanganna at 1490 m elevation. The new species can be distinguished from all known congeners by the following combination of characters: relatively large size (females up to 28.3 mm), head large, Finger I subequal or shorter than II, the tip of Finger IV surpassing the base of the distal tubercle on Finger III when fingers are adpressed, fingers with preaxial keel-like lateral folds, best developed on Fingers II and III, toes moderately webbed with folded flaplike fringing, symmetrical cloacal tubercles present, dorsolateral stripe absent, ventrolateral stripe present, inconspicuous, oblique lateral stripe present, often broken in spots. *Anomaloglossus megacephalus* has been previously confused with *A. tepuyensis,* a taxon described from Auyantepui in Venezuela.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The genus *Anomaloglossus* contains twenty-four species—some of them previously assigned to the genus *Colostethus*—many of which apparently have restricted distribution ranges (Grant *et al.* 2006). *Anomaloglossus* species are easily distinguished from other Aromobatidae by the synapomorphic presence of a median lingual process (Grant *et al.* 2006).

Anomaloglossus species display considerable variation in reproductive biology. The six species for which data on reproductive behaviour are available have terrestrial eggs (*i.e.* non-aquatic). After hatching, tadpoles are transported on males' dorsum to a suitable body of water, except in *A. stepheni* (Martins, 1989) (tadpole endotrophic, nidicolous), and in *A. degranvillei* (Lescure, 1975) (tadpole endotrophic, developing on the male's back). In phytotelm-breeding species like *A. beebei* (Noble, 1923), tadpoles hatch from eggs laid on leaves above the water-filled axis of bromeliads and slide into the bromeliad tank; males transport them only occasionally, for instance when there is no food in the bromeliad tank (Kok *et al*. 2005). Maternal care (here laying of trophic eggs) is reported in two species [*A. beebei* and *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006a)]. Tadpole deposition sites are invariable within species and range from phytotelmata [*e.g. A. beebei*, *A. roraima* (La Marca, 1998)], to small forest puddles [*e.g. A. kaiei*, *A. praderioi* (La Marca, 1998)] and to running water [*e.g. A. tepuyensis* (La Marca, 1998)].

The genus is reported to occur on the Pacific slopes of the Andes in Colombia and Ecuador (three species), in the Amazonas state of Brazil (one species) and in the Guiana Shield (21 species), where most species (16 species, 67% of all known *Anomaloglossus*) occur in the uplands and highlands of the Pantepui region, a biogeographic province referring to the complex of mountains mainly derived from the sandstone of the Roraima Group in southern Venezuela, west-central Guyana and northern Brazil [see Myers & Grant (2009), Barrio-Amorós *et al.* (2010), Frost (2010), and Kok (2010) for number of known species and detailed species distributions].

Because of the sometimes large intraspecific variability, *Anomaloglossus* can be morphologically difficult to distinguish [*e.g. A. baeobatrachus* (Boistel & de Massary, 1999) and *A. stepheni*], particularly in preservative. Several areas within the distribution of the genus are still largely unexplored and cryptic species are probably not uncommon in the genus (Fouquet *et al*. 2007).

Grant *et al.* (2006) included an *Anomaloglossus* specimen collected during the Royal Ontario Museum Ayanganna Expedition in 2000 in their phylogenetic study, and cautiously identified it as *A. tepuyensis*—a species described from Auyantepui in Venezuela—on the basis of morphology. Grant *et al.* (2006: 120) aptly mentioned that their identification "*will likely require revision*" and predicted "*additional specimens and/or molecular data will reveal that these are different species*". MacCulloch & Lathrop (2009) followed Grant *et al.*'s (2006) tentative identification. In the meantime two additional *Anomaloglossus* specimens became available from Mt. Ayanganna and Maringma Tepui, Guyana and PJRK had the opportunity to examine the type series of most *Anomaloglossus* from the Pantepui region in the context of a taxonomic redefinition of the Pantepui species. Direct comparisons indicated that the specimens from Guyana are not conspecific with *A. tepuyensis* from the type locality and further morphological comparisons showed that the Guyanese populations represent an undescribed taxon, which is described herein.

MATERIAL AND METHODS

Specimens were collected by hand and euthanized by immersion in Xylocaine or in a mixture of clove oil, ethanol and water. Tissue (a piece of liver or thigh muscle) was removed from most specimens and preserved in 95-100% ethanol. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens have been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) and the Royal Ontario Museum (ROM); tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (VUB) and ROM (see Appendix for material examined).

Coordinates and elevations were acquired using a Garmin 60CSx Global Positioning System unit and referenced to map datum WGS84.

All morphometric data were taken from the preserved specimens by the same person (BW) [except HL2, HL3, HW, and BEL (taken by PJRK)], to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital caliper. For ease of comparison, the description mainly follows the pattern of recent descriptions in the genus (*e.g.* Kok *et al.* 2006a, Myers & Donnelly 2008, Kok 2010). Measurements were taken and abbreviated as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL1); (3) head length from angle of jaw to tip of snout (HL2); (4) midline distance from snout tip to an imaginary line between anterior arm insertions when arms at right angle with body (HL3); (5) head width at level of angle of jaws (HW); (6) snout length from anterior corner of eye to tip of snout (SL); (7) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (8) internarial distance (IN); (9) eye length (EL); (10) interorbital distance (IO); (11) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (12) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (13) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (14) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (15) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (16) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (17) width of disc on Finger III (WFD); (18) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (19) width of disc on Toe IV (WTD); (20) tibia length from outer edge of flexed knee to heel (TIL); (21) upper arm length from anterior insertion with the body to outer edge of flexed elbow (AL); (22) midline distance from an imaginary line between anterior arm insertions when arms at right angle with body to an imaginary line between anterior thigh insertions when thighs at right angle with body (BEL).

Webbing formulae follow Savage & Heyer (1967), with modifications proposed by Myers & Duellman (1982) and Savage & Heyer (1997). Relative lengths of fingers were compared according to Kaplan (1997), using the distance from the proximal edge of the palmar tubercle to the tip of each finger.

Colour pattern in life was taken from field notes and colour photographs. Sex and maturity were determined by the presence/absence of vocal slit(s) and by dissection. Internal soft anatomy was examined by dissection of preserved specimens.

Comparisons of external character states are based both on original descriptions and examination of museum specimens, usually including the type series (see Appendix for material examined). Since examination of comparative type series sometimes revealed discrepancies between type specimens and original descriptions, our diagnoses may differ from those usually proposed.

Taxonomy follows Grant *et al*. (2006). Institutional acronyms follow Frost (2010).

NEW SPECIES DESCRIPTION

Anomaloglossus megacephalus sp. nov.

Figs. 1–4; Table 1

Anomaloglossus tepuyensis (La Marca, 1998) in part; Grant *et al*. (2006: 120, 158)
Anomaloglossus tepuyensis (La Marca, 1997 [sic]); MacCulloch & Lathrop (2009: 11, figs. 5–6, plate B)

Holotype. IRSNB 1986 (field number PK 1881), an adult female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 20 November 2007 at 16h30, eastern base of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05° 12’ 37”N, 060° 33’ 59”W, 1060 m elevation).

Paratypes. ROM 39637-38, adult females collected by Amy Lathrop and Carter Cox, 28 October 2000, northeastern plateau of Mount Ayanganna, Cuyuni-Mazaruni District, Guyana (05° 24’ N, 59° 57’ W, 1490 m elevation).

Etymology. The specific epithet is a combination of *mega* (Greek meaning "large") and *cephalus* (Greek meaning “head”), which refers to the large head of the species and is used as a noun in apposition.

Adult definition and diagnosis. (1) large-sized *Anomaloglossus* (male unknown, female 27.3–28.3 mm SVL); (2) body robust, but relatively more slender than most known congeners, head large; (3) skin on dorsum smooth to granular, more tuberculate posteriorly, skin on venter smooth to slightly granular; (4) Finger I subequal or shorter than II; (5) tip of Finger IV surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed; (6) distal tubercle on Finger IV present; (7) condition of Finger III in males unknown; (8) fingers with keel-like lateral folds (*sensu* Myers & Donnelly 2008), best developed preaxially on Fingers II and III; (9) toes moderately webbed, with well-developed folded flaplike fringing (*sensu* Myers & Donnelly 2008); (10) tarsal keel well-defined, weakly curved, slightly tuberclelike; (11) presence of black arm gland in males (*sensu* Grant & Castro-Herrera 1998, see also Grant *et al.* 2006) unknown; (12) symmetrical cloacal tubercles present; (13) pale paracloacal mark present; (14) dorsolateral stripe absent in female (condition unknown in males); (15) ventrolateral stripe present, inconspicuous; (16) oblique lateral stripe present, broken in spots or relatively well-defined; (17) condition of sexual dichromatism in throat colour unknown; (18) condition of sexual dichromatism in ventral colouration unknown; (19) iris with metallic pigmentation and pupil ring; (20) large intestine anteriorly pigmented; (21) colour of testes unknown; (22)

mature oocytes partly pigmented; (23) median lingual process short, wider than long, tapered (24) maxillary teeth present, small.

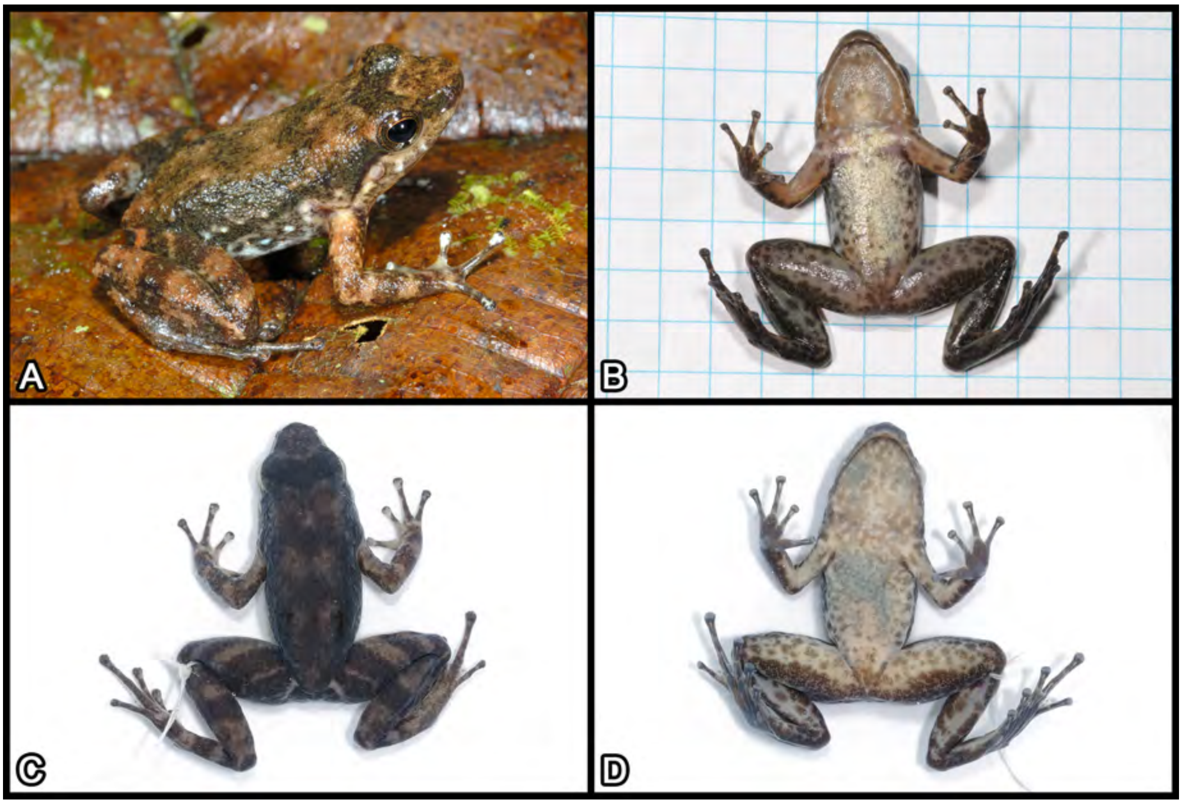

Figure **1.** *Anomaloglossus megacephalus* **sp. nov.** A: Dorsolateral view of the holotype in life (IRSNB 1986, 27.3 mm SVL). B: Ventral view of the holotype in life. C: Dorsal view of the preserved holotype. D: Ventral view of the preserved holotype. Photos by PJRK.

Description of the Holotype. An adult female 27.3 mm SVL in excellent condition of preservation. Dorsal skin granular, more tuberculate posteriorly; ventral skin slightly granular. In preservative, a barely distinct epidermal ridge borders the tip of snout dorsally. Dorsal surface of hind limbs granular and tuberculate, with two distinct symmetrical enlarged tubercles located laterally between urostyle and vent (Fig. 1; see Grant *et al.* 1997 for a description and illustration of the cloacal tubercles).

Head longer than wide (HL2 > HW), greatest width 34% of SVL. Snout bluntly pointed in lateral view, extending past the lower jaw, bluntly pointed in ventral and dorsal views. Nares located close to tip of snout, directed posterolaterally; nares visible from front, barely visible from above and below; posterior rim of naris bordered behind by a crescent-shaped ridge; rim bearing a small tuberclelike prominence posterodorsally, this “bump” is distinct in frontal, dorsal and ventral views; internarial distance 40% of greatest head width. Canthus rostralis well defined; loreal region straight, sloping outward to lip. Interorbital distance 83% of eye length, 90% of upper eyelid width. Snout length 123% of eye length, 49% of head length; distance from anterior corner of eye to posterior margin of naris 60% of eye length. Postrictal tubercles inconspicuous. Tympanic membrane inconspicuous, round, concealed posterodorsally by a diffuse supratympanic swelling; tympanic annulus prominent anteroventrally; tympanum 43% of eye length, separated from eye by a distance equal to 23% of eye length. Midline distance from tip of snout to arm insertion greater than distance from arm insertion to thigh insertion (HL3 > BEL).

Forearm slightly longer than upper arm, no distinct ulnar fold. Hand moderate in size, HAND III 27% of SVL, 78% of HW. Relative length of fingers III > IV > I ≥ II. Fingers unwebbed. Discs of fingers expanded, disc on Finger IV widest, discs on other fingers subequal. Fingers with keel-like lateral folds (*sensu* Myers & Donnelly 2008), best developed pre- and (slightly) postaxially on Finger II and preaxially on Finger III (Fig. 2 A).

Palmar tubercle large, rounded, slightly heart-shaped; thenar tubercle smaller, elliptical; one or two round to ovoid subarticular tubercles (one each on Fingers I and II, two each on Fingers III and IV, with distal tubercles on Finger III and IV slightly less conspicuous). A very low, barely distinct outer metacarpal fringe. Tip of Finger IV distinctly surpassing the base of distal subarticular tubercle on Finger III when fingers adpressed. No fleshy supracarpal fold atop wrist (Fig. 2 A).

Hind limbs robust, moderately long, with heel of adpressed leg reaching anterior corner of eye; TIL 49% of SVL. Relative lengths of adpressed toes IV > III > V > II > I; first toe short, slightly surpassing the base of subarticular tubercle of second toe. Toe discs expanded, slightly larger than finger discs, largest on Toes II and IV. Feet moderately webbed; all toes with well developed folded flaplike fringing (*sensu* Myers & Donnelly 2008), except on postaxial edge of Toe V on the right side. Webbing formula **I** 0^{+}–2^{-} **II** 1^{-}–2 1/2 **III** 2^{-}–3^{+} **IV** 3 1⁄3–2^{-} **V** (Fig. 2 A).

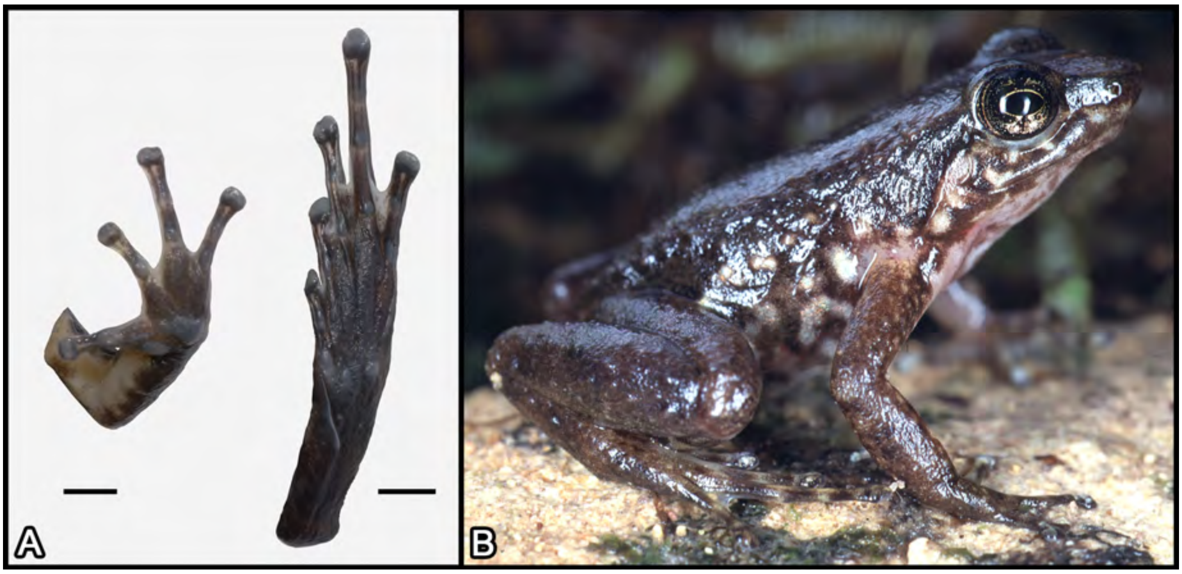

Figure **2.** *Anomaloglossus megacephalus* **sp. nov.** A: Ventral views of left hand (left) and left foot (right) of the female holotype (IRSNB 1986, 27.3 mm SVL). Scale bars are 2 mm. B: ROM 39638, female paratype (27.9 mm SVL), from Mt. Ayanganna. Photos by PJRK (A) and AL (B).

Inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, round, about half the size of the inner; a distinct oval medial metatarsal tubercle present on both sides. One to three round to ovoid subarticular tubercles (one each on Toes I and II, two each on

Toes III and V, and three on Toe IV, with distal tubercle on Toe IV the smallest and least conspicuous). A strong outer metatarsal fold coextensive with the folded flaplike fringing on Toe V, almost reaching the outer metatarsal tubercle on the left side; outer metatarsal fold absent on the right side. A slightly tuberclelike tarsal keel weakly curved at proximal end, extending proximolaterad from preaxial edge of inner metatarsal tubercle, not continuous with the fringe along the outer edge of the first toe (Fig. 2 A).

Maxillary teeth present, small. Tongue longer than wide, wider and free posteriorly, with rounded margin; median lingual process short, wider than long, tapered.

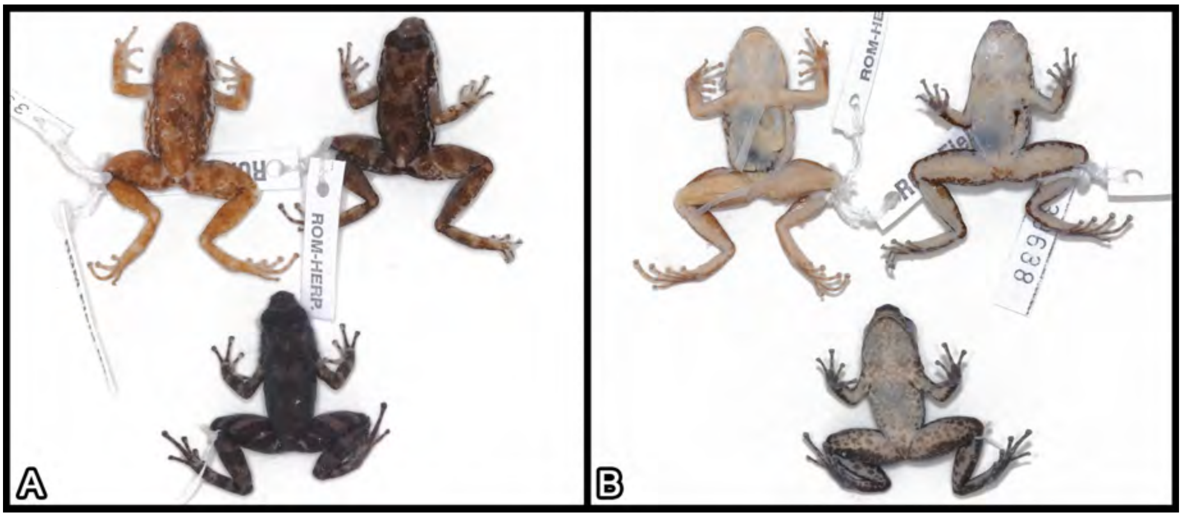

Figure **3.** *Anomaloglossus megacephalus* **sp. nov.**, showing intra- and interpopulational variation in dorsal (A) and ventral (B) pattern in preservative. Two upper specimens are from Mt. Ayanganna: ROM 39637 (upper left, female 28.3 mm SVL) and ROM 39638 (upper right, female 27.9 mm SVL). Lower specimen is the holotype (female 27.3 mm) from Maringma Tepui. Photos by PJRK.

Colour of the Holotype in life. Dorsal ground colour medium brown, with a dark brown V-shaped interorbital bar slightly outlined with light creamish brown, followed by two less defined dark brown bars, the first more or less V-shaped, at the level of arm insertion, the second just anterior to sacrum. Small, poorly defined, dark brown flecks on snout, between and on dorsal bars. Upper surface of arm light brown with well-defined dark brown transverse bands on forearm and wrist, a less defined one on elbow; upper surface of thigh, shank, and foot light brown with well-defined dark brown transverse bands. A yellow wash on the anterior face of the thigh. Flanks dark brown, slightly lighter ventrally with a few bluish irregular spots and a few whitish irregular blotches on the lower part forming a broken inconspicuous ventrolateral stripe. A few white spots (covering small tubercles) form a broken oblique lateral stripe that does not extend to arm insertion. No dorsolateral stripe. Upper lip creamish brown suffused with melanophores, two bluish marks below eye; loreal region and side of head dark brown; tympanum area light creamish brown concealed in a poorly defined light stripe from posterior corner of eye to arm insertion. A dark brown stripe is present on the anterior edge of upper arm, tapering from arm insertion to forearm. Throat light brown, blotched with white and dark brown; belly light grey, blotched with dark brown, blotches more numerous and larger laterally. Undersurface of upper arm light brown with a few dark markings; undersurface of forearm blackish; undersurface of thigh and shank light grey blotched with dark brown; rear of thigh and cloacal region blackish. Pale reddish orange paracloacal marks present. Tip of digits whitish. Palms and soles black. Iris mostly orange-bronze, darkened with black suffusion, with two oblique metallic white marks separated by a black triangular mark below pupil (Fig. 1 A–B).

Colour of the Holotype in preservative. Dorsal ground colour brown, with a dark brown V-shaped interorbital bar slightly outlined with light brown, followed by two less defined dark brown bars, the first more or less V-shaped, at the level of arm insertion, the second just anterior to sacrum. Small, poorly defined, dark brown flecks on snout, between and on dorsal bars. Upper surface of arm light brown with well-defined dark brown transverse bands on elbow, forearm and wrist; upper surface of leg light brown with well-defined dark brown transverse bands on thigh, shank, and foot. Flanks dark brown, with some irregular spots and a few whitish irregular blotches on the lower part forming a broken inconspicuous ventrolateral stripe. A few white spots (covering small tubercles) form a broken oblique lateral stripe that does not extend to arm insertion. No dorsolateral stripe. Upper lip dirty brown suffused with melanophores, two whitish marks below eye; loreal region and side of head black; distinct whitish stripe extending from posterior corner of eye to arm insertion including most of tympanum. A dark brown stripe is present on the anterior edge of upper arm, tapering from arm insertion to forearm. Throat and belly whitish, blotched with dark brown. Undersurface of upper arm whitish with a few dark markings; undersurface of forearm blackish; undersurface of thigh whitish blotched with dark brown; undersurface of shank light grey blotched with dark brown; rear of thigh and cloacal region blackish. Light brown paracloacal marks present. Palms and soles black (Fig. 1 B–C).

Variation. See Table 1 for morphometric measurements of the holotype and the paratypes and Figs. 2 B and 3 for intra- and interpopulational variation.

Symmetrical enlarged cloacal tubercles are clearly visible in the holotype. Those tubercles are present, but less visible in the paratypes probably due to an artefact of preservation (cloacal tubercles are most visible in well preserved specimens).

Only the holotype and one paratype have a medial metatarsal tubercle, a character that is sometimes present in other *Anomaloglossus* species as well.

Only the holotype lacks folded flaplike fringing on the postaxial edge of Toe V and a coextensive strong outer metatarsal fold on the right side, indicating an aberrant condition.

An additional difference between the holotype and the paratypes is the length of Finger I, which is slightly longer than II in the holotype on the left hand (*vs.* shorter in the two paratypes), and subequal on the right hand (*vs.* shorter in the two paratypes).

Toe webbing variation in females (male unknown) is **I** 0^{+}-2^{-} **II** (1^{-}-$1^{1/2}$)–($2^{1/2}$-3^{-}) **III** (2^{-}-2)–(3^{+}-$3^{1/2}$) **IV** ($3^{1/3}$- $3^{1/2}$)–(2^{-}-2) **V**.

The condition of the oblique lateral stripe is variable among specimens, from a series of light spots/blotches extending diagonally from the groin across the flanks and barely reaching the level of the insertion of the arm (*e.g.* IRSNB 1986) to an almost solid, clearly visible stripe extending diagonally from the groin across the flanks to the level of the insertion of the arm, then breaking in a series of light spots almost reaching the eye (*e.g.* ROM 39638). Slight variation also occurs between the right and the left flank.

In life, ROM 39638 was darker and the dark dorsal bars less detectable (Fig. 2 B).

Character	IRSNB 1986	ROM 39637	ROM 39638
SVL	27.3	28.3	27.9
HL1	8.8	8.5	9.1
HL2	10.5	10.7	10.8
HL3	12.2	10.8	11.7
HW	9.2	9.9	9.6
SL	4.3	4.4	4.2
EN	2.1	2.2	2.3
IN	3.8	3.5	3.6
EL	3.5	3.6	3.5
IO	2.9	3.1	2.8
TYM	1.5	1.4	1.5
FAL	5.7	5.8	6.6
HAND I	5.4	5.0	5.6
HAND II	5.2	5.9	5.9
HAND III	7.3	8.0	7.6
HAND IV	6.0	6.2	6.1
WFD	0.9	1.0	1.1
FL	12.7	13.4	14.3
WTD	1.2	1.2	1.2
TIL	13.5	13.9	14.5
AL	5.7	5.6	5.6
BEL	10.5	10.8	12.0

Table **1.** Morphometric measurements (in mm) of the type series of *Anomaloglossus megacephalus*. Abbreviations are defined in the text. Male is unknown.

Tadpole description. Two tadpoles were collected in a stream at 1490 m on Mt. Ayanganna. Description and illustrations of one of the two stage-25 tadpoles are provided in MacCulloch and Lathrop (2009: 11, under *Anomaloglossus tepuyensis*).

Comparison with other known *Anomaloglossus* tadpoles occurring in the Pantepui region.- Tadpoles of *A. megacephalus* most resemble those of *A. parkerae* (Meinhardt & Parmalee, 1996) and *A. tepuyensis*, which are also deposited in streams. The tadpole of *A. parkerae* was described by Duellman (1997), that of *A. tepuyensis* by Myers & Donnelly (2008). Both descriptions contain drawings and written descriptions. Two items are noteworthy: (1) Duellman (1997) describes the oral disc of *A. parkerae* as “not emarginate”, whereas Myers & Donnelly (2008) describe the oral disc of *A. tepuyensis* as “emarginate”. The oral disc margins of these two species are very similar (Duellman 1997, fig. 12; Myers & Donnelly 2008, fig. 17) and we follow Grant *et al.* (2006) in describing the oral discs of *Anomaloglossus* as emarginate; (2) Duellman (1997) describes the LTRF of *A. parkerae* as 2(1)/3, although the oral disc illustrated shows a LTRF 2(2)/3. This is obviously an error and the LTRF of *A. parkerae* is 2(2)/3, like in *A. tepuyensis* and *A.*

megacephalus.

Although there are few quantifiable differences among the larvae of *Anomaloglossus megacephalus*, *A. parkerae* and *A. tepuyensis*, the tadpole of *A. megacephalus* markedly differs from that of *A. parkerae* and *A. tepuyensis* in having a longer tail [tail length of stage-25 tadpoles is 68% of total length in *A. megacephalus* (n=2) *vs*. 62-63% in *A. parkerae* (n=4) and *A. tepuyensis* (n=29) tadpoles in the same stage], in having the maximum height of tail similar to body height (distinctly higher in *A. parkerae* and *A. tepuyensis*), and in having the upper fin noticeably lower than tail musculature at midtail (higher or equal in *A. parkerae* and *A. tepuyensis*).

When compared to other known *Anomaloglossus* tadpoles from the Pantepui region, *A. megacephalus* differs from *A. beebei* and *A. roraima* by stream habitat (phytotelmata habitat in *A. beebei* and *A. roraima*); from *A. kaiei* and *A. praderioi* in having the upper fin slightly increasing in length from tail-body junction [first quarter of upper fin straight before increasing in length to about midlength in *A. kaiei* (n=30) and *A. praderioi* (n=11)]; and from *A. tamacuarensis* (Myers & Donnelly, 1997) in having a longer tail [body length of stage-25 tadpoles is 68% of total length in *A. megacephalus* (n=2) *vs*. 63-65% in *A. tamacuarensis* (n=12) tadpoles in the same stage], and in having less marginal papillae and shorter lateral processes.

Distribution and ecology. *Anomaloglossus megacephalus* is currently only known from the eastern base of Maringma Tepui, Guyana, where it occurs at 1060 m elevation in low-canopy forest, and from the northeast plateau of Mt. Ayanganna, Guyana on the basis of two specimens collected at 1490 m elevation in dense low-canopy, high-tepui forest (Fig. 4).

Anomaloglossus megacephalus appears to be uncommon and elusive, with only three specimens collected. It is a diurnal species, the holotype was found on the sandy bank of a small forest stream. The Ayanganna specimens were collected in wet forest not closely associated with stream banks.

Egg deposition site unknown. Tadpoles are deposited in streams. Advertisement call is unknown.

Distinguishing among *Anomaloglossus* species from the Pantepui region. We first present a focussed comparison between the new species and the ten *Anomaloglossus* species known to occur in the Eastern Pantepui District (*i.e.* east of the Rio Caroní). The Rio Caroní likely acts as a biogeographic barrier for *Anomaloglossus* species since no species has been reported to occur on both sides of the river in the Guiana highlands of Venezuela and Guyana (it must be noted that very few Pantepui anurans are known to occur on both sides of the river). But, in order to provide a more comprehensive comparison, we also compared the new species with the six known *Anomaloglossus* species that occur in the Western Pantepui District (*i.e.* west of the Rio Caroní) in the Guiana highlands of Venezuela.

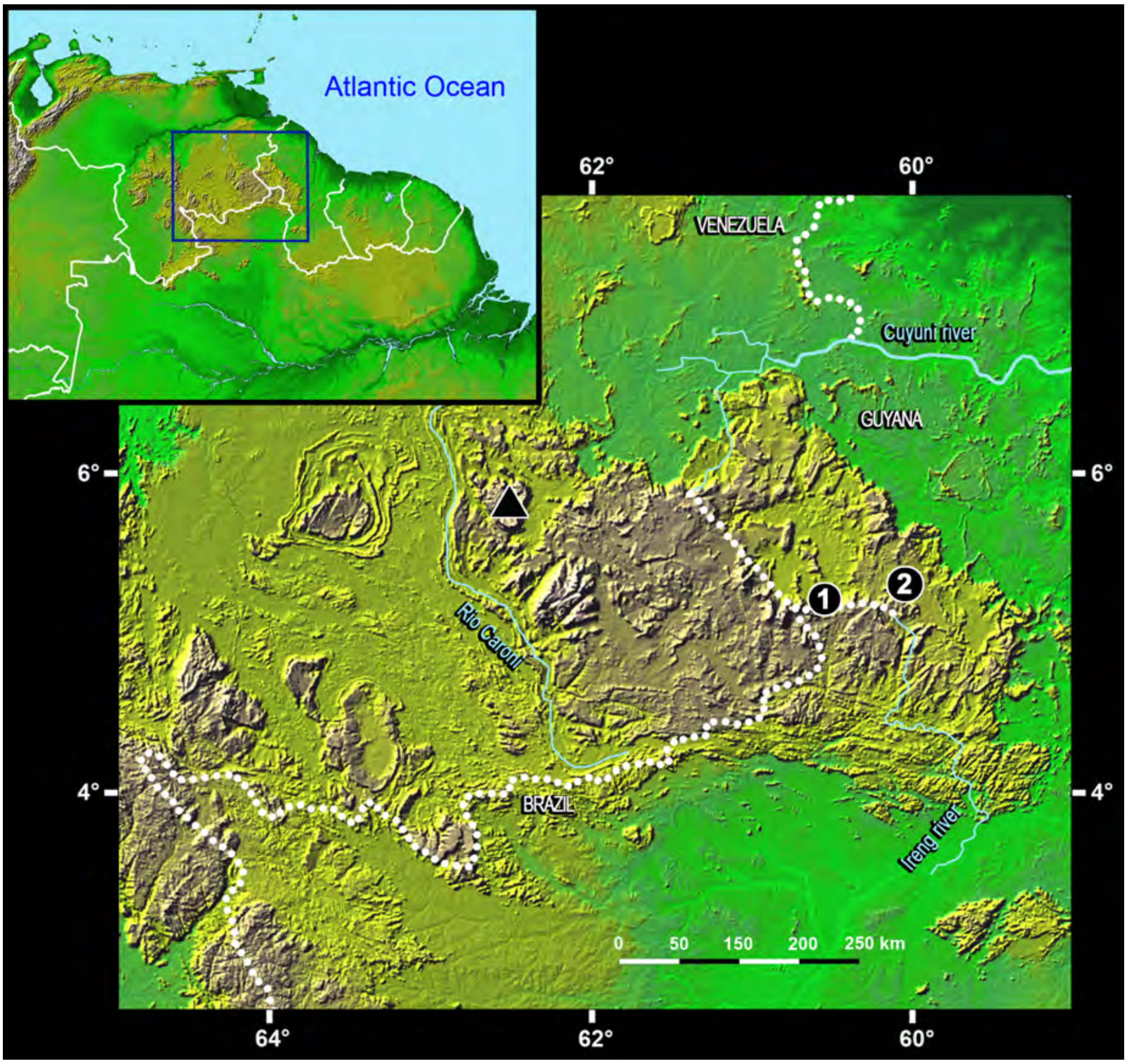

Figure **4.** Map of the eastern Pantepui region showing the known distributions of *Anomaloglossus megacephalus* **sp. nov.** (circles): 1 = type locality, Mount Maringma, Guyana; 2 = Mount Ayanganna, Guyana. The type locality of *A. tepuyensis* is indicated by a triangle. Maps elaborated after a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388.

Eastern Pantepui *Anomaloglossus* species.

Anomaloglossus megacephalus can be distinguished from *A. beebei* by (characters of *A. beebei* in parentheses, see also Kok *et al*. 2006b and Kok & Kalamandeen 2008) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (18.7 mm in *A. beebei*, n=27), fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes not folded), toes with folded flaplike fringing (fringes not folded), throat in adult female blotched (immaculate), palm dark brown to black (yellowish), distinct dark bands on thigh and shank (absent), dark interorbital V-shaped band (absent).

Anomaloglossus megacephalus can be distinguished from *A. breweri* (Barrio-Amorós, 2006) by (characters of *A. breweri* in parentheses) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (23.8 mm in *A. breweri*, n=1), throat in adult female blotched (immaculate), median lingual process short, wider than long, tapered (distinctly longer than wide, tip pointed).

Anomaloglossus megacephalus can be distinguished from *A. kaiei* by (characters of *A. kaiei* in parentheses, see also Kok & Kalamandeen 2008) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (19.8 mm in *A. kaiei*, n=25), fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes not folded), toes moderately webbed (basally webbed), dorsolateral stripe absent (present), oblique lateral stripe present (absent), throat in adult female blotched (immaculate).

Anomaloglossus megacephalus can be distinguished from *A. murisipanensis* (La Marca, 1998) in having (characters of *A. murisipanensis* in parentheses, all based on the preserved holotype, which is a juvenile and the only known specimen) fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes barely detectable), more webbing on toes, symmetrical cloacal tubercles present (absent), tarsal keel weakly to distinctly curved, slightly tuberclelike (straight, not tuberclelike), oblique lateral stripe always present, even if broken in spots (not distinguishable), no white stripe between naris and eye in preservative (present).

Anomaloglossus megacephalus can be distinguished from *A. praderioi* by (characters of *A. praderioi* in parentheses, see also Kok 2010) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (22.7 mm in *A. praderioi*, n=1), Finger IV longer than I (equal), tip of Finger IV always surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (barely reaching the base), toes moderately webbed with folded flaplike fringing (basally webbed, folded flaplike fringing not present on all toes), dorsolateral stripe absent (present), oblique lateral stripe present (absent), throat in adult female blotched (immaculate).

Anomaloglossus megacephalus can be distinguished from *A. roraima* in having (characters of *A. roraima* in parentheses) fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes barely distinct, not distinctly folded), all toes with folded flaplike fringing (absent), webbing on toes moderate (absent).

Anomaloglossus megacephalus can be distinguished from *A. rufulus* (Gorzula, 1990) in having (characters of *A. rufulus* in parentheses) webbing on toes moderate (rudimentary), and most remarkably by ventral colour pattern; light with a few dark brown blotches in *A. megacephalus* (dark brown marbled with white blotches in *A. rufulus*).

The new species superficially most resembles *A. parkerae*, *A. tepuyensis* (with which it has been confused), and *A. triunfo* (Barrio-Amorós, Fuentes-Ramos & Rivas-Fuenmayor, 2004), in sharing a similar dorsal pattern. It should be noted that *A. triunfo* is a possible synonym of *A. tepuyensis* (Kok & Barrio-Amorós unpubl. data, see also comments by Myers & Donnelly 2008). *Anomaloglossus parkerae* is distinguished from *A. tepuyensis* and *A. triunfo* only by a few characters such as size, definition of dorsal pattern, and condition of finger and toe fringes (Myers & Donnelly 2008). Adults of *A. megacephalus* can notably be distinguished from those three similar taxa in having a more slender body (*Anomaloglossus parkerae, A. tepuyensis* and *A. triunfo* are distinctly stockier frogs), a comparatively longer snout and a larger, somewhat more massive head [See Fig. 5 for close comparison between *A. megacephalus* and *A. tepuyensis* and *A. parkerae*; compare also with Duellman's (1997: 10) colour plate of *A. parkerae*, fig. 30 (showing *A. parkerae*) in Lötters *et al.* (2007), and figs. 13, 15 and 16 illustrating *A. tepuyensis* in Myers & Donnelly (2008); see also below for further comments], and in having symmetrical cloacal tubercles (absent in all females of *A. parkerae, A. tepuyensis* and *A. triunfo* examined).

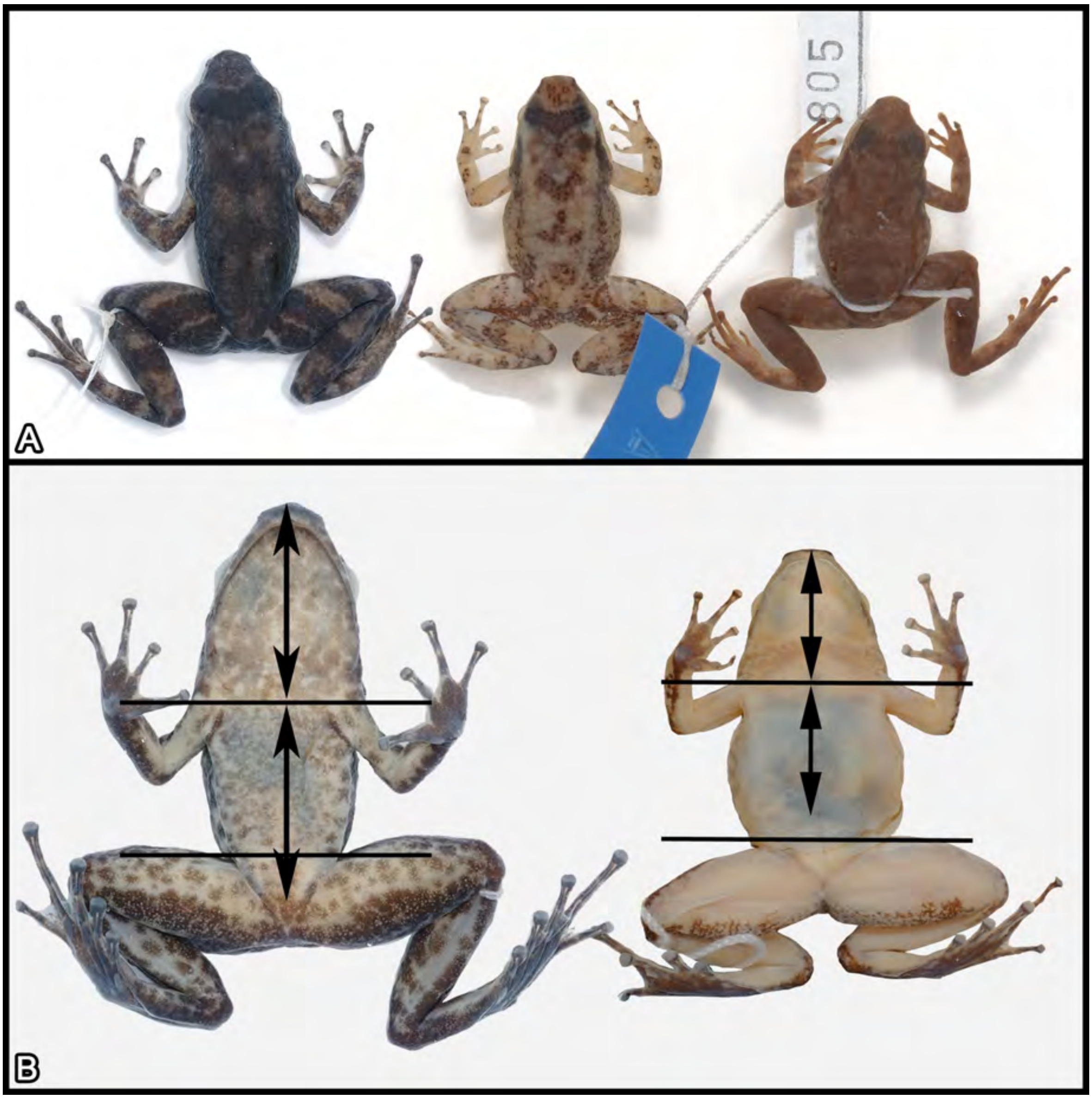

Figure **5.** Comparison of *Anomaloglossus megacephalus* **sp. nov.** and the similar *A. tepuyensis* and *A. parkerae*. A: Dorsal view of preserved specimens of (from left to right) *A. megacephalus* **sp. nov.** (IRSNB 1986, 27.3 mm SVL)**,** *A. tepuyensis* (MHNLS 17401, 23.3 mm SVL) and *A. parkerae* (MHNLS 11089, 23.2 mm SVL). B: Comparison between midline distance from snout tip to an imaginary line between anterior arm insertions and the same distance reported posteriorly from the same imaginary line in *A. megacephalus* **sp. nov.** and *A. tepuyensis*. In most *A. megacephalus* specimens (left, IRSNB 1986, 27.3 mm SVL) the distance reaches or surpasses the anterior insertion of thigh, whereas in all specimens of *A. tepuyensis* examined (right, MHNLS 17401, 23.3 mm SVL), the distance fails to reach the thigh. Photos by PJRK.

Direct comparison of specimens shows a difference in head size in *Anomaloglossus megacephalus* compared to the similar *A. parkerae*, *A. tepuyensis* and *A. triunfo*, as confirmed by plotting of morphometric proportions. Comparison of HL3 with BEL indicates that the new species proportionally has a longer head than *A. tepuyensis* (Fig. 6). In order to distinguish between those similar species, the midline distance from the tip of the snout to an imaginary line between anterior insertions of upper arms is measured, and that distance is then extended posteriorly from the same imaginary line. In two of the three available *A. megacephalus* adult specimens the distance reaches or surpasses the anterior insertion of thigh, whereas in all adult specimens of *A. parkerae, A. tepuyensis* and *A. triunfo* examined (n = 20), the distance fails to reach the thigh insertion (see Fig. 5 B). It is noteworthy to mention that the only specimen of *A. megacephalus* in which HL3 is not longer than BEL is in poor preservation state.

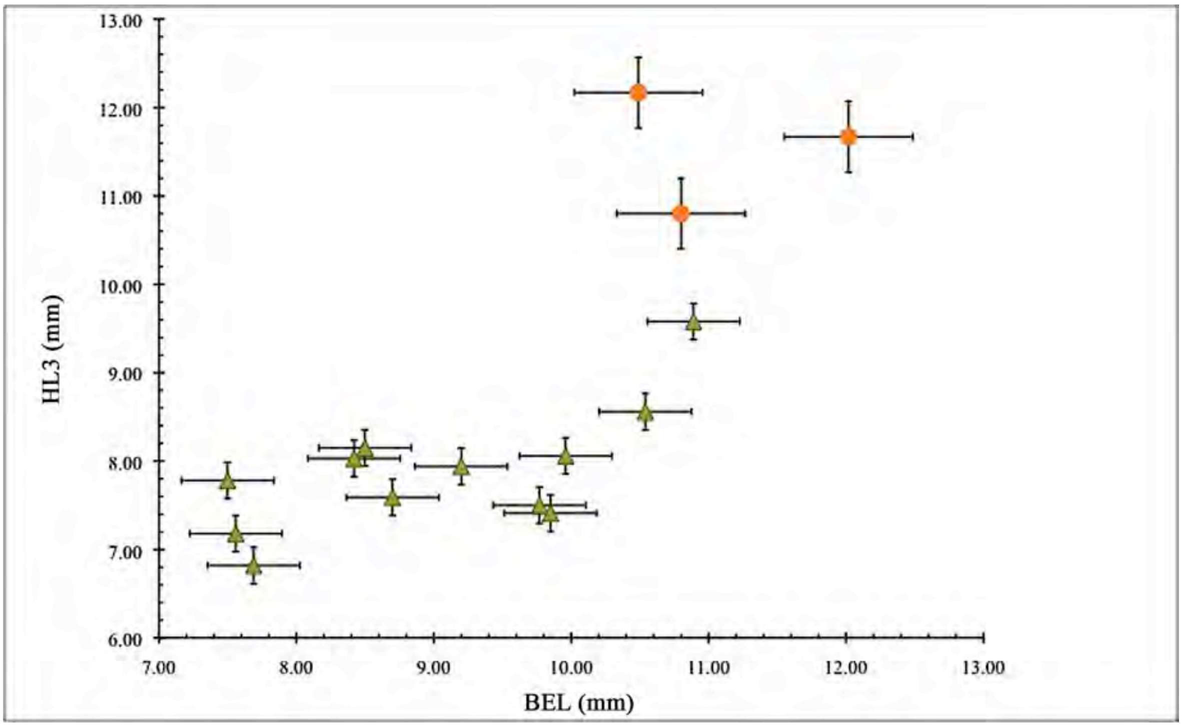

Figure **6.** Graph showing correlation between HL3 and BEL with standard errors for adult female specimens of *Anomaloglossus tepuyensis* (green triangles) and *A. megacephalus* **sp. nov**. (orange circles). Abbreviations are defined in the text. The graph clearly shows that the head of *A. megacephalus* **sp. nov**. is proportionally longer that the head of *A. tepuyensis*.

Western Pantepui *Anomaloglossus* species.

Among the Western Pantepui *Anomaloglossus* species, *A. ayarzaguenai* (La Marca, 1998) and *A. moffetti* Barrio-Amorós and Brewer-Carías, 2008 are the geographically closest species to *A. megacephalus* (*ca.* 400 km airline to the west). *Anomaloglossus ayarzaguenai* and *A. moffetti* are very similar to each other, geographically close (from Cerro Jaua and Cerro Sarisariñama, respectively) and possible synonyms (Kok & Barrio-Amorós unpubl. data). *Anomaloglossus megacephalus* is distinguished from *A. ayarzaguenai* and *A. moffetti* in having a comparatively longer snout, and a larger, somewhat more massive head [compare Figs. 1 and 2 B with fig. 4 a–c illustrating *A. moffetti* in Barrio-Amorós & Brewer-Carías (2008)], in having a distinct tympanum in life (barely distinct in *A. ayarzaguenai* and *A. moffetti*), separated from eye by 42–60% of its greatest length (25% or less in *A. ayarzaguenai* and *A. moffetti*), and in lacking a dark area spotted with white ventrolaterally at the level of arm insertion (always present in *A. ayarzaguenai* and *A. moffetti*).

Anomaloglossus megacephalus mostly differs from *A. guanayensis* (La Marca, 1998) by (characters of *A. guanayensis* in parentheses) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (23.5 mm in *A. guanayensis*, n=3), and in having less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers).

Anomaloglossus megacephalus can be distinguished from *A. parimae* (La Marca, 1998) by (characters of *A. parimae* in parentheses) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (23.1 mm in *A. parimae*, n=2), in having a short, wider than long median lingual process (slender, noticeably longer than wide), and in having distinctly more webbing on toes.

Anomaloglossus megacephalus can be distinguished from *A. shrevei* (Rivero, 1961) in having (characters of *A. shrevei* in parentheses) a weakly to distinctly curved, slightly tuberclelike tarsal keel, (short, straight, not tuberclelike), less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers), and dark blotches on throat and belly (throat and belly immaculate).

Anomaloglossus megacephalus mostly differs from *A. tamacuarensis* by (characters of *A. tamacuarensis* in parentheses) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (25.0 mm in *A. tamacuarensis*, n=2), in having a comparatively longer snout, and a larger, somewhat more massive head [compare Figs. 1 and 2 B with figs. 11 and 13 illustrating *A. tamacuarensis* in Myers & Donnelly (1997)], less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers), a conspicuous tympanum (inconspicuous), and in having a short, wider than long median lingual process (slender, noticeably longer than wide).

Discussion. Although progress has been made, we are still far from having a full understanding of the *Anomaloglossus* species richness in the Pantepui region. Based on the material available to us, there are at least two undescribed *Anomaloglossus* species in the Ayanganna and Wokomung massifs in Guyana. One of them was reported as *A.* "Ayanganna" in Grant *et al.* (2006) and subsequently as *A.* cf. *praderioi* in Kok (2010). Another possible undescribed species occurs on Mt. Wokomung, but additional evidence is needed to formally exclude conspecificity with *A. megacephalus*.

Grant *et al.* (2006) reported another undescribed species from the area (*A.* "Thomasing") from Mt. Tomasing, Guyana that we have not examined, but which—according to the data provided by Grant *et al.* (2006)—is closely related (and possibly conspecific) with *A. megacephalus*. More data (ecological, morphological and molecular) are needed to resolve this.

Species limits are sometimes difficult to define on morphology alone, and as pointed out by Kok (2010), any new *Anomaloglossus* description should ideally include tadpole and call descriptions, and data on natural history. However, this is sometimes hardly achievable, especially in regions difficult to explore and where additional expeditions are unlikely in the near future.

Our preliminary molecular results indicate that uncorrected pairwise distances based on a fragment of *ca.* 550 base pairs of the 16S rRNA gene (GenBank accession number DQ502128 + the authors unpublished data) between *Anomaloglossus tepuyensis* from the type locality and *A. megacephalus* varies between 6.9 and 7.1%, while uncorrected pairwise distance between known populations of *A. megacephalus* is only 0.17%. It should be stressed that low genetic distances (based on a fragment of the 16S rRNA gene) between morphologically well distinguishable sister taxa is not uncommon in the genus (the authors, unpubl. data). The same was recently reported in the genus *Ameerega* (Dendrobatidae, sister group of Aromobatidae), in which genetic distances of *ca*. 2% (based on a fragment of the 16S rRNA gene) or less between species is not uncommon (see Lötters *et al*. 2005, 2009). This emphasizes the need for integrative taxonomy and shows the limits of the use of a universal threshold of genetic distance to identify amphibian species.

ACKNOWLEDGMENTS

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APPENDIX 1. ADDITIONAL MATERIAL EXAMINED

Anomaloglossus ayarzaguenai.— Venezuela: *Estado Bolívar*: Cerro Jaua, MHNLS 12949 (holotype), MHNLS 12950–51 (paratypes).

Anomaloglossus beebei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 13721–26, 13728–54, ULABG 6817 (ex IRSNB 13727), IRSNB 13779–81 (tadpoles).

Anomaloglossus breweri.— Venezuela: *Estado Bolívar*: Aprada Tepui, Cueva del Fantasma, MHNLS 17044 (holotype), MHNLS 17045–46 (paratypes).

Anomaloglossus guanayensis.— Venezuela: *Estado Bolívar*: Serranía de Guanay, MHNLS 10708 (holotype), MHNLS 10712–10714 (paratypes), 10716–10717 (paratypes), 10724–10725 (paratypes).

Anomaloglossus kaiei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 1938 (holotype), IRSNB 1939–64 (paratypes), IRSNB 14419 (2 specimens), IRSNB 14422–26, IRSNB 14433–35, IRSNB 14437–40, IRSNB 14443, IRSNB 14446–51, IRSNB 14454–57, IRSNB 13755–78 (tadpoles), IRSNB 14432 (tadpoles), IRSNB 14436 (tadpole), IRSNB 14444–45 (tadpoles), IRSNB 14452–53 (tadpoles), ROM 42999, Mount Wokomung, ROM 43321, ROM 43327, ROM 43330, ROM 43333; *Cuyuni-Mazaruni District*: Wayalayeng, IRSNB 14922–24, Maringma Tepui, IRSNB 14925–31.

Anomaloglossus moffetti.— Venezuela: *Estado Bolívar*: Sarisariñama-tepui, EBRG 4645 (holotype), EBRG 4646–51 (paratypes).

Anomaloglossus murisipanensis.— Venezuela: *Estado Bolívar*: Murisipan-Tepui, MHNLS 11385 (holotype).

Anomaloglossus parimae.— Venezuela: *Estado Amazonas*: Cerro Delgado Chalbaud, ULABG 4221 (holotype), ULABG 4212–20 (paratypes), ULABG 4222–26 (paratypes).

Anomaloglossus parkerae.— Venezuela: *Estado Bolívar*: Sierra de Lema, Salto El Danto, MHNLS 2901, MHNLS 11088–89 (topotypic specimens).

Anomaloglossus praderioi.— Guyana: *Cuyuni-Mazaruni District*: Maringma Tepui, IRSNB 14403–13, IRSNB 14414–16 (tadpoles); Venezuela: *Estado Bolívar*: Mount Roraima ULABG 4196 (holotype), MHNLS 11272 (paratype), Sierra de Lema, EBRG 5569.

Anomaloglossus roraima.— Venezuela: *Estado Bolívar*: Mount Roraima, ULABG 4197 (holotype).

Anomaloglossus rufulus.— Venezuela: *Estado Bolívar*: Amuri-Tepui, Chimantá Massif, MHNLS 10361 (holotype).

Anomaloglossus tamacuarensis.— Venezuela: *Estado Amazonas*: Sierra Tapirapecó, north base of Pico Tamacuari, MBUCV 6430–33 (paratypes).

Anomaloglossus tepuyensis.— Venezuela: *Estado Bolívar*: Auyantepui, ULABG 2557 (holotype), Cucurital River, MHNLS 14404–05, Purumay River, MHNLS 14924–25, MHNLS 14940–41, MHNLS 15687, Quebrada Atapere, MHNLS 15924, MHNLS 17359–60, MHNLS 17383, Quebrada Tucutupan, MHNLS 17401, Quebrada Rutapa, MHNLS 17361.

Anomaloglossus triunfo.— Venezuela: *Estado Bolívar*: Cerro Santa Rosa, Serranía del Supamo, EBRG 4756 (holotype), EBRG 4757–59 (paratypes).

6

A New Highland Species of *Pristimantis* Jiménez de la Espada, 1871 (Anura: Strabomantidae) from the Pantepui Region, Northern South America

P. J. R. Kok, D. B. Means & F. Bossuyt

Abstract
A new strabomantid frog of the genus *Pristimantis* Jiménez de la Espada, 1871 is described from the Eastern Pantepui Region, Guiana Shield, northern South America. The new species, *Pristimantis aureoventris* **sp. nov.**, is known so far from two neighbouring tepuis, namely Wei Assipu Tepui (type locality) at the border between Guyana and Brazil and Mount Roraima in Guyana, and occurs between 2210–2305 m elevation. The new taxon is distinguished from all known congeners by the following combination of characters: Finger I < II; tympanum distinct; basal webbing between Toes IV–V; broad lateral fringes on fingers and toes; ventral skin areolate; vocal slits absent in male; two non-spinous whitish nuptial pads and vocal sac present in male; high degree of pattern polymorphism; throat, chest, and belly golden yellow, usually with reddish brown to dark brown mottling; internal organs little or not visible through the ventral skin in life. The call of the new species consists of bouts of a single amplitude-modulated (decreasing to the end) note repeated at a rate of *ca.* 18 notes/min with a dominant frequency ranging from 2180 to 2430 Hz.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The genus *Pristimantis* Jiménez de la Espada, 1871 was resurrected by Heinicke *et al.* (2007), who split the speciose genus *Eleutherodactylus* into three genera on the basis of molecular evidence: *Eleutherodactylus* was restricted to the "Caribbean Clade", the members of the "South American Clade" were allocated to the genus *Pristimantis*, whereas the members of the "Middle American Clade" were allocated to the genus *Craugastor*. Soon after, further molecular support for this hypothesis was provided by Hedges *et al.* (2008), who allocated *Pristimantis* and 16 additional genera previously placed in the family Brachycephalidae by Frost *et al.* (2006) in the new family Strabomantidae.

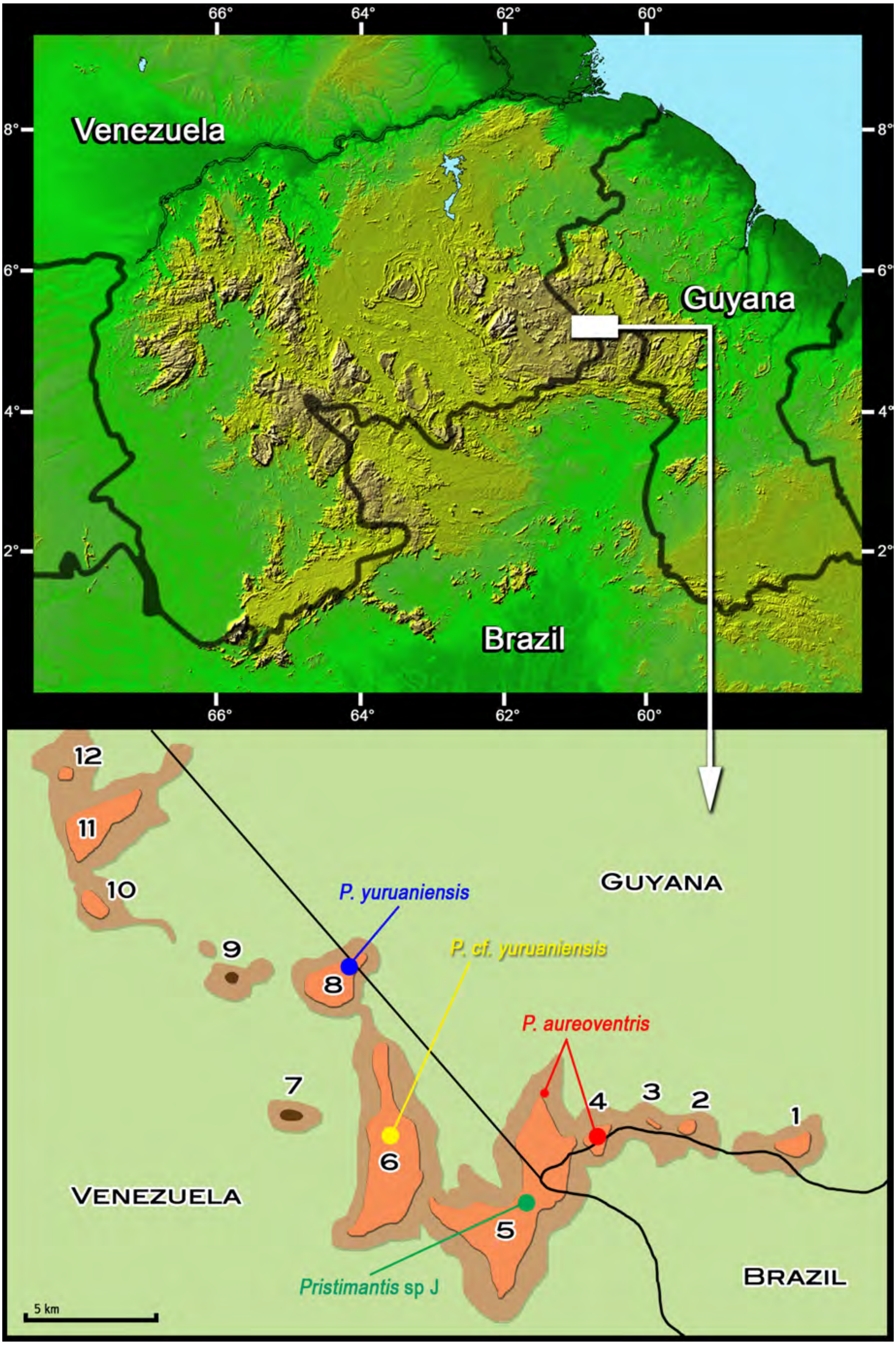
Recently, Heinicke *et al.* (2009) erected the new family Ceuthomantidae and the new genus *Ceuthomantis* to accommodate a new species from the Pakaraima Mountains of Guyana (*C. smaragdinus* Heinicke, Duellman, Trueb, Means, MacCulloch & Hedges, 2009), and proposed the placement of *Pristimantis aracamuni* (Barrio-Amorós & Molina, 2006) and *P. cavernibardus* (Myers & Donnelly, 1997) in the new family and genus based on morphological similarities. Barrio-Amorós (2010) then described *Pristimantis cf. cavernibardus* from Sarisariñama Tepui as *Ceuthomantis duellmani*.

To date, the genus *Pristimantis* contains more than 430 described species, 21 of which are distributed in the Pantepui region (Barrio-Amorós *et al.* 2010, Frost 2011), a biogeographic province referring to the complex of mountains (most of them called "tepuis") mainly derived from the sandstone of the Roraima Group in southern Venezuela, northwestern Guyana and northern Brazil (McDiarmid & Donnelly 2005) (Fig. 1). Among these 21 species, six only seem to be restricted to tepui summits and upper slopes, occurring above 2000 m elevation [*i.e. P. cantitans* (Myers & Donnelly, 1996), *P. pruinatus* (Myers & Donnelly, 1996), and *P. yaviensis* (Myers & Donnelly, 1996) from 2150 m on Cerro Yaví, *P. marahuaka* (Fuentes-Ramos & Barrio-Amorós, 2004) from 2450 m on Cerro Marahuaka, *P. muchimuk* Barrio-Amorós, Mesa, Brewer-Carías and McDiarmid, 2010 from 2325 m on Churi Tepui in the Chimanta Massif, and *P. yuruaniensis* Rödder and Jungfer, 2008 from 2300 m on Yuruani Tepui].

According to McDiarmid & Donnelly (2005), several tepui summit *Pristimantis* species are still awaiting description, and only a few of the 20 unnamed species they listed were recently described (*e.g. Pristimantis auricarens* Myers & Donnelly, 2008 from Auyantepui and *P. yuruaniensis* from Yuruani Tepui).

Wei Assipu Tepui, sometimes called "Little Roraima", is a poorly explored table-top mountain reaching *ca.* 2260 m elevation, located *ca.* 2 km airline (summit to summit distance) east of Mount Roraima at the border between Guyana and Brazil. An expedition to the summit of the tepui in November 2009 resulted in the discovery of an additional, distinctive *Pristimantis* species, which was also collected on the upper slopes of Mount Roraima. The new taxon is described below.

Figure **1.** (next page)**.** Map of the Pantepui region, with enlarged white rectangle corresponding to the Eastern Tepui Chain: 1 = Maringma Tepui, 2 = Yakontipu, 3 = Appokailang, 4 = Wei Assipu Tepui, 5 = Mount Roraima, 6 = Kukenan Tepui, 7 = Achipo Tepui, 8 = Yuruani Tepui, 9 = Guadacapiapu Tepui, 10 = Karaurin Tepui, 11 = Ilu Tepui, 12 = Tramen Tepui. Areas in orange indicate summits higher than 2000 m elevation; areas in dark brown indicate summits lower than 2000 m; areas in light brown indicate tepui slopes above 1500 m elevation.


66°
64°
62°
60°
8°
6°
4°
2°
Venezuela
Guyana
Brazil
12
11
10
9
8
7
6
5
4
3
2
1
P. yuruaniensis
P. cf. yuruaniensis
P. aureoventris
Pristimantis sp J
GUYANA
VENEZUELA
BRAZIL
5 km

MATERIAL AND METHODS

Specimens were collected by hand and euthanized by immersion in 2% Xylocaine. Tissue (a piece of liver or thigh muscle) was removed from most specimens and preserved in 95-100% ethanol. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens have been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB); tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (VUB) (see Appendix for material examined).

Coordinates and elevations were acquired using a Garmin 60CSx Global Positioning System unit and referenced to map datum WGS84.

Terminology for morphological characters mostly follows Lynch & Duellman (1997), Savage *et al.* (2004), Kok & Kalamandeen (2008), and Duellman & Lehr (2009). All morphometric data were taken from the preserved specimens to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper. For ease of comparison, the description mainly follows the pattern of recent descriptions in the genus (*e.g.* Myers & Donnelly 2008, Barrio-Amorós *et al*. 2010). Classical measurements for the genus were taken and abbreviated as follows: (1) snout-vent length, from tip of snout to posterior margin of vent (SVL); (2) head length from angle of jaw to tip of snout (HL); (3) greatest width of the head (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance, taken between the median margins of the nares (IN); (7) eye length, horizontal distance from the anterior margin to the posterior margin of the eye (EL); (8) interorbital distance, taken between the median margins of the orbits (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (11) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (12) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (13) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (14) width of disc on Finger III (WFD); (15) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (16) width of disc on Toe IV (WTD); (17) tibia length from outer edge of flexed knee to heel (TIL).

Colour pattern in life was taken from field notes and colour digital photographs. Sex and maturity were determined by the presence or absence of nuptial pads (once it was established that adult males of the new species have nuptial pads) or by dissection and direct examination of gonads when sex remained doubtful. Internal soft anatomy was examined by dissection of preserved specimens.

Comparisons of external character states are based both on original descriptions and examination of museum specimens (see Appendix for material examined).

Recordings of advertisement calls were taken in the field at a distance of less than 1 m from the calling male with a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder using Maxell DM60 digital audiotape (holotype) or with a Sennheiser ME66/K6 microphone attached to a Marantz PMD661 solid state recorder (uncollected *Pristimantis yuruaniensis* recorded for comparison purpose). The calls were analysed at a sampling rate of 44100 Hz using Raven Pro version 1.4 software (Charif *et al.*, 2010).

Temporal variables measured included: call duration (= note duration); inter-call interval (beginning of one call to beginning of the next); and call rate (= number of calls per minute). The dominant (emphasized) frequency of the note was measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 150 Hz). Air temperature at the call sites was measured with a Hanna digital pH/thermometer.

Because preliminary molecular analyses based on a fragment of *ca*. 550 base pairs of the 16S rRNA gene (the authors, unpublished data) indicate that syntopic specimens from the summit of Wei Assipu Tepui cluster into two morphologically undifferentiated clades separated by 0.89–1.25% uncorrected pairwise distance (divergence within each of these clades varies from 0–0.36%) we decided to select specimens of one of these two clades to serve as the type series, assigning the others and specimens for which molecular data are unavailable to “referred specimens” (see Discussion).

Taxonomy follows Hedges *et al*. (2008). Institutional acronyms follow Frost (2011).

NEW SPECIES DESCRIPTION

***Pristimantis aureoventris* sp. nov.**

Figs. 2–7; Table 1

Holotype. IRSNB 4152 (field number PK 2152), an adult male collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 17 November 2009 at 20h00, summit of Wei Assipu Tepui, Cuyuni-Mazaruni District, Guyana (05° 13’ 05”N, 060° 42’ 15”W, 2210 m elevation).

Paratopotypes (n=2)**.** IRSNB 4153 (field number PK 2066), a female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 3 November 2009, and IRSNB 4154 (field number PK 2087), a subadult female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 4 November 2009.

Referred specimens (n=10)**.** IRSNB 15821–22 (field numbers PK 2162–63), females; IRSNB 15820, IRSNB 15823 (field numbers PK 2085, PK 2086), males; IRSNB 15824–27 (field numbers PK 2107–08, PK 2114, PK 2117), males; IRSNB 15637 (field number PK 2158), a very small juvenile, all collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry on the summit of Wei Assipu Tepui between 3–19 November 2009. IRSNB 15643 (field number CPI 10484), a male collected by D. Bruce Means, 17 November 2006, from *ca*. 300 m below the base of the ultimate cliff of the northern “Prow” of Mount Roraima, Cuyuni-Mazaruni District, Guyana (05° 15’N, 060° 43’W, 2305 m elevation).

Etymology. The specific name *aureoventris* is a noun in apposition derived from the Latin words “*aureus*” meaning golden, and “*ventris*” meaning venter, and refers to the golden ventral face of the new species.

Generic allocation. To date, there is no identifiable morphological synapomorphy supporting the genus *Pristimantis* (Hedges *et al.* 2008). We assign the new taxon to the genus *Pristimantis* based on molecular phylogenetic relationships (the authors, unpublished data) as well as on its morphological characteristics, which fall into the range of other *Pristimantis* species.

Definition and diagnosis. A small species of the genus *Pristimantis* currently not assigned to any species group, but morphologically most similar to species of the non-monophyletic *unistrigatus* species group (*sensu* Hedges *et al*. 2008, see Discussion) mainly characterized in having Finger I shorter than II, Toe V longer than III, extending to the distal edge of the distal subarticular tubercle of Toe IV when toes are adpressed, and by the absence of cranial crests and the presence of vomerine teeth. The new species is characterized by the following combination of characters: (1) dorsal skin shagreened to slightly granular, rarely with some conical tubercles, faint middorsal raphe in life, ventral skin areolate; (2) tympanum distinct, less than half the size of the eye; (3) snout rounded to subovoid in dorsal view, rounded to slightly sloping in profile, canthus rostralis nearly straight to concave, round; (4) upper eyelid smooth to slightly granular, usually with one or two distinctly enlarged tubercles on each eyelid; (5) choanae small, oval, dentigerous processes of vomers small, oblique, V-shaped, posterior and medial to choanae, each bearing 2–5 teeth; (6) absence of vocal slits in males, but presence of a shallow vocal sac and of two white non-spinous nuptial pads; (7) Finger I shorter than II; (8) fingers with broad lateral fringes; (9) ulnar tubercles low, inconspicuous, not forming a distinct line in preservative, but more conspicuous in life, sometimes forming a row; (10) tarsal tubercles low, inconspicuous, not forming a distinct line, calcar tubercles present, not pronounced; (11) inner metatarsal tubercle oval, two to four times the size of the round outer metatarsal tubercle; (12) toes with broad lateral fringes, webbing basal between Toes IV-V, Toe V longer than III, usually surpassing the proximal edge of the distal tubercle on Toe IV when toes are adpressed; (13) in life dorsal colouration highly variable, ranging from light golden brown, medium or dark brown to dark brown with two broad light brown longitudinal stripes mottled with dark brown and finely edged by a cream line; a W-shaped marking may be present on scapula; ill-defined light brown oblique bands are usually present on flanks with similarly coloured ill-defined cross-bands on legs; broad light greyish brown bands may be present on flanks, dark brown dorsolateral bands may be present as well; a faint dark interorbital bar is usually visible; the snout is sometimes paler than body with some dark markings; a dark brown to black postocular stripe across upper and posterior parts of tympanum is present in most specimens; the groin is usually black or brown, sometimes with some small golden spots; a conspicuous reddish orange flashmark on groin may be visible; arms and legs often have a reddish or orangish tint. In preservative dorsal colouration brown to dark brown, the same patterns as described in life faded, but are still visible; (14) males 19.6–22.7 mm SVL, females 24.0–29.0 mm.

Compared to the 21 *Pristimantis* species distributed in the Pantepui region, *P. aureoventris* is immediately distinguished from *P. stegolepis* (Schlüter & Rödder, 2007), *P. vilarsi* (Melin, 1941), and *P. zeuctotylus* (Lynch & Hoogmoed, 1977) in having F I < II (F I > II in *P. stegolepis*, *P. vilarsi* and *P. zeuctotylus*); from *P. auricarens*, *P. jester* Means and Savage, 2007, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis* in having a distinct tympanum (indistinct in *P. auricarens*, *P. jester*, *P. marahuaka*, *P. muchimuk*, and *P. yaviensis*); from *P. avius* (Myers & Donnelly, 1997), *P. cantitans*, *P. inguinalis* (Parker, 1940), *P. marmoratus* (Boulenger, 1900), *P. memorans* (Myers & Donnelly, 1997), *P. pruinatus*, *P.*

pulvinatus (Rivero, 1968), and *P. sarisarinama* Barrio-Amorós and Brewer-Carías, 2008 in lacking vocal slits in male (vocal slits present in male of *P. avius*, *P. cantitans*, *P. inguinalis*, *P. marmoratus*, *P. memorans*, *P. pruinatus*, *P. pulvinatus*, and *P. sarisarinama*); from *P. dendrobatoides* Means and Savage, 2007 in having lateral fringes on fingers and toes (absent in *P. dendrobatoides*), in having a shagreened to slightly granular dorsal skin (covered with large granular tubercles in *P. dendrobatoides*), and by the presence of nuptial pads in male (absent in *P. dendrobatoides*); from *P. guaiquinimensis* (Schlüter & Rödder, 2007) and *P. tepuiensis* (Schlüter & Rödder, 2007) by its much smaller size in adult male (male SVL max 22.7 mm [n=8] in *P. aureoventris vs.* 33.6 mm [n=2] in *P. guaiquinimensis*, and 34.7 mm [n=1] in *P. tepuiensis*), by the presence of nuptial pads in male (absent in *P. guaiquinimensis* and *P. tepuiensis*), by the presence of vomerine teeth (absent in *P. guaiquinimensis* and *P. tepuiensis*), and in having lateral fringes on fingers and toes (absent in *P. guaiquinimensis* and *P. tepuiensis*); from *P. saltissimus* Means and Savage, 2007 in having lateral fringes on fingers and toes (absent in *P. saltissimus*), and by the presence of nuptial pads in male (absent in *P. saltissimus*); from *P. yuruaniensis* by its smaller size in adult female (female SVL max 29.0 mm [n=3] in *P. aureoventris vs.* 32.2 mm [n=5] in *P. yuruaniensis*), by having the ventral part golden yellow in life, usually with reddish brown to dark brown mottling, opaque with internal organs not, or barely visible through the skin (ventral part whitish, orangish or brown speckled with minute brownish dots in life, translucent, internal organs well visible through the skin in *P. yuruaniensis*), by having a higher degree of pattern polymorphism, and by having a less tuberculate skin.

Description of the Holotype. An adult male 20.4 mm SVL (Fig. 2) in very good condition of preservation, except a few small scars on back and upper arms. Head slightly longer than wide (HW 90.4% of HL), wider than body, HW 39.9% of SVL, cranial crests absent. Snout rounded in dorsal view, slightly sloping in profile; canthus rostralis nearly straight, round, loreal region slightly concave, sloping outward to lip; nares slightly protuberant, directed posterolaterally. Upper eyelid width narrower than IO; upper eyelid slightly granular with two barely discernible enlarged tubercles on each eyelid (better visible in life). Tympanum distinct, but not conspicuous, slightly obscured posteriorly, vertically oval, TYM 29% of EL, separated from eye by about half its length; supratympanic fold originating at corner of eye, failing to reach shoulder, slightly arched; small postrictal tubercles evident. Choanae small, oval, slightly kidney-shaped, not concealed by palatal shelf of maxillary arch; dentigerous processes of vomers slightly smaller than choanae, oblique, V-shaped, posterior and medial to choanae, each bearing 3 to 4 teeth. Tongue much longer than wide, rounded posteriorly, posterior 2/3 free. Vocal slits absent, shallow subgular vocal sac present, seemingly not very distensible.

Dorsal skin shagreened, almost smooth on head; middorsal raphe faint; no scapular folds or ridges visible; dorsal surfaces of limbs shagreened; flanks granular. Throat smooth; venter areolate (coarsely granular); posteroventral thigh and cloacal region areolate; weak discoidal fold anterior to groin; ulnar tubercles low, inconspicuous, not forming a distinct line in preservative, but more visible in life with three of them more prominent, forming a row.

Finger I 85% of II; relative length of adpressed fingers III > IV > II > I; adpressed Finger I failing to reach proximal edge of subdigital pad of Finger II; broad pre- and postaxial lateral fringes on fingers; presence of two whitish non-spinous nuptial pads, one adjacent to thenar tubercle and having about the same size, the other on the posterodorsal side of the thumb, having about the same size as the subarticular tubercle on Finger I. Finger discs expanded, with wide digital pads, broader than long, slightly rounded; distal median edge rounded. Palmar tubercle large, deeply bifid, V-shaped; thenar tubercle large, ovoid; subarticular tubercles large, round; supernumerary tubercles present, relatively large and protuberant (Fig. 3).

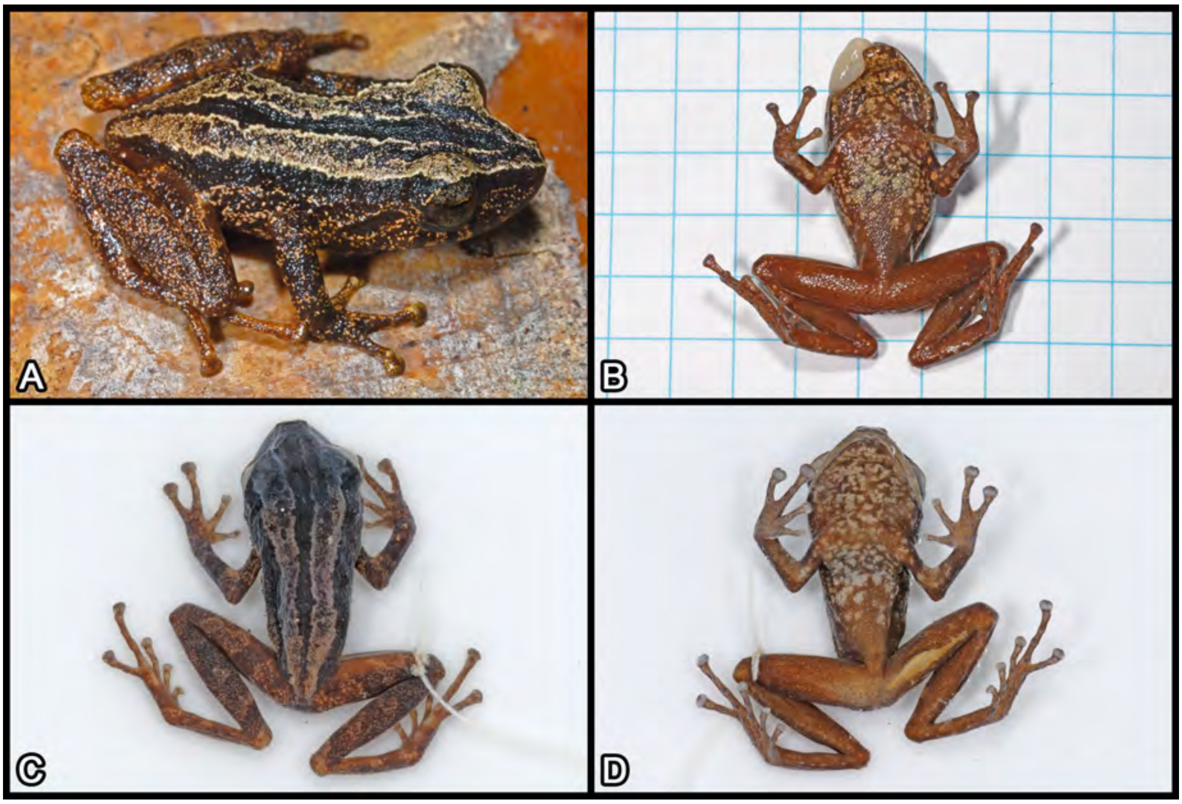


Figure **2.** *Pristimantis aureoventris* **sp. nov.** A: Dorsolateral view of the male holotype in life (IRSNB 4152, 20.4 mm SVL). B: Ventral view of the anaesthetized holotype. C: Dorsal view of the preserved holotype. D: Ventral view of the preserved holotype. Photographs by Philippe J.R. Kok.

Hind limbs relatively long; heels overlap when held at right angles to sagittal plane; TIL 55.7% SVL; FL 45.8% SVL. Relative length of adpressed toes IV > V > III > II > I; tip of Toe V extends to distal edge of ultimate subarticular tubercle of Toe IV, tip of III to the distal edge of the penultimate subarticular tubercle of IV. Toe discs as wide or narrower than finger discs, WFD/WTD = 1.11, with wide digital pads. Toes with broad pre- and postaxial lateral fringe, except on Toe I where fringes are barely visible; webbing basal between Toes IV-V. Inner metatarsal tubercle elongate, oval, about twice the size of the round outer metatarsal tubercle; supernumerary plantar tubercles low and round; subarticular tubercles large and protuberant. Calcar tubercles indistinct. Tarsal tubercles low, inconspicuous, not forming a distinct line; inner tarsal fold not visible (Fig. 3).

Figure **3.** *Pristimantis aureoventris* **sp. nov.** Ventral views of left hand (left) and left foot (right) of the male holotype (IRSNB 4152, 20.4 mm SVL). Scale bars = 1 mm (left) and 1.5 mm (right). Photographs by Philippe J.R. Kok.

Measurements of the Holotype (mm). SVL 20.4; HL 9.0; HW 8.2; SL 3.5; EN 2.3; IN 1.8; EL 3.2; IO 2.5, TYM 0.9; HAND I 3.6; HAND II 4.2; HAND III 5.8; HAND IV 4.7; WFD 1.1; FL 9.4; WTD 1.0; TIL 11.4.

Colour of the Holotype in life. Dorsal ground colour dark brown with two broad light brown longitudinal stripes mottled with dark brown and finely edged by a cream line, extending from tip of snout to vent. Flanks dark brown with ill-defined light brown oblique bands; limbs adorned with similarly coloured ill-defined cross-bands. Arms and legs have a reddish tint. Broad dark brown postocular stripe across upper and posterior parts of tympanum, not contacting eye and failing to reach shoulder; broad dark brown canthal stripe; ill-defined dark brown labial bars from eye to upper lip. Posterior and anterior surfaces of thighs reddish brown, slightly mottled with golden. Throat, chest, and upper belly golden yellow with reddish brown mottling, lower belly and under surfaces of limbs reddish brown; internal organs not visible through the skin. Palms and soles dark brown. Iris greenish bronze, with fine black venation and a median horizontal reddish streak (Fig. 2).

Colour of the Holotype in preservative. After 14 months in preservative, patterns and colours faded, but remain roughly the same. The golden ventral colour and the light brown stripes and bands became greyish. Arms and legs still have a slightly reddish tint (Fig. 2).

Variation. See Table 1 for measurements, and Figs. 4–6 for intrapopulational variation.

The most striking variation occurs in colour and pattern, which are very variable among living individuals (Fig. 4). The holotype is the only specimen having a striped dorsal pattern. Among the other specimens available, the dorsal colouration in life ranges from light golden brown (*e.g.* IRSNB 15823, adult male) to dark brown (*e.g.* IRSNB 15827, adult male), sometimes with a W-shaped marking on scapula (*e.g.* IRSNB 15820 and IRSNB 15643, adult males, and IRSNB 4154, subadult female). One male (IRSNB 15825) has a dark brown dorsum with broad light greyish brown bands on flanks; two individuals (IRSNB 4153, adult female, and IRSNB 15826, adult male) have a brownish dorsum with ill-defined dark brown dorsolateral bands. The ill-defined light brown oblique bands on flanks and the similarly coloured ill-defined cross-bands on legs may be absent (*e.g.* IRSNB 15820, adult male). A faint dark interorbital bar is usually visible (absent in the holotype), this bar being conspicuous in IRSNB 4154 (subadult female). In three individuals (IRSNB 4154, subadult female, IRSNB 15824 adult male, IRSNB 15825, adult male) the snout is paler than body (tan) with some dark markings (a black inverted triangle in IRSNB 4154). A dark brown to black postocular stripe across upper and posterior parts of tympanum is present in all specimens from Wei Assipu Tepui, that stripe is poorly detectable in the Roraima specimen. Groin is usually black or brown, sometimes with some small golden spots; one male (IRSNB 15827) had a conspicuous reddish orange flashmark on its groin in life (Fig. 7), which became white after preservation. Arms and legs usually have a reddish or orangish tint; IRSNB 15824 (adult male) had the posterior and anterior surfaces of thighs, the tibio-tarsal articulation, and part of the feet including Toes III–IV bright red; IRSNB 15825 (adult male) had the tibio-tarsal articulation distinctly paler (light grey) than the legs (dark brown); IRSNB 4154 (subadult female) had the anterior surface of thighs, the posterior surface of shanks, and part of the feet including Toes III–IV orange, a similar pattern is visible in IRSNB 15826 (adult male), but much less vivid. In other specimens, the posterior and anterior surfaces of thighs are reddish brown to dark brown, slightly mottled with golden. Under surfaces of limbs are reddish brown to dark brown, often heavily spotted with golden. Mottling on venter varies from reddish brown to dark brown, almost black, and is variably extensive; two individuals (IRSNB 15823, adult male from Wei Assipu Tepui, and IRSNB 15643, adult male from Mount Roraima, see Figs. 4, 6) lack mottling on venter. Due to the golden colouration of the venter, internal organs are little (IRSNB 15822, adult female) or not (holotype and other specimens) visible through the ventral skin in life (Figs. 2, 4). Iris colouration is variable, some individuals lack the median horizontal reddish streak (*e.g.* IRSNB 15822, adult female); IRSNB 15820 (adult male) has a blue-green iris (Fig. 4). In preservative all specimens became darker and variation in colour and pattern is less visible, but is still discernible (Fig. 5).

Character	**Males Wei Assipu Tepui**	**Females Wei Assipu Tepui**	**Subadult female Wei Assipu Tepui**	**Male Mount Roraima**
	(*n*=7)	**(*n*=3)**	**(*n*=1)**	**(*n*=1)**
SVL	21.6 ± 0.8 (20.4–22.7)	26.8 (24.0–29.0)	17.7	19.6
HL	9.2 ± 0.3 (8.6–9.6)	11.6 (10.7–12.2)	7.4	8.4
HW	8.5 ± 0.3 (7.9–8.8)	10.4 (9.7–11.2)	6.8	8.3
SL	3.8 ± 0.2 (3.5–4.1)	4.5 (4.5–4.6)	3.1	3.8
EN	2.5 ± 0.2 (2.2–2.6)	3.1 (2.9–3.3)	2.1	2.4
IN	2.0 ± 0.1 (1.8–2.2)	2.2	1.8	1.9
EL	3.1 ± 0.2 (2.9–3.3)	3.3 (3.1–3.5)	2.1	3.1
IO	2.6 ± 0.2 (2.3–2.9)	3.2 (3.1–3.3)	2.0	2.5
TYM	1.1 ± 0.1 (0.9–1.3)	1.4	1.0	0.8
HAND I	3.7 ± 0.2 (3.4–4.0)	4.9 (4.4–5.4)	3.0	3.3
HAND II	4.4 ± 0.2 (4.2–4.8)	5.6 (5.2–6.0)	3.4	3.8
HAND III	6.1 ± 0.2 (5.8–6.3)	8.0 (7.0–8.1)	4.7	5.1
HAND IV	4.9 ± 0.2 (4.6–5.2)	6.1 (5.8–6.4)	3.8	4.1
WFD	1.1 ± 0.1 (1.0–1.3)	1.3 (1.2–1.4)	0.7	1.0
FL	9.4 ± 0.3 (9.0–9.6)	11.6 (10.9–12.0)	7.4	8.1
WTD	1.1 ± 0.1 (1.0–1.2)	1.4 (1.3–1.6)	0.6	1.0
TIL	11.7 ± 0.2 (11.4–12.1)	14.9 (14.8–15.5)	9.5	10.5

Table **1.** Measurements (in mm) of specimens of *Pristimantis aureoventris* **sp. nov**. Abbreviations are defined in the text. Mean ± SD (when sample > 3) are followed by the range in parentheses.

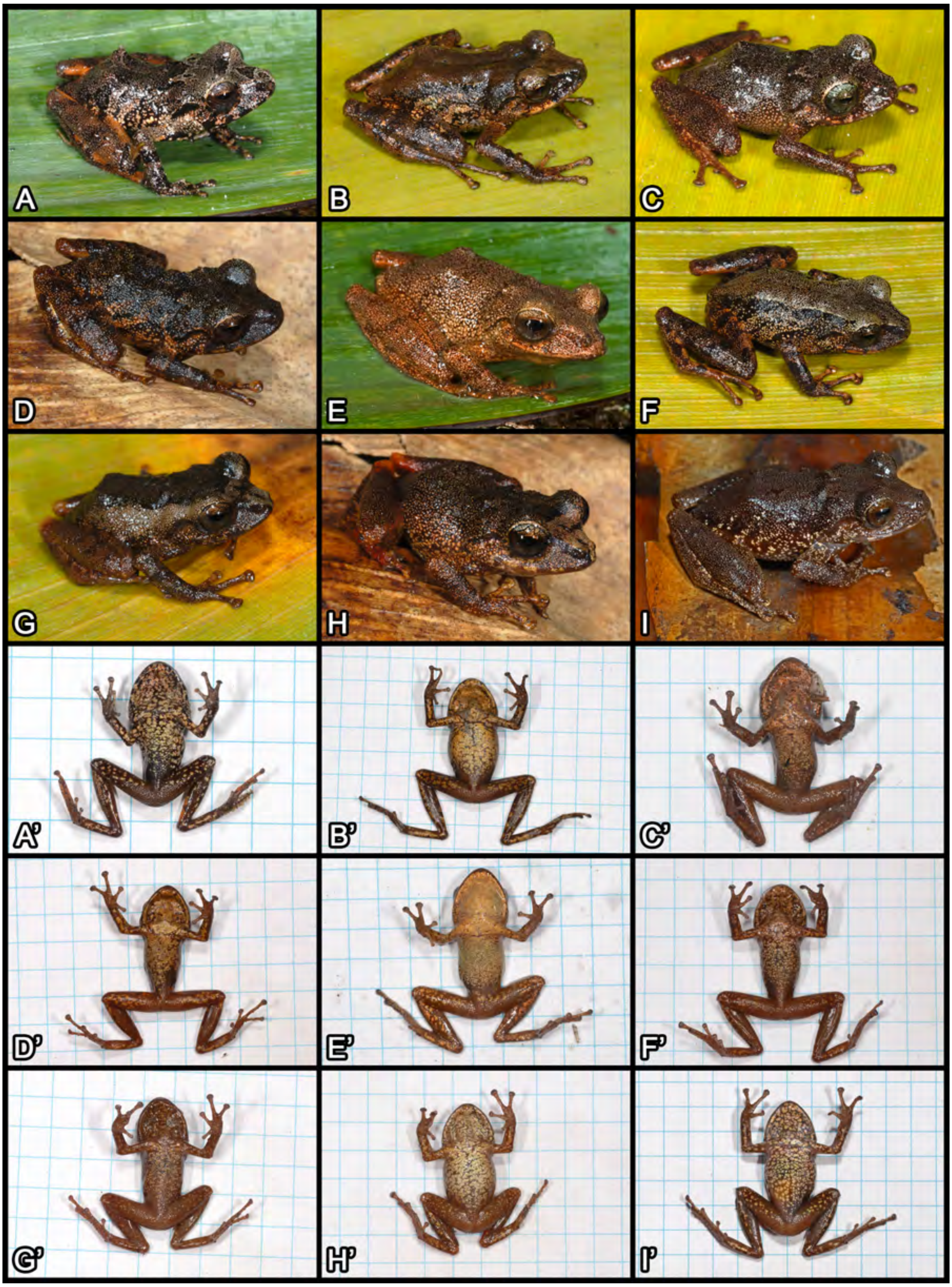


Figure **4.** *Pristimantis aureoventris* **sp. nov.** Intrapopulation variation in dorsal and ventral colour in living specimens from Wei Assipu Tepui. A-A': IRSNB 4154, subadult female, 17.7 mm SVL. B-B': IRSNB 4153, adult female, 24.0 mm SVL. C-C': IRSNB 15820, adult male, 21.4 mm SVL. D-D': IRSNB 15827, adult male, 22.3 mm SVL. E-E': IRSNB 15823, adult male, 22.6 mm SVL. F-F': IRSNB 15826, adult male, 22.7 mm SVL. G-G': IRSNB 15825, adult male, 20.9 mm SVL. H-H': IRSNB 15824, adult male, 21.0 mm SVL. I-I': IRSNB 15822, adult female, 27.3 mm SVL. Photographs by Philippe J.R. Kok.

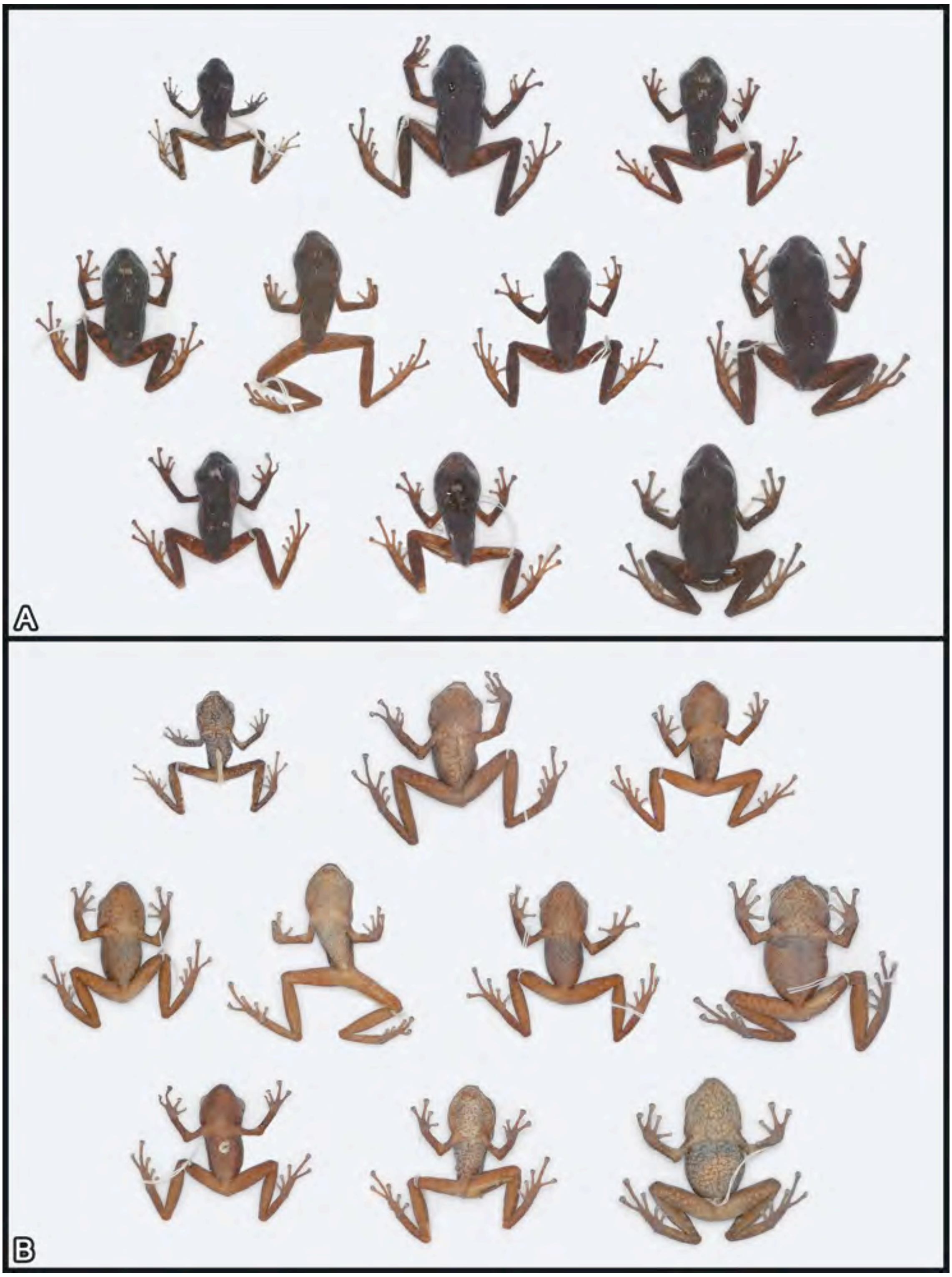


Figure **5.** *Pristimantis aureoventris* **sp. nov.** Intrapopulation variation in dorsal (above) and ventral (below) colour in preserved specimens from Wei Assipu Tepui. First row, from left to right: IRSNB 4154, subadult female, 17.7 mm SVL, IRSNB 4153, adult female, 24.0 mm SVL, IRSNB 15820, adult male, 21.4 mm SVL. Second row, from left to right: IRSNB 15827, adult male, 22.3 mm SVL, IRSNB 15823, adult male, 22.6 mm SVL, IRSNB 15826, adult male, 22.7 mm SVL, IRSNB 15821, adult female, 29.0 mm SVL. Third row, from left to right: IRSNB 15825, adult male, 20.9 mm SVL, IRSNB 15824, adult male, 21.0 mm SVL, IRSNB 15822, adult female, 27.3 mm SVL. Photographs by Philippe J.R. Kok.

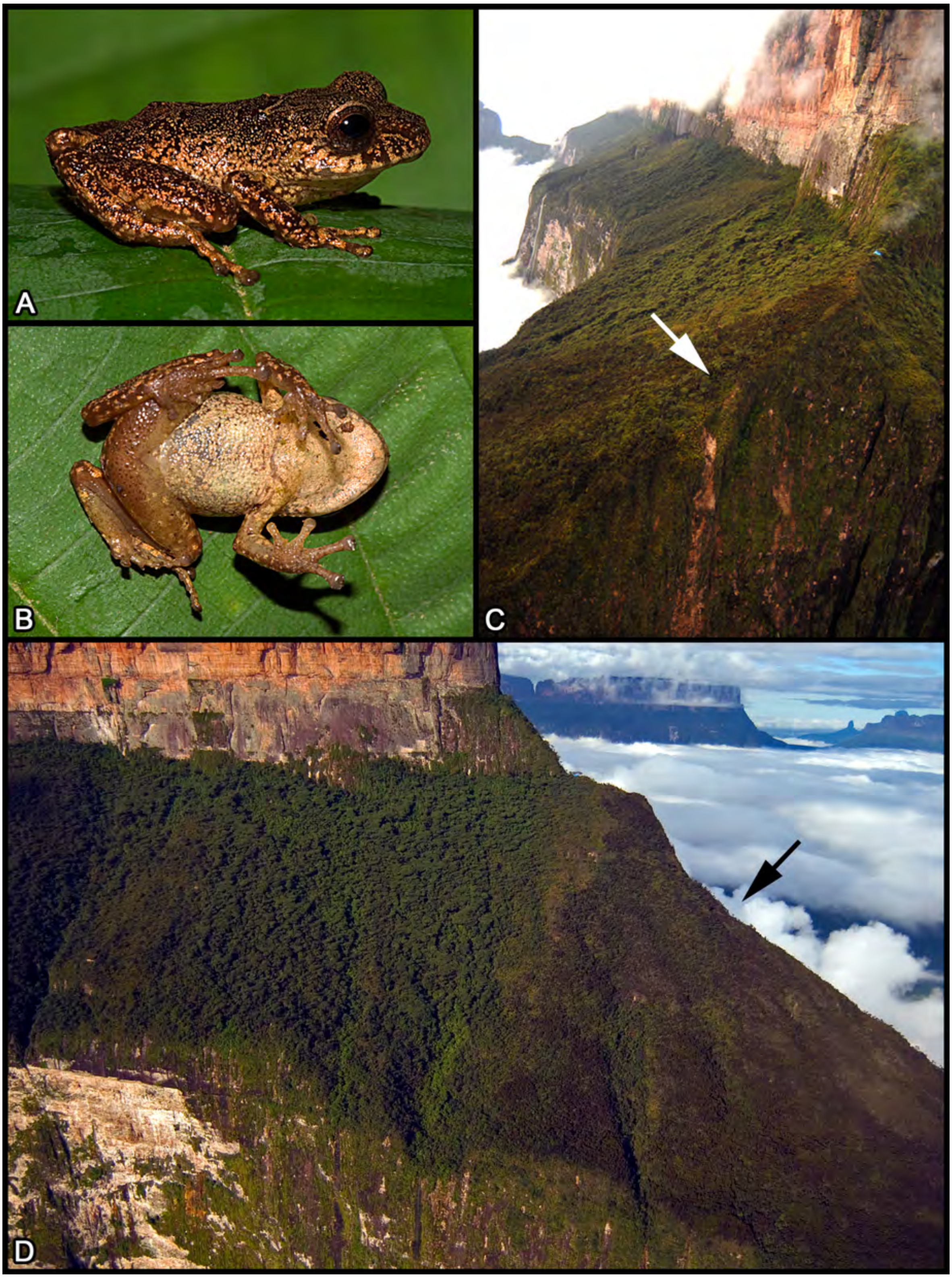


Figure **6.** *Pristimantis aureoventris* **sp. nov.** A: Dorsolateral view of IRSNB 15643, 19.6 mm SVL, male referred specimen from the upper slopes of Mount Roraima. B: Ventral view of the same specimen while alive. C, D: Aerial photographs of the base of the ultimate cliff of the northern Prow of Mount Roraima, arrows indicate the exact place where the specimen was collected; a small part of Wei Assipu Tepui is visible on the upper left on image C. Photographs by D. Bruce Means.

Figure **7.** *Pristimantis aureoventris* **sp. nov.** Groin region showing the conspicuous reddish orange flashmark in the adult male IRSNB 15827. Photograph by Philippe J.R. Kok.

Dorsal skin texture is slightly variable, most individuals having the dorsal skin shagreened to slightly granular. One specimen however (IRSNB 15827, adult male) has small conspicuous conical tubercles on anterior dorsum and legs, as is the case in the tiny (7.1 mm SVL) referred juvenile (IRSNB 15637). Few small conical tubercles are also visible on legs of most of the specimens. Small scapular tubercles were visible in seven individuals of both sexes in life (IRSNB 15822–24, IRSNB 15827, IRSNB 15643), but these tubercles are barely seen on the preserved animals and are absent in the holotype. Eyelid tubercles can be conspicuous (*e.g.* in IRSNB 15824, adult male) or barely visible (*e.g.* in IRSNB 15820, adult male).

Number of teeth on dentigerous processes of vomers varies from two to five; they are absent in the very small juvenile (IRSNB 15637).

A weak discoidal fold anterior to groin is visible only in the holotype and in two other specimens (IRSNB 15826, adult male, IRSNB 4153, adult female).

The tip of Toe V fails to reach the distal edge of the ultimate subarticular tubercle of Toe IV on both sides in one female (IRSNB 4153), and on one side in four individuals of both sexes (IRSNB 15822–24, IRSNB 15643).

No obvious sexual dimorphism is noted, except in size (females are larger than males).

Other differences among available specimens are considered minor.

Advertisement call. The following description is based on a sample of 21 advertisement calls from the male holotype (IRSNB 4152), recorded on the summit of Wei Assipu Tepui (05° 13’ 05”N, 060° 42’ 15”W, 2210 m elevation), on 17 November 2009 at 20h00, air temperature 15.0°C. The male was calling concealed between the basal leaves of an *Orectanthe sceptrum* (Xyridaceae) growing *ca.* 150 cm above the ground on the wall of a 300-cm deep small crevice.

Temporal structure. The advertisement call of *Pristimantis aureoventris* consists of a soft, single, unpulsed note (perceived by the human ear as a small drop falling in the water). Calls are apparently emitted in bouts of about 20 calls (variation of the number of calls in each bout is unknown). The call rate was 18 calls/min based on a 1-min period. The mean call duration is 0.021 ± 0.002 and varies from 0.017 to 0.023 s. The inter-call interval is rather uniform and has a mean of 3.097 ± 0.275 and a range of 2.730–3.610 s (Fig. 8A).

Spectral structure. Three harmonics are apparently developed, with the fundamental frequency dominating (mean: 2295, range: 2180–2430 Hz) (Fig. 8A). The third harmonic contains slightly more sound energy than the second. The three harmonics show a feeble “U-shaped” frequency modulation (Fig. 8A).

Comparisons. Unfortunately, very few detailed descriptions of *Pristimantis* advertisement calls are available from the highlands of the Pantepui region. Myers and Donnelly (1996) provided analyses of unvouchered calls of different individuals of two highland *Pristimantis* species (tentatively assigned to *P. cantitans* and *P. pruinatus*) from Cerro Yaví, a massif located *ca.* 680 km W airline from Wei Assipu Tepui, and Rödder and Jungfer (2008) described the call of *P. yuruaniensis* from Yuruani Tepui located *ca.* 19 km airline NW from Wei Assipu Tepui.

The call of *P. aureoventris* mostly differs from the calls described from Cerro Yaví in call duration and fundamental frequency: call duration varies from 0.017 to 0.023 s in *P. aureoventris vs.* 0.047 to 0.075 s in the type I call (presumably *P. cantitans*) and *vs.* 0.028 to 0.056 s in the type II call (presumably *P. pruinatus*) of Myers and Donnelly (1996); fundamental frequency varies from 2180–2430 Hz in *P. aureoventris vs.* 1520–1720 Hz in the type I call and *vs.* 2440–2660 Hz in the type II call of Myers and Donnelly (1996).

To the human ear, the call of *P. yuruaniensis* sounds more or less similar to that of *P. aureoventris*, but higher-pitched. Analysis indicates differences in note duration (0.017–0.023 s in *P. aureoventris vs.* 0.093–0.139 s in *P. yuruaniensis*), in fundamental frequency (2180–2430 Hz in *P. aureoventris vs.* 1860–2080 Hz in *P. yuruaniensis*), in inter-call interval (2.730–3.610 s in *P. aureoventris vs.* 0.504–1.968 s in *P. yuruaniensis*), and in harmonics structure (three harmonics showing a feeble “U-shaped” frequency modulation in *P. aureoventris vs.* five indistinctly modulated harmonics in *P. yuruaniensis*). Additionally, the distribution of sound energy decreases progressively through the higher harmonics in *P. yuruaniensis*, while in *P. aureoventris* the third harmonic contains slightly more sound energy than the second (compare Fig. 8A with Fig. 8B). Some of these variations could be caused by intrinsic parameters (*e.g.* size variation, see Duellman & Trueb 1986). Apparent similarity between calls of Pantepui *Pristimantis* species might be interpreted as a plesiomorphic trait.

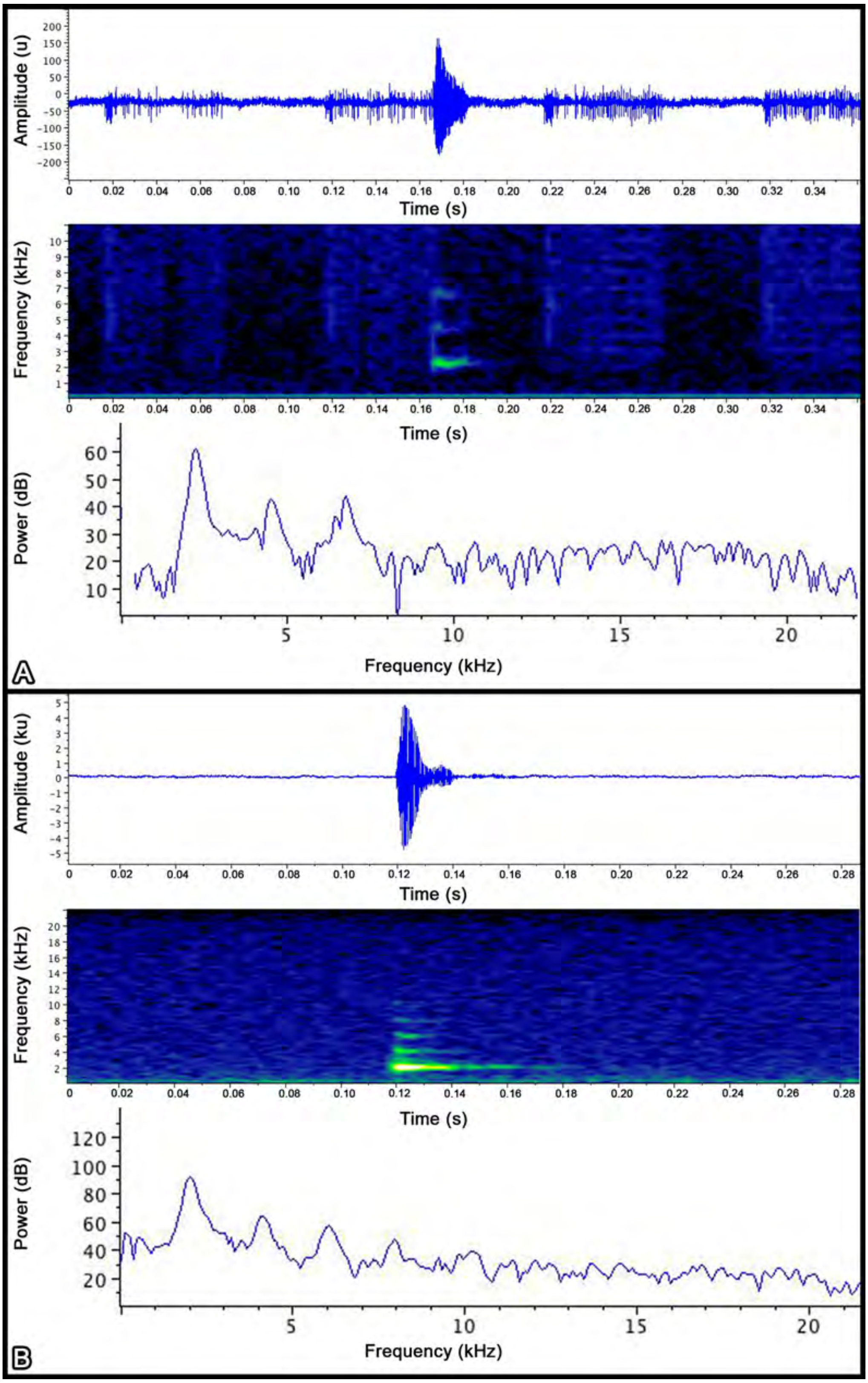


Figure **8.** A. Vocalisation of *Pristimantis aureoventris* **sp. nov.** Oscillogram, spectrogram, and power spectrum of one call of the male holotype recorded at 15.0°C temperature. B. Vocalisation of *Pristimantis yuruaniensis*. Oscillogram, spectrogram, and power spectrum of one call of a topotypic uncollected male recorded at 15.0°C temperature.

Distribution and ecology. *Pristimantis aureoventris* is currently known only from the type locality—the summit of Wei Assipu Tepui (at 2210 m elevation) at the border between Guyana and Brazil—and from near the base of the ultimate cliff of the northern “Prow” of Mount Roraima in Guyana at about 2305 m elevation (Figs. 1, 6, 9). According to the GPS, Wei Assipu Tepui reaches a maximum elevation of *ca.* 2260 m above sea level. Wei Assipu Tepui summit area is about 3 km2 and is level with a large number of fractures, some of them very deep and impassable without the use of climbing equipment—like the “Sima de los Guácharos”, which is more than 100 m deep (see Carreño *et al.* 2002). The Wei Assipu Tepui summit vegetation is the classic “tepui vegetation”, with large areas of coarse herbs mixed with woody subshrubs on peat soils, some quaking bogs and extensive patches of dwarf forests dominated by *Bonnetia roraimae* (Theaceae). The terrestrial bromeliads *Brocchinia tatei* and *B. reducta* are especially abundant, as well as *Stegolepis guianensis* (Rapateaceae), *Orectanthe sceptrum* (Xyridaceae), and *Heliamphora nutans* (Sarraceniaceae). Temperature and hygrometry were recorded from the summit of Wei Assipu Tepui between 9–11 November 2009. A thermo-hygrometer was placed under a small rock in a bare rock area on the summit. The maximum temperature recorded was 29°C (day), the minimum temperature recorded was 13°C (night). Maximum hygrometry recorded was 74% (night), minimum hygrometry was 24% (day). Temperature in the base camp (located under two very large boulders, close to a small forest) was as low as 11°C at night and hygrometry reached 98% during misty nights and mornings. Few rains occurred during our stay in November 2009, which was mostly very dry.

Culminating at 2810 m elevation, Mount Roraima is the highest tepui and second highest point in the Pantepui region (after Pico de la Neblina in the southwest, which reaches about 3000 m elevation). Roraima summit plateau area is about 34 km2. The plateau is very rocky and its vegetation is very sparse. The reader is referred to Huber (1995a, b) for description of the vegetation and physical features of Mount Roraima.

Mount Roraima and Wei Assipu Tepui are very close to each other (about 2 km airline between summits) and the vegetation at the Roraima site was similar to that on Wei Assipu Tepui, but on an inclined talus slope (see below).

Pristimantis aureoventris was found to be mainly nocturnal. Four specimens collected on Wei Assipu Tepui, including the calling male holotype, were found concealed between the basal (brown) leaves of *Orectanthe sceptrum* (Xyridaceae); four other specimens (including the tiny juvenile) were collected between brown leaves at the base of *Brocchinia tatei* (Bromeliaceae); one female was found sitting on bare rock at night; a subadult female was collected at night, sitting on a branch of a small tree about 100 cm above the ground; and one specimen was collected by chance, while escaping from dense vegetation.

The individual from near the base of the ultimate cliff of Mount Roraima's northern "Prow" was taken about 10h00 as it jumped across a trail among dense tank bromeliads (*Brocchinia tatei*) and woody subshrubs in what MacInnes (1974) called the El Dorado Swamp. The "swamp" is a patch of tepui summit vegetation dominated by *Bonnetia roraimae, Brocchinia tatei, Heliamphora nutans, Utricularia humboldtii, Stegolepis guianensis, Orectanthe sceptrum*, and other plants that grow on the inclined, flattish ridge that extends about 1 km north beyond the end of the "Prow" between elevations 1850 and 2200 m (Fig. 6). A completely different forest vegetation dominated by several species of broad-leaved angiosperms including a *Schefflera* sp., Leguminosae, Clusiaceae, palms, and tree ferns of the genus *Cyathea*, with understory shrubs of Melastomataceae, grows at the same elevations leading south on the talus slope below the eastern cliff of Mount Roraima all the way to a small saddle connecting Mount Roraima to Wei Assipu. Two nights of collecting in this cliff-base forest did not turn up frogs of any species.

Figure **9.** A. Aerial photograph of Wei Assipu Tepui (right) and Mount Roraima (left). B. Aerial photograph of Wei Assipu Tepui, Mount Roraima is well visible on the upper left. C. Summit of Wei Assipu Tepui. D. Typical vegetation in which specimens of *Pristimantis aureoventris* **sp. nov.** were collected. E. Clutch of four eggs in a dead pitcher of a *Heliamphora nutans* plant (pitcher removed from original location for photographic purpose). F. Close-up photograph of the four eggs inside the pitcher. Photographs by Philippe J.R. Kok.

Males call at night, hidden in plants among dense vegetation and are usually exceedingly difficult to locate. None of the several males heard calling was exposed. The species is apparently abundant, but specimens are difficult to collect. We are aware of two previous expeditions on the summit of Wei Assipu Tepui during which amphibians were collected (see for instance Villarreal *et al*. 2002), but none of them found *Pristimantis* *aureoventris*.

Two clutches of eggs were found on the summit of Wei Assipu Tepui, both were in a dead (brown) pitcher at the base of two different *Heliamphora nutans* plants (Sarraceniaceae). Genomic DNA was extracted from one egg of each clutch, and DNA barcoding established conclusively adult and egg conspecificity (0% uncorrected pairwise distance). The first clutch was found on 5 November 2009 in a plant growing at the bottom of a small, very humid crevice (*ca.* 300 cm deep) and contained five eggs measuring 5.25–5.62 mm. The second clutch was found on 7 November 2009, at the edge of another small, very humid crevice (*ca.* 600 cm deep) and contained four eggs measuring 5.53–6.10 mm (Fig. 9).

Discussion. The new taxon is morphologically most similar to species assigned to the artificial *unistrigatus* species group (*sensu* Hedges *et al.* 2008). Considering that the *unistrigatus* group is largely non-monophyletic (see for instance Hedges *et al.* 2008: 15), we prefer not to include the new species in it. It is expected that further molecular and morphological data will indicate that the Pantepui species *sensu stricto* (*i.e.* highland species) are well distinct from the original *unistrigatus* group of Lynch (1976) and that of Lynch and Duellman (1997).

Among described *Pristimantis* species, the geographically closest highland species to *P. aureoventris* is *P. yuruaniensis*, which occurs on the summit of Yuruani Tepui, about 19 km (airline) NW of Wei Assipu Tepui (see Fig. 1). Both taxa inhabit very similar environments, and although superficially similar, these highland species diverge in some morphological characters (*i.e.* size, skin condition) and colour pattern, including the fact that *P. aureoventris* exhibits a high degree of pattern polymorphism, while *P. yuruaniensis* is a poorly variable species, with a distinct sexual dichromatism (males are light orangish brown, females are dark brown, see Fig. 10). Additionally, the ventral face of *P. yuruaniensis* in life is translucent, whitish, orangish or brown speckled with minute brownish dots, with internal organs well visible through the skin; conversely, that of *P. aureoventris* is opaque, golden yellow with reddish brown to dark brown mottling, with internal organs little or not visible through the skin (compare Fig. 4 with Fig. 10). Another interesting difference resides in the tongue morphology, *P. yuruaniensis* having a broad, short round tongue, rarely slightly longer than broad (only one of the five specimens examined has the tongue slightly longer than wide), whereas the tongue of *P. aureoventris* is very long, always much longer than wide. According to the data available, the number of eggs laid by each species is different: 4–5 in *P. aureoventris vs.* 9 in *P. yuruaniensis* (PJRK pers. obs., Rödder & Jungfer 2008). Furthermore, although more or less similar to the human ear, their calls are significantly different. We consider both species distinct because they are geographically isolated (isolated lineage segments), morphologically reliably diagnosable and have different advertisement calls.

Mägdefrau & Mägdefrau (1994) and Rödder & Jungfer (2008) suggested the presence of *P. yuruaniensis* on the summit of Kukenan Tepui (located 10 km airline SE to Yuruani Tepui), mostly based on overall similarities of specimens and identical call (although apparently none of the Kukenan specimens were collected). The specimen from Kukenan Tepui reported as *P. cf. yuruaniensis* illustrated in Rödder & Jungfer (2008: 64) might belong to a still undescribed species and more investigations are needed before confirming the occurrence of *P. yuruaniensis* on Kukenan Tepui.

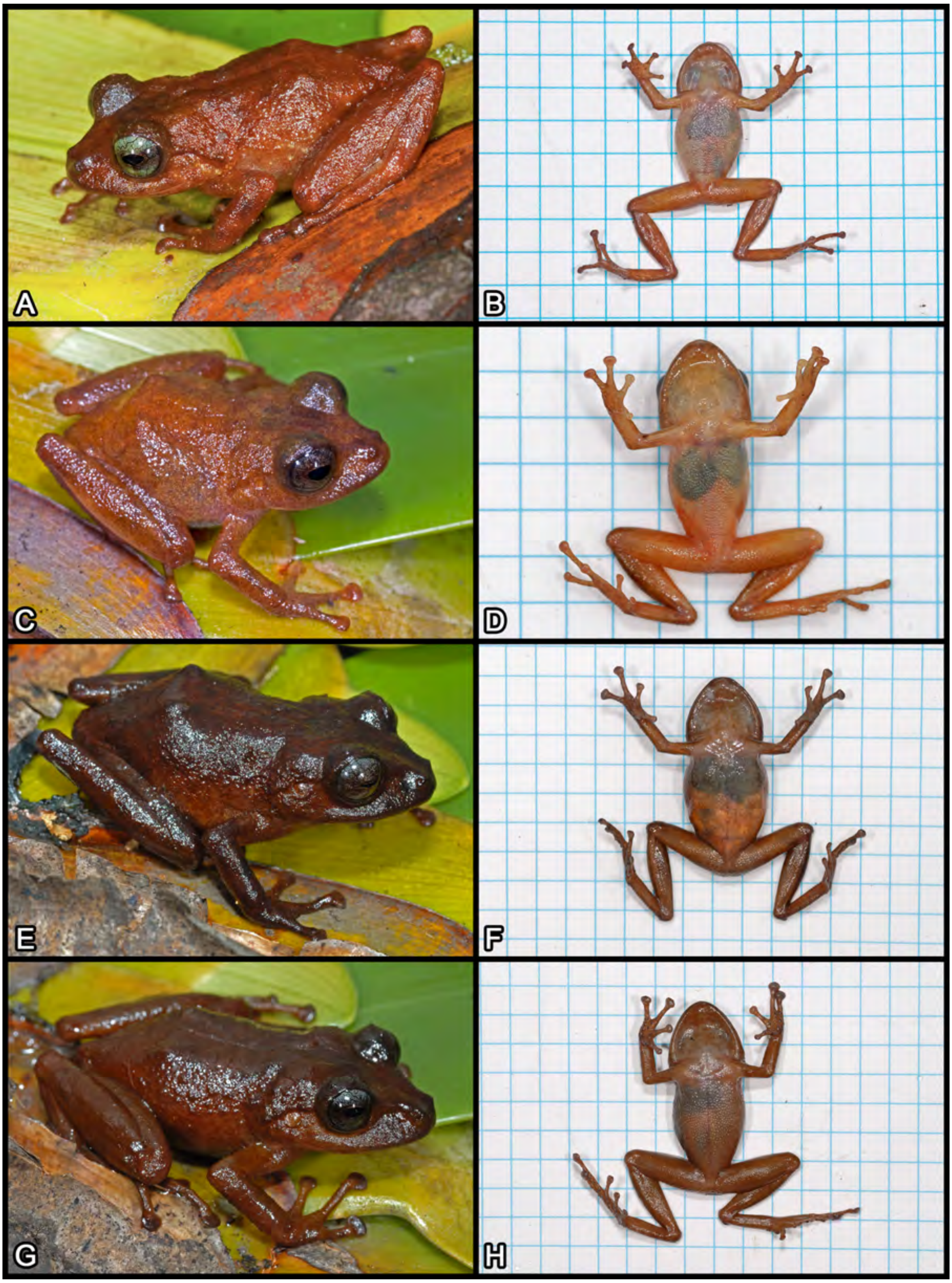


Figure **10.** *Pristimantis yuruaniensis* from the type locality (Yuruani Tepui). Intrapopulation variation and sexual dichromatism in dorsal and ventral colour in living specimens. A: Dorsolateral view of the male IRSNB 15640, 23.8 mm SVL. B: Ventral view of the same specimen. C: Dorsolateral view of the male IRSNB 15641, 24.0 mm SVL. D: Ventral view of the same specimen. E: Dorsolateral view of the female IRSNB 15638, 32.1 mm SVL. F: Ventral view of the same specimen. G: Dorsolateral view of the female IRSNB 15639, 32.2 mm SVL. H: Ventral view of the same specimen. Photographs by Philippe J.R. Kok.

Because it might mislead future new species descriptions and comparisons, it should be noted that the original description of *Pristimantis yuruaniensis* (Rödder & Jungfer 2008) contains errors, some probably attributable to the poor state of preservation of the type series. Examination of one paratype (SMNS 09855, an adult female) as well as four additional topotypic specimens (IRSNB 15638–39, adult females, IRSNB 15640–41, adult males) shows that (character states reported in the original description of *P. yuruaniensis* are between parentheses): *P. yuruaniensis* has an areolate ventral skin in life ("smooth"), dentigerous processes of vomers bear 1–6 teeth ("no vomerine dentigerous processes", although the paratype SMNS 09855 has 3–5 teeth on each vomer), vocal slits absent in males, presence of two whitish nuptial pads on thumb (characters unknown because no male was available), fingers with broad lateral fringes ("fingers without lateral keels"), toes with broad lateral fringes ("toes without lateral keels", although fringes are well visible on the paratype SMNS 09855), basal webbing between Toes IV-V ("no webbing"). Additionally, figure 4B in Rödder & Jungfer (2008: 65) suggests that in *P. yuruaniensis* Toe V is almost equal to Toe III when toes are adpressed. This is contradicted by examination of the paratype SMNS 09855 and the additional topotypic specimens mentioned above, in which Toe V reaches at least the proximal edge of the distal subarticular tubercle on Toe IV, and is distinctly longer than Toe III.

McDiarmid & Donnelly (2005) reported an undescribed *Pristimantis* species from the summit of Mount Roraima ("*Eleutherodactylus* sp J"). Although there seems to be morphological differences between "*Eleutherodactylus* sp J" and *Pristimantis aureoventris* (César Barrio-Amorós, pers. comm), we have not examined specimens from the summit of Roraima and tissue samples from these specimens are unavailable. We therefore cannot exclude that these taxa are conspecific.

The presence of at least one same anuran species on both Mount Roraima and Wei Assipu Tepui has been reported (*Oreophrynella quelchii*, see Villarreal *et al*. 2002), and the occurrence of the same *Pristimantis* species on both of these neighbouring tepuis is not surprising. However it still remains unknown why some species sometimes occur on two or more different tepui summits, while some seem restricted to a single summit.

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APPENDIX. ADDITIONAL MATERIAL EXAMINED

Pristimantis dendrobatoides.— Guyana: *Potaro-Siparuni District*: Wokomung Massif, USNM 563662 (holotype), USNM 563661 (paratopotype), USNM 564161–64, ROM 43317 (paratypes).

Pristimantis inguinalis.— Guyana: *East Berbice-Corentyne District*: New River, BMNH 1947.2.16.6 (formerly 1939.1.1.1) (holotype), BMNH 1947.2.16.7 (formerly 1939.1.1.2) (paratype).

Pristimantis jester.— Guyana: *Potaro-Siparuni District*: Wokomung Massif, USNM 563631 (holotype), USNM 563632 (paratopotype), USNM 563633, ROM 43303, ROM 43306 (paratypes).

Pristimantis marmoratus.— Guyana: *Cuyuni-Mazaruni District*: foot of Mount Roraima, BMNH 1947.2.16.92 (formerly 99.3.25.19) (holotype).

Pristimantis pulvinatus.— Venezuela: *Estado Bolívar*: La Escalera, IRSNB 15654.

Pristimantis saltissimus.— Guyana: *Potaro-Siparuni District*: Wokomung Massif, USNM 563639 (holotype), USNM 563634–37, USNM 563640–41, USNM 563644–45 (paratopotypes), USNM 563638, USNM 563642–43, USNM 563646–51, USNM 563665–79 (paratypes), IRSNB 15644–53 (topotypic specimens).

Pristimantis yuruaniensis.— Venezuela: *Estado Bolívar*: Yuruani Tepui, IRSNB 15638–41 (topotypic specimens), SMNS 09855 (paratype).

7

A New Species of *Anadia* (Reptilia, Squamata) from the Venezuelan "Lost World", Northern South America

P. J. R. Kok & G. A. Rivas

Abstract

A new gymnophthalmid lizard of the genus *Anadia* Gray, 1845 is described from the summit of Abakapá-tepui, Bolívar state, Venezuela, between 2200–2242 m elevation. The new species, *Anadia mcdiarmidi* **sp. nov.**, is endemic to the Chimantá Massif and seemingly also occurs on Amurí-tepui and Murei-tepui. The new taxon is mainly distinguished from all known congeners by the following combination of characters: body fairly robust, dorsal scales small and quadrangular, middorsal scales 53-57, suboculars large, subequal in size, with sometimes one scale slightly protruding downward between 4th and 5th supralabial, nasal entire, without sub-nostril groove, body uniform greyish to bluish brown in life, devoid of any conspicuous pattern in males, venter immaculate golden grey in life, femoral pores 9–10 on each side in males, preanal pores absent, hemipenis globose, weakly bilobed, bordered by numerous flounces (>20) bearing comblike rows of minute weakly mineralized spinules. The presence of a species of *Anadia*, a primarily Andean genus, on the top of tepuis is of considerable interest to the understanding of the Pantepui biogeography.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

Gymnophthalmid lizards of the genus *Anadia* Gray, 1845 may be gracile, narrow-headed and semi-arboreal or mostly terrestrial, more robust with a broader head (Oftedal, 1974). This genus is primarily Andean, with 17 currently recognized species distributed in the Ecuadorian Andes (*A. petersi* Oftedal, 1974), Colombian Andes [*A. altaserrania* Harris & Ayala, 1987, *A. bogotensis* (Peters, 1863), *A. pulchella* Ruthven, 1926], Venezuelan Andes [*A. bitaeniata* Boulenger, 1903, *A. brevifrontalis* (Boulenger, 1903), *A. hobarti* La Marca & García-Pérez, 1990, *A. pamplonensis* Dunn, 1944], the central coastal range in Venezuela [*A. marmorata* (Gray, 1846), *A. steyeri* Nieden, 1914], the eastern coastal range in Venezuela (*A. blakei* Schmidt, 1932, *A. pariaensis* Rivas, La Marca & Oliveros, 1999), and at lower elevations from Costa Rica to southwestern Ecuador and in southeastern Venezuela [*A. ocellata* Gray, 1845, *A. vittata* Boulenger, 1913, *A. bumanguesa* Rueda-Almonacid & Caicedo, 2004, *A. rhombifera* (Günther, 1859), *A. escalerae* Myers, Rivas & Jadin, 2009].

Oftedal (1974) provided a comprehensive review of the genus, which is still authoritative and included 11 species. Since Oftedal's work five additional species have been described in the genus: two from Colombia (*A. altaserrania* and *A. bumanguesa*), one from the Venezuelan Andes (*A. hobarti*), one from the peninsula of Paria in Venezuela (*A. pariaensis*), and one from the La Escalera region, Bolívar state in southeastern Venezuela (*A. escalerae*), which to date constitutes the easternmost locality for the genus. *Anadia pamplonensis* was removed from the synonymy of *A. bitaeniata* by Harris & Ayala (1987). The monophyly of the genus is still in question (Myers et al., 2009) and phylogenetic relationships are mostly unknown.

In 1978 Roy McDiarmid (Smithsonian Institution) accompanied by the Venezuelan explorer Charles Brewer-Carías collected an *Anadia* species on the summit of Murei-tepui in the Chimantá Massif (Gorzula, 1992; McDiarmid & Donnelly, 2005). Although the species was supposed to be described by McDiarmid and Harris (as stated by Gorzula, 1992), Gorzula (1992) reported it from the Chimantá Massif as *Anadia breweri* (a *nomen nudum* according to Gorzula & Señaris, 1999; Myers & Donnelly, 2008; and Myers et al., 2009) based on McDiarmid's specimen and additional material collected by the "Grupo Científico Chimantá". The species was subsequently reported as "*Anadia* species a" by Gorzula & Señaris (1999), who mentioned it from three tepuis in the Chimantá Massif: Abakapá-tepui, Amurí-tepui, and Murei-tepui, and as "*Anadia* sp. A" by McDiarmid & Donnelly (2005), who also reported it from the three same mountains. The species is illustrated as *Anadia breweri* in a recent book by Brewer-Carías & Audy (2010, unnumbered figure on page 210). Surprisingly, no description ever appeared and the status of the new species (including its generic allocation) remains uncertain.

A recent expedition to Abakapá-tepui in the Chimantá Massif led in the framework of a study on the evolution of the Pantepui herpetofauna resulted in the rediscovery of the species, which is described below on the basis of four specimens.

MATERIAL AND METHODS

Specimens were collected by hand and euthanized by intra-peritoneal injection of 2% Xylocaine. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens have been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB), Brussels, Belgium. Coordinates and elevations of localities were acquired using a Garmin 60CSx Global Positioning System unit and referenced to map datum WGS84.

Comparisons of external character states are based both on original descriptions and examination of museum specimens (see Appendix for material examined). Terminology for morphological characters and scale counts mostly follow Oftedal (1974) and Myers et al. (2009). All morphometric data were taken from the preserved specimens to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper. For ease of comparison, the description mainly follows the pattern of Myers et al. (2009). The following measurements and scale counts were taken and abbreviated as follows: (1) snout-vent length, from tip of snout to posterior margin of vent (SVL); (2) tail length, from posterior margin of vent to tip of tail (TL); (3) head length, from tip of snout to anterior margin of ear opening (HL); (4) greatest width of head (HW); (5) greatest depth of head (HD); (6) snout-axilla length (SAL); (7) neck length, from posterior edge of ear opening to forearm held at right angle to body (NL); (8) axilla-groin distance (= trunk length), from base of forelimb to base of hind limb (AXG); (9) forelimb length, from axilla to tip of claw of longest digit (FlL); (10) hind limb length, from groin to tip of claw of longest digit (HlL); (11) number of subdigital lamellae under Finger IV (SLF); (12) number of subdigital lamellae under Toe IV (SLT); (13) number of middorsal scales, from postoccipitals to the level of posterior edge of thigh held at right angle to body (MD); (14) number of ventrals in longitudinal rows, counted at midbody and including small ventrolateral rectangular plates (VL); (15) number of ventrals in transverse rows, counted between collar and vent [thus including preanals, which as pointed out by Oftedal (1974) are frequently difficult to distinguish from ventrals in the genus] (VT); (16) number of scales around midbody, counted at mid-distance between collar and vent (SAM); (17) number of supralabials (SL); (18) number of infralabials (IL); and (19) number of femoral pores under each thigh (FP).

Males' genitalia were everted in the field by injection of 10% formalin at the base of the tail just prior preservation. The left hemipenis of the holotype and both hemipenes of the adult male paratype (IRSNB 2674) were dissected in the laboratory, soaked over night in a solution of 2% potassium hydroxide, washed with distilled water, and filled with petroleum jelly, mostly following the methods described by Manzani & Abe (1988) and modified by Pesantes (1994) and Zaher (1999). To highlight the calcareous spinules the organs were subsequently stained 24 hours in 1% potassium hydroxide saturated with Alizarin Red [method adapted from Uzzell (1973)], and stored in 70% ethanol. Terminology of hemipenis description mostly follows Dowling & Savage (1960), Savage (1997), Zaher (1999), and Myers et al. (2009).

Colour pattern in life was taken from field notes and colour digital photographs. Sex was determined by the presence/absence of hemipenes (base of tail dissected when hemipenes were not everted in the field). Taxonomy follows Oftedal (1974), Pellegrino et al. (2001) and Rodrigues et al. (2005). Institutional acronyms follow Frost (2011).

RESULTS

Anadia mcdiarmidi sp. nov.

(Figs. 1–7; Table 1)

Anadia breweri (*nomen nudum*); Gorzula (1992: 276, figs. 168-171)
Anadia species a; Gorzula & Señaris (1999: 114-115, fig. 88)
Anadia sp. A; McDiarmid & Donnelly (2005: 514)
Anadia breweri (*nomen nudum*); Brewer-Carías & Audy (2010: 210, unnumbered figure)

Holotype. IRSNB 2677 (field number PK 3565), an adult male collected by Philippe J. R. Kok, 3 May 2011 at 11h39, summit of Abakapá-tepui, Bolívar state, Venezuela (05° 11' 09"N, 062° 17' 36"W, 2201 m elevation).

Paratopotypes (n=3)**.** One adult male (IRSNB 2674, field number PK 3578) collected by Philippe J. R. Kok, 6 May 2011 at 9h40, summit of Abakapá-tepui, Bolívar state, Venezuela (05° 10' 50"N, 062° 17' 49"W, 2242 m elevation), one juvenile male (IRSNB 2675, field number PK 3577) collected by Philippe J. R. Kok, 6 May 2011 at 9h10, summit of Abakapá-tepui, Bolívar state, Venezuela (05° 11' 00"N, 062° 17' 34"W, 2200 m elevation), and another juvenile male (IRSNB 2676, field number PK 3589) collected by Philippe J. R. Kok, 9 May 2011 at 9h00, summit of Abakapá-tepui, Bolívar state, Venezuela (05° 11' 07"N, 062° 17' 19"W, 2204 m elevation).

Etymology. The specific epithet is a noun in the genitive case, honouring Roy McDiarmid, North American herpetologist (Smithsonian Institution), for his contribution to the knowledge of the Pantepui herpetofauna.

Generic allocation. The new species is placed in the genus *Anadia* because it fits the 11 diagnostic traits for the genus proposed by Oftedal (1974): dorsal scales smooth, essentially homogeneous; no distinct rows of much smaller scales between lateral scales; ventral scales smooth, quadrangular; head scales smooth, without striation; single frontonasal separating nasals; paired prefrontals; several large pigmented palpebrals; gular scales smooth, essentially homogeneous, with no distinctly enlarged longitudinal rows; 7-10 large preanal scales [maximum 9 in Oftedal (1974)]; femoral pores conspicuous in adult males; and limbs well developed, pentadactyl with all toes clawed.

Definition and diagnosis. A fairly robust species currently not assigned to any species group. The new species is characterized by the following combination of characters: (1) size small, body robust (maximum known SVL 62.2 mm); (2) tail longer than SVL; (3) dorsal scales small, quadrangular; (4) middorsal scales 53-57; (5) suboculars large, unequal in size, with sometimes one scale slightly protruding downward between 4th and 5th supralabial, suboculars separated from palpebrals by 2-3 rows of mostly inconspicuous tiny scales, a few of them distinctly enlarged with angular downward protrusion between suboculars (6) nasal entire, without sub-nostril groove; (7) 3-4 large pigmented palpebrals; (8) body uniform beige or greyish to bluish brown in life, devoid of any conspicuous pattern in males; (9) absence of any dark line on side of head in adult males; (10) venter immaculate golden grey in life; (11) femoral pores 9-10 on each side in males, unknown in females; (12) preanal pores absent; (13) hemipenis globose, weakly bilobed, bordered by numerous flounces (>20, including about eight medioproximal asulcate flounces) bearing comblike rows of minute weakly mineralized spinules, *sulcus spermaticus* divided in the crotch by a small fleshy bumplike structure, *sulcus* branches barely detectable.

The new taxon is immediately distinguished from *Anadia ocellata*, *A. vittata*, *A. rhombifera*, and *A. petersi* [all members of the *ocellata* group of Oftedal (1974)] and *A. bogotensis* [single member of the *bogotensis* group of Oftedal (1974)] in having quadrangular dorsal scales (subhexagonal in species of the *ocellata* group, imbricate in *A. bogotensis*), and in lacking a subnostril groove or divided nasal (nasal divided or subnostril groove present in species of the *ocellata* group and in *A. bogotensis*); from *A. altaserrania* [a member of the *bitaeniata* group of Oftedal (1974) according to Harris & Ayala (1987)] in having prefrontals (lacking in *A. altaserrania*), in having more femoral pores in males (9-10 in *A. mcdiarmidi vs.* 3-4 in *A. altaserrania*), and in having a higher number of middorsal scales (53-57 in *A. mcdiarmidi vs.* 45-47 in *A. altaserrania*); from *A. bitaeniata, A. brevifrontalis, A. hobarti, A. pamplonensis,* and *A. pulchella* [all members of the *bitaeniata* group of Oftedal (1974) according to La Marca & García-Pérez (1990)] in having a higher number of middorsal scales (53-57 in *A. mcdiarmidi vs.* maximum 50 in species of the *bitaeniata* group); from *A. blakei* and *A. marmorata* [members of the *marmorata* group of Oftedal (1974)] in having a higher number of middorsal scales (more than 50 in *A. mcdiarmidi vs.* less than 35 in *A. blakei* and *A. marmorata*); from *A. bumanguesa* [a member of the *bitaeniata* group of Oftedal (1974) according to Rueda-Almonacid & Caicedo (2004), but a possible synonym of *A. steyeri* and thus a member of the *steyeri* group of Oftedal (1974) according to Rivas et al. (in press)] in having a lower number of scales around midbody (35-36 in *A. mcdiarmidi vs.* 41 in *A. steyeri*), and in having pigmented palpebrals (unpigmented in *A. bumanguesa*); from *A. pariaensis* (not assigned to any species group in the original description) in having a much lower number of middorsal scales (54-57 in *A. mcdiarmidi vs.* 70-72 in *A. pariaensis*); from *A. steyeri* [single member of the *steyeri* group of Oftedal (1974)] in having a lower number of scales around midbody (35-36 in *A. mcdiarmidi vs.* 40-45 in *A. steyeri*); and from *A. escalerae* (not assigned to any species group in the original description), the geographically closest relative, in having a robust body (slender in *A. escalerae*), in having smooth dorsal scales (weakly keeled in *A. escalerae*), in lacking dorsolateral stripes (present in *A. escalerae*), in having a lower number of middorsal scales (54-57 in *A. mcdiarmidi vs.* 63 in *A. escalerae*), and in having a lower number of scales around midbody (35-36 in *A. mcdiarmidi vs.* 40 in *A. escalerae*).

Description of the Holotype. An adult male in good condition (Figs. 1A, C, 2, 3, 4, 6), with 62.2 mm SVL and 110.0 mm TL (see also Table 1). A rather robust *Anadia* species with moderately long limbs (digits overlap when limbs are adpressed along body). Snout attenuate, flat in profile. HL 25% of SVL, 1.5 times longer than wide, 1.6 times wider than high; head conspicuously wider than neck. Neck long, 68% of HL, 35% of AXG. SAL 93% of AXG, 46% of SVL. Body wider than deep. Tail dorsoventrally flattened, about 1.8 times longer than SVL. Limbs pentadactyl with all digits clawed. Forelimb 27% of SVL, 52% of AXG; hind limb 36% of SVL, 73% of AXG.

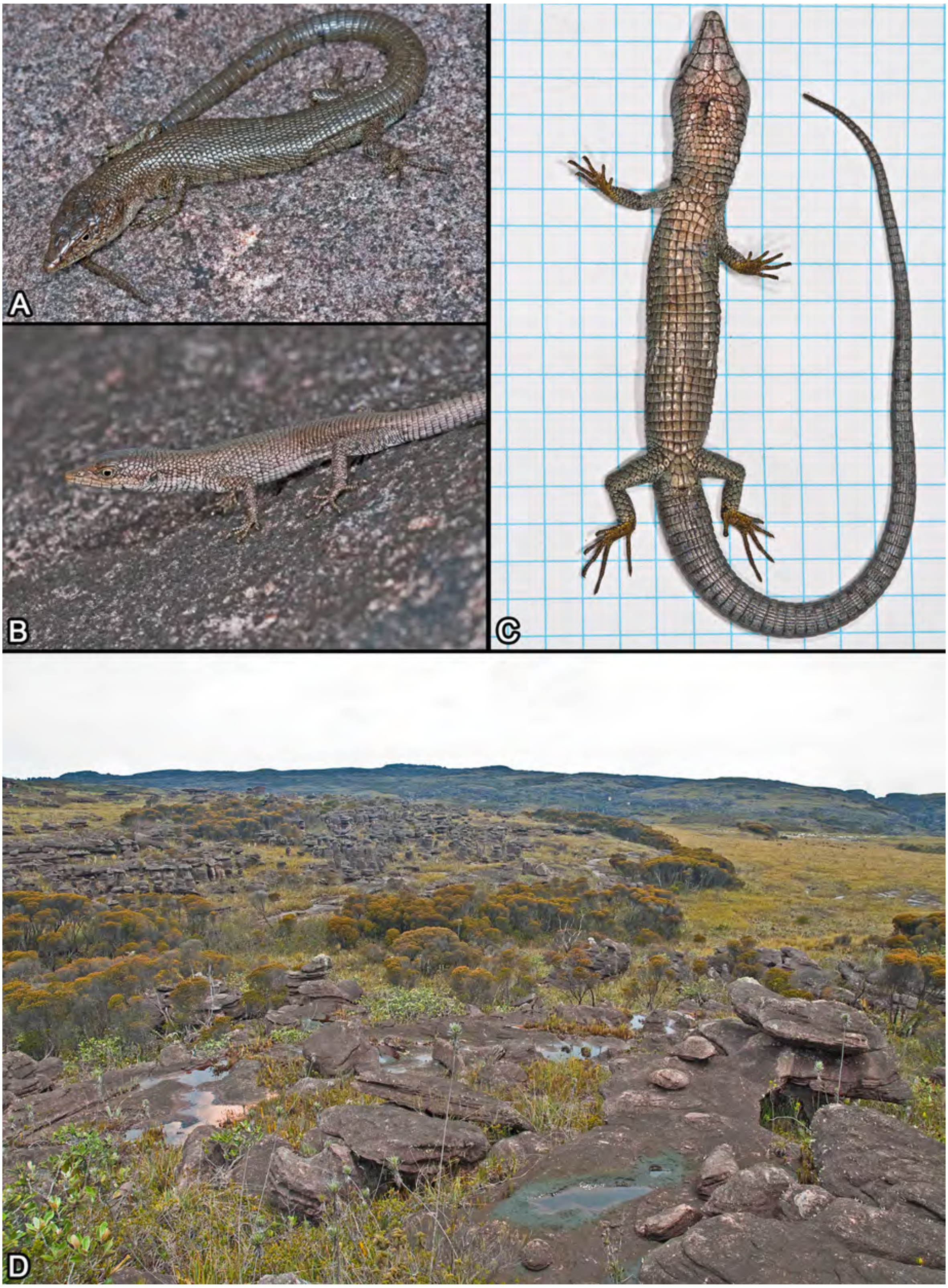

Figure **1.** *Anadia mcdiarmidi* **sp. nov.** A. IRSNB 2677, male holotype in life. B. IRSNB 2675, juvenile male paratype in life. C. Ventral view of the anaesthetized holotype (grid squares = 5 mm). D. Summit of Abakapá-tepui, looking NW, showing the macrohabitat of the new species (3 May 2011). Photographs by Philippe J.R. Kok.

Scutellation on the dorsal surface of head is typical for the genus [see fig. 1 in Oftedal (1974)], except the condition of the parietals and interparietal (see below and Figs. 2, 7). The frontal is damaged, the frontoparietals are slightly damaged. Head scales are smooth with a few minute scattered pits, those pits are especially concentrated on the upper and posterior margins of supralabials, on the lower and posterior margins of infralabials, and on the posterior margin of rostral.

Rostral much wider than deep, laterally in contact with nasals and first supralabial, dorsally in contact with large frontonasal. Frontonasal with nearly straight anterior margin, posteriorly pointed. Paired prefrontals in contact, medial suture short. Frontal damaged, but obviously wider anteriorly and with blunt anterior point. Paired frontoparietals slightly damaged, with long medial suture, in contact with interparietal, parietals, and two posterior supraoculars. Three large supraoculars subequal in size. Interparietal divided into about two scales unequal in size. Parietals not extending as far as interparietal posteriorly, divided into two scales on the left side, into four scales on the right side. A series of six small to large occipitals (postparietals) circling the common posterior margin of parietals and interparietal.

Nasal scale entire, with a small indentation situated anterodorsally to nostril on the left side. Nasal scale in contact with rostral, posteriorly in contact with prefrontal, and in broad contact with loreal. Loreal large, pentagonal, in broad contact with first superciliary (= presuperciliary) and frenocular, in point contact with preocular. One small preocular, three postoculars. First superciliary large, followed by four shorter superciliaries. No small azygous scale between superciliaries and supraoculars. Frenocular followed posteriorly by three suboculars. Third subocular slightly extending to lip between supralabials 4-5 on the left side only. Suboculars separated from palpebrals by 2-3 poorly defined rows of mostly inconspicuous tiny scales, two of them distinctly enlarged with angular downward protrusion between suboculars. Seven supralabials.

Eight ciliaries along upper eyelid. Lower eyelid scales translucent, slightly pigmented, with four higher-than-wide palpebrals.

Temporal scales subimbricate, smooth, with flat surfaces, slightly larger above and smaller below. Ear opening broad, ovoid, slightly inclined posterodorsally, edged with small, slightly pebblelike scales; tympanum recessed, pigmented.

Underside of head with six infralabials on each side. A large mental followed by a large postmental in contact with first two infralabials. Two pairs of large genials in broad contact medially, in lateral contact with infralabials 3-4; two pair of postgenials, the first pair large, each scale in contact with last genial and infralabials 4-5, the second pair much smaller, each scale in contact with first postgenial and in point contact with fifth infralabial. Gulars arranged in transverse rows, becoming slightly larger posteriad, culminating in a well-defined collar row of eight subequal scales; no distinctly enlarged longitudinal rows. Side of neck between ear and collar pebbled with subequal irregularly shaped juxtaposed scales.

Middorsal scales 54. Dorsal scales on neck subimbricate, irregularly shaped, with rounded surfaces. Dorsal body scales smooth, juxtaposed, mainly quadrangular, a few irregularly shaped, but most are longer than wide, in transverse rows only. Lateral scales smooth, similar to dorsals, but smaller.

Ventral scales much wider than dorsals, smooth, juxtaposed, quadrangular, slightly longer than wide except for *ca.* four median longitudinal rows of square to wider than long scales on belly; in 14 longitudinal rows at midbody and 31 transverse rows between collar and vent.

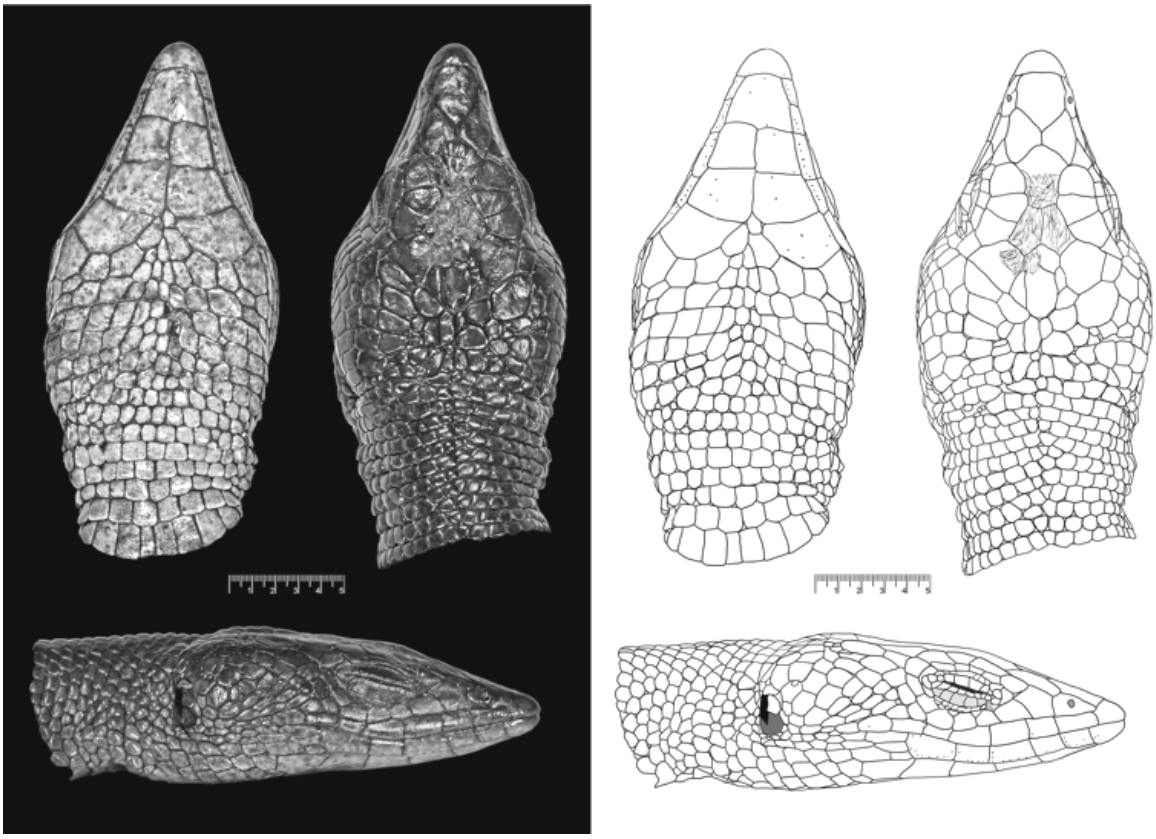

Figure **2.** *Anadia mcdiarmidi* **sp. nov.** Ventral, dorsal, and lateral views of the head of the holotype (IRSNB 2677). Scale lines = 5 mm. Photographs by Philippe J.R. Kok.

Eight marginal preanal scales anterior to vent, the middle two narrower than the adjacent lateral ones, most outer ones very small. Femoral pores well developed, in swollen pore scales mostly in linear contact; 9 pores on left thigh, 10 on right. Pores do not extend onto preanal area (Fig. 3).

Caudal scales smooth, subimbricate, rectangular, in transverse rows around tail.

Scales on dorsal surfaces of arm large, smooth, imbricate; ventral surfaces of arm with similar, but smaller and less imbricate scales. Hind limbs with large, smooth subimbricate to imbricate scales on anterior face of thighs and on lower legs; scales similar but smaller on ventral side of thigh. Dorsal and posterior sides of thigh with much smaller, irregularly shaped juxtaposed scales.

Moderate-size, imbricate scales atop hands and feet. Supradigital scales single; upper and lower ungual-sheath scales covering base of claws, leaving tips well exposed. Palms and soles with small slightly raised juxtaposed scales (Fig. 4). Two enlarged smooth thenar scales at base of pollex. Subdigital lamellae mostly single. Lamellae under first (**I**) through fifth (**V**) finger (right/left side): **I**: 7/6, **II**: 9/9, **III**: 11/11, **IV**: 13/14, **V**: 10/9. Lamellae under first (**I**) through fifth (**V**) toe (right/left side): **I**: 6/6, **II**: 10/10, **III**: 14/12, **IV**: 17/15, **V**: 15/6 (large part of Toe V missing on left side).

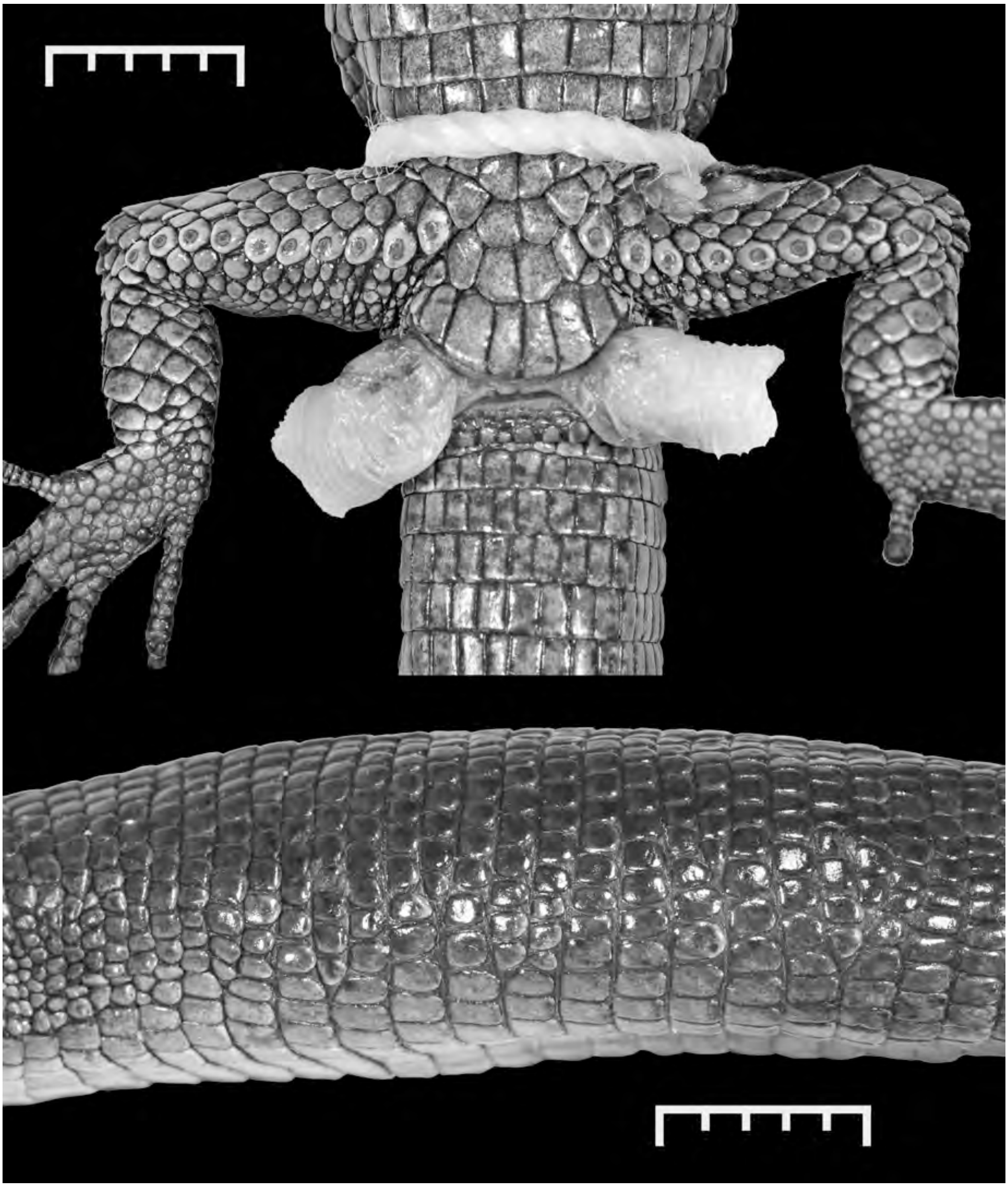

Figure **3.** *Anadia mcdiarmidi* **sp. nov.** Subpelvic region of the preserved male holotype (IRSNB 2677), showing preanal scales and femoral pores, and trunk of the preserved holotype in lateral view (head to left), showing scalation at midbody. Scale lines = 5 mm. Photographs by Philippe J.R. Kok.

Tongue lanceolate; proximal two-third unpigmented, distal one-third heavily pigmented, including fork. Upper surface behind fork covered with imbricate scalelike papillae that extend onto ventrolateral sides of tongue. Raised medioventral side of tongue with numerous (>10) of thin, oblique, anteriorly converging and pointed (chevronlike) infralingual plicae; anterior pair of plicae swollen, bluntly pointed and larger than those following. Very shallow medioventral groove.

Figure **4.** *Anadia mcdiarmidi* **sp. nov.** Left hand and right foot of the holotype (IRSNB 2677) in life. Scale line = 5 mm. Photographs by Philippe J.R. Kok.

Anterior maxillary and dentary teeth conical, unicuspid, with no or very feeble recurvature, becoming larger posteriorly.

The left hemipenis (Fig. 5) extends about four subcaudal rows when adpressed to the tail, and is about 7.0 mm in length and 4.0 mm across its widest point when fully everted (organ not maximally expanded because one of the lobes was slightly damaged during the eversion process). Hemipenial body globose, tapered near the base, weakly and symmetrically bilobed. *Sulcus spermaticus* broader near crotch, relatively shallow, curving about halfway around the base of the organ, then running medially towards the lobes. *Sulcus* flanked by a narrow nude area on each side, and divided in the crotch by a small fleshy bumplike structure, from where two narrow, ill-defined and barely detectable *sulcus* branches seem to extend laterally into the folded thickened “ear-like” tissues of each lobe towards the apices of the lobes. Lobes are complexly folded, not flattened terminally, and *sulcus* branches seem to end in small depressions (from which residual seminal fluid was removed before hemipenis preparation).

Very base of hemipenis nude, pigmented in life. Lateral and asulcate faces of the organ with a series of roughly equidistant oblique plicae or flounces with weakly calcified spinules. Twenty-three rows of flounces extending along the organ. Basal flounces shorter, almost in straight transverse lines, the three first rows almost continuous across the hemipenial base, except for narrow nude areas on each lateral face and for nude areas edging each side of the *sulcus spermaticus*; five subsequent rows continuous across hemipenial body (except for nude areas edging each side of the *sulcus spermaticus*), with the seventh and eight rows distinctly pointing medially towards the apex on the asulcate face (those eight flounces proximal to the median nude space of the asulcate face correspond to the "medioproximal asulcate flounces" *sensu* Myers et al. 2009); fifteen remaining rows chevron-shaped, also circling the organ, but separated by a broad median nude space on the asulcate face and by the nude areas edging each side of the *sulcus spermaticus*. The *plicae* bear comblike rows of minute weakly mineralized spinules that project slightly from the edges of the *plicae* and usually increase in size towards the lateral faces and the basal part of the organ (staining of the spinules by Alizarin Red is well visible under the microscope although not observable in Fig. 5).

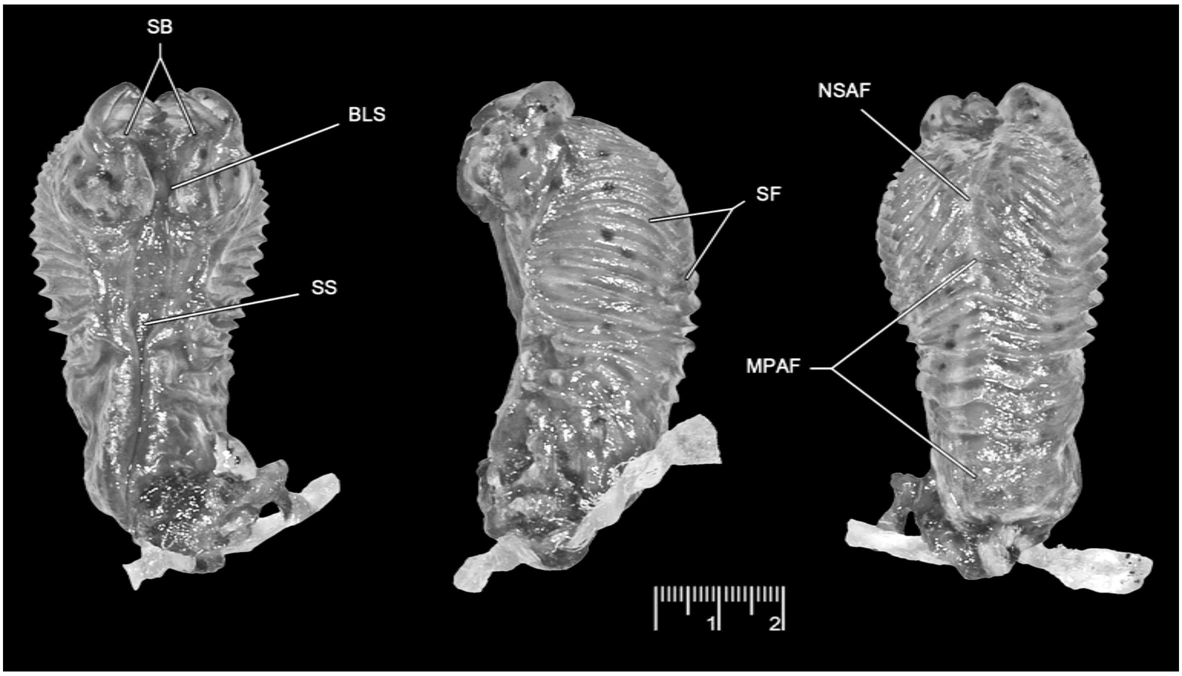

Figure **5.** *Anadia mcdiarmidi* **sp. nov.** The left fully everted—not maximally expanded—hemipenis of the holotype (IRSNB 2677). Left: sulcate side. Centre: lateral view, turned with sulcate side facing left. Right: asulcate side. BLS = fleshy bumplike structure, MPAF = medioproximal asulcate flounces, NSAF = median nude space of the asulcate face, SB = *sulcus* branches, SF = spinulate flounces, SS = *sulcus spermaticus*. Scale line = 2 mm. Although staining of the spinules by Alizarin Red is well visible under the microscope, the structures are not clearly observable in the figure. Photographs by Philippe J.R. Kok.

Colour of the Holotype in life. Dorsum greyish to bluish brown depending on light intensity, devoid of any conspicuous pattern, but with a few scattered black scales on flanks. Arms and legs, including digits, greyish brown with a few scattered black scales; rear of thighs with a few ill-defined dark markings. Ventral surfaces of head and body golden grey, ventral surfaces of legs and tail bluish grey, palms and soles lemon yellow speckled with brown and yellowish orange scales. Tympanum dark brown, iris pale yellow (Figs. 1 A, C, 4).

Colour of the Holotype in preservative. After approximately two months in preservative, the dorsal surfaces became dark brown (looking slightly peppered when specimen is in liquid), the ventral surfaces are metallic blue, except the anterior surface of head, which is light grey (Fig. 6). Palms and soles are grey. Tympanum is dark brown. It is worthwhile to note that the ventral skin, and some parts that are light grey (like the anterior underside of head), turn blue or bluer when pressure is applied to the skin.

Variation in paratypes. The paratypes consist in one adult male (SVL 60.4 mm), and two juvenile males (SVL from 38.2 to 42.6 mm). Table 1 provides measurements of the type series, and Fig. 1B shows one of the juvenile paratypes in life (IRSNB 2675).

One of the main differences among specimens of the type series is the occurrence of a presupraocular scale in the three paratypes (absent in the holotype); that presupraocular scale is divided on both sides in IRSNB 2675. IRSNB 2676 has four suboculars on both sides (*vs.* three in the holotype and other paratypes). Supralabial counts are consistent, but infralabial counts vary from 5 (n=1) to 7 (n=1, one side only). Pits on head scales are inconspicuous in the two juveniles (*vs.* well visible in the adult males). Suboculars are always separated from palpebrals by 2-3 poorly defined rows of inconspicuous tiny scales. In IRSNB 2674 three of these scales (*vs.* two in the holotype) are distinctly enlarged (larger than in holotype) with angular downward protrusion between suboculars. In both juvenile paratypes, only one of these scales is only slightly enlarged and slightly protrudes between suboculars. The condition of the parietals and interparietal is highly variable among specimens and none of the specimens examined has complete interparietal and parietals, which are always divided in several smaller scales (see Fig. 7 for comparison). Number of middorsal scales varies from 53 to 57. Ventrals are in 11 to 14 longitudinal rows and in 29 to 30 transverse rows. The number of femoral pores varies from 8 to 10. Preanals vary from 7 to 10.

The fully everted, maximally expanded, right hemipenis of the adult male paratype (IRSNB 2674) is identical to the holotype's organ, except that maximal expansion makes the *sulcus spermaticus* bifurcation and the *sulcus* branches even more difficult to appreciate. Maximal expansion does not highlight hemipenial features that would have been overlooked in the not maximally expanded hemipenis of the holotype. The hemipenis is 6.6 mm in length and 4.0 mm across its widest point when everted; there are twenty-four rows of flounces extending along the organ, *ca.* eight of which are medioproximal asulcate flounces.

Colour in life ranges from beige to dark greyish, sometimes bluish, brown dorsally, depending on light intensity. Rear of thighs usually has a few ill-defined dark markings. Some blue markings may be visible around ear, or at the base of the tail, or on ventral parts. Ventral parts range from golden grey to pale yellow. One of the juvenile paratypes (IRSNB 2675, see Fig. 1B) has two poorly defined dark brown stripes between eye and ear. In preservative all specimens became dark brown dorsally, looking slightly peppered when in liquid. Ventral parts are always metallic blue (Fig. 6). Tympanum in preserved specimens varies from dark brown to blue or golden blue.

Figure **6.** *Anadia mcdiarmidi* **sp. nov.** Intrapopulation variation in dorsal (above) and ventral (below) colour pattern in preserved specimens. From left to right: IRSNB 2677, IRSNB 2674, IRSNB 2676, IRSNB 2675. Photographs by Philippe J.R. Kok.

Distribution and ecology. The new species is known only from the Chimantá Massif in Venezuela (Fig. 8) where it has been reported from Abakapá-tepui (type locality), Amurí-tepui, and Murei-tepui (sometimes named Eruoda-tepui, see Discussion) between *ca.* 2100-2600 m elevation (McDiarmid & Donnelly, 2005). The species is probably widespread in the Chimantá Massif.

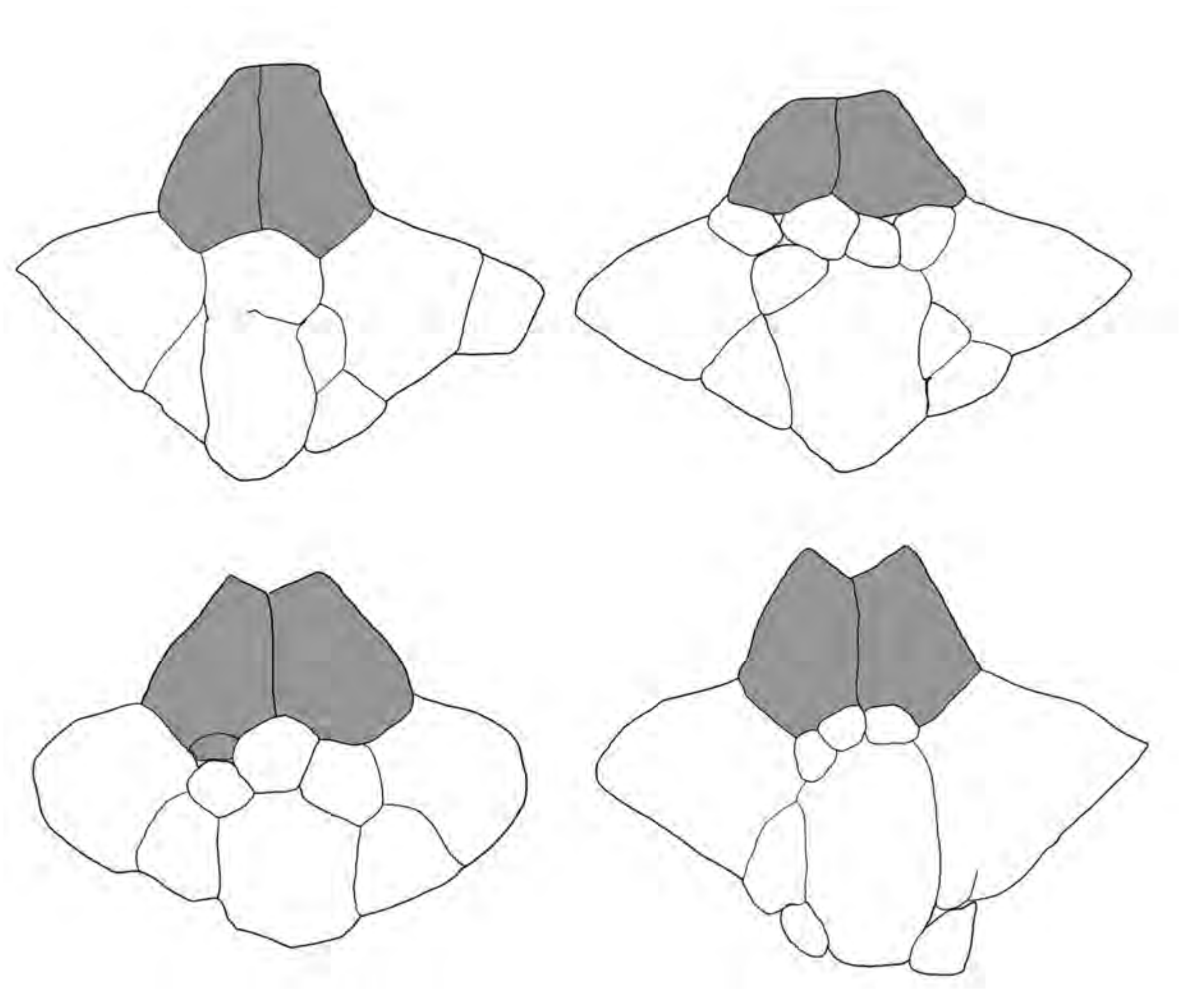

Figure **7.** *Anadia mcdiarmidi* **sp. nov.** Intrapopulation variation in the condition of the parietals and the interparietal (frontoparietals in grey). Top, from left to right: IRSNB 2677, IRSNB 2676; bottom, from left to right: IRSNB 2675, IRSNB 2674. Drawings not at scale.

Anadia mcdiarmidi is diurnal and inhabits open, mostly flat sandstone areas on tepui summits (Fig. 1 D). The holotype and two paratypes were collected during the day under rocks; IRSNB 2674 was found during the day, crawling in a small crack between rocks. Two white fertile eggs (both measuring 12.3 mm) and several older eggshells attributable to the new species were found under a large rock, suggesting that a same suitable nesting site may be reused [as already postulated by Gorzula (1992)], and that females lay two eggs at a time. The only other lizard found syntopic with *Anadia mcdiarmidi* was *Neusticurus* cf. *rudis*, which was also mainly found under rocks.

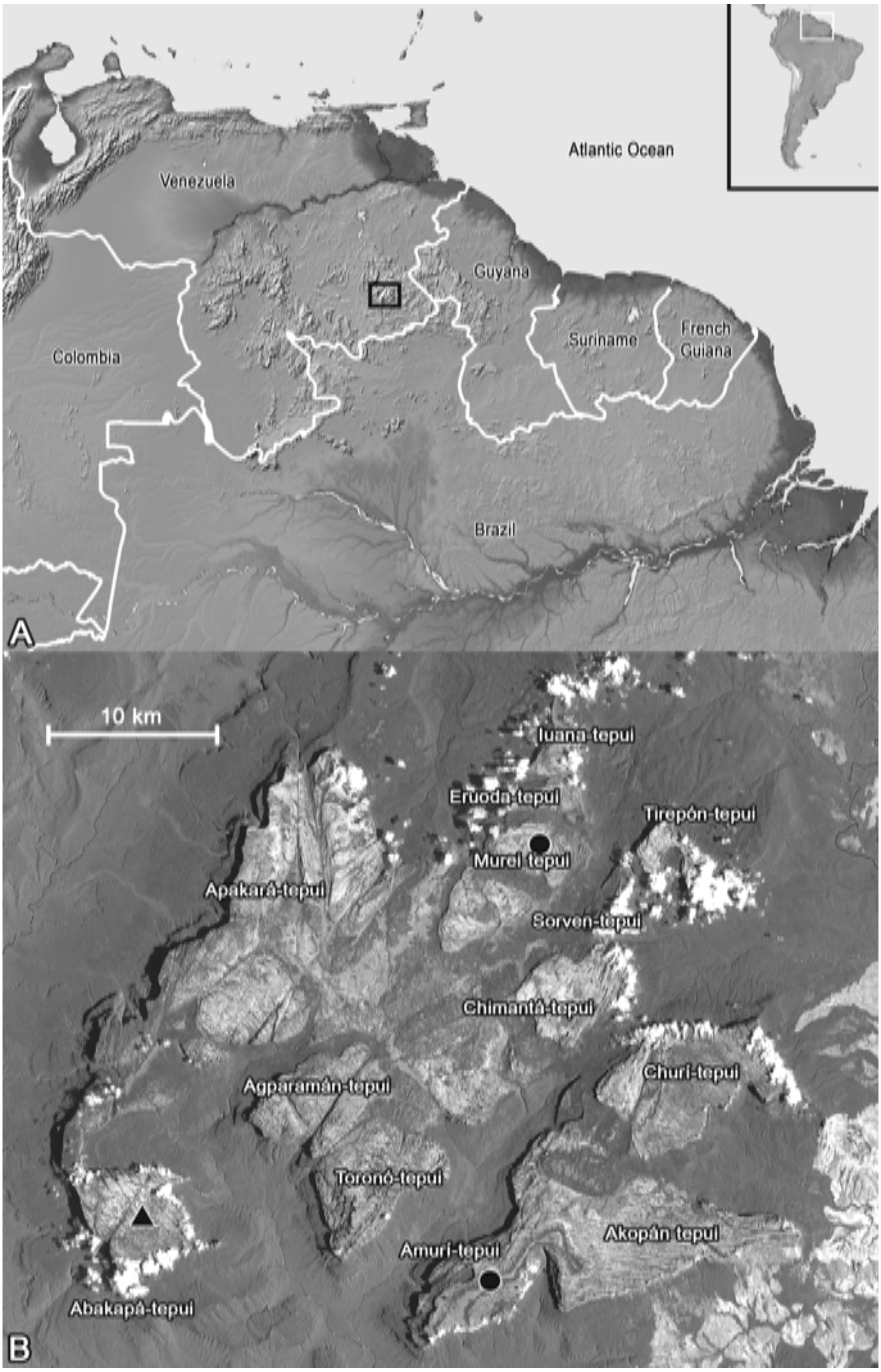

Figure **8.** Map of the Guiana Shield region (A), with enlarged black rectangle corresponding to the Chimantá Massif (B). Black triangle indicates type locality, black dots indicate other know localities for the species.

Specimen	IRSNB 2677	IRSNB 2674	IRSNB 2675	IRSNB 2676
Sex	M	M	Juvenile M	Juvenile M
SVL	62.2	60.4	38.2	42.6
TL	110.0	57.0[1]	29.7[1]	74.0
HL	15.8	13.6	9.0	10.2
HW	10.8	8.7	5.8	6.6
HD	6.7	5.7	3.9	4.4
SAL	28.4	23.8	14.6	18.9
NL	10.8	6.7	5.2	6.0
AXG	30.7	29.9	18.4	19.8
FlL	16.6	16.6	10.2	11.6
HlL	22.4	18.5	14.3	15.6
SLF	13/14[2]	14/13[2]	12/13[2]	13/14[2]
SLT	17/17[2]	17/17[2]	17/15[2]	17/17[2]
MD	54	53	53	57
VL	14	12	14	11
VT	31	29	31	30
SAM	36	35	35	35
SL	7/7[2]	7/7[2]	7/7[2]	7/7[2]
IL	6/6[2]	6/6[2]	7/6[2]	5/5[2]
FP	10/9[2]	9/9[2]	9/8[2]	10/10[2]

Table **1.** Sex, measurements (in mm) and scale counts of the type series of *Anadia mcdiarmidi* **sp. nov**. M = male, [1] = tail incomplete or obviously regenerated, [2] = data corresponding to right/left side, other abbreviations are defined in the text.

Discussion. As stated above, the new species has been mentioned previously in four publications: Gorzula (1992), Gorzula & Señaris (1999), McDiarmid & Donnelly (2005), and Brewer-Carías & Audy (2010), but none of these publications provides any comprehensive morphometric data, except a SVL of 86 mm and a TL of 77 mm (suggesting a broken tail) in a large adult male (catalogued as MHNLS 10772, probably the largest known specimen), and a SVL of 65 mm in a gravid female catalogued as MHNLS 10765 (Gorzula & Señaris, 1999). The few published photographs [figs 168-171 in Gorzula (1992), fig. 88 in Gorzula & Señaris (1999), and an unnumbered figure on page 210 in Brewer-Carías & Audy (2010)] and data (Gorzula, 1992; Gorzula & Señaris, 1999) conform to the new species description and add the following information: (1) large males obviously have a wider head than females, a character shared by several *Anadia* species (*e.g. A. bogotensis*, *A. brevifrontalis*, *A. petersi*, *A. rhombifera*), (2) females may have one or two faint darker stripes between orbit and ear (as also seen in one of our juvenile male paratypes), (3) the known maximal size in the species is apparently 86 mm SVL.

Although Eruoda-tepui and Murei-tepui (occasionally spelled Murey-tepui) are sometimes considered the same mountain (e.g. Gorzula & Señaris, 1999), we consider them as separate tepuis (see Fig. 8). McDiarmid & Donnelly (2005) provide 05° 22’N, 062° 05’W as the coordinates for Murei-tepui, and clearly mention that it is the locality where *Anadia* sp. A (here described as *Anadia mcdiarmidi*) has been collected. Eruoda-tepui is located north to Murei-tepui, and no report of the new species has been recorded from that mountain yet.

Pellegrino et al. (2001) tentatively assigned the genus *Anadia* to the family Cercosaurinae (tribe Cercosaurini) on the basis of morphology and our preliminary molecular results (Kok, unpublished) corroborate this. Members of the genus *Anadia* have not been included in any modern phylogenetic study and relationships between species, as well as their relationships with apparently close genera like *Euspondylus*, remain unknown. The genus *Euspondylus* Tschudi, 1845 is ill defined (see Oftedal, 1974; Myers et al., 2009) and is mainly distinguished from *Anadia* by the presence of distinct rows of much smaller scales between lateral scales (in *Anadia* lateral scales are subequal and mostly in unbroken transverse rows with dorsal scales). A single study was conducted to test the phylogenetic position of *Euspondylus acutirostris* (Peters, 1863) based on its cranial osteology and myology (Montero et al., 2002). Results from Montero et al. (2002) show *E. acutirostris* nested in a clade containing three species of *Anadia*, thus suggesting that both genera are synonyms. However, Myers et al. (2009: 11) highlighted that one of the *E. acutirostris* specimens used by Montero and colleagues could have been misidentified and could actually be an *Anadia marmorata*, which is currently impossible to determine because that specimen was dissected for the osteological portion of their study. Therefore, the phylogenetic position of *Anadia*, intrageneric relationships within *Anadia*, and relationships to *Euspondylus* remain an enigma.

Based on morphology only it is challenging to infer relationships of the new taxon with other *Anadia* species because many characters of the new species could be adaptations to high mountain habitat, and thus shared by other high mountain species that may not be closely related. At this stage the lack of adequate tissue sampling among *Anadia* species hampers any sound molecular analyses.

The origin of the Pantepui biodiversity still remains an evolutionary enigma (e.g. Rull, 2009) and the discovery of a species of *Anadia* (primarily an Andean genus) apparently endemic to tepui summits is of considerable interest to the understanding of the processes underlying the origin and evolution of the Pantepui herpetofauna. This matter is beyond the scope of this paper and is subject of ongoing research that will be presented elsewhere.

ACKNOWLEDGEMENTS

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APPENDIX. ADDITIONAL COMPARATIVE MATERIAL EXAMINED

Anadia blakei.– (1). Venezuela: *Sucre*: Cerro Humo, Península de Paria, EBRG 2746.

Anadia marmorata.– (2). Venezuela: *Aragua*: Estación Biológica de Rancho Grande, 1100 m, EBRG 3423. *Distrito Capital*: sector Jerenba Parque Nacional Macarao, 2300 m (living specimen to be deposited at EBRG).

Anadia escalerae.– (1). Venezuela: *Bolívar*: La Escalera, 132 km SE Río Cuyuní (= 46 km SE km 88) on the road to Santa Elena de Uairén, EBRG 1998 (holotype).

Euspondylus acutirostris.– (3). Venezuela: *Aragua*: Carretera El Junquito-Colonia Tovar, a 1.5ha a la derecha del arco de la Colonia Tovar, 2350 m. MHNLS 17474. *Falcón*: Sierra de San Luis, cerro Galicia, La Soledad, 1200 m. EBRG 3971. *Yaracuy*: Pico el Tigre, Parque Nacional Yurubí, 1700 m (living specimen to be deposited at EBRG).

8

A Redescription of *Anomaloglossus praderioi* (La Marca, 1998) (Anura: Aromobatidae: Anomaloglossinae), with Description of its Tadpole and Call

P. J. R. Kok

Abstract
Anomaloglossus praderioi was originally described as *Colostethus praderioi* by E. La Marca in 1998 on the basis of two male specimens. The present paper provides a redescription of the species on the basis of new material from Maringma Tepui in Guyana and an additional specimen from Sierra de Lema in Venezuela. The redescription includes descriptions of the tadpole and vocalisation. Anomaloglossus praderioi is a medium-sized species mainly distinguished from its known congeners in having Fingers I, II and IV equal in length, the tip of Finger IV barely reaching the base of the distal subarticular tubercle on Finger III when fingers are adpressed, Fingers II and III with preaxial keel-like lateral folds, toes basally webbed with folded flaplike fringing except on Toes IV–V, symmetrical cloacal tubercles present, thin pale dorsolateral stripe present from tip of snout to tip of urostyle, ventrolateral stripe inconspicuous, never straight, oblique lateral stripe absent, throat in male grey to very dark grey, almost solid black, with black blotches, throat in female bright orange, almost immaculate. The tadpole is dark brown to black, exotrophic, benthic, LTRF 2(2)/3. The advertisement call consists of long trains of a single note repeated at a rate of 61–76 notes/min with a dominant frequency ranging from 3,562 to 3,856 Hz. The species is reported from eastern Venezuela and western Guyana and inhabits montane medium-canopy forest at elevations between 1,310–1,950 m above sea level.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The genus *Anomaloglossus* currently contains 23 species, of which 20 are *cis*-Andean and three are *trans*-Andean. The majority of taxa have restricted distributions in the Guiana Shield. The monophyly of the genus is supported by the presence of the median lingual process (Grant *et al.,* 2006). The few *trans*-Andean species are placed in the genus *Anomaloglossus* due to the synapomorphic presence of the median lingual process, but they have not yet been included in quantitative phylogenetic analyses because of lack of material (Grant *et al.,* 2006; Myers & Grant, 2009). *Anomaloglossus* species are fascinating animals displaying interesting diversity in their reproductive biology. Some species have endotrophic tadpoles [*e.g. A. degranvillei* (Lescure, 1975)], some are phytotelm breeders with partly oophagous larvae [*e.g. A. beebei* (Noble, 1923)], some species deposit tadpoles in small temporary pools with females occasionally supplying trophic eggs [*e.g. A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006)], while others sometimes deposit larvae in running water [*e.g. A. tepuyensis* (La Marca, 1998)].

La Marca (1998) originally named *Anomaloglossus praderioi* (see Myers & Donnelly, 2008:143 for comment on date of publication) on the basis of two adult males collected between 1,800–1,950 m elevation on the slopes of Mt. Roraima, Estado Bolívar, Venezuela. The species' name rarely appeared in the literature since the original description (Barrio-Amorós, 1998, 2004; Grant *et al.*, 2006), except in the diagnoses of new congeneric taxa. Besides the few data given in the original description, close to nothing is known about the species.

Grant *et al.* (2006) included *Anomaloglossus praderioi* in their phylogenetic study on the basis of samples from two specimens collected at 1,310 m elevation on the slopes of Mt. Roraima, Cuyuni-Mazaruni District, Guyana. This represented the first and only range extension, although minor and not explicitly stated. Grant *et al.* (2006:120) also briefly commented on the morphological similarities between *A. praderioi* and the Guyanan *A. "degranvillei"* (which is *Anomaloglossus kaiei*), but did not examine the type series of *A. praderioi.*

Unfortunately several *Anomaloglossus* descriptions overlook—or erroneously describe—important diagnostic characters. Many are poorly illustrated and are based on very few specimens. Some descriptions are based on a single immature individual and in many cases colour in life is unknown, which is problematic since some diagnostic colour features may disappear or become less conspicuous in preservative (*e.g.* dorsolateral stripe). As in other poorly known taxa, lack of comprehensive morphological data prevents adequate comparison with putative new species. Additional descriptions and a more complete understanding of the morphology of the little-known species are crucial to ensure the identity of new material.

Eleven specimens of *Anomaloglossus praderioi,* as well as 14 tadpoles, were collected during a recent expedition in the eastern Roraima tepui chain in Guyana, and the vocalisation of the species was recorded. Examination of museum material allowed the detection of an additional specimen. On the basis of this new material (listed in Appendix), and comparison with the holotype and the paratype of *A. praderioi,* I present herein a new description of the taxon based on morphology and call, including the first illustration in colour of the species as well as the first description of its tadpole. A new diagnosis is provided and new observations on the ranges of *A. praderioi* and of the morphologically similar *A. kaiei* are discussed. The IUCN Red List Category of *A. praderioi* is also discussed.

MATERIAL AND METHODS

The newly collected specimens of *Anomaloglossus praderioi* are from the southeastern slope of Maringma Tepui (05°12’16”N, 060°34’39”W, 1,376 m elevation, Fig. 1), Cuyuni-Mazaruni District, Guyana, where 10 adult individuals (nine males, one female), one juvenile, and 14 tadpoles were secured. Specimens were fixed in 10% formalin for several days and transferred to 70% ethanol (adults and juvenile) or preserved in 10% formalin (12 tadpoles) for permanent storage. A piece of liver was extracted from seven specimens prior to fixation and preserved in 95% ethanol for later molecular analyses. Two tadpoles were preserved in 95% ethanol for the same purpose. Specimens were deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB), tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (see Appendix for material examined). Colour in life is described from digital photographs and field notes. Sex was confirmed by the presence of vocal slits. All measurements were taken on the preserved specimens, to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper or an ocular micrometer.

One additional juvenile specimen, misidentified as *Anomaloglossus parkerae,* was detected in the EBRG collections.

Abbreviations and standard measurements for adults are as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL); (3) head width at level of angle of jaws (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance (IN); (7) eye length (EL); (8) interorbital distance (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (11) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (12) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (13) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (14) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (15) width of disc on Finger III (WFD); (16) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (17) width of disc on Toe IV (WTD); (18) tibia length from outer edge of flexed knee to heel (TIL); (19) upper arm length from anterior insertion with the body to outer edge of flexed elbow (AL). Webbing formulae are those of Savage & Heyer (1967), with modifications proposed by Myers & Duellman (1982) and Savage & Heyer (1997). For ease of comparison, toe webbing is considered basal when it reaches – but does not distinctly surpass – the basal subarticular tubercle on Toes II–V, and moderate when it reaches an area between the basal and the second subarticular tubercle on Toes II–V. Relative lengths of fingers were compared according to Kaplan (1997), using the distance from the proximal edge of the palmar tubercle to the tip of each finger.

Three lots of tadpoles were collected, two from two different small temporary pools (nine individuals total), the other from the back of one male (five individuals). Developmental stages of tadpoles follow Gosner (1960); terminology and oral disc characters follow Altig & McDiarmid (1999). Colour in life is described from field notes. Abbreviations and standard measurements for tadpoles are as follows: (1) total length from tip of snout to tip of tail (TL); (2) body length from tip of snout to junction of posterior body and tail musculature (BL); (3) tail length from junction of posterior body and tail musculature to tip of tail (TAL); (4) greatest body width (BW); (5) highest body height (BH); (6) head width at level of eyes (HW); (7) tail muscle height at base of tail (TMH); (8) tail muscle width at base of tail (TMW); (9) maximum height of tail (MTH); (10) eye-naris distance (END); (11) naris-snout distance (NSD); (12) internarial distance (IND); (13) interorbital distance (IOD); (14) eye diameter (ED). The oral disc of a 24.5 mm long, stage-39 formalin preserved tadpole was dissected, critical-point dried and coated with gold following the usual protocol (Echeverría, 1997; Kok & Kalamandeen, 2008) for scanning electron microscopy (SEM). Observations and photomicrographs were made with a FEI Quanta-200 environmental scanning electron microscope (ESEM). Ethanol-preserved tadpoles were not included in Table 2 because ethanol caused soft tissue desiccation and body deformation.

Three minutes of advertisement calls were recorded at a distance of less than 1 m from two calling males (one of them collected) using a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder using Maxell DM60 digital audiotape. The calls were analysed at a sampling rate of 44,100 Hz using Raven version 1.3 software (Charif *et al.*, 2008). Temporal variables measured included: call duration (= note duration); inter-call interval (beginning of one call to beginning of the next); and call rate (= number of calls per minute). The dominant (emphasized) frequency of the note was measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 120 Hz). Air temperature at the call sites was measured with a Hanna digital pH/thermometer and varied from 19.8–20°C.

Taxonomy follows Grant *et al.* (2006). Institutional acronyms follow Frost (2009).

RESULTS

New description of *Anomaloglossus praderioi* (la Marca, 1998)

Figs. 2–7

Adult definition and diagnosis. (1) medium-sized *Anomaloglossus* (males 19.5–22.4 mm SVL, female 22.7 mm SVL); (2) body robust; (3) skin on dorsum shagreened to finely granular, more granular posteriorly, skin on venter smooth to shagreened; (4) Fingers I, II and IV equal in length; (5) tip of Finger IV barely reaching the base of the distal subarticular tubercle on Finger III when fingers adpressed; (6) distal tubercle on Finger IV present; (7) Finger III slightly swollen in males (preaxial keeling distinctly more developed than in females); (8) Fingers II and III with preaxial keel-like lateral folds (*sensu* Myers & Donnelly, 2008); (9) toes basally webbed, with folded flaplike fringing (*sensu* Myers & Donnelly, 2008), except on Toe IV (preaxial only) and Toe V; (10) tarsal keel weakly to distinctly curved, slightly tuberclelike; (11) black arm gland absent in male (*sensu* Grant & Castro-Herrera, 1998, see also Grant *et al.,* 2006), but presence of a glandular supracarpal pad in both sexes (larger in male in which it usually extends further on the forearm); (12)

symmetrical cloacal tubercles present; (13) pale paracloacal mark present; (14) thin pale dorsolateral stripe present in both sexes, from tip of snout to tip of urostyle, usually slightly narrower on body than on head (dorsolateral stripe unnoticeable in preserved specimens);

Figure **1.** Map of the eastern Pantepui region showing the known distribution of *Anomaloglossus praderioi:* **1:** Type locality, Venezuelan slope of Mt. Roraima; **2:** Guyanan slope of Mt. Roraima; **3:** Maringma Tepui, Guyana; **4:** Sierra de Lema, Venezuela. Question marks indicate possible extension of distribution (*see* text for details). Maps elaborated after a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa. gov/catalog/PIA03388.

(15) ventrolateral stripe inconspicuous, never straight; (16) oblique lateral stripe absent; (17) obvious dichromatism in throat colour, throat of male grey to very dark grey, almost solid black, with black blotches, throat of female bright orange, almost immaculate except for a few lighter blotches and a few melanophores on chin and lower lip; (18) obvious dichromatism in ventral colouration, chest and anterior part of belly in male grey to dark grey with black blotches, posterior part of belly bright orange, belly in female bright orange, immaculate; (19) iris with metallic pigmentation and pupil ring; (20) large intestine extensively pigmented; (21) testes cream, unpigmented; (22) mature oocytes partly pigmented; (23) median lingual process short, tapered (24) maxillary teeth present, small.

Comparison with other species. The following comparisons of some external character states are based both on original descriptions and examination of type specimens (see Appendix for material examined). Examination of comparative type series sometimes revealed discrepancies between type specimens and original descriptions (*e.g.* sex, skin texture, length of Finger I *vs.* II, condition of fringes on fingers and toes), which explains that the following diagnosis may differ from those usually proposed (see Discussion).

Twenty-three species of *Anomaloglossus* are recognized, many of which apparently have restricted ranges. Compared to the nine other *Anomaloglossus* species known to occur in the Eastern Pantepui District (*i.e.* east of the Rio Caroní, which obviously acts as a biogeographic barrier for *Anomaloglossus* species) in the Guiana highlands of Venezuela and Guyana, *A. praderioi* can easily be distinguished from *A. beebei* by (characters of *A. beebei* in parentheses) larger size (female SVL max 22.7 mm in *A. praderioi vs.* 18.7 mm in *A. beebei*), skin on dorsum shagreened to finely granular (granular), ventral skin smooth to shagreened (granular), Fingers I and II equal in length (Finger I < Finger II), Fingers II and III with preaxial keel-like lateral folds (fringes not folded), most toes with folded flaplike fringing (fringes not folded), toes basally webbed (moderately webbed), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (when present dorsolateral stripe originates from posterior corner of eye), throat in adult male grey to almost black, with black blotches (immaculate yellow), chest and anterior part of belly in male grey to dark grey with black blotches (immaculate yellow), palm dark brown to black (yellowish), distinct dark bands on thigh and shank (absent), dark interorbital band (absent); from *A. breweri* (Barrio-Amorós, 2006) by (characters of *A. breweri* in parentheses) Fingers I and II equal in length (Finger I < Finger II), tip of Finger IV barely reaching base of distal subarticular tubercle on Finger III when fingers adpressed (goes beyond), toes basally webbed (moderately webbed), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (absent), oblique lateral stripe absent (present, often broken into small spots), throat in adult male grey to almost black, with black blotches (dirty white), belly bright orange in both sexes (dirty white in male, yellow in female); from *A. kaiei* by (characters of *A. kaiei* in parentheses) larger size (female SVL max 22.7 mm in *A. praderioi vs.* 19.8 mm in *A. kaiei*), Fingers II and III with preaxial keel-like lateral folds (fringes not folded), dorsolateral stripe from tip of snout to tip of urostyle (always originates from posterior corner of eye), throat in adult male grey to almost black, with black blotches (never deep grey or solid black), chest and anterior part of belly in male grey to dark grey with black blotches (greyish without black blotches); belly bright orange in both sexes (cream in male, orangish yellow in female); from *A. murisipanensis* (La Marca, 1998) by (characters of *A. murisipanensis* in parentheses) Fingers I and II equal in length (Finger I < Finger II), tip of Finger IV barely reaching base of distal subarticular tubercle on Finger III when fingers adpressed (goes beyond), toes basally webbed (moderately webbed), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (absent), belly immaculate in female (covered with melanophores), tarsal keel weakly to distinctly curved, slightly tuberclelike (straight, not tuberclelike); from *A. parkerae* (Meinhardt & Parmelee, 1996) by (characters of *A. parkerae* in parentheses) Fingers I and II equal in length (Finger I < Finger II), tip of Finger IV barely reaching base of distal subarticular tubercle on Finger III when fingers adpressed (goes beyond), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (absent), oblique lateral stripe absent (usually present, often broken into small spots), toes basally webbed (moderately webbed), throat in adult male grey to almost black, with black blotches (orange yellow); from *A. roraima* (La Marca, 1998) by (characters of *A. roraima* in parentheses) skin on dorsum shagreened to finely granular (granular), ventral skin smooth to shagreened (granular), Fingers I and II equal in length (Finger I < Finger II), Fingers II and III with preaxial keel-like lateral folds (fringes not folded), most toes with folded flaplike fringing (fringes not or very feebly folded), feet basally webbed (no webbing); from *A. rufulus* (Gorzula, 1990) in having (characters of *A. rufulus* in parentheses) dorsolateral stripe from tip of snout to tip of urostyle (absent), posterior part of belly never marbled (ventral part entirely marbled); from *A. tepuyensis* by (characters of *A. tepuyensis* in parentheses) Fingers I and II equal in length (Finger I < Finger II), tip of Finger IV barely reaching base of distal subarticular tubercle on Finger III when fingers adpressed (goes beyond), toes basally webbed (moderately webbed), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (absent), oblique lateral stripe absent (usually present, often broken into small spots), throat in adult male grey to almost black, with black blotches (never deep grey or solid black, usually grey with white flecking), belly bright orange in both sexes (grey, greenish grey, or greenish yellow); from *A. triunfo* (Barrio-Amorós, Fuentes-Ramos & Rivas-Fuenmayor, 2004) by (characters of *A. triunfo* in parentheses) Fingers I and II equal in length (Finger I < Finger II), tip of Finger IV barely reaching base of distal subarticular tubercle on Finger III when fingers adpressed (goes beyond), toes basally webbed (moderately webbed), symmetrical cloacal tubercles present (absent), dorsolateral stripe from tip of snout to tip of urostyle (absent), oblique lateral stripe absent (present, often broken into small spots), throat in adult male grey to almost black, with black blotches (white).

Adult description. The main differences from the original description are italicized and quoted between brackets; see Table 1 for morphometric measurements of the holotype (ULABG 4196) and the paratype (MHNLS 11272) of *Anomaloglossus praderioi* compared to new material. Adult males 19.5–22.4 mm SVL, single known adult female slightly larger at 22.7 mm SVL. Dorsal skin shagreened to finely granular, becoming more granular posteriorly and on hind limbs [*dorsal skin reported as smooth in the original description* (piel de dorso lisa) *probably due to an artefact of preservation*]; ventral skin smooth to shagreened. A low, more or less distinct, epidermal ridge usually borders the tip of snout dorsally; this ridge is usually more visible in preserved specimens. Dorsal surface of hind limbs granular, with two distinct symmetrical enlarged tubercles located laterally between urostyle and vent in 10 specimens (83%); these tubercles are not easily distinguishable from other surrounding tubercles in the other specimens, possibly due to an artefact of preservation.

Head slightly wider than long, greatest width 34–35% SVL. Snout bluntly pointed in lateral view, extending past lower jaw, truncate to bluntly pointed in ventral and dorsal views. Nares located close to tip of snout, directed posterolaterally; nares visible from front, barely visible from above and below; posterior rim of naris bordered behind by a crescent-shaped ridge; rim bearing a small tuberclelike prominence posterodorsally, this “bump” usually visible from in front, above and below; internarial distance 38–39% greatest head width. Canthus rostralis slightly rounded; loreal region concave, sloping outward to lip. Interorbital distance as long as eye length, longer than upper eyelid. Snout length 130–134% eye length, 51–52% head length; distance from anterior corner of eye to posterior margin of naris 67–69% eye length. Postrictal tubercles few and inconspicuous. Tympanic membrane inconspicuous, round, concealed posterodorsally by a diffuse supratympanic swelling; tympanic annulus usually visible anteroventrally; tympanum 45–48% eye length.

Character	Holotype, Mount Roraima (male)	Paratype, Mount Roraima (male)	Males from Maringma tepui (*n*=9)	Female from Maringma tepui (*n*=1)	Juvenile from Maringma tepui (*n*=1)	Juvenile from Sierra de Lema (*n*=1)
SVL	19.5	22.4	21.2 ± 0.42 (20.5–21.9)	22.7	15.0	16.7
HL	6.1	6.6	6.9 ± 0.29 (6.5–7.3)	7.4	5.3	5.0
HW	6.8	6.8	7.3 ± 0.19 (7.1–7.6)	7.9	5.2	5.8
SL	2.9	3.3	3.5 ± 0.16 (3.3–3.8)	3.9	2.7	2.6
EN	1.5	1.8	1.8 ± 0.11 (1.6–1.9)	2.0	1.2	1.5
IN	2.5	2.5	2.8 ± 0.14 (2.7–3.1)	3.1	2.1	2.3
EL	2.6	2.8	2.7 ± 0.13 (2.5–2.9)	2.9	1.9	2.5
IO	2.4	2.6	2.7 ± 0.19 (2.4–3.0)	2.9	1.9	1.9
TYM	1.2	1.0	1.3 ± 0.11 (1.2–1.5)	1.3	0.9	1.0
FAL	4.3	4.6	4.8 ± 0.20 (4.4–5.1)	4.9	3.4	3.0
HAND I	3.8	3.9	4.0 ± 0.19 (3.7–4.3)	4.3	2.5	-
HAND II	3.8	3.9	4.0 ± 0.16 (3.8–4.3)	4.3	2.5	-
HAND III	5.3	5.4	5.5 ± 0.17 (5.2–5.8)	5.8	3.5	-
HAND IV	3.8	3.9	4.0 ± 0.17 (3.8–4.3)	4.3	2.5	-
WFD	0.6	0.6	0.7 ± 0.07 (0.6–0.8)	0.6	0.4	-
FL	9.0	9.0	9.2 ± 0.41 (8.6–9.9)	9.8	6.0	6.7
WTD	0.8	0.7	0.8 ± 0.07 (0.7–0.9)	0.8	0.6	-
TIL	10.3	10.2	10.7 ± 0.27 (10.3–11.0)	11.9	7.6	8.0
AL	4.4	4.8	5.8 ± 0.34 (5.5–6.5)	6.4	3.8	3.8

Table **1.** Morphometric measurements (in mm) of the holotype (ULABG 4196) and the paratype (MHNLS 11272) of *Anomaloglossus praderioi,* new material from Maringma Tepui, Guyana, and an additional specimen from Sierra de Lema, Venezuela. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

Forearm shorter than upper arm length, no distinct ulnar fold, but sometimes a row of low tubercles instead. Hand moderate, its length 26% SVL, 73–75% greatest head width. Relative length of fingers III > IV = II = I. Fingers unwebbed. Discs of fingers expanded, disc on Finger I widest. Fingers II and III with preaxial keel-like lateral folds (*sensu* Myers & Donnelly, 2008), distinctly more developed in males, which have a slightly swollen Finger III (Fig. 2A–B) [*Finger III reported as not swollen in male in the original description* (dedo III de la mano en machos no engrosado), *probably because female was not available and thus comparison impossible*].

Figure **2.** *Anomaloglossus praderioi*, showing ventral views of hand and foot. **A:** Left hand (left) and left foot (right) of a female specimen (IRSNB 14404, 22.7 mm SVL). **B:** Left hand (left) and left foot (right) of a male specimen (IRSNB 14403, 20.9 mm SVL). Black arrows highlight sexual dimorphism in preaxial third finger keeling, showing a slightly swollen third finger in male. Scale bars are 2 mm.

Palmar tubercle large, rounded; thenar tubercle smaller, elliptical; one or two round to ovoid subarticular tubercles (one each on Fingers I and II, two each on Fingers III and IV, with distal tubercle on Finger IV less conspicuous). No distinct outer metacarpal fringe. Tip of Finger IV barely reaching the base of distal subarticular tubercle on Finger III when fingers adpressed (Fig. 2A–B) [*although this is not shown on fig. 8 in the original description the same condition applies to the holotype*]. No fleshy supracarpal fold atop wrist, but presence of a glandular supracarpal pad in both sexes (larger in male in which it usually extends further on the forearm).

Hind limbs robust, moderately long, with heel of adpressed leg reaching posterior corner of eye to snout; tibia 50–52% SVL. Relative lengths of adpressed toes IV > III > V > II > I; first toe short, usually reaching the base of subarticular tubercle of second toe. Toe discs expanded (moderately on Toe I), subequal or slightly larger than finger discs. Feet basally webbed; toes with folded flaplike fringing (*sensu* Myers & Donnelly, 2008), except on Toe IV (preaxial only) and Toe V. Webbing formula I (2–2^-)–2^+ II (2^-–1 3/4)–3^+ III (3–3^-)–(4–4^+) IV 4 3/4–(3–3^+) V (Fig. 2 A–B).

Inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, round, about half the size of the inner. One to three round to ovoid subarticular tubercles (one each on Toes I and II, two each on Toes III and V, and three on Toe IV, with distal tubercle on Toe IV the smallest and least conspicuous). No examined specimen has a medial metatarsal tubercle. A weak outer metatarsal fold from proximal subarticular tubercle on Toe V to outer metatarsal tubercle. A slightly tuberclelike tarsal keel weakly to distinctly curved at proximal end, usually extending proximolaterad from preaxial edge of inner metatarsal tubercle, not distinctly continuous with the fringe along the outer edge of the first toe (Fig. 2A–B) [*reported as short, straight and not tuberclelike nor swollen in the original diagnosis* (pliegue tarsal corto, recto, no terminado ni en engrosamiento ni en tubérculo), *but as short, straight, conspicuous with posterior margin slightly swollen* (conspicuo, corto, con borde posterior recto y ligeramente engrosado) *in the description of the holotype; this character is variable among the specimens examined*].

Maxillary teeth present, small. Tongue longer than wide, free posteriorly, with rounded margin; median lingual process short, tapered. Vocal slits bilateral, large, extending from edge of tongue to angle of jaw.

Colour in life. Dorsal ground colour varies from light greyish brown to reddish brown or dark brown, usually with one to three dark brown to black triangular, diamond-shaped or diffuse hourglass markings from interorbital to presacral region. Upper surface of arm light brown to yellowish or orangish brown; upper surfaces of leg light greyish brown to dark grey with dark brown to black transverse bands on thigh, shank and foot; in most living specimens one of the transverse bands is larger and more conspicuous than others, which can sometimes be absent or barely visible (Figs. 3A–B, D–F; 4A–C; 5A). Adult males with grey to very dark grey throat, almost solid black, with black blotches, throat colour extending onto chest and anterior part of belly [*the original diagnosis – based on two male specimens – mentions that there is no marking on the chest, although the throat is covered by punctuate melanophores* (sin marcas sobre el pecho, aunque hay una punteadura fina de melanóforos que cubren toda la garganta), *but later in the text, describing the colour of the male holotype in life La Marca mentioned that throat, chest and anterior part of belly are black with small white spots* (garganta, pecho, parte anterior y lados del vientre, de color negro con manchitas blancas)]; posterior part of belly bright orange (Figs. 3C; 4A'–C'). Adult female with bright orange throat, almost immaculate except a few lighter blotches and a few melanophores on chin and lower lip; belly bright orange (Fig. 3C). Juvenile with light grey throat; belly yellowish, bright orange on its posteriormost part (Fig. 5A'). Flanks light grey to light reddish brown (males) or yellowish brown (female), usually with some small white or sky blue flecks more concentrated on the lower part, not forming a straight ventrolateral stripe (*sensu* Grant *et al.*, 2006). However, some inconspicuous yellowish elongate spots may occur and can be interpreted as a broken stripe[1]. Oblique lateral stripe absent. Distinct thin pale dorsolateral stripe present in both sexes and in the juvenile, extending from tip of snout to tip of urostyle, usually slightly narrower on body than on head [*this character was overlooked in the original description* (sin banda dorsolaterales claras y oscuras) *because it was exclusively based on preserved specimens, see below*]. A wide dark brown band of variable width present below the dorsolateral stripe, extending from tip of snout laterally around the body and above the vent, containing most of the tympanum and usually tapering posteriorly from axilla. Upper lip light to dark grey, suffused with melanophores and sometimes with a few sky blue flecks in males, yellow with few melanophores in female. A black stripe extends from posterior margin of eye to axilla region and is usually underlined by a white to light grey (males) or bright yellow line

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[1] The ventrolateral stripe condition is not very contributive in diagnosing *Anomaloglossus* species since it seems intraspecifically variable and its occurrence is subject to interpretation. In known species in which it is detectable it is always broken and/or poorly defined.

(female); a white or light grey (males) or yellow spot (female) at arm insertion. Usually a black stripe on anterior and posterior edges of upper arm, tapering from arm insertion to forearm; dark area on upper surface of wrist. Undersurfaces of arm and thigh bright to dark orange, undersurface of shank yellowish brown with black flecks an spots (more extensive in males). Pale, creamish brown, paracloacal marks present. Toes and digits with sky blue dots in both sexes. Palms and soles dark brown to black. Iris metallic reddish bronze in males, metallic bronze in female, with fine dark brown reticulation in both sexes (Figs. 3–4).

Figure **3.** *Anomaloglossus praderioi,* showing intrapopulation variation in colour in life and strong sexual throat and ventral dichromatism. **A:** Dorsolateral view of IRSNB 14403, male 20.9 mm SVL. **B:** Dorsolateral view of IRSNB 14404, female 22.7 mm SVL. **C:** Ventral views of male (left, IRSNB 14403) and female (right, IRSNB 14404). **D:** Dorsolateral view of IRSNB 14405, male 20.9 mm SVL. **E:** Dorsolateral view of IRSNB 14406, male 21.3 mm SVL. **F:** Dorsolateral view of IRSNB 14408, male 21.2 mm SVL.

Colour in preservative. After 18 months in preservative, the dorsal ground colour of the Maringma specimens varies from light or pinkish grey to dark greyish brown, with one to three dark brown to black triangular, diamond-shaped or diffuse hourglass markings from interorbital to presacral region. Upper surface of arm varies from cream to greyish brown, upper surface of leg varies from cream to dark grey, all dark markings remain well visible. Flanks are light to dark grey, usually with some white flecks on the lower part or rarely with a few elongate spots, which in a few dark males can be interpreted as an inconspicuous broken ventrolateral stripe (see footnote above). Although the dorsolateral line completely disappeared in all specimens (unnoticeable even under magnification), the wide dark brown band of variable width extending from tip of snout laterally around the body and above the vent is still distinct. The orange ventral colouration faded to creamish white, males still have noticeably darker throat, chest and anterior belly, usually with conspicuous black spots [*the original diagnosis – based on two male specimens – mentions that there are no markings on the chest, although the throat is covered by punctuate melanophores* (sin marcas sobre el pecho, aunque hay una punteadura fina de melanóforos que cubren toda la garganta), *but later in the text, describing the colour of the male holotype in preservative La Marca stated that throat, chest and anterior part of belly are dark with irregular small spots* (el patrón pardo oscuro con manchitas irregulares del fondo se repite en la garganta, pecho y parte anterior del vientre); *examination of the type series indicates that in preservative the holotype of* A. praderioi *has distinctly darker chest and anterior belly, and the paratype has chest and most of belly very dark*]; throat of female creamish white with a few melanophores on chin and lower lip. Pale paracloacal marks still visible, palms and soles black (Fig. 6). The holotype (13 years in preservative), the paratype (20 years in preservative) and the specimen from Sierra de Lema (14 months in preservative) conform well to this description.

Tadpole description. The following description – except oral disc – is based on an *Anomaloglossus praderioi* tadpole in stage 28 (IRSNB 14415a, Fig. 7A) that was collected in a small temporary pool. All values are in millimetres. See Table 2 for additional measurements and descriptive statistics for 14 meristic characters based on 11 tadpoles of stages 26–39.

Type 4 tadpole (Orton, 1953), exotrophic, benthic ecomorphological guild (Lannoo *et al.*, 1987; Altig & Johnson, 1989). Total length 22.4; body length 8.8 (39.3% total length), tail length 13.6 (60.7%). Body ovoid and depressed; highest body width 5.3, highest body height 4.2; snout bluntly rounded in dorsal and lateral views. Naris very small, circular, directed anterodorsally, opening 1.0 from tip of snout; distance from naris to anterior margin of eye 0.7; internarial distance 1.5, 30.6% head width at level of eyes. Eyes dorsal and directed laterally; eye diameter 0.8; interorbital distance 1.7, 34.7% head width at level of eyes. Spiracle sinistral, tube free, opening directed posterodorsally; tube length 1.0; tube transverse width 0.4; distance from tip of snout to spiracular opening 3.5, 39.8% body length. Vent tube 1.0, dextrally attached to ventral fin, opening directed dextrally. Developing hind limb bud 0.4 in length, 0.2 in width. Caudal musculature robust, highest at junction of body and tail, deeper than fins, tapering to tail terminus, terminating slightly anterior to tail tip; tail muscle width at base of tail 1.8, tail muscle height at base of tail 1.8. Upper fin originates at junction of body and tail, equal in height to lower fin, except in the first quarter of tail where it is distinctly lower; upper fin almost straight in its first quarter before increasing in height to about midlength; upper tail fin height 0.9, lower tail fin height 0.9, at midtail. Lateral-line system not detectable.

Oral disc description is based on an *Anomaloglossus praderioi* tadpole in stage 39 (IRSNB 14416b, Fig. 7B–C). Oral disc located anteroventrally, emarginated on left side only (aberrant condition, other tadpoles have oral disc emarginated on both sides); transverse width 2.0 (35.7% body width, 44.6% head width); border of disc surrounded with *ca.* 72 marginal papillae, *ca.* 30 on posterolateral margins of anterior labium, *ca.* 42 on entire posterior labium; gap in papillae on anterior labium *ca.* 1.3; all papillae small, tapered, blunt-tipped, subequal, *ca.* 0.08; submarginal papillae present on posterior labium, where papillae are arranged in two more or less distinct rows; lower jaw sheath V-shaped, narrower than upper jaw sheath; each side of upper sheath sigmoid; both upper and lower sheaths serrated; medial serrations blunttipped, lateral ones pointed; serrations extend entire length of sheaths, but do not include lateral processes (Fig. 7B). Labial tooth row formula 2(2)/3; labial teeth numerous, moderately long, strongly curved, bearing *ca.* 15 cusps (Fig. 7C); tooth row A-1 complete, slightly longer than A-2; tooth row A-2 interrupted medially; lower tooth rows complete, shorter than A-1; tooth row P-1 slightly longer than P-2 and P-3, which are subequal.

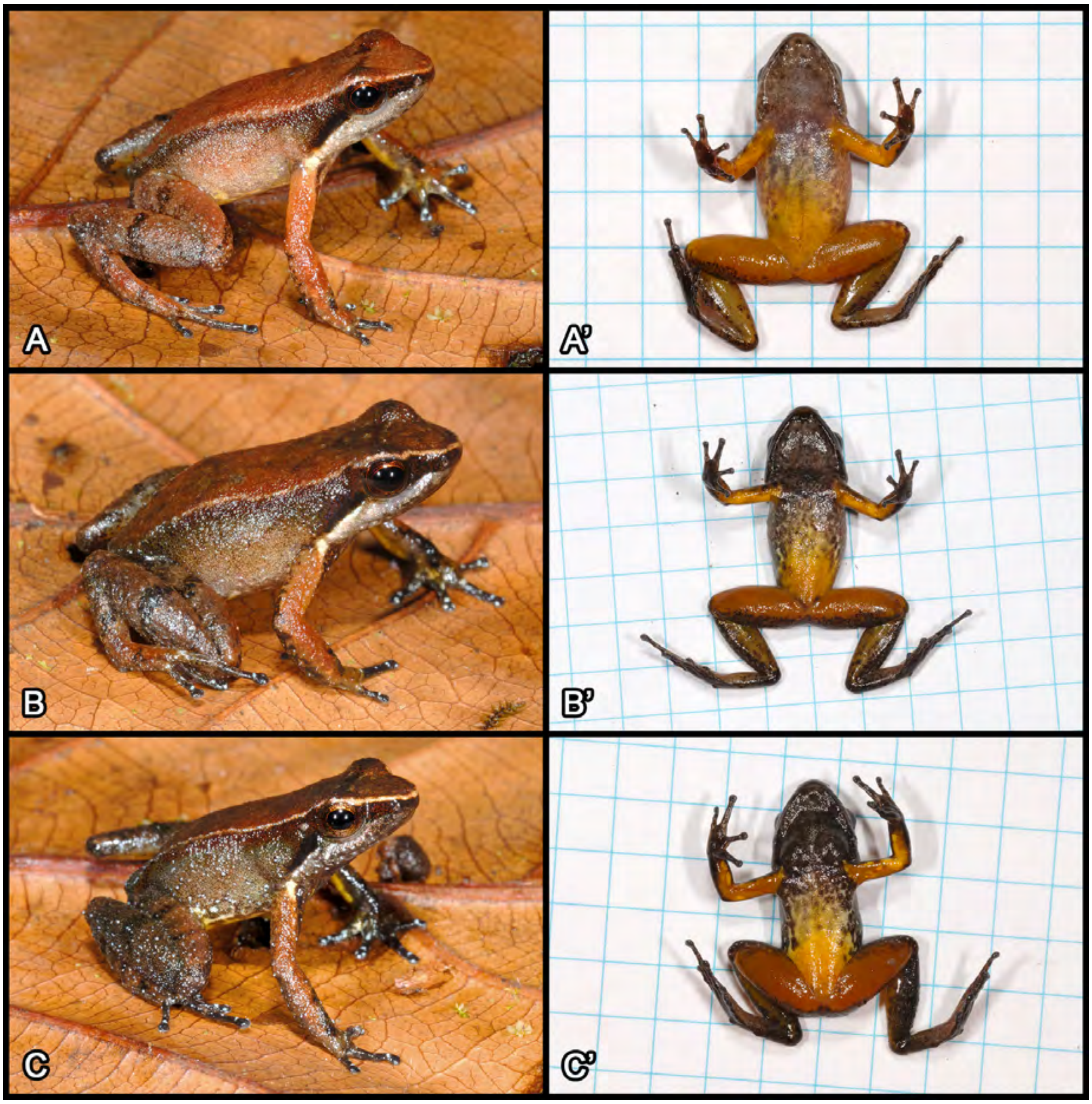

Figure **4.** *Anomaloglossus praderioi*, showing intrapopulation variation in dorsal and ventral colour in males in life. **A:** Dorsolateral view of IRSNB 14409, 21.1 mm SVL. **A':** Ventral view of the same specimen. **B:** Dorsolateral view of IRSNB 14410, 21.6 mm SVL. **B':** Ventral view of the same specimen. **C:** Dorsolateral view of IRSNB 14407, 20.5 mm SVL. **C':** Ventral view of the same specimen.

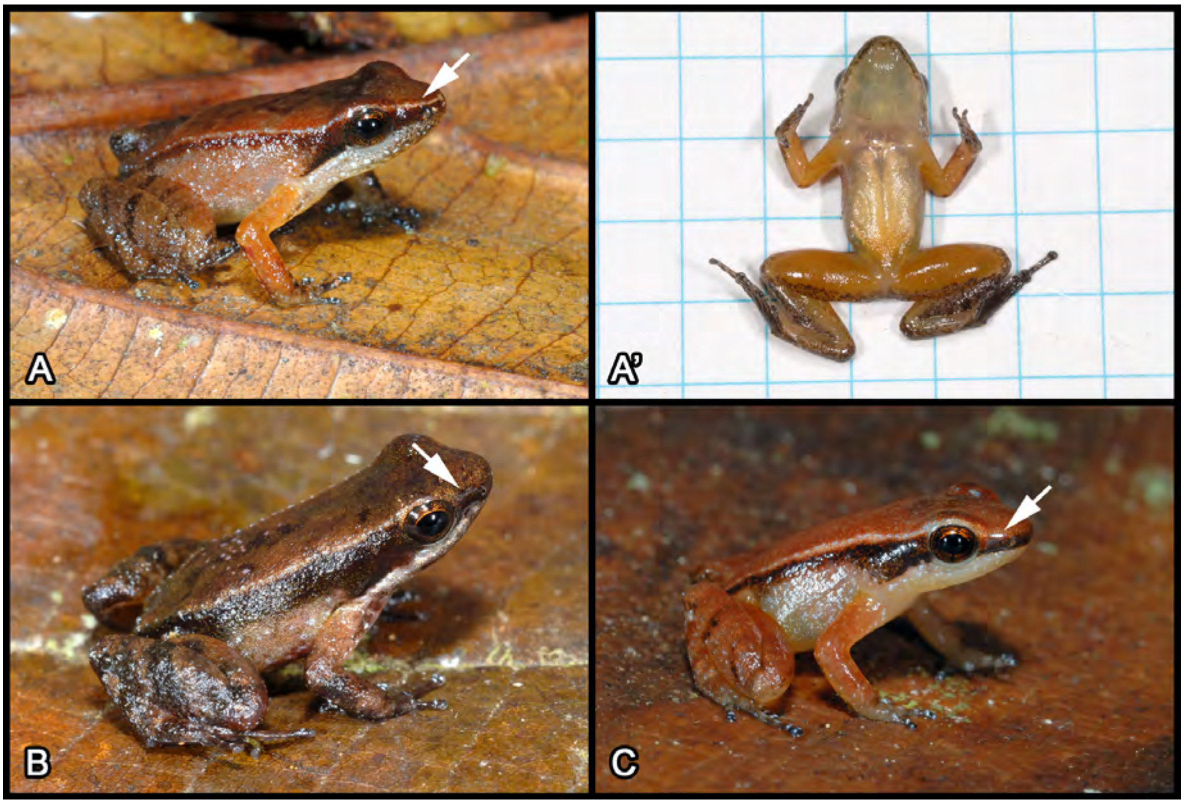

Figure **5.** Comparison between *Anomaloglossus praderioi* and the sympatric, morphologically similar, *A. kaiei*. **A:** Dorsolateral view of a juvenile *A. praderioi* (IRSNB 14411, 15.0 mm SVL). **A':** Ventral view of the same specimen. **B:** Dorsolateral view of an adult male *A. kaiei* from the southeastern slope of Maringma Tepui at 1,060 m elevation (IRSNB 14417, 19.5 mm SVL). **C:** Dorsolateral view of a juvenile *A. kaiei* from the surrounding of Wayalayeng village, eastern base of Maringma Tepui at 678 m elevation (IRSNB 14418, 13.2 mm SVL). Arrows highlight presence/absence of dorsolateral line between tip of snout and eye, a character that readily distinguish between the species.

Colour of tadpole in life. Dark brown to black with scattered lighter flecks on sides; caudal musculature and upper fin with scattered black flecks; lower fin translucent.

Colour of tadpole in preservative. Background colour brown to dark brown. Venter translucent with some scattered melanophores. Caudal musculature and upper fin with scattered dark brown flecks, lower fin mostly immaculate (Fig. 7A).

Ontogenetic changes. Changes in body size are summarized in Table 2. There is no remarkable ontogenetic change, the lateral line system is still difficult to detect in stage-39 tadpoles, in which a short, discontinued infraorbital branch originating from near upper labium is barely visible. A very short superior trunk branch is barely visible as well. Distal lower fin is slightly more pigmented in stage-28 and stage-39 tadpoles. Number of rows of marginal papillae on posterior labium is variable (from one in most stages-26–28 tadpoles to two in stage-39 tadpoles). Size of A-2 gap is variable and apparently not related to age.

Comparison with other known *Anomaloglossus* tadpoles occurring in the Eastern Pantepui District. The tadpole of *A. praderioi* is immediately distinguished from that of *A. beebei* in being dark brown to black (pale yellow to golden in *A. beebei*), and benthic (arboreal in *A. beebei*, which breeds exclusively in bromeliads phytotelmata). Most benthic *Anomaloglossus* tadpoles are very similar and difficult to distinguish, especially in preservative. Although similar to the tadpoles of *A. parkerae* and *A. tepuyensis*, the tadpole of *A. praderioi* differs from those species in having the first quarter of the upper fin straight before increasing in length to about midlength (*vs.* upper fin gradually increasing in length from tail-body junction), a character apparently common to all non-riparian species. The tadpole of *A. kaiei* is also very similar, sharing the same upper fin characteristic, but is distinctly smaller at equal stages (*e.g.* range of total length in stage-27 tadpoles 12.6–16.4 in *A. kaiei vs.* 17.5–22.4 in *A. praderioi*) and has maximum tail height always lower than body height (*vs.* subequal to slightly higher).

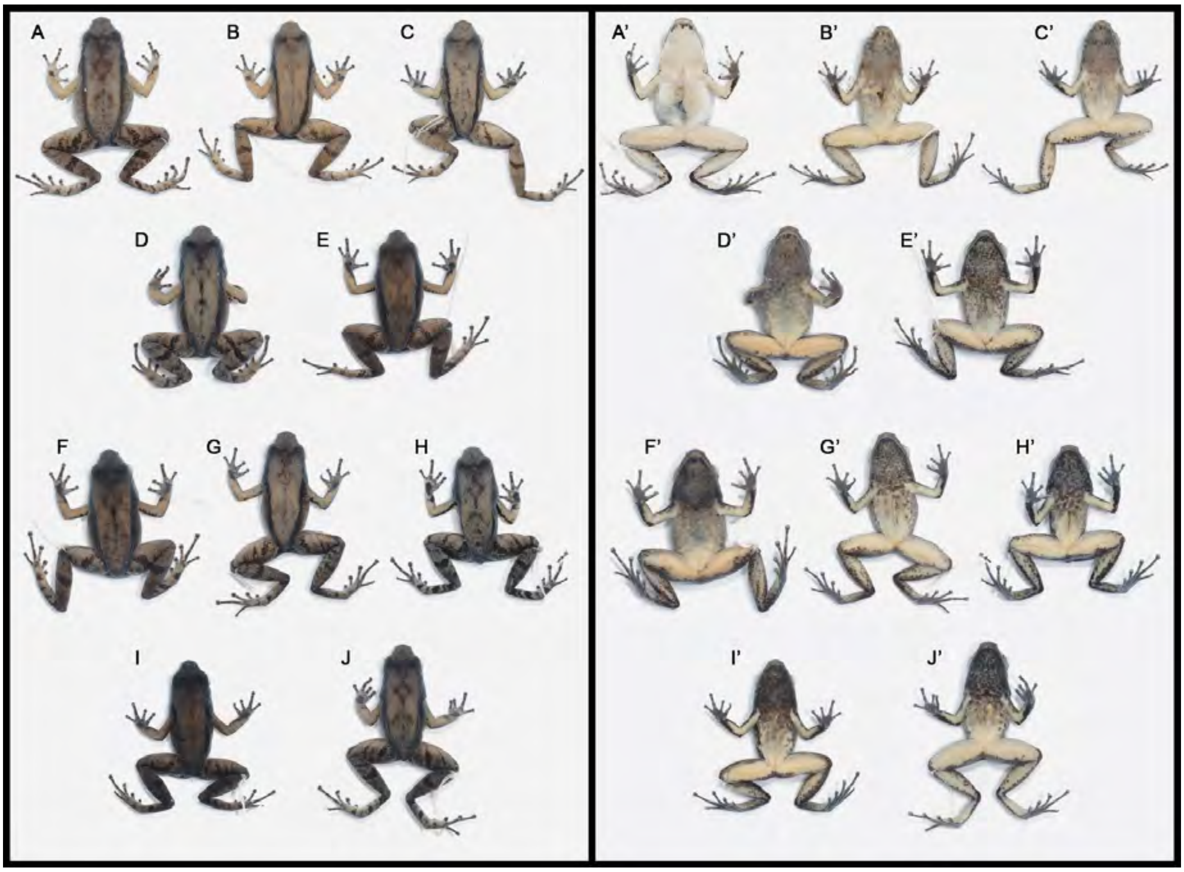

Figure **6.** *Anomaloglossus praderioi*, showing intrapopulation variation in dorsal (left) and ventral (right) pattern in preservative. **A-A':** IRSNB 14404, female 22.7 mm SVL. **B-B':** IRSNB 14409, male 21.1 mm SVL. **C-C':** IRSNB 14408, male 20.9 mm SVL. **D-D':** IRSNB 14413, male 21.9 mm SVL. **E-E':** IRSNB 14410, male 21.6 mm SVL. **F-F':** IRSNB 14412, male 21.4 mm SVL. **G-G':** IRSNB 14406, male 21.3 mm SVL. **H-H':** IRSNB 14403, male 21.2 mm SVL. **I-I':** IRSNB 14407, male 20.5 mm SVL. **J-J':** IRSNB 14405, male 20.9 mm SVL.

Advertisement call. The following description is based on a sample of 20 advertisement calls from two males (10 calls per male), IRSNB 14410 and an unvouchered specimen, both individuals recorded on the southeastern slope of Maringma Tepui, on 24 November 2007 between 14h30–15h00, air temperature 19.8–20°C. IRSNB 14410 was calling alone (Fig. 8A–B), whereas the unvouchered specimen was calling antiphonally with other males in the background (Fig. 8C–D).

Temporal structure. The advertisement call of *Anomaloglossus praderioi* consists of long trains of a single, variably pulsed note (Figs. 8–10). Amplitude modulations (pulses) are variably evident in the oscillograms and range from two to four (Figs. 9–10). The call rate varies between 65–76 (IRSNB 14410) and 61–66 calls/min (unvouchered individual) based on a 3 min period. The mean call duration for the two males is 0.045 ± 0.002 and varies from 0.041 to 0.049 s. The inter-call interval is not uniform and has a mean of 0.960 ± 0.248 and a range of 0.554–1.502 s. A slight decrease in call rate and note duration, and an increase in inter-call interval and amplitude modulation are noticeable in the unvouchered specimen (see Table 3), which was calling antiphonally with other males in the background at the same air temperature (Fig. 8, Fig. 9 *vs.* 10).

Spectral structure. Six to seven harmonics are developed, with the fundamental frequency dominating (mean: 3,709, range: 3,562–3,856 Hz) (Figs. 9–10). The distribution of sound energy decreases progressively through the higher harmonics. The dominant frequency is slightly modulated upwards.

Comparison with other *Anomaloglossus* calls. Only one *Anomaloglossus* species for which calls are known produces a single note per call: *A. degranvillei*, which does not occur in the Pantepui region but in French Guiana and Suriname and likely in adjacent Brazil (Frost, 2009). The call of *A. degranvillei* can notably be distinguished from that of *A. praderioi* by lower call rate (42 *vs.* 61–76 in *A. praderioi*), higher dominant frequency (4,280–4,640 *vs.* 3,562–3,856 in *A. praderioi*), and in having the dominant frequency located in the second harmonic (in the fundamental harmonic in *A. praderioi*).

Distribution and natural history. *Anomaloglossus praderioi* is currently known from two localities in eastern Venezuela: at 1,374 m elevation in the Sierra de Lema (currently the western and northernmost known locality), and between 1,800–1,950 m elevation on the slopes of Mt. Roraima (type locality), and two localities in Guyana: at 1,310 m elevation on the slopes of Mt. Roraima, and at 1,376 m elevation on the slopes of Maringma Tepui (currently the eastern and southernmost known locality) (Fig. 1). *Anomaloglossus praderioi* seems thus restricted to undisturbed forests at elevations between 1,310–1,950 m and is probably restricted to the eastern part of the Eastern Pantepui District (see Discussion). It is expected to be discovered in suitable habitat along the Pakaraima Mountains range in Guyana and northern Brazil as well as in the eastern part of the Sierra de Lema and the Sierra de Rinocote in Venezuela.

Anomaloglossus praderioi occurs in undisturbed montane medium-canopy forest with abundant epiphytes and mosses and rich undergrowth (Fig. 11). The species is locally abundant and was never found syntopic with the sympatric *A. kaiei*, which never occurs above 1,060 m elevation. All specimens were collected during the day, on the ground, never closely associated with water bodies. Males emitted vocalisations the entire day. Courtship was not observed and oviposition site is unknown. A male was found carrying five tadpoles on his back; tadpoles are deposited in small temporary pools.

Character	Stage 26 (*n*=5)	Stage 27 (*n*=3)	Stage 28 (*n*=1)	Stage 31 (*n*=1)*	Stage 39 (*n*=2)
TL	16.1 ± 0.5 (15.5–16.8)	19.2 ± 2.8 (17.5–22.4)	21.1	26.5	24.9 ± 0.4 (24.5–25.3)
BL	5.2 ± 0.1 (5.0–5.3)	7.0 ± 1.8 (5.3–8.8)	8.6	–	7.9 ± 0.2 (7.7–8.1)
TAL	11.0 ± 0.4 (10.5–11.5)	12.2 ± 1.4 (10.8–13.6)	12.5	–	17.0 ± 0.2 (16.8–17.2)
BW	3.0	4.7 ± 0.6 (4.2–5.3)	5.6	–	5.6
BH	2.2 ± 0.1 (2.1–2.4)	3.5 ± 0.6 (3.0–4.2)	4.2	–	4.1
HW	2.7 ± 0.1 (2.6–2.9)	4.2 ± 0.6 (3.7–4.9)	4.6	–	4.7 ± 0.1 (4.5–4.8)
TMH	1.4	1.6 ± 0.2 (1.5–1.8)	1.8	–	2.6 ± 0.2 (2.4–2.8)
TMW	1.3	1.5 ± 0.3 (1.3–1.8)	1.8	–	2.5
MTH	2.4	3.5 ± 0.6 (3.0–4.1)	4.0	–	4.4 ± 0.2 (4.2–4.5)
END	0.5 ± 0.09 (0.3–0.5)	0.6 ± 0.1 (0.5–0.7)	0.8	–	0.9 ± 0.05 (0.8–0.9)
NSD	0.6 ± 0.05 (0.5–0.6)	0.8 ± 0.2 (0.7–1.0)	1.0	–	0.7
IND	0.9 ± 0.1 (0.8–1.0)	1.2 ± 0.3 (1.0–1.5)	1.4	–	1.6 ± 0.1 (1.5–1.7)
IOD	1.0 ± 0.09 (0.8–1.0)	1.4 ± 0.3 (1.2–1.7)	1.5	–	1.5 ± 0.05 (1.4–1.5)
ED	0.5 ± 0.06 (0.5–0.6)	0.7 ± 0.06 (0.7–0.8)	0.7	–	1.2 ± 0.1 (1.1–1.3)

Table **2.** Morphometric measurements (in mm) of tadpoles of *Anomaloglossus praderioi*. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses. * tadpole lost before complete measurements were taken.

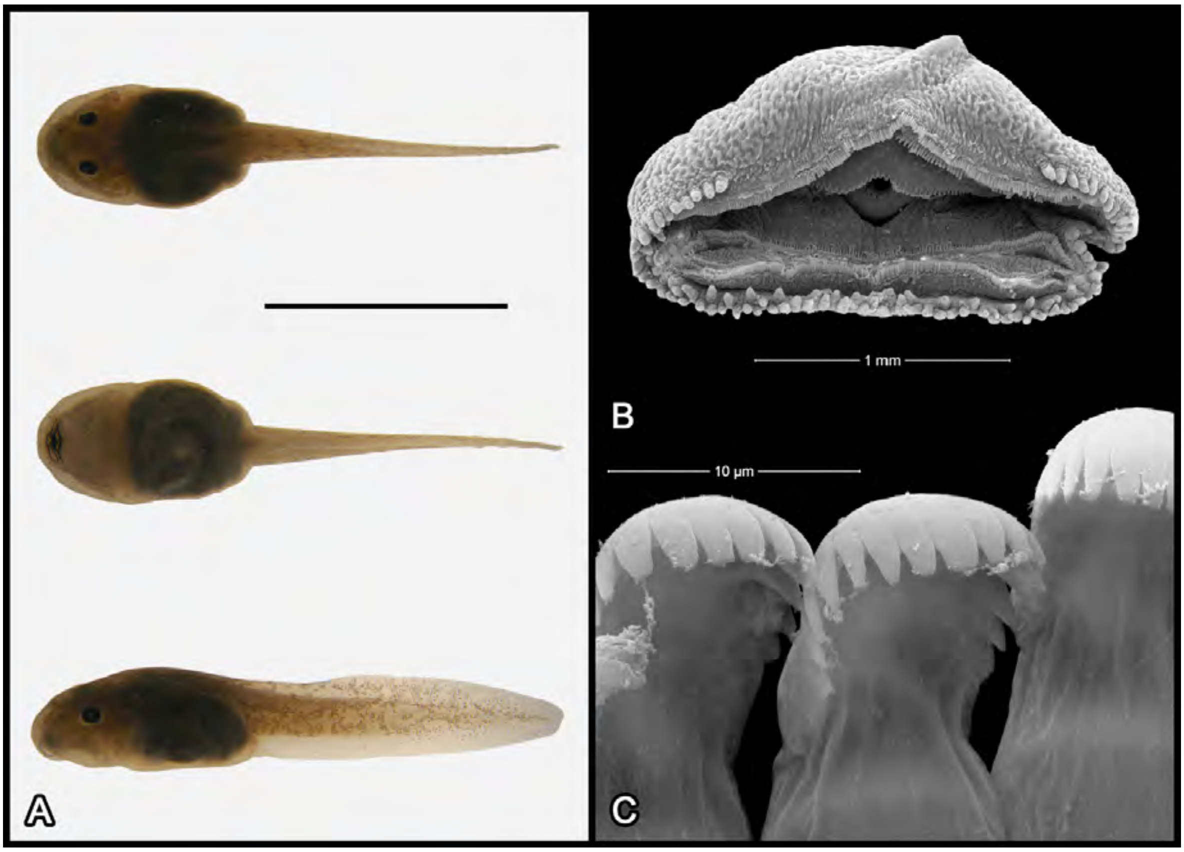

Figure **7.** Tadpole of *Anomaloglossus praderioi.* **A:** Dorsal, ventral and lateral views of IRSNB 14415a, a stage-28 tadpole in preservative. Scale bar is 10 mm. **B:** Photomicrograph of the oral disc of IRSNB 14416b, a stage-39 tadpole (130x magnification), teeth row A-2 mostly hidden by A-1. **C:** Photomicrograph of labial teeth of the same specimen (13000x magnification).

Individual	Call rate (calls/min)	Note duration (s)	Inter-call interval (s)	Dominant frequency (Hz)
IRSNB 14410, calling alone	69.7 ± 4.64 (65–76)	0.045 ± 0.002 (0.043–0.049)	0.838 ± 0.2 (0.554–1.153)	3856
Unvouchered specimen, calling antiphonally with other males in the background	63.3 ± 2.05 (61–66)	0.042 ± 0.001 (0.041–0.043)	1.112 ± 0.2 (0.730–1.502)	3562

Table **3.** Measurements of acoustic parameters for two males *Anomaloglossus praderioi*. Mean ± SD are followed by the range in parentheses. Temperature varied from 19.8–20°C.

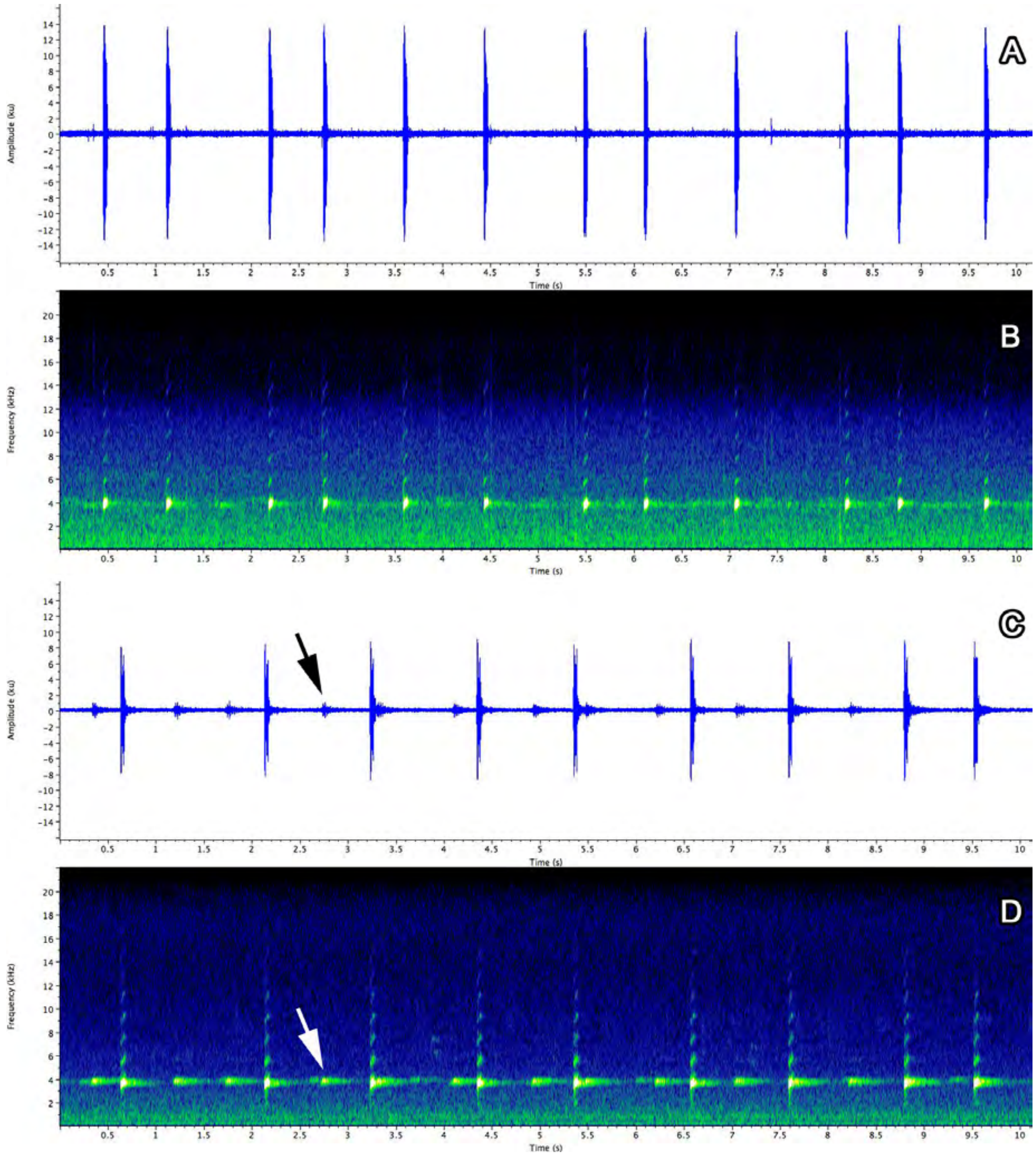

Figure **8.** Vocalisation of *Anomaloglossus praderioi.* **A:** Oscillogram. **B:** Spectrogram (recording of IRSNB 14410). **C:** Oscillogram. **D:** Spectrogram (recording of an unvouchered specimen). Arrows indicate another male calling antiphonally. Temperature varied from 19.8–20°C.

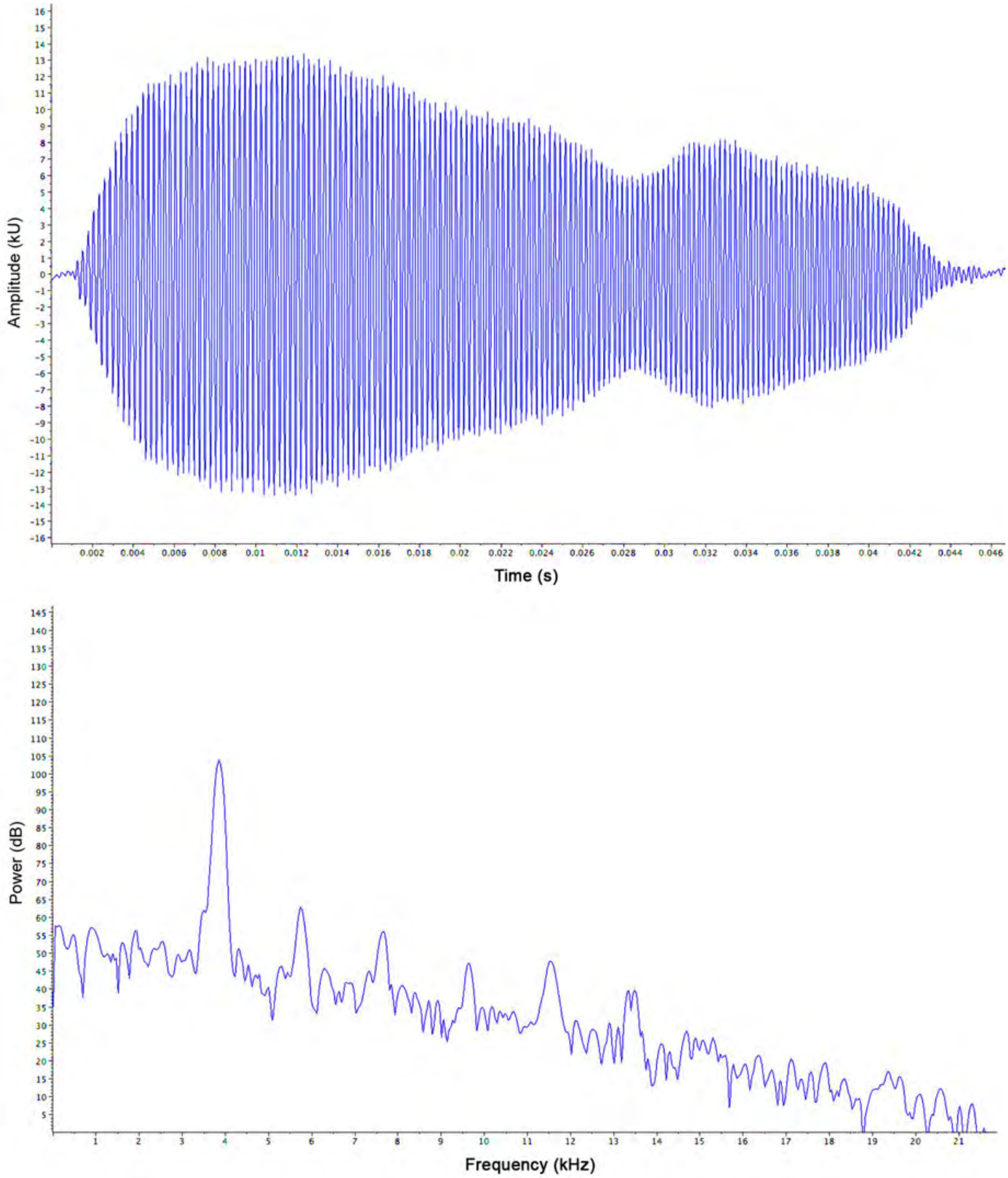

Figure **9.** Vocalisation of *Anomaloglossus praderioi*. Expanded oscillogram of the first note in Fig. 8A–B showing slight amplitude modulation (top) and spectral slice of the same note (bottom). Temperature varied from 19.8–20°C.

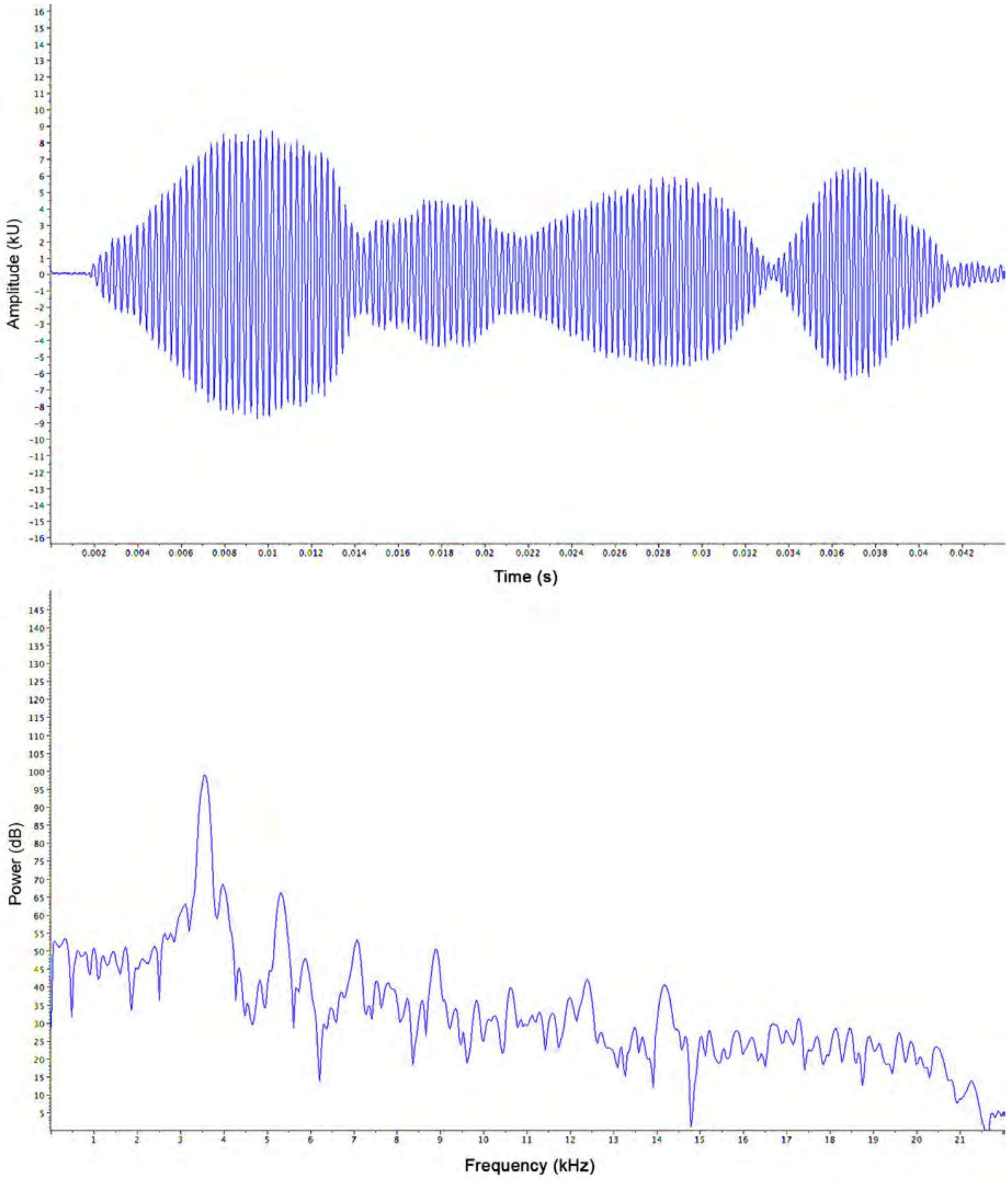

Figure **10.** Vocalisation of *Anomaloglossus praderioi*. Expanded oscillogram of the first note in Fig. 8C–D showing strong amplitude modulation (top) and spectral slice of the same note (bottom). Temperature varied from 19.8–20°C.

Figure **11.** Habitat of *Anomaloglossus praderioi* on the southeastern slope of Maringma Tepui, Guyana, at 1,370 m elevation.

Discussion. Poor and/or inaccurate original descriptions not only prevent correct identification of new material, but also impede new species descriptions. The problem is of course exacerbated when authors do not examine holotypes and faithfully follow original descriptions as a basis for diagnosing new species (see a striking example in Kok & Rivas Fuenmayor, 2008). The genus *Anomaloglossus* is particularly affected by this problem because many species have been described on the basis of few preserved specimens – sometimes a single immature individual (*e.g. A. murisipanensis, A. roraima*) with no additional material available. Important diagnostic characters, such as dorsolateral lines, may be lost in preserved specimens: the original description of *A. praderioi* mentions that the species lacks dorsolateral lines, which is true in preservative, but these lines are conspicuous in living specimens.

I recently had the opportunity to examine type series of most *Anomaloglossus* from the Pantepui region (northeastern South America) in the context of a taxonomic redefinition of the species, which confirmed the presence of a median lingual process in all of them and revealed significant discrepancies between some type specimens and original descriptions. Inconsistencies concerned wrong determination of sex, wrong evaluation of age, and inaccurate descriptions of important diagnostic characters such as skin texture, length of Finger I *vs.* II, and condition of fringes on fingers and toes. New descriptions of these taxa on the basis of newly collected material are in great demand to avoid misidentifications, confusing diagnoses, and descriptions of synonyms. Since examining type series might be problematic (most museums refuse now to lend type material), good redescriptions and redefinitions of species are invaluable (*e.g.* Myers & Donnelly, 2008). Descriptions of new *Anomaloglossus* species without examining comparative type material should not be prevented, but the greatest caution should be exercised.

An additional problem in the genus *Anomaloglossus* is the great intraspecific variability in some taxa and the apparent occurrence of cryptic species that are morphologically almost impossible to distinguish (*e.g. A. baeobatrachus* and *A. stepheni*), especially in preservative. Ideally, redescriptions – and new taxa descriptions – should include tadpole, call, and data on natural history. Phylogenetic analyses are also critical, and probably necessary to support species identity and detect cryptic taxa.

I examined a series of *Anomaloglossus* sp from Mt. Wokomung and Mt. Ayanganna, Guyana (ROM specimens, see Appendix) that are superficially very similar to *A. praderioi* and possibly conspecific. However, I decided to not include this material collected about 100 km east of the type locality (see Fig. 1) in the present work because specimens from these populations differ from *A. praderioi* in discrete morphological characters and probably belong to a cryptic undescribed taxon. Pending additional morphological and molecular evidence I currently consider these populations as *Anomaloglossus* cf. *praderioi*. Grant *et al.* (2006:121) reached a similar conclusion notably finding 8.3% uncorrected pairwise distance between Cytochrome *b* sequences of a specimen from Mt. Ayanganna [called "Ayanganna" in Grant *et al.* (2006)] and two specimens of *A. praderioi* from near the type locality.

Due to its relatively wide range and apparently healthy populations occurring in pristine habitat (especially in Guyana), I suggest that *Anomaloglossus praderioi* be classified as "Least Concern" (LC) in accordance with the criteria of IUCN (2001). However, because of possible chytridiomycosis outbreak, known Venezuelan populations should be monitored.

The range of *Anomaloglossus kaiei* is here reported to be broader than was previously known (see Kok, 2008). It occurs from Kaieteur National Park to the slopes of Maringma Tepui, at elevations between 150–1,060 m. The species is also present on the slopes of Mt. Wokomung. If some *Anomaloglossus* probably do have restricted distributions, some other species are widespread, and lowland and "tepui slopes" species should be expected to be more widespread that previously thought.

Resumen

Anomaloglossus praderioi fue originalmente descrito como *Colostethus praderioi* por E. La Marca en 1998 con dos ejemplares machos. El presente artículo ofrece una redescripción detallada de la especie basada en nuevos ejemplares de Maringma Tepui, en Guyana y ejemplares adicionales de la Sierra de Lema, en Venezuela. La redescripción incluye la vocalización y descripción del renacuajo. Anomaloglossus praderioi es de tamaño mediano y se distingue principalmente de sus congéneres por los siguientes caracteres: los dedos I, II y IV con igual longitud; punta del dedo IV apenas llega a la base del tubérculo subarticular distal del dedo III, cuando estos son colocados juntos; dedos II y III con la quilla preaxial y pliegues laterales; dedos de los pies palmeados basalmente, excepto en los dedos IV–V; simétricos tubérculos cloacales presentes; franja delgada

dorsolateral de color pálido, la cual va desde la punta del hocico hasta la punta de urostilo; banda ventrolateral inconspicua, nunca recta; banda lateral oblicua ausente. Macho con garganta de color gris a gris muy oscuro, casi negro uniforme. En hembras la garganta es de color naranja brillante, casi inmaculada. La larva es castaño oscuro a negro, de hábitos exotróficos y bentónicos, LTRF 2 (2)/3. La llamada de advertencia consiste de largas series de una nota sencilla repetida a un ritmo de 61–76 notes/min con una frecuencia dominante que va desde 3,562 a 3,856 Hz. La especie queda registrada para el sureste de Venezuela y oeste de Guyana, habitando bosques montanos con cobertura media en elevaciones entre los 1,310–1,950 m s.n.m.

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APPENDIX . ADDITIONAL SPECIMENS EXAMINED

Anomaloglossus beebei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 13721-26, 13728-53, ULABG 6817 (ex IRSNB 13727), IRSNB 13754 (tadpoles), IRSNB 13779-81 (tadpoles).

Anomaloglossus breweri.— Venezuela: *Estado Bolívar*: Aprada Tepui, Cueva del Fantasma, MHNLS 17044 (holotype), MHNLS 17045-46 (paratypes).

Anomaloglossus kaiei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 1938 (holotype), IRSNB 1939-64 (paratypes), IRSNB 14420-57, IRSNB 13755-78 (tadpoles), ROM 42999; Cuyuni-Mazaruni District, Wayalayeng, IRSNB 14922-24, Maringma Tepui, IRSNB 14925-31, Mount Wokomung, ROM 43321, ROM 43327, ROM 43330, ROM 43333.

Anomaloglossus murisipanensis.— Venezuela: *Estado Bolívar*: Murisipan-Tepui, MHNLS 11385 (holotype).

Anomaloglossus parkerae.— Venezuela: *Estado Bolívar*: Sierra de Lema, Salto El Danto, MHNLS 2901, MHNLS 11088–89.

Anomaloglossus praderioi.— Guyana: *Cuyuni-Mazaruni District*: Maringma Tepui, IRSNB 11403–13, IRSNB 14414–16 (tadpoles); Venezuela: *Estado Bolívar*: Mount Roraima ULABG 4196 (holotype), MHNLS 11272 (paratype), Sierra de Lema, EBRG 5569.

Anomaloglossus cf *praderioi*.— Guyana: *Cuyuni-Mazaruni District*: Mount Wokomung, ROM 43320, ROM 43322–26, ROM 43328–29, ROM 43331–32, ROM 43896, Mount Ayanganna ROM 39639.

Anomaloglossus roraima.— Venezuela: *Estado Bolívar*: Mount Roraima, ULABG 4197 (holotype).

Anomaloglossus rufulus.— Venezuela: *Estado Bolívar*: Amuri-Tepui, Chimantá Massif, MHNLS 10361 (holotype).

Anomaloglossus tepuyensis.— Venezuela: *Estado Bolívar*: Auyantepui: ULABG 2557 (holotype), Cucurital River, MHNLS 14404–05, Purumay River, MHNLS 14924–25, MHNLS 14940–41, MHNLS 15687, Quebrada Atapere, MHNLS 15924, MHNLS 17359–60, MHNLS 17383, Quebrada Tucutupan, MHNLS 17401, Quebrada Rutapa, MHNLS 17361.

Anomaloglossus triunfo.— Venezuela: *Estado Bolívar*: Cerro Santa Rosa, Serranía del Supamo, EBRG 4756 (holotype), EBRG 4757–59 (paratypes).

9

A New Diagnosis and Description of *Anomaloglossus roraima* (La Marca, 1998) (Anura: Aromobatidae: Anomaloglossinae), with Description of its Tadpole and Call

P. J. R. Kok, B. Willaert & D. B. Means

Abstract

The frog *Anomaloglossus roraima* was originally described as *Colostethus roraima* by E. La Marca in 1998 on the basis of a single immature female collected at 2700 m elevation on the upper slopes of Mount Roraima, a tepui (table mountain) located in southeastern Venezuela. We herein provide a redescription of the species on the basis of new material from Wei-Assipu-tepui and Maringma-tepui in Guyana. The redescription includes the first descriptions of the tadpole and vocalisation. *Anomaloglossus roraima* is a small-sized species mainly distinguished from its known congeners in having Finger I < II; fingers with narrow pre- and postaxial unfolded fringes; toes unwebbed (although rudimentary webbing is sometimes present between Toe III and IV) with narrow pre- and postaxial unfolded fringes; symmetrical cloacal tubercles present; dorsolateral stripe usually present, often inconspicuous; ventrolateral stripe absent; oblique lateral stripe absent; no obvious sexual dichromatism in throat, chest and ventral colour patterns. The tadpole is large, black, exotrophic, arboreal, LTRF 2(2)/3. The advertisement call consists of a single note repeated at a rate of 8.5–17 notes/min with a dominant frequency ranging from 4107 to 4362 Hz. The species is restricted to a small area in the Eastern Tepui Chain in southeastern Venezuela and western Guyana and mainly inhabits large bromeliads in tepui scrub and high-tepui meadows at elevations between 1860–2700 m above sea level. The discovery on different tepui summits and upper slopes of a species previously reported as having a highly restricted range is important for the understanding of the biogeography of the Pantepui region.

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INTRODUCTION

The genus *Anomaloglossus* was erected by Grant *et al.* (2006) to accommodate all the species formerly included in *Colostethus* that have a median lingual process (MLP), an unusual anatomic structure also known in some Asian and African ranoid frogs (Grant *et al.*, 1997). According to Grant *et al.* (2006) *Anomaloglossus* is sister to *Rheobates,* a genus reported from the Cordillera Central and the Cordillera Oriental in Colombia. Twenty-nine *Anomaloglossus* species are currently recognized (Kok, 2010; Kok *et al.*, 2010; Ouboter and Jairam, 2012; Myers *et al.*, 2012), 18 of which being reported as endemic to Pantepui (Frost, 2013). The genus *Anomaloglossus* includes several species having very restricted distributions in the Guiana Shield, sometimes reported from the summit of a single tepui only, whereas the genus is reported to have some representatives in the Andes, in Panama, and a single species in the Amazonian lowlands (Frost, 2013). Grant *et al.* (2006) pointed out that more taxon sampling is needed to clarify relationships between *cis*-Andean species and those occurring west of the Andes (= *trans*-Andean) and that the *trans*-Andean species having a median lingual process must be included in phylogenetic analyses to corroborate their placement in *Anomaloglossus*. Grant *et al.* (2012) and Myers *et al.* (2012) recently suggested that the Panamian and *trans*-Andean *Anomaloglossus* form a clade phylogenetically distant from the *cis*-Andean *Anomaloglossus* and should be reallocated to a different genus. This would leave *Anomaloglossus* with 25 species, all restricted to the Guiana Shield and peripheral lowland areas.

Anomaloglossus species have a biphasic life cycle, eggs are usually laid on the ground, and the tadpoles are carried by the male to a suitable body of water (*e.g.* streams, puddles). Phytotelm-breeding species have specific ecological niche preferences. In those species, eggs are laid on bromeliad leaves and tadpoles slide into the bromeliad tank.

As already pointed out by Kok (2010) and Kok *et al.* (2010) several *Anomaloglossus* descriptions overlook and/or erroneously describe important diagnostic characters. Most are poorly illustrated (photographs of many *Anomaloglossus* species in life are not available) and are based on very few specimens. This is a significant obstacle to accurate comparisons between species, but also with possible new taxa. Redescriptions of those poorly known species and a more complete understanding of their morphology are thus of primary importance.

The distribution of many tepui taxa is very poorly known and the discovery of the occurrence of a same *Anomaloglossus* species on several tepui summits/upper slopes is central to understanding the biogeography of the area.

Anomaloglossus roraima was originally described in 1998 by Enrique La Marca (see Myers & Donnelly, 2008: 143 for comment on date of publication) in his revision of the genus *Colostethus* from the Venezuelan Guayana. The description was solely based on the holotype, an immature female collected in 1996 at 2700 m elevation on “La Rampa” just below the summit of Mount Roraima, Estado Bolívar, Venezuela. As for many *Anomaloglossus* species known only from the type series, the species’ name rarely appeared in the literature since the original description (*e.g.* Barrio-Amorós, 1998, 2004; McDiarmid & Donnelly, 2005; Grant *et al.*, 2006, MacCulloch *et al.*, 2007), except in the diagnoses of new congeneric taxa. Besides the few data provided in the original description, no information is available about the species, which is considered as highly restricted (*i.e.* restricted to a single tepui) by McDiarmid & Donnelly (2005).

Grant *et al.* (2006) included *Anomaloglossus roraima* in their phylogenetic study on the basis of DNA samples from two specimens and a tadpole collected by DBM between 1860–2350 m elevation on the north slopes of Mount Roraima, Cuyuni-Mazaruni District, Guyana. The authors indicated that *A. roraima* breeds in phytotelmata and suggested a sister-species relationship with *A. beebei* (Noble, 1923) (the only other known phytotelm-breeding *Anomaloglossus* species) based on molecular evidence. The purpose of Grant *et al.* (2006) was not to redefine the species and they did not examine the type specimen of *A. roraima*, however they concluded that their additional specimens–all from close to the type locality– sufficiently agreed with the original description to be considered conspecific.

As already pointed out by Kok (2010) and Kok *et al.* (2010) several *Anomaloglossus* descriptions overlook and/or erroneously describe important diagnostic characters. Most are poorly illustrated (photographs of many *Anomaloglossus* species in life are not available) and are based on very few specimens. This is a significant obstacle to accurate comparisons between species, but also with possible new taxa. Redescriptions of those poorly known species and a more complete understanding of their morphology are thus of primary importance. The distribution of many tepui taxa is very poorly known and the discovery of the occurrence of a same *Anomaloglossus* species on several tepui summits/upper slopes is central to understanding the biogeography of the area.

Thirty additional specimens of *Anomaloglossus roraima*, as well as 24 tadpoles, were collected at two different localities in the Eastern Tepui Chain in Guyana, and the vocalization of the species was recorded at both sites. On the basis of this new material (listed in the Appendix), and direct comparison with the holotype of *A. roraima*, we provide below a redescription of the taxon based on morphology and call as well as the first description of its tadpole. An updated diagnosis is provided and the IUCN Red List Category of *A. roraima* is discussed.

MATERIAL AND METHODS

The newly collected specimens of *Anomaloglossus roraima* are from the summit of Maringma-tepui (05° 12’ 57”N, 060° 35’ 07”W, between 2000–2100 m elevation, Fig. 1), Cuyuni-Mazaruni District, Guyana, where 13 adult individuals (six males, seven females), one sub-adult female, six juveniles, and seven tadpoles were secured, and from the summit of Wei-Assipu-tepui, at the border between Guyana and Brazil (05° 13’ 05”N, 060° 42’ 23”W, between 2200–2300 m elevation, Fig. 1) where seven adult individuals (two males, five females), two sub-adult females, one juvenile, and 17 tadpoles were collected. Additional specimens and tadpoles were collected at the base of the ultimate cliffs of the "Prow" of Mount Roraima in Guyana by DBM, but these specimens could not be recovered and are therefore not included in the morphological analyses.

Specimens were euthanized by immersion in a 2% Xylocaine solution, fixed in 10% formalin for several days and transferred to 70% ethanol (adults and juveniles) or preserved in 10% formalin (20 tadpoles) for permanent storage. A piece of liver and/or thigh muscle was taken from 15 specimens prior to fixation and preserved in 95% ethanol for later molecular analyses. Four tadpoles were preserved in 95% ethanol for the same purpose. Specimens were deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) and tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (see Appendix for material examined).

Color in life is described from digital photographs and field notes. Sex and maturity were determined by the presence/absence of vocal slit(s) and by dissection when sex determination was doubtful. Internal soft anatomy was examined by dissection of preserved specimens. All morphometric data were taken from the preserved specimens by the same person (BW during his master internship at the IRSNB), to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper or an ocular micrometer.

Abbreviations and standard measurements for adults are as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL); (3) head width at level of angle of jaws (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance (IN); (7) eye length (EL); (8) interorbital distance (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (11) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (12) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (13) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (14) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (15) width of disc on Finger III (WFD); (16) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (17) width of disc on Toe IV (WTD); (18) tibia length from outer edge of flexed knee to heel (TIL); (19) upper arm length from anterior insertion with the body to outer edge of flexed elbow (AL). Relative lengths of fingers were compared according to Kaplan (1997), using the distance from the proximal edge of the palmar tubercle to the tip of each finger.

Three lots of tadpoles were collected, all from terrestrial tank bromeliads (*Brocchinia tatei*, Bromeliaceae). Developmental stages of tadpoles follow Gosner (1960); terminology and oral disc characters follow Altig & McDiarmid (1999). Color in life is described from field notes and color photographs. Abbreviations and standard measurements for tadpoles are as follows: (1) total length from tip of snout to tip of tail (TL); (2) body length from tip of snout to junction of posterior body and tail musculature (BL); (3) tail length from junction of posterior body and tail musculature to tip of tail (TAL); (4) greatest body width (BW); (5) highest body height (BH); (6) head width at level of eyes (HW); (7) tail muscle height at base of tail (TMH); (8) tail muscle width at base of tail (TMW); (9) maximum height of tail (MTH); (10) eye-naris distance (END); (11) naris-snout distance (NSD); (12) internarial distance (IND); (13) interorbital distance (IOD); (14) eye diameter (ED). The oral disc of a 28.7 mm long, stage-27 formalin preserved tadpole was dissected, critical-point dried, and coated with gold following the usual protocol (Echeverría, 1997; Kok & Kalamandeen, 2008) for scanning electron microscopy (SEM). Observations and photomicrographs were made with a FEI Quanta-200 environmental scanning electron microscope (ESEM). Ethanol-preserved tadpoles were not included in Table 2 because ethanol caused soft tissue desiccation and body deformation.

Advertisement calls were recorded (1.5 to 3 minutes) at a distance of less than 1 m from one calling male collected on Maringma-tepui and one uncollected male on Wei-Assipu-tepui using a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder using Maxell DM60 digital audiotape. The calls were analysed at a sampling rate of 44100 Hz using Raven version 1.4 software (Charif *et al*., 2010). Temporal variables measured included: call duration (= note duration); inter-call interval (beginning of one call to beginning of the next); and call rate (= number of calls per minute) (Kok & Kalamandeen, 2008). The dominant (emphasized) frequency of the note was measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 120 Hz) (Kok & Kalamandeen, 2008). Air temperature at the call sites was measured with a Hanna digital pH/thermometer and was 17°C at both sites.

Taxonomy follows Grant *et al*. (2006). Institutional acronyms follow Frost (2013).

RESULTS

Redescription of *Anomaloglossus roraima* (La Marca, 1998)

(Figs. 2–8)

Adult definition and diagnosis. (1) Small-sized *Anomaloglossus* (males 16.5–19.0 mm SVL, females 16.5–19.3 mm SVL); (2) body robust; (3) skin on dorsum fairly variable, rarely smooth, usually shagreen to finely granular, more granular posteriorly, skin on venter smooth to shagreen; (4) Finger I < II; (5) tip of Finger IV reaching or surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (when the distal subarticular tubercle on Finger III is visible, see below); (6) distal tubercle on Finger IV present, although often barely distinguishable; (7) Finger III faintly swollen in some males (preaxial and postaxial keeling weakly more developed than in females, only visible under magnification); (8) fingers with narrow pre- and postaxial unfolded fringes (best visible under magnification); (9) toes unwebbed–although rudimentary webbing is sometimes present between Toes III-IV–with narrow pre- and postaxial unfolded fringes (best visible under magnification); (10) tarsal keel weakly curved, slightly tuberclelike, not extending from metatarsal tubercle; (11) black arm gland absent in male (*sensu* Grant & Castro-Herrera, 1998, see also Grant *et al*., 2006); (12) symmetrical cloacal tubercles present; (13) pale paracloacal mark usually absent; (14) thin pale dorsolateral stripe present or absent in both sexes, when present it extends from the anterior or posterior corner of eye to the level of anterior thigh insertion (dorsolateral stripe less conspicuous in preserved specimens); (15) ventrolateral stripe absent; (16) oblique lateral stripe absent; (17) no obvious sexual dichromatism in throat color; (18) no obvious sexual dichromatism in ventral coloration; (19) iris with metallic pigmentation and pupil ring; (20) large intestine extensively pigmented; (21) testes cream, unpigmented; (22) mature oocytes darkly pigmented; (23) median lingual process short, tapered; (24) maxillary teeth present, small.

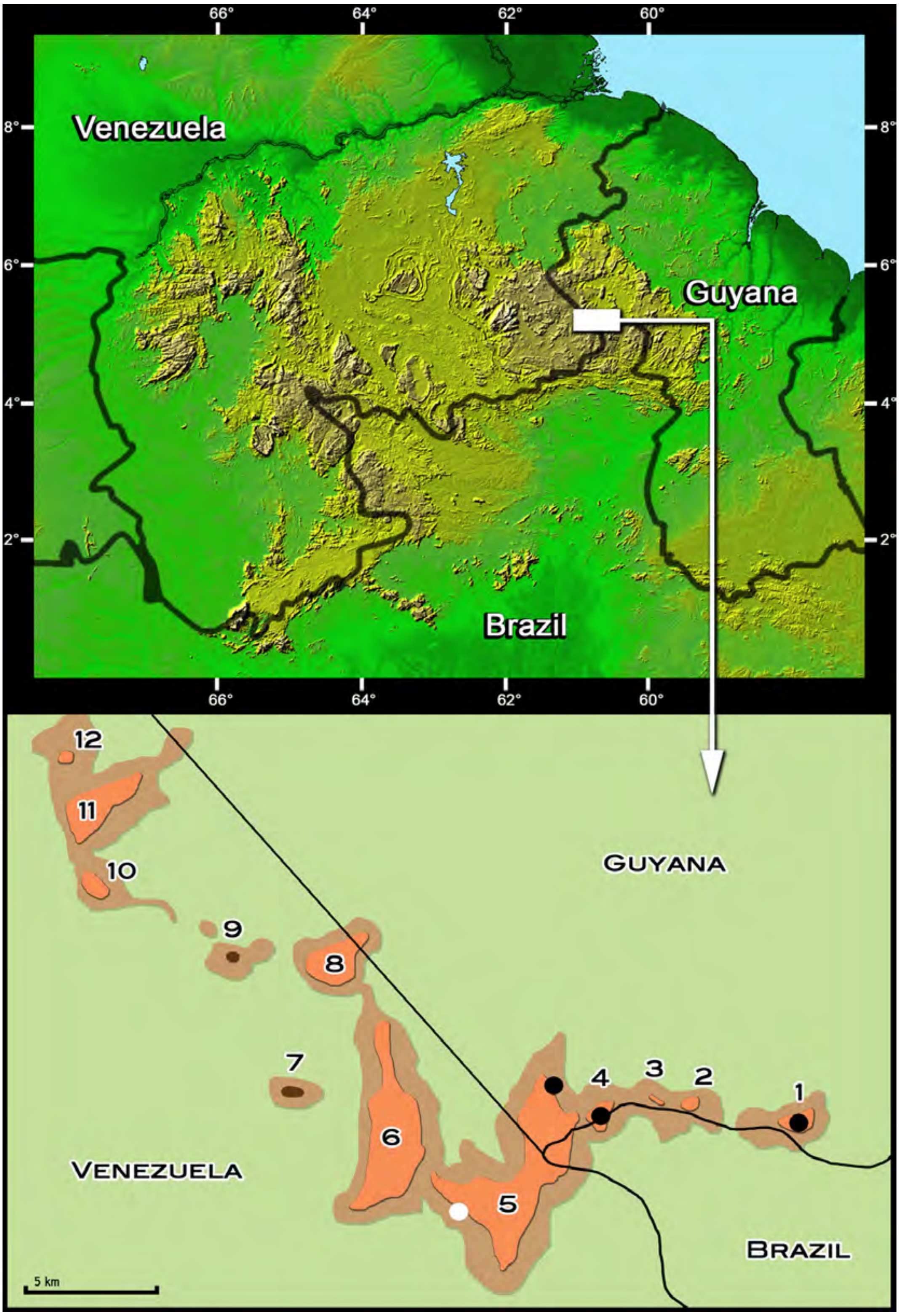

Figure **1.** Map of the Pantepui region, with enlarged white rectangle corresponding to the Eastern Tepui Chain: 1 = Maringma-tepui, 2 = Yakontipu-tepui, 3 = Appokailang-tepui, 4 = Wei-Assipu-tepui, 5 = Mount Roraima, 6 = Kukenan-tepui, 7 = Achipo-tepui, 8 = Yuruani-tepui, 9 = Guadacapiapu-tepui, 10 = Karaurin-tepui, 11 = Ilu-tepui, 12 = Tramen-tepui. Areas in orange indicate summits higher than 2000 m elevation; areas in dark brown indicate summits lower than 2000 m; areas in light brown indicate tepui slopes above 1500 m elevation. Dots show collecting localities of *Anomaloglossus roraima* (white dot = type locality, black dots = new localities).

Comparison with other species. Twenty-nine species of *Anomaloglossus* are currently recognized (Frost, 2013), many of which apparently have restricted ranges. Eleven *Anomaloglossus* species are known to occur in the Eastern Pantepui District in the Guiana highlands of Venezuela and Guyana (*i.e.* east of the Rio Caroní, which likely acts as a biogeographic barrier for *Anomaloglossus* species since no species has been reported to occur on both sides of the river): *A. beebei*, *A. breweri* (Barrio-Amorós, 2006), *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet and Bourne, 2006), *A. megacephalus* Kok, MacCulloch, Lathrop, Willaert and Bossuyt, 2010, *A. moffetti* Barrio-Amorós and Brewer-Carías, 2008, *A. parkerae* (Meinhardt and Parmelee, 1996), *A. praderioi* (La Marca, 1998), *A. murisipanensis* (La Marca, 1998), *A. rufulus* (Gorzula, 1990), *A. tepuyensis* (La Marca, 1998), and *A. triunfo* (Barrio-Amorós, Fuentes-Ramos and Rivas, 2004). *Anomaloglossus roraima* is readily distinguished from these species in having adult females reaching less than 20 mm SVL [adult females of all other known *Anomaloglossus* species from the area exceed 20 mm SVL, except in *A. beebei*, *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006), and *A. triunfo*[1] (Barrio-Amorós, Fuentes-Ramos & Rivas, 2004)] and by lacking toe webbing (webbing basal to extensive in all other known *Anomaloglossus* species from the area).

Adult description. Major differences from the original description are italicized between brackets; see Table 1 for morphometric data of the holotype of *Anomaloglossus roraima* (ULABG 4197, illustrated in Fig. 2) compared to new material (partly illustrated in Figs. 3–7). Adult males 16.5–19.0 mm SVL (n = 8), adult females 16.5–19.3 mm SVL (n = 12). Dorsal skin texture fairly variable, from smooth (uncommon) to finely granular, becoming more granular posteriorly and on hind limbs; ventral skin smooth to shagreen. Dorsal surface of hind limbs granular, with two distinct symmetrical enlarged tubercles located laterally between urostyle and vent in 23 specimens (77% of our sample); these tubercles are less easily distinguishable in the other specimens, possibly due to an artefact of preservation.

Head wider than long, greatest width 36% of SVL in males, 35% in females. Snout rounded in lateral view, extending past lower jaw, broadly rounded in ventral and dorsal views. Nares located close to tip of snout, directed posterolaterally; nares visible from front, barely visible from above and not visible from below; internarial distance 33% of greatest head width in both sexes. Canthus rostralis barely defined, rounded; loreal region concave, sloping outward to lip. Interorbital distance slightly shorter than eye length, shorter than upper eyelid. Snout length 104% of eye length in both sexes, 45% (in males) to 46% (in females) of head length; distance from anterior corner of eye to posterior margin of naris 60% (in males) to 62% (in females) of eye length. Postrictal tubercles usually few and inconspicuous. Tympanic membrane poorly recessed, inconspicuous, round, much smaller than eye, concealed posterodorsally by a more or less prominent supratympanic swelling; tympanic annulus usually detectable anteroventrally.

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[1] Barrio-Amorós *et al.* (2004) reported one of the paratypes of *Anomaloglossus triunfo* to be an adult female. Upon re-examination by PJRK that specimen (EBRG 4758) proved to be a subadult individual. Therefore none of the specimens examined by Barrio-Amorós *et al.* (2004) is an adult female, and the correct female size is still unknown in that species. We believe that *Anomaloglossus triunfo* is likely a synonym of *A. tepuyensis* La Marca, 1998.

Forearm subequal to upper arm length, no distinct ulnar fold, but sometimes a row of low tubercles instead. Hand moderate, its length 27% (in males) to 28% (in females) of SVL; hand length 77% (in males) to 79% (in females) of greatest head width. Relative length of fingers III > IV > II > I. Fingers unwebbed. Discs of fingers expanded, disc on Finger IV slightly widest. Fingers with narrow pre- and postaxial unfolded fringes (*sensu* Myers & Donnelly, 2008), Finger III faintly swollen in some males (preaxial and postaxial keeling weakly more developed than in females, only visible under magnification; Fig. 3 A–B).

Palmar tubercle large, rounded to ovoid; thenar tubercle smaller, elliptical; one, rarely two round to ovoid subarticular tubercles (one each on Fingers I and II, usually one–rarely two–each on Fingers III and IV, with distal tubercle on these fingers usually barely detectable). No distinct outer metacarpal fringe. Tip of Finger IV reaching or surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (when the distal subarticular tubercle on Finger III is visible, which is rarely the case; Fig. 3 A–B) [*although the distal subarticular tubercle on Finger III is well visible on fig. 9 in the original description, it is in fact barely detectable on the holotype; the opposite is true for the basal subarticular tubercle on Finger III, which is not seen on fig. 9 in the original description although it is well visible on the holotype*]. No fleshy supracarpal fold atop wrist.

Hind limbs moderately robust, moderately long, with heel of adpressed leg reaching posterior to anterior corner of eye; tibia 51% (in males) to 52% (in females) of SVL. Relative lengths of adpressed toes IV > III > V > II > I; first toe short, usually, but not always reaching the base of subarticular tubercle of second toe. Toe discs moderately expanded, subequal or slightly larger than finger discs. Feet unwebbed, although rudimentary webbing is sometimes present between Finger III and IV; toes with narrow pre- and postaxial unfolded fringes (*sensu* Myers & Donnelly, 2008) that are best visible under magnification.

Inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, round, between half and two-third the size of the inner. One to three round to ovoid subarticular tubercles (one each on Toes I and II, two each on Toes III and V, and three on Toe IV, with distal tubercle on Toe IV the smallest and least conspicuous). A medial metatarsal tubercle is detectable at least on one side in 50% of the specimens examined. Outer metatarsal fold absent. A straight or weakly curved tuberclelike tarsal keel not extending from metatarsal tubercle (Fig. 3 A–B).

Maxillary teeth present, small. Tongue longer than wide, free posteriorly, with rounded margin; median lingual process short, tapered. Vocal slits bilateral, large, extending from edge of tongue to angle of jaw.

Color in life.- Dorsal ground color varies from tan to shades of light brown, sometimes monochromatic (Figs. 4B, 5A, 5C) but often with dark brown pigment arranged as limited (Figs. 4C, 4D, 5D) to heavy (Figs. 4A, 5B) mottling, the mottles having no particular shape. Upper surface of arm and forearm slightly lighter than ground color, sometimes reddish, the upper arm with tiny, faint white dots and the forearm with 1–3 transverse dark brown bands. Upper surface of thigh, shank, and heel identical with dorsal ground color and having 1–3 transverse dark brown mottles often forming poorly distinct bands. Dorsal ground color set off from flanks by the same quality of dark brown pigment as dorsal mottles, forming along the contact a poorly defined, slightly lighter, narrow dorsolateral stripe. Dark flank pigment runs posterior from the naris through the middle of the eye and expands to the top of the shoulder arching over the tympanum. Posterior to the shoulder, the flank pigment sometimes is continuously dark brown but in other examples breaks up into the same kinds of mottles mixed with dorsal ground color as on the back. Upper lip under the naris posterior to the shoulder the same uniformly tan to light brown dorsal ground color, but sometimes invaded partially by dark flank pigment. Belly yellowish (Fig. 4A') to light rusty colour in both sexes (Figs. 4B', 4C', 4D', 5C', 5D'), but sometimes heavily suffused with dark brown, uniform (Fig 5A') or mottled (Fig. 5B') pigment in some males. Chin undersurface slightly lighter in tone, sometimes with a few dark brown mottles or completely suffused with dark pigment (Figs. 5A', 5B'). Undersurfaces of front and hind legs darker in tone than the belly and often mottled (Figs. 5B', 5D') or completely suffused with dark brown pigment (Figs. 5A', 5C'). Undersurfaces of hands, feet, and toes uniformly dark brown. Toe tips of manus and pes dorsally dark brown set off prominently from the lighter coloured dorsal ground colour of the rest of the toes by a sky blue narrow transverse band. Iris light rusty brown above, dark brown pigment through the middle of the eye, light rusty brown below.

Colour of juvenile.- In one juvenile, the dorsal ground colour was light gray with dark mottling between the eyes and upper back. Flanks were similarly gray with no darker pigment but a narrow, tan, faint dorsolateral stripe was present from the naris to the urostyle. A narrow zone of dark pigment ran posterior to the naris through the iris and ends on the cheek and shoulder as in the adult, but somewhat less prominently. Dorsal surface of upper arms and forearms were reddish brown with about ten round white to light gray spots on each part of the arm. Ground color of dorsal surfaces of the thigh, shank, and heel were light gray-brown with one or two darker crossbands. Undersurfaces of arms and legs were reddish-yellow in color with a light suffusion of dark pigment over the legs. Belly and throat were yellowish but peppered with light gray specks that double in size on the chin that is blackish anteriorly. Toes of both manus and pes are dark brown to black with light gray speckles and a prominent light blue band across the base of the ultimate phalange. Iris as in the adult.

Color in preservative.- After 12 years in preservative, the yellow and red pigments of the holotype have disappeared leaving only dark gray to brown pigments uniformly suffused over the dorsum and prominent as transverse bands across the forearm (1 band), thigh (2), shank (2), heel (1), and foot (1). Brown pigment also is present on the toe tips, undersurfaces of the manus, pes, forearm, heel, anterior and posterior surfaces of the forearm, and lightly suffused over the dorsal surfaces of the legs between the darker crossbands. The belly, chin, and undersurfaces of the upper arm, leg, and shank were pigmentless (Fig. 2). After about four years in preservative, five males and eight females displayed a similar loss of yellow and red color as in the holotype. Dark gray to brown pigments remained as a dorsal suffusion with varying degrees of darker mottling (Fig. 6) on the belly and undersurfaces of the arms and legs. In all cases, the dark pigments were retained as they were present in life, but the yellow and red pigments presumably were dissolved out of the skin in preservatives. Limited dark mottling may occur on the otherwise colorless undersurfaces of the chin, belly, and legs and a suffusion of dark pigment may increase posteriorly (Fig. 6).

Character	Subadult female holotype (ULABG 4197)	Adult males from Wei-Assipu-tepui (*n*=2)	Adult females from Wei-Assipu-tepui (*n*=5)	Adult males from Maringma-tepui (*n*=6)	Adult females from Maringma-tepui (*n*=7)
SVL	15.4	17.8 ± 1.2 (16.6–18.9)	17.5 ± 0.8 (16.5–18.8)	17.9 ± 0.8 (16.5–19.0)	18.6 ± 0.8 (17.4–19.3)
HL	4.3	5.6 ± 0.3 (5.3–5.8)	5.6 ± 0.3 (5.3–6.2)	5.4 ± 0.3 (5.0–5.8)	5.8 ± 0.3 (5.2–6.0)
HW	5.1	6.4 ± 0.5 (5.9–6.8)	6.1 ± 0.2 (5.9–6.3)	6.3 ± 0.3 (5.9–6.7)	6.5 ± 0.3 (6.1–7.0)
SL	2.6	2.5 ± 0.2 (2.3–2.6)	2.5 ± 0.1 (2.3–2.6)	2.5 ± 0.2 (2.3–2.8)	2.6 ± 0.2 (2.3–2.8)
EN	1.2	1.5 ± 0.1 (1.4–1.5)	1.5 ± 0.1 (1.3–1.5)	1.5 ± 0.1 (1.3–1.6)	1.5 ± 0.1 (1.4–1.6)
IN	1.7	2.1 ± 0.2 (1.9–2.2)	2.0	2.0 ± 0.1 (1.9–2.1)	2.2 ± 0.1 (2.1–2.4)
EL	2.2	2.4 ± 0.1 (2.3–2.5)	2.5 ± 0.1 (2.4–2.6)	2.4 ± 0.1 (2.2–2.6)	2.5 ± 0.1 (2.3–2.6)
IO	2.0	2.0 ± 0.2 (1.8–2.2)	1.9 ± 0.1 (1.8–2.1)	2.0 ± 0.1 (1.8–2.1)	2.1 ± 0.1 (2.0–2.2)
TYM	-	0.8 ± 0.1 (0.7–0.8)	0.8 ± 0.1 (0.6–0.9)	0.9 ± 0.1 (0.8 –1.1)	0.9 ± 0.1 (0.8–1.2)
FAL	3.9	4.1	4.2 ± 0.2 (4.0–4.4)	4.2 ± 0.1 (4.1–4.4)	4.2 ± 0.3 (3.7–4.5)
HAND I	2.8	3.1 ± 0.2 (2.9–3.2)	3.1 ± 0.1 (3.0–3.4)	3.2 ± 0.2 (3.0–3.5)	3.2 ± 0.2 (2.9–3.4)
HAND II	3.2	3.5 ± 0.1 (3.4–3.5)	3.6 ± 0.1 (3.4–3.8)	3.6 ± 0.2 (3.4–3.9)	3.6 ± 0.2 (3.2–3.8)
HAND III	4.4	4.8 ± 0.1 (4.7–4.8)	4.9 ± 0.0 (4.9–5.0)	5.0 ± 0.1 (4.8–5.2)	5.0 ± 0.3 (4.4–5.3)
HAND IV	3.3	4.0 ± 0.1 (3.9–4.0)	3.8 ± 0.1 (3.6–3.9)	3.8 ± 0.2 (3.6–4.1)	3.9 ± 0.3 (3.5–4.3)
WFD	0.6	0.6 ± 0.1 (0.6–0.7)	0.7 ± 0.1 (0.6–0.8)	0.7 ± 0.1 (0.6–0.8)	0.7 ± 0.1 (0.5–0.9)
FL	7.0	8.1 ± 0.2 (7.9–8.3)	8.0 ± 0.1 (7.8–8.2)	8.2 ± 0.3 (7.9–8.7)	8.4 ± 0.4 (7.7–8.8)
WTD	0.5	0.8 ± 0.1 (0.7–0.8)	0.6 ± 0.1 (0.5–0.7)	0.7 ± 0.1 (0.6–0.8)	0.8 ± 0.0 (0.7–0.8)
TIL	8.3	9.4 ± 0.1 (9.3–9.4)	9.3 ± 0.1 (9.0–9.4)	9.2 ± 0.4 (8.6–9.8)	9.2 ± 0.4 (8.7–10.0)
AL	3.4	4.5 ± 0.1 (4.4–4.5)	4.1 ± 0.1 (4.0–4.3)	4.4 ± 0.3 (4.1–4.9)	4.5 ± 0.2 (4.1–4.8)

Table **1.** Measurements (in mm) of the holotype (ULABG 4197) of *Anomaloglossus roraimae* and new material from Maringma-tepui and Wei-Assipu-tepui, Guyana. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

Figure **2.** *Anomaloglossus roraima*, preserved subadult female holotype (ULABG 4197). **A:** Dorsal view. **B:** Ventral view. Scale bars are 5 mm. **C:** Left hand. **D:** Left foot. Scale bars are 2 mm. Photos by Philippe J.R. Kok.

Undersurfaces of forearms, hands, and feet dark brown. Undersurfaces of the chin, belly, and rear legs white (or pigmentless as in the holotype) with varying degrees of dark brown pigment suffused in increasing intensityposteriorward, often appearing in mottled patches (especially under the chin) and culminating in two males (IRSNB 15898, IRSNB 15864) with all ventral surfaces very dark brown (Fig. 6).

Tadpole description.- The following description–except oral disc–is based on an *Anomaloglossus roraima* tadpole in stage 28 (IRSNB 15903-e, Fig. 8 A) collected in the phytotelma of a *Brocchinia tatei* (Bromeliaceae) on Wei-Assipu-tepui. All values are in millimetres. See Table 2 for additional measurements and descriptive statistics for 14 meristic characters based on 19 tadpoles of stages 25–44.

Type 4 tadpole (Orton, 1953), exotrophic, arboreal Type 2 (Lannoo *et al*., 1987; Altig & Johnson, 1989). Total length 26.1; body length 10.2 (39% of total length); tail length 15.9

(61% of total length). Body ovoid and depressed; greatest body width 6.4, highest body height 4.2; snout bluntly rounded in dorsal and lateral views. Naris very small, circular, directed anterodorsally, opening 1.5 from tip of snout; distance from naris to anterior margin of eye 0.9; internarial distance 1.4, 26% of head width at level of eyes. Eyes dorsal and directed dorsolaterally; eye diameter 1.0; interorbital distance 2.6, 49% of head width at level of eyes. Spiracle sinistral, tube free, opening directed posterodorsally; tube length 0.9; tube transverse width 1.0; distance from tip of snout to spiracular opening 5.7, 56% of body length. Vent tube 0.8, dextrally attached to ventral fin, opening directed dextrally. Developing hind limb bud 0.4 in length, 0.3 in width. Caudal musculature robust, highest at mid-length between body and tail tip, deeper than fins, tapering to tail terminus, terminating slightly anterior to tail tip; tail muscle width at base of tail 2.0; tail muscle height at base of tail 2.5. Upper fin originates posterior to junction of body and tail (Fig. 8 A), mostly equal in height to lower fin; upper fin gradually increasing in height to slightly before tip; upper tail fin height 0.9, lower tail fin height 1.1, at midtail. Lateral-line system with an infraorbital branch originating near upper labium and terminating just behind the eye; a longitudinal branch originating near lower labium and meeting the angular branch; an angular branch originating below eye and terminating onto the ventral surface; a lateroventral branch originating near lower labium, in contact with the longitudinal branch and the angular branch at its extremities; a short middle body branch curving above spiracle, dropping posteroventrally and terminating before mid-body length.

Figure **3.** *Anomaloglossus roraima*, showing ventral views of hand and foot. **A:** Left hand (left) and left foot (right) of a male specimen (IRSNB 15888, 17.3 mm SVL). **B:** Left hand (left) and left foot (right) of a female specimen (IRSNB 15885, 17.4 mm SVL). Scale bars are 2 mm. Photos by Philippe J.R. Kok.

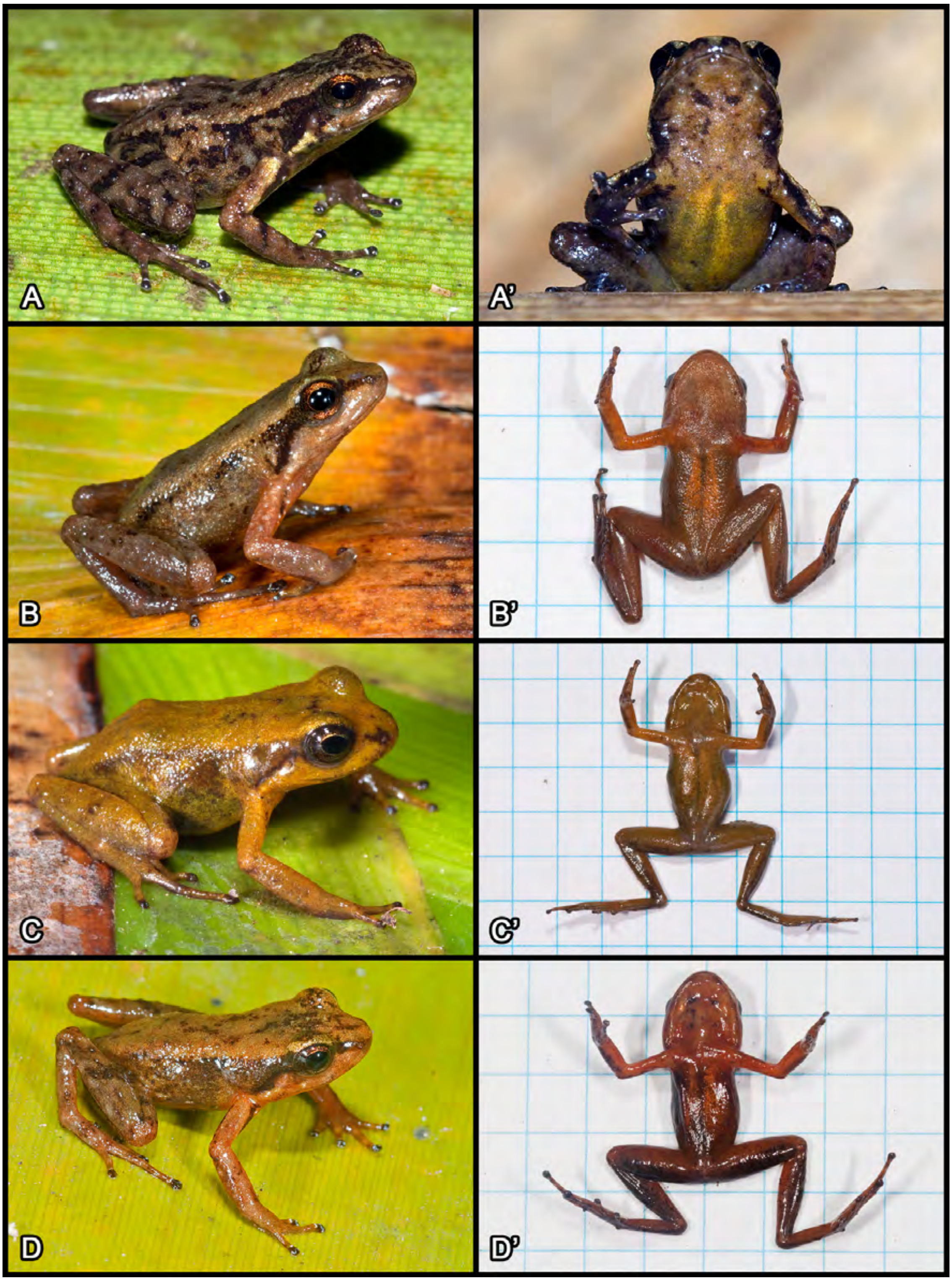

Figure **4.** *Anomaloglossus roraima*, showing inter- and intrapopulation variation in color in life. **A:** Dorsolateral view of CPI-10212 (sex and SVL unknown) from Mount Roraima. **A':** Ventral view of the same specimen. **B:** Dorsolateral view of IRSNB 15905, male 16.6 mm SVL from Wei-Assipu-tepui. **B':** Ventral view of the same specimen. **C:** Dorsolateral view of IRSNB 15865, male 18.9 mm SVL from Wei-Assipu-tepui. **C':** Ventral view of the same specimen. **D:** Dorsolateral view of IRSNB 15909, female 16.5 mm SVL from Wei-Assipu-tepui. **D':** Ventral view of the same specimen. Grid squares = 5 mm. Photos A-A' by D. Bruce Means, B-D' by Philippe J.R. Kok.

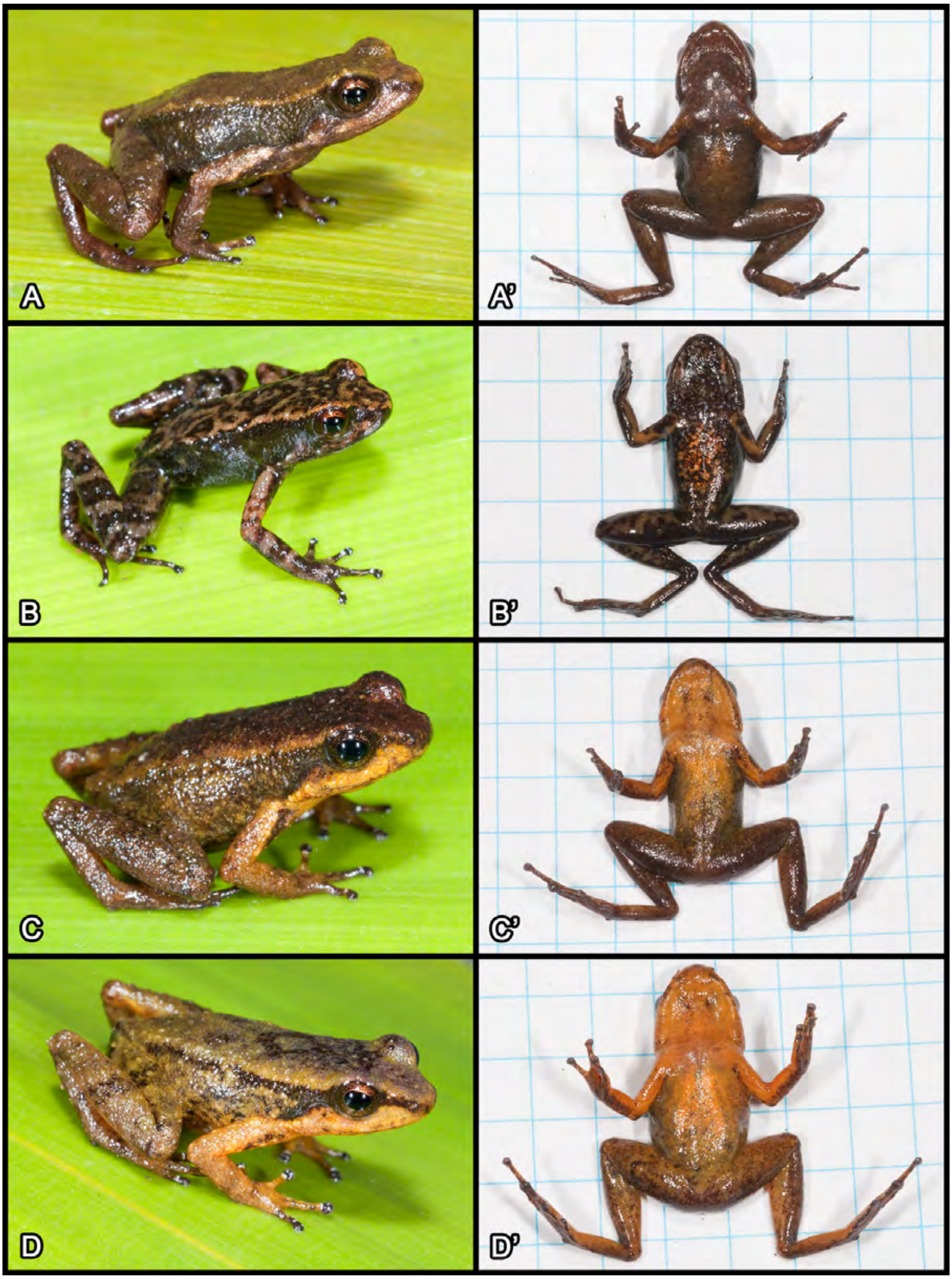

Figure **5.** *Anomaloglossus roraima*, showing intrapopulation variation in color in life. **A:** Dorsolateral view of IRSNB 15901, male 18.1 mm SVL from Maringma-tepui. **A':** Ventral view of the same specimen. **B:** Dorsolateral view of IRSNB 15864, male 16.5 mm SVL from Maringma-tepui. **B':** Ventral view of the same specimen. **C:** Dorsolateral view of IRSNB 15887, female 19.3 mm SVL from Maringma-tepui. **C':** Ventral view of the same specimen. **D:** Dorsolateral view of IRSNB 15883, female 18.9 mm SVL from Maringma-tepui. **D':** Ventral view of the same specimen. Grid squares = 5 mm. Photos by Philippe J.R. Kok.

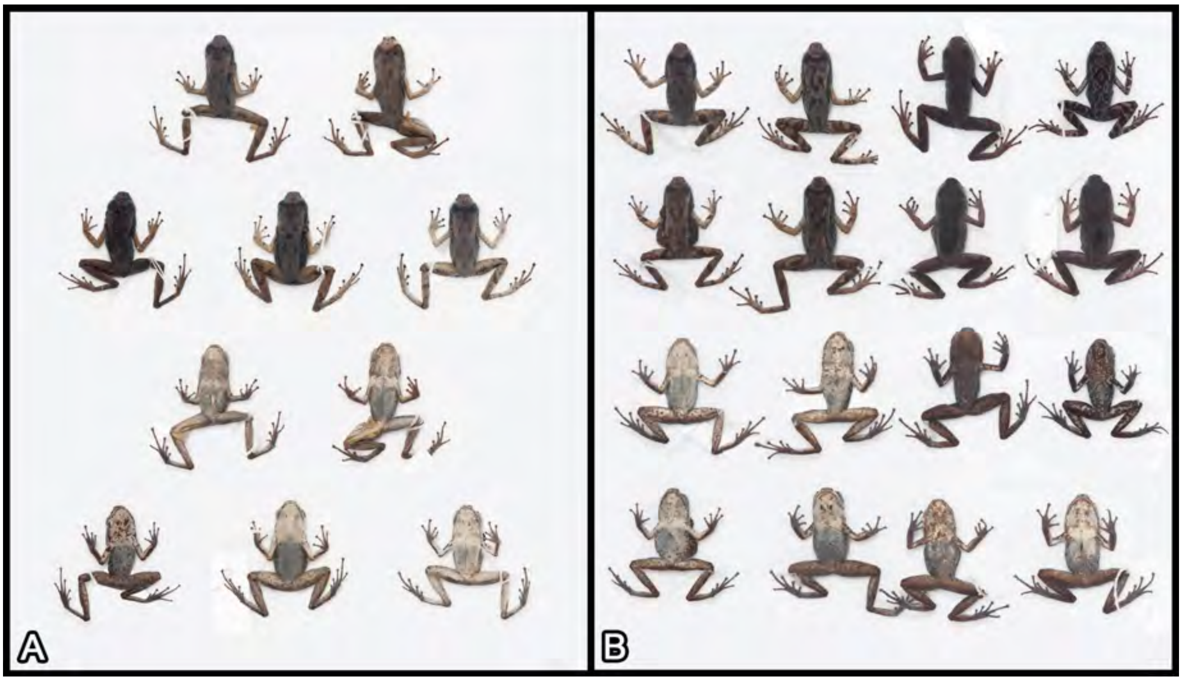

Figure **6.** *Anomaloglossus roraima*, showing inter- and intrapopulation variation in dorsal and ventral pattern in preservative. **A**: specimens from Wei-Assipu-tepui, first row, dorsal pattern in males, from left to right: IRSNB 15905, 18.9 mm SVL, IRSNB 15865, 16.6 mm SVL; second row, dorsal pattern in females, from left to right: IRSNB 15904, 17.1 mm SVL, IRSNB 15908, 19.2 mm SVL, IRSNB 15906, 17.2 mm SVL; third and fourth row, ventral patterns of the same specimens. **B**: specimens from Maringma-tepui, first row, dorsal pattern in males, from left to right: IRSNB 15888 17.3 mm SVL, IRSNB 15886, 18.4 mm SVL, IRSNB 15898, 19.0 mm SVL, IRSNB 15864, 16.5 mm SVL; second row, dorsal pattern in females, from left to right: IRSNB 15885, 17.4 mm SVL, IRSNB 15891, 19.1 mm SVL, IRSNB 15893, 18.6 mm SVL, IRSNB 15887, 19.3 mm SVL; third and fourth row, ventral patterns of the same specimens. Photos by Philippe J.R. Kok.

Oral disc description is based on a tadpole in stage 27 (IRSNB 15902-f, Fig. 8 B). Oral disc located anteroventrally, laterally emarginated; transverse width 2.9; border of disc surrounded with *ca.* 60 marginal papillae, *ca.* 16 on posterolateral margins of anterior labium, *ca.* 44 on entire posterior labium; gap in papillae on anterior labium *ca.* 0.4; all papillae small, tapered, blunt-tipped, subequal; a few submarginal papillae present on posterior labium, where papillae are mostly arranged in a weak double row; lower jaw sheath slightly V-shaped, slightly higher than upper jaw sheath; each side of upper sheath slightly curved, not sigmoid; both upper and lower sheaths serrated; medial serrations blunt-tipped, lateral ones pointed; serrations extend entire length of sheaths, but do not include lateral processes (Fig. 8 B). Labial tooth row formula 2(2)/3; labial teeth numerous, moderately long, strongly curved, bearing *ca.* 15–20 cusps; tooth row A-1 complete, slightly longer than A-2; tooth row A-2 interrupted medially; lower tooth rows complete, shorter than A-1; tooth row P-2 slightly longer than P-1 and P-3, which are subequal.

Color of tadpole in life.- Black with few scattered lighter flecks on sides; caudal musculature and fins with scattered light gray flecks (Fig. 7 B).

Color of tadpole in preservative.- Background color, including venter, dark brown. Caudal musculature brown with scattered light gray flecks, fins translucent with scattered dark brown flecks (Fig. 8 A).

Ontogenetic changes.- Changes in body size are summarized in Table 2. There is no remarkable ontogenetic change, the lateral-line system is well detectable in stages 25-40, with an infraorbital branch originating near upper labium and terminating below or just behind the eye; a longitudinal branch originating near lower labium and meeting the angular branch; an angular branch originating below eye and terminating onto the ventral surface; a lateroventral branch originating near lower labium, often in contact with the longitudinal branch and the angular branch; in one stage-40 specimen a short supraorbital branch originating near upper labium and terminating just before the nostril; a middle body branch curving above spiracle, dropping posteroventrally and usually terminating near the end of the body. Lateral line system less developed after stage 42, absent in one stage-44 specimen; only a short angular branch detectable in another stage-44 specimen. From stage 39 onward, larvae have marginal papillae on posterior labium arranged in a double row, while smaller tadpoles have a weakly doubled row of papillae, sometimes with a single row retained on lateral edges of posterior labium.

Comparison with other known Anomaloglossus *tadpoles occurring in the Eastern Pantepui District.*- The tadpole of *A. roraima* is immediately distinguished from all known *Anomaloglossus* tadpoles (except that of *A. beebei*, see Kok *et al.*, 2006b for comparison) in being arboreal and exotrophic (other known *Anomaloglossus* tadpoles are either lentic or lotic and exotrophic, or nidicolous and/or endotrophic). The tadpole of *A. beebei* (the only known species that also breeds exclusively in bromeliad phytotelmata) is pale yellow to golden and has a higher upper fin originating from tail-body junction (vs. black with a low upper fin originating posterior to junction of body and tail in *A. roraima*). Although most benthic *Anomaloglossus* tadpoles are roughly similar and sometimes difficult to distinguish, especially in preservative, the tadpoles of *A. kaiei* and *A. praderioi* (La Marca, 1998) are immediately distinguished from the tadpole of *A. roraima* by their smaller size at equal stage (range of total length in stage-27 tadpoles is 12.6–16.4 in *A. kaiei*, 17.5–22.4 in *A. praderioi vs.* 24.0–27.8 in *A. roraima*, see Kok *et al.*, 2006a and Kok, 2010 for comparison). The tadpole of *A. roraima* mainly differs from the tadpoles of *A. parkerae* (Meinhardt & Parmelee, 1996) and *A. tepuyensis* (La Marca, 1998) in having a lower upper fin originating posterior to junction of body and tail (*vs.* higher upper fin originating from tail-body junction, see illustrations in Duellman, 1997 and in Myers & Donnelly, 2008 for comparison).

Advertisement call.- The following description is based on two advertisement calls from two different males: IRSNB 15901 from Maringma-tepui (recorded on 29/11/2007 at 9h00) and an unvouchered specimen from Wei-Assipu-tepui (recorded on 19/11/2009 at 9h30), both individuals were calling at 17°C air temperature, in bromeliads. Measurements of acoustic parameters for each individual recorded are provided in Table 3. The data presented below are inferred from the calls of both individuals.

Temporal structure.- The advertisement call of *Anomaloglossus roraima* consists in a single note repeated at a rate of 8.5–17 calls/min. A weak amplitude modulation is present and is most visible in the male from Maringma-tepui. Mean call duration is 0.143s ± 0.027 (range: 0.113–0.201s). The inter-call interval is not uniform and has a mean of 4.391s ± 2.130 and a range of 2.689–13.659s (Fig. 9).

Spectral structure.- Five to six harmonics are developed with the dominant frequency located in the second harmonic (mean: 4229 Hz ± 130; range: 3939–4362 Hz), although this is not always obvious. Frequency modulation is not detectable (Fig. 9).

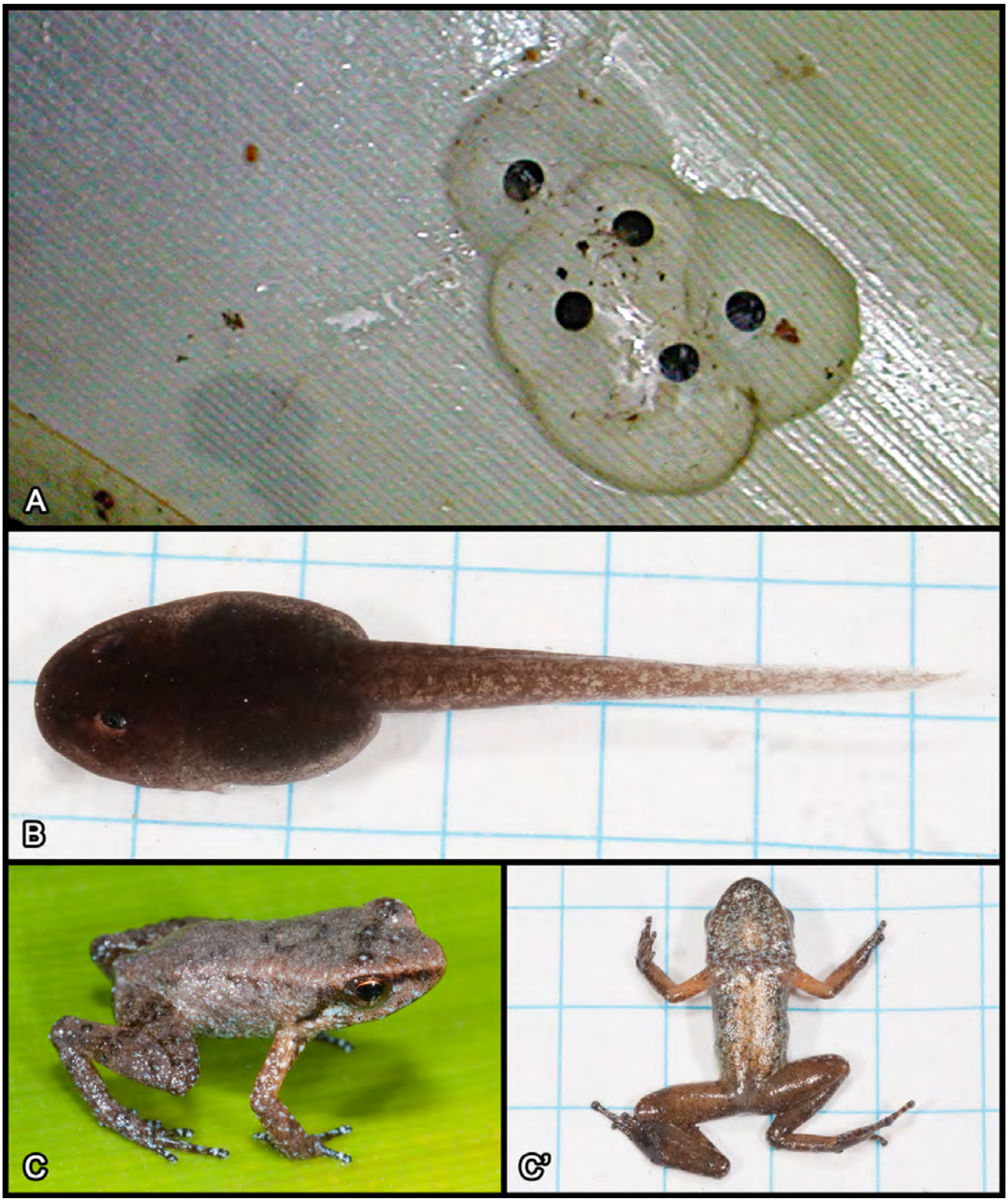

Figure **7.** Egg clutch, tadpole, and juvenile of *Anomaloglossus roraima* in life. **A:** Egg clutch deposited on a leaf of a terrestrial tank bromeliad *Brocchinia tatei*. **B:** IRSNB 15902-c, a stage-27 tadpole. **C:** Dorsolateral view of IRSNB 15884, 11.3 mm SVL, a juvenile of *A. roraima* collected on Maringma-tepui. **C':** Ventral view of the same specimen. Grid squares = 5 mm. Photo A by D. Bruce Means, B-C' by Philippe J.R. Kok.

Character	**Stage 25 (*n*=1)**	**Stage 26 (*n*=2)**	**Stage 27 (*n*=3)**	**Stage 28 (*n*=2)**	**Stage 38 (*n*=1)**	**Stage 39 (*n*=2)**	**Stage 40 (*n*=2)**	**Stage 41 (*n*=1)**	**Stage 42 (*n*=3)**	**Stage 44 (*n*=2)**
TL	18.9	25.1 ± 0.3 (24.8–25.3)	25.8 ± 1.6 (24.0–27.8)	27.8 ± 1.7 (26.1–29.5)	31.6	28.1 ± 1.4 (26.7–29.5)	30.4 ± 0.2 (30.2–30.6)	32.0	32.6 (*n*=1)	22.9 (*n*=1)
BL	7.0	9.6 ± 0.1 (9.5–9.7)	9.6 ± 0.6 (9.1–10.5)	10.0 ± 0.3 (9.7–10.2)	11.1	9.4 ± 0.1 (9.2–9.5)	9.9 ± 0.5 (9.4–10.3)	10.2	9.8 ± 1.0 (8.4–10.5)	10.1 ± 0.1 (10.0–10.2)
TAL	11.9	15.5 ± 0.2 (15.3–15.6)	16.2 ± 1.1 (14.8–17.3)	17.9 ± 2.0 (15.9–19.8)	20.5	18.8 ± 1.6 (17.2–20.3)	20.6 ± 0.3 (20.3–20.8)	21.8	22.1 (*n*=1)	12.7 (*n*=1)
BW	4.5	6.6 ± 0.2 (6.4–6.7)	6.2 ± 0.3 (5.9–6.7)	6.7 ± 0.3 (6.4–7.0)	7.2	7.1 ± 0.2 (6.9–7.3)	7.3 ± 0.0 (7.2–7.3)	7.0	5.2 ± 0.7 (4.4–6.1)	4.5 ± 0.3 (4.2–4.8)
BH	2.8	4.0 ± 0.5 (3.8–4.1)	3.7 ± 0.3 (3.3–3.9)	4.5 ± 0.3 (4.2–4.7)	4.7	4.6 ± 0.1 (4.4–4.7)	4.6 ± 0.2 (4.4–4.8)	4.8	4.4 ± 0.4 (3.9–5.0)	3.9 ± 0.2 (3.8–4.1)
HW	4.1	5.5	5.3 ± 0.2 (5.2–5.6)	5.6 ± 0.3 (5.3–5.8)	6.1	5.7 ± 0.1 (5.6–5.8)	5.6	5.5	5.0 ± 0.5 (4.4–5.6)	3.7 ± 0.2 (3.4–3.9)
TMH	1.4	2.7 ± 0.2 (2.5–2.8)	2.3 ± 0.4 (1.9–2.8)	2.3 ± 0.3 (2.5–2.8)	2.7	2.5	2.5	2.3	2.1 ± 0.2 (1.9–2.3)	1.5 ± 0.2 (1.4–1.7)
TMW	1.3	2.3	2.3 ± 0.2 (2.0–2.5)	2.2 ± 0.1 (2.0–2.3)	2.7	2.5 ± 0.2 (2.3–2.7)	2.7	2.5	2.4 ± 0.3 (2.0–2.7)	2.1 ± 0.2 (1.9–2.2)
MTH	2.7	3.8	3.6 ± 0.2 (3.3–3.9)	4.0 ± 0.2 (3.8–4.1)	4.4	4.0 ± 0.1 (3.9–4.1)	4.2 ± 0.0 (4.1–4.2)	3.9	3.5 ± 0.5 (3.0–4.1)	2.2 ± 0.5 (1.7–2.7)
END	0.6	0.8 ± 0.1 (0.7–0.8)	0.8 ± 0.0 (0.8–0.9)	0.9	1.1	1.0 ± 0.1 (0.9–1.1)	1.0 ± 0.2 (0.8–1.2)	0.8	1.2 ± 0.0 (1.1–1.2)	0.9 ± 0.2 (0.7–1.1)
NSD	0.8	0.9 ± 0.1 (0.8–0.9)	1.1	1.1 ± 0.0 (1.0–1.1)	1.5	1.2 ± 0.1 (1.1–1.3)	1.2 ± 0.2 (1.0–1.3)	1.1	1.0 ± 0.2 (0.8–1.3)	0.8 ± 0.1 (0.7–0.8)
IND	1.1	1.5 ± 0.1 (1.4–1.6)	1.4 ± 0.0 (1.3–1.4)	1.5 ± 0.1 (1.4–1.6)	1.8	1.6	1.7	1.6	1.4 ± 0.0 (1.4–1.5)	1.5 ± 0.1 (1.4–1.6)
IOD	1.6	2.1 ± 0.1 (2.0–2.1)	2.1 ± 0.1 (2.0–2.3)	2.5 ± 0.1 (2.3–2.6)	1.6	1.2 ± 0.1 (1.1–1.3)	1.5 ± 0.1 (1.4–1.6)	1.2	1.6 ± 0.2 (1.4–1.8)	1.5 ± 0.1 (1.4–1.6)
ED	0.7	1.0	1.0 ± 0.1 (0.8–1.1)	1.0	1.1	1.3 ± 0.1 (1.1–1.4)	1.3 ± 0.1 (1.2–1.4)	1.2	1.4 ± 0.0 (1.4–1.5)	1.4

Table **2.** Measurements (in mm) of tadpoles of *Anomaloglossus roraima*. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

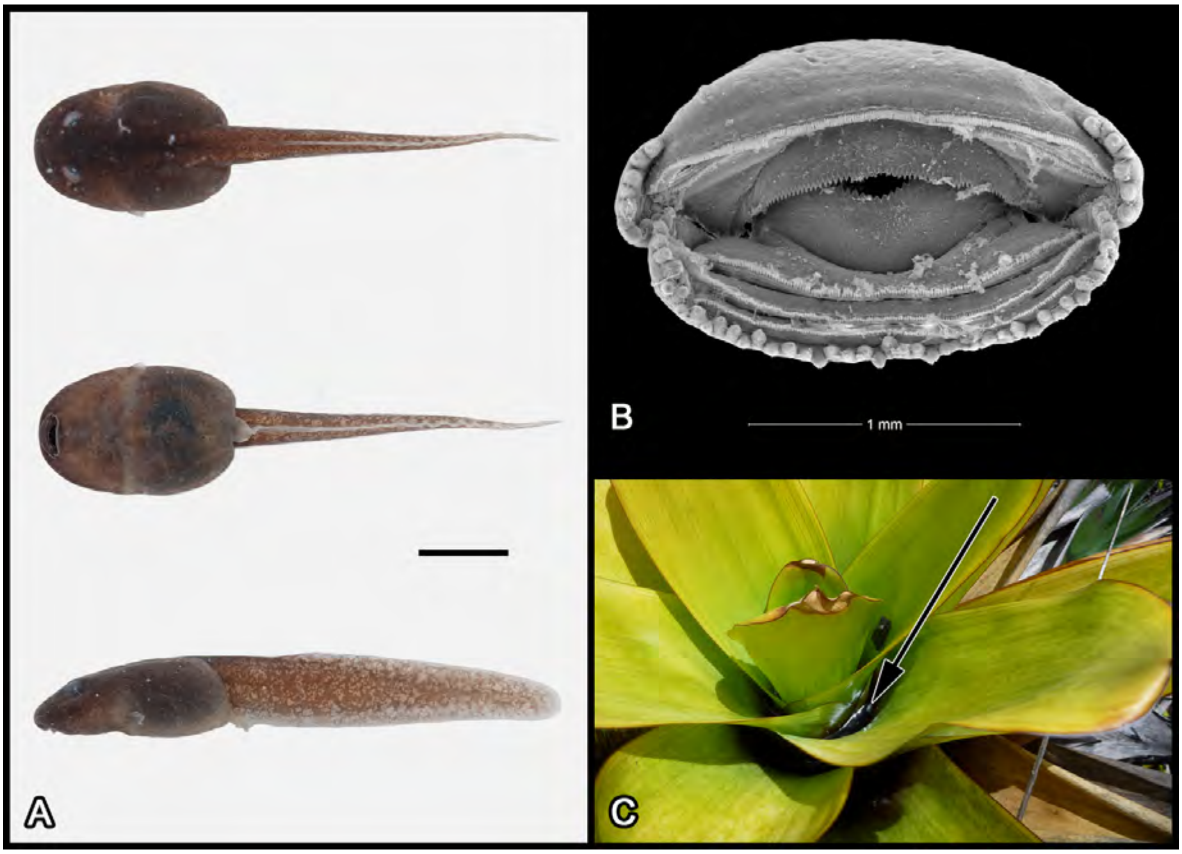

Figure **8.** Tadpole of *Anomaloglossus roraima* in preservative, and larvae microhabitat. **A:** Dorsal, ventral and lateral views of IRSNB 15903-e, a stage-28 tadpole. Scale bar is 5 mm. **B:** Photomicrograph of the oral disc of IRSNB 15902-f, a stage-27 tadpole (140x magnification). **C:** A terrestrial tank bromeliad *Brocchinia tatei* with black arrow showing tadpole microhabitat (the frog seen above the arrow is a *Tepuihyla* sp). Photos by Philippe J.R. Kok.

Individual	**Call rate (calls/min)**	**Note duration (s)**	**Inter-call interval (s)**	**Dominant frequency (Hz)**
IRSNB 15901, Maringma-tepui	8.5	0.186 ± 0.006 (0.178–0.201)	6.835 ± 2.465 (4.432–13.659)	4034 ± 81.098 (3939–4132)
Unvouchered specimen, Wei-Assipu-tepui	17	0.127 ± 0.004 (0.113–0.136)	3.560 ± 1.162 (2.689–10.665)	4299 ± 49.473 (4107–4362)

Table **3.** Measurements of acoustic parameters for two *Anomaloglossus roraima* males from two different tepui summits. Mean ± SD are followed by the range in parentheses. Temperature was 17°C at both sites.

Intraspecific (interpopulational) variation.- Some variation is present between the calls of the male from Maringma-tepui and the male from Wei-Assipu-tepui. Call duration in the Maringma male is slightly longer, dominant frequency lower, and inter-call interval longer (Table 3). Furthermore the amplitude in notes in the Maringma male's call is more obviously modulated (Fig. 10) and the first harmonic more difficult to detect. It should be noted that although air temperature was the same during both recordings, the hygrometry was much higher during the recording of the Maringma male (*ca.* 90% during a cloudy misty day) than during the recording of the Wei-Assipu male (*ca.* 30% during a dry sunny day). It is unknown whether the differences between the calls were related to the hygrometry level or whether they merely reflect intraspecific variation, but in any case they were not substantial.

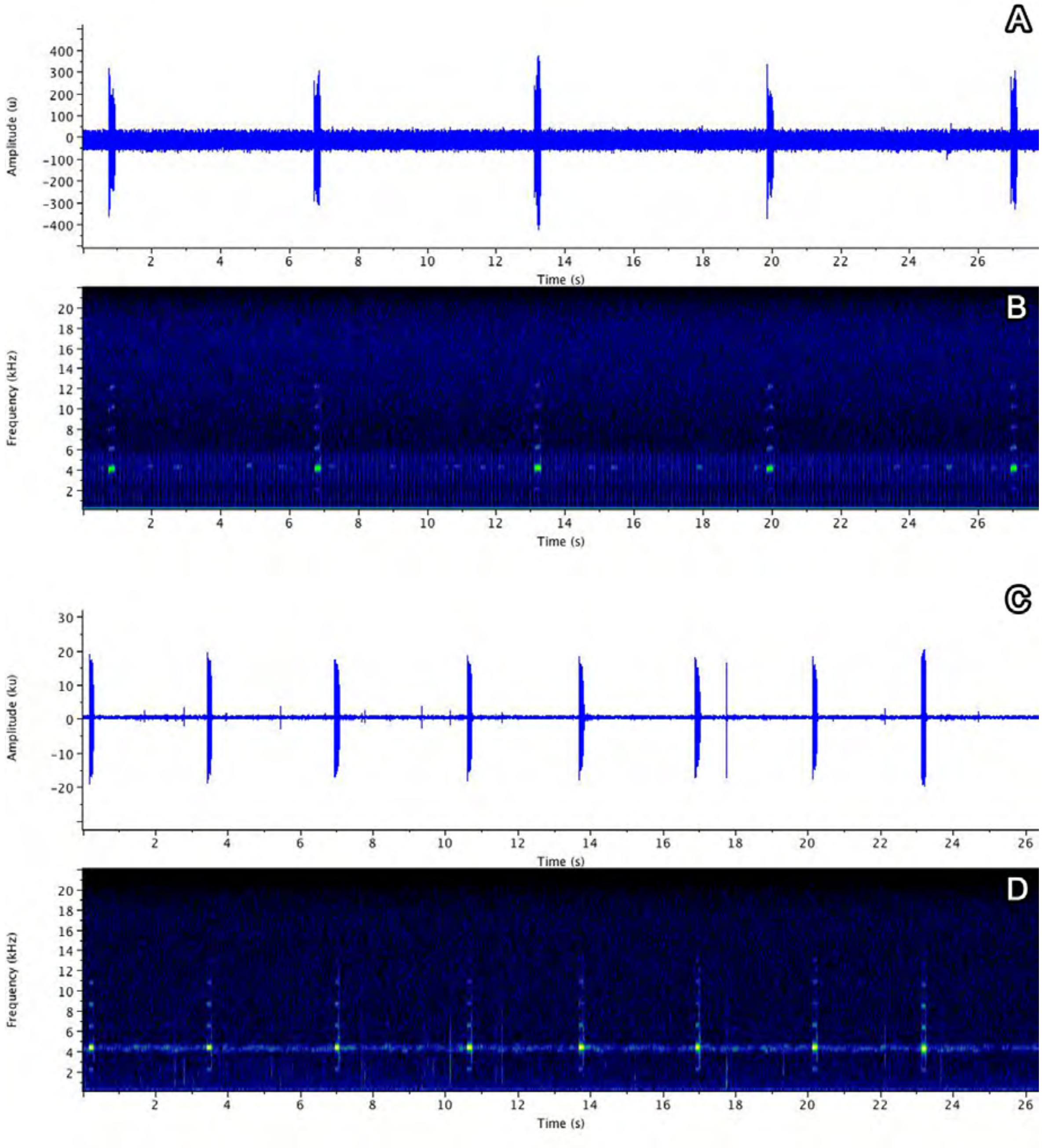

Figure **9.** Vocalization of *Anomaloglossus roraima*. **A:** Oscillogram. **B:** Spectrogram (recording of IRSNB 15901 from Maringma-tepui). **C:** Oscillogram. **D:** Spectrogram (recording of an unvouchered specimen from Wei-Assipu-tepui). Temperature was 17°C in both cases.

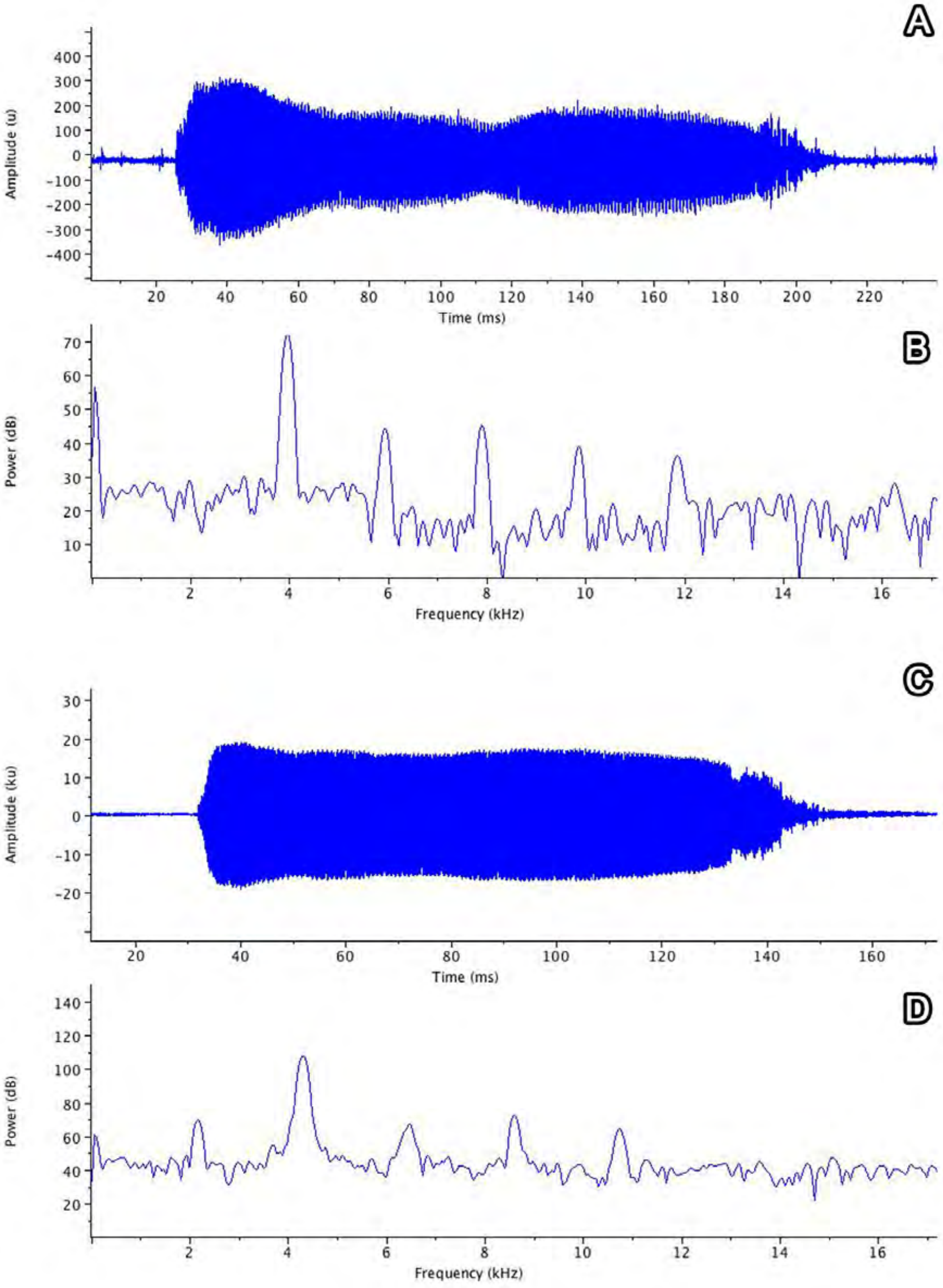

Figure **10.** Vocalization of *Anomaloglossus roraima*. **A-B:** Expanded oscillogram of the first note in Fig. 9 A-B showing slight amplitude modulation (A) and spectral slice of the same note showing poorly defined fundamental frequency at *ca.* 2 kHz (B). **C-D:** Expanded oscillogram of the first note in Fig. 9 C-D showing absence of significant amplitude modulation (C) and spectral slice of the same note showing a well detectable fundamental frequency at *ca.* 2 kHz (D). Temperature was 17°C in both cases.

Comparison with other Anomaloglossus *calls.*- Only three *cis*-Andean *Anomaloglossus* species for which calls are known produce a single note per call: *A. degranvillei* (Lescure, 1975), a riparian species that does not occur in the Pantepui region but in French Guiana and Suriname and likely in adjacent Brazil (Frost, 2013), and *A. praderioi*, which is sympatric with *A. roraima* on the upper slopes of Mount Roraima (Kok, 2010), and *A. surinamensis* Ouboter and Jairam, 2012, a riparian species that does not occur in the Pantepui region but in eastern Suriname. The call of *A. degranvillei* (see Lescure and Marty, 2001 for comparison) is the most similar to that of *A. roraima*, having a similar dominant frequency (4280–4640 vs. 3939–4362 in *A. roraima*) located in the second harmonic. It is however easily distinguished by the higher call rate (42 vs. 8.5–17 in *A. roraima*). In *A. praderioi* the call rate is much higher (61–76), the dominant frequency is slightly lower (3562–3856), and is located in the fundamental harmonic (vs. 3939–4362 with dominant frequency located in the second harmonic in *A. roraima*, even if this is not always obvious). Furthermore, in *A. praderioi* the dominant frequency is slightly modulated upwards, while there is no such frequency modulation detectable in *A. roraima*. Comparison with the call of *A. surinamensis* is made difficult by the brevity of the description, but in *A. surinamensis* (see Ouboter and Jairam, 2012 for comparison) the dominant frequency is reported to be 4550–4950Hz (vs. 3939–4362Hz in *A. roraima*) and the call rate faster than in *A. degranvillei* (therefore much faster than in *A. roraima*, see above).

Distribution and natural history.- *Anomaloglossus roraima* is currently known only from the upper slopes and summits of three tepuis in southeastern Venezuela and western Guyana: between 1860–2700 m elevation on the slopes of Mount Roraima (type locality, currently the westernmost known locality), between 2200–2300 m elevation on the summit of Wei-Assipu-tepui, and between 2000–2100 m elevation on the summit of Maringma-tepui (currently the easternmost known locality; Fig. 1). *Anomaloglossus roraima* seems restricted to tepui scrub and high-tepui meadow at elevations between 1860–2700 m and is probably restricted to the eastern part of the Eastern Pantepui District. It is expected to be discovered in suitable habitat between Mount Roraima and Maringma-tepui in Guyana (*e.g.* on Yakontipu-tepui and on Appokailang-tepui, both still unexplored herpetologically), and likely between Mount Roraima and Kukenan-tepui in Venezuela.

Anomaloglossus roraima breeds in the large terrestrial bromeliad *Brocchinia tatei* (Fig. 11). The species is locally common and was found sympatric with *A. praderioi* on the upper slopes of Mount Roraima only. All specimens were collected during the day, in large terrestrial tank bromeliads or on the ground close to these bromeliads, usually along rivulets and small puddles. A very small juvenile (IRSNB 15884, 11.3 mm SVL, Fig. 7 C-C’) was collected moving on the ground close to bromeliads, another one (lost) was found during patch sampling (5 x 5 m patch) among plant rootlets under the ground. Males emitted vocalizations the entire day, but significantly more males were calling during misty days. Courtship was not observed. Eggs are deposited in low number (*ca.* five) on the leaves of terrestrial tank bromeliads (Fig. 7A). No male was found carrying tadpoles on his back, and we hypothesize that reproduction in this species is similar to that in its sister species *Anomaloglossus beebei* (see Kok et *al.*, 2005, 2006b for details). We found up to 29 tadpoles in a same bromeliad phytotelma, which indicates that several clutches can be deposited in a same plant.

Figure **11.** Habitat of *Anomaloglossus roraima*. **A:** Patch of *Brocchinia tatei* on the upper northern slope of Mount Roraima, Guyana, at *ca.* 2300 m elevation. **B:** A large *Brocchinia tatei* on the upper northern slope of Mount Roraima, Guyana, at *ca.* 2300 m elevation. **C:** Numerous *Brocchinia tatei* between escarpments on the summit of Wei-Assipu-tepui, Guyana, at *ca.* 2150 m elevation. **D:** Thick vegetation including a *Brocchinia tatei* on the summit of Maringma-tepui, Guyana, at *ca.* 2100 m elevation. Photos A-B by D. Bruce Means, C-D by Philippe J.R. Kok.

In phytotelmata of *Brocchinia tatei* on Wei-Assipu-tepui and at the base of the ultimate cliffs of the "Prow" of Mount Roraima, we found abundant small (<15 cm), brown earthworms (Clitellata: Glossoscolescidae) and a small aquatic cricket, *Hydrolutos roraimae* (Orthoptera: Anostostomatidae) that may be a predator on frog eggs and tadpoles.

Phylogenetic relationships.- As highlighted by Grant *et al.* (2006) and Kok *et al.* (2012), *Anomaloglossus roraima* is sister to *A. beebei*. Both species are the only known *Anomaloglossus* that use bromeliad phytotelmata as habitat for their larvae. Kok *et al.* (2012, supplementary material) showed that the clade containing *A. beebei* and *A. roraima* (arboreal tadpoles with confirmed trophic egg-laying in *A. beebei*, highly hypothesized in *A. roraima*) is sister to a clade containing *A. kaiei*, *A. praderioi*, and a still undescribed taxon from Mount Wokomung (lentic tadpoles with confirmed trophic egg-laying in *A. kaiei*, potential in *A. praderioi* and the still unnamed taxon). The clade containing these species with arboreal/lentic tadpoles diverged from clades containing species mostly with lotic or endotrophic tadpoles.

Discussion. Comparison of our specimens with the holotype of *Anomaloglossus roraima* leaves no doubt about their belonging to the same species. Our additional specimens also agree well with the original species definition (La Marca, 1998) except in a few aspects that are mostly La Marca's misinterpretation of character states and inconsistencies in illustrations. Several important diagnostic characters were unknown by La Marca because his description is based on a single immature female. We hope that our detailed redescription will facilitate specimens' identification.

Like many other *Anomaloglossus* species, *A. roraima* displays an impressive intraspecific variation in color pattern. This phenotypic variability, coupled with the fact that the species occurs on different tepuis, could lead to inappropriate taxonomic decisions (*i.e.* describing populations from different tepuis as new), which has been done in the past with other Pantepui taxa (see Kok *et al.*, 2012). Genetic divergences between populations of *A. roraima* from different tepuis are surprisingly low (0–0.2% in 16S, less than 0.8% in ND1, see Kok *et al.*, 2012) and strongly advocate against the recognition of these populations as separate species, as also indicated by morphological and call analyses.

In their supplementary material, Santos *et al.* (2009) argued that the taxonomic division of Dendrobatidae into two families by Grant *et al.* (2006) [referred by Santos and colleagues to as Allobatidae (*lapsus calami* for Aromobatidae) and Dendrobatidae] is "*unnecessary and adds no new information*". They thus proposed to return Dendrobatidae to a single family. Apart from the fact that Santos *et al*. (2009) consistently use "Allobatidae" instead of Aromobatidae—which might arise questions about their proper reading of Grant *et al*. (2006)—their proposition is in contradiction with the topology of the phylogenetic trees these authors proposed which, as mentioned by Santos *et al.* (2009) themselves, is similar to the phylogenetic hypotheses of Grant *et al.* (2006). We disagree with Santos *et al*. (2009) and still consider Aromobatidae as a distinct family and refer the reader to Brown *et al*. (2011) for further discussion about the relevance and adequacy of the taxonomic corrections proposed by Santos *et al*. (2009).

Due to its restricted range (area of occupancy severely fragmented and estimated to be less than 2000 km^2, with species found at less than 10 locations) and continuing decline of habitat quality caused by (1) the many local fires affecting tepui slope vegetation ignited by Amerindians in Venezuela (see Tate, 1930; Means, 1995), (2) an increase of mostly unregulated tourism on Mount Roraima (Castillo, 2005), and (3) global warming (Nogué *et* *al*., 2009) we suggest that *Anomaloglossus roraima* be classified as “Vulnerable” (VU) in accordance with the criteria B2 a, b (iii) of IUCN (2001).

Resumen

La rana *Anomaloglossus roraima* fue originalmente descrito como *Colostethus roraima* por E. La Marca en 1998 con base a un único e inmaduro ejemplar hembra, recolectado a 2700 m de elevación sobre la parte alta del monte Roraima, un tepui (macizo montañoso) localizado en el sureste de Venezuela. Se ofrece una redescripción de la especie con base a nuevos ejemplares del Wei-Assipu-tepui y Maringma-tepui en Guyana. La redescripción incluye su vocalización y descripción de la larva. *Anomaloglossus roraima* es una especie de pequeño tamaño y se diferencia de otras especies dentro del genero por tener el dedo de la mano I < II con aristas pre-y postaxiales que son angostas y sin doblés; dedos del pie sin membrana (aunque una membrana rudimentaria esta algunas veces presente entre los dedos III y IV) y con aristas pre-y postaxiales que son angostas y sin doblés; tubérculos cloacales simétricos presentes; línea dorsolateral usualmente presente, con frecuencia inconspicua; línea ventrolateral ausente, línea lateral oblicua ausente; sin un obvio dicromatismo sexual en la garganta, pecho y en el diseño de la coloración ventral. La larva es grande, negra, exotrofica, arbórea, LTRF 2(2)/3. El canto de llamado reproductivo consiste de una única nota repetida a una tasa de 8.5–17 notas/minuto, con una frecuencia dominante que va de 4107 a 4362 Hz. La especie esta restringida a una pequeña área dentro de la Cadena de Tepuyes del Este, en el sureste de Venezuela y oeste de Guyana, donde esta habita principalmente sobre grandes bromelias en arbustales y vegetación rala altotepuyana, en elevaciones entre 1860–2700 m sobre el nivel del mar. El descubrimiento de esta especie en diferentes cimas de tepuyes y en sus laderas, la cual había sido previamente señalada como un habitante restringido a las tierras altas, es importante para el entendimiento de la biogeografía del la región del Pantepui.

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APPENDIX . ADDITIONAL SPECIMENS EXAMINED

Anomaloglossus beebei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 13721-26, 13728-53, ULABG 6817 (ex IRSNB 13727), IRSNB 13754 (tadpoles), IRSNB 13779-81 (tadpoles).

Anomaloglossus breweri.— Venezuela: *Estado Bolívar*: Aprada Tepui, Cueva del Fantasma, MHNLS 17044 (holotype), MHNLS 17045-46 (paratypes).

Anomaloglossus kaiei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 1938 (holotype), IRSNB 1939-64 (paratypes), IRSNB 14420-57, IRSNB 13755-78 (tadpoles), ROM 42999; Cuyuni-Mazaruni District, Wayalayeng, IRSNB 14922-24, Maringma Tepui, IRSNB 14925-31, Mount Wokomung, ROM 43321, ROM 43327, ROM 43330, ROM 43333.

Anomaloglossus murisipanensis.— Venezuela: *Estado Bolívar*: Murisipan-Tepui, MHNLS 11385 (holotype).

Anomaloglossus parkerae.— Venezuela: *Estado Bolívar*: Sierra de Lema, Salto El Danto, MHNLS 2901, MHNLS 11088-89.

Anomaloglossus praderioi.— Guyana: *Cuyuni-Mazaruni District*: Maringma Tepui, IRSNB 11403-13, IRSNB 14414-16 (tadpoles); Venezuela: *Estado Bolívar*: Mount Roraima ULABG 4196 (holotype), MHNLS 11272 (paratype), Sierra de Lema, EBRG 5569.

Anomaloglossus cf *praderioi*.— Guyana: *Cuyuni-Mazaruni District*: Mount Wokomung, ROM 43320, ROM 43322-26, ROM 43328-29, ROM 43331-32, ROM 43896, Mount Ayanganna ROM 39639.

Anomaloglossus roraima.— Guyana, *Cuyuni-Mazaruni District*: Wei-Assipu-tepui, IRSNB 15851, IRSNB 15865, IRSNB 15904-11, 15903 a-g (tadpoles), Maringma-tepui, IRSNB 15864, IRSNB 15883-901, 15902 a-m (tadpoles). Venezuela, *Estado Bolívar*: Mount Roraima, ULABG 4197 (holotype).

Anomaloglossus rufulus.— Venezuela: *Estado Bolívar*: Amuri-Tepui, Chimantá Massif, MHNLS 10361 (holotype).

Anomaloglossus tepuyensis.— Venezuela: *Estado Bolívar*, Auyantepui: ULABG 2557 (holotype), Cucurital River, MHNLS 14404-05, Purumay River, MHNLS 14924-25, MHNLS 14940-41, MHNLS 15687, Quebrada Atapere, MHNLS 15924, MHNLS 17359-60, MHNLS 17383, Quebrada Tucutupan, MHNLS 17401, Quebrada Rutapa, MHNLS 17361.

Anomaloglossus triunfo.— Venezuela: *Estado Bolívar*: Cerro Santa Rosa, Serranía del Supamo, EBRG 4756 (holotype), EBRG 4757-59 (paratypes).

10

LOW GENETIC DIVERSITY IN TEPUI SUMMIT VERTEBRATES

P. J. R. KOK, R. D. MACCULLOCH, D. B. MEANS, K. ROELANTS,
I. VAN BOCXLAER & F. BOSSUYT

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Photo courtesy of C. Brewer-Carías

MAIN TEXT

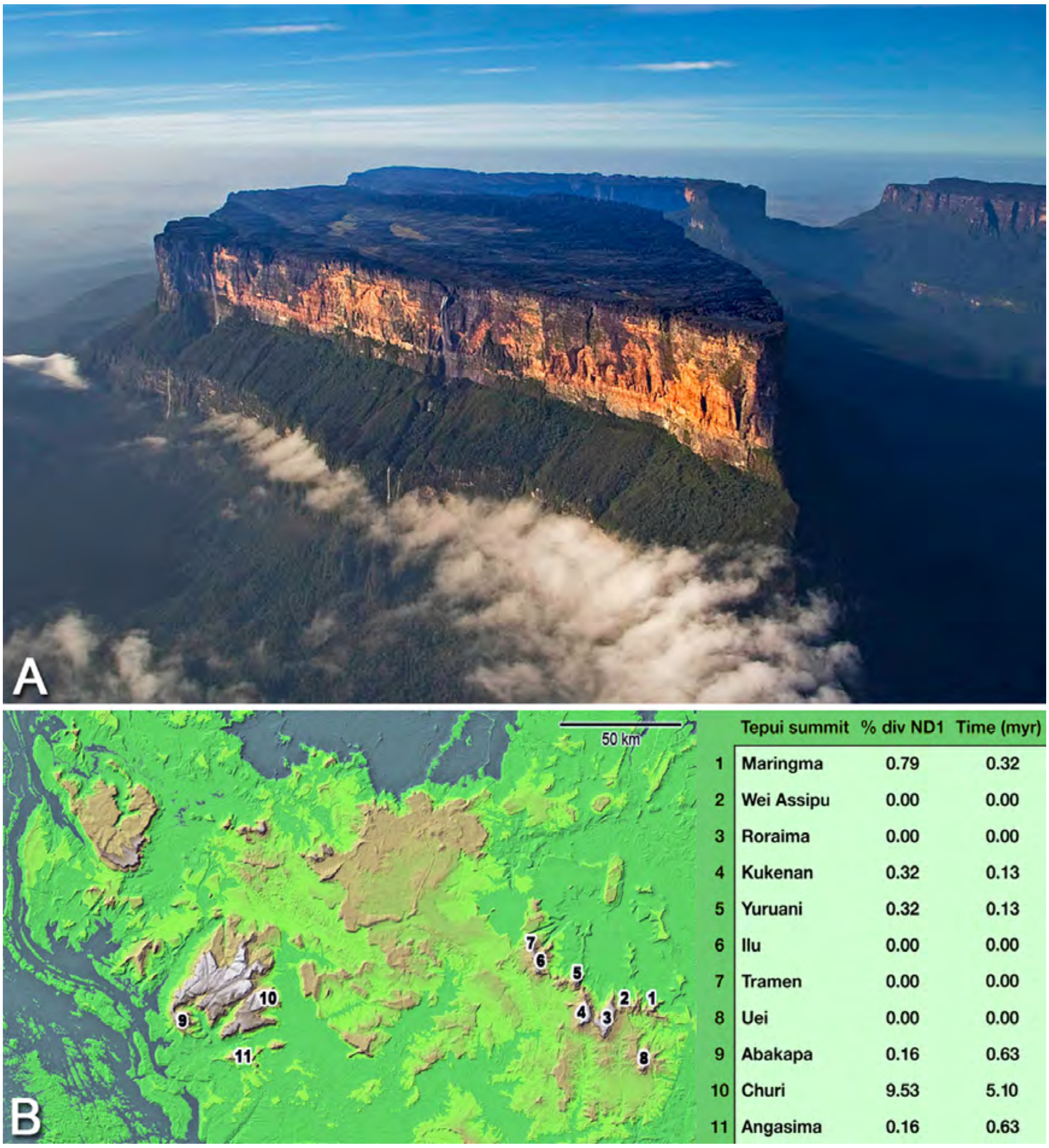
The Pantepui region of South America, located in southern Venezuela, northern Brazil, and western Guyana, is characterized by table mountains (tepuis) made of Proterozoic (> 1.5 billion years old) sandstone–the highest reaching nearly 3 km–that are isolated from their surroundings by up to 1000 m vertical cliffs (Fig. 1A). Tepuis are among the most inaccessible places on earth (Supplemental information), and the majority of their summits have been less visited than the moon. Due to its ancient age and topography [1, 2], this region has been assumed to be an ideal nursery of speciation and a potential inland counterpart to oceanic archipelagos [3, 4]. High endemism has been reported for the flora (25% in vascular plants) and fauna (68.5% in amphibians and reptiles) of single tepuis [5, 6], and an ancient origin has been postulated for some of these organisms. But, it has also been suggested that a few taxa living in habitats extending from lowlands to summits (e.g., savannah) invaded some of the more accessible tepuis only recently [6-8]. Taken at face value, the overall timing and extent of biotic interchange between tepui summits has remained unstudied. Here, we show that recent faunal interchange among currently isolated tepui summits has been extensive, and affected even taxa living in some of the most tepui-specific habitats and on the most inaccessible summits.

We used a comprehensive sampling of five Pantepui amphibian genera (*Anomaloglossus*, *Oreophrynella*, *Pristimantis*, *Stefania* and *Tepuihyla*) and one reptile family (Gymnophthalmidae)–the most conspicuous vertebrates on tepui summits–from 17 tepuis in the Eastern Pantepui region and surrounding uplands. If individual tepui summits were indeed reservoirs of ancient endemism, phylogenetic analyses of these taxa would identify genetically distinct populations on each tepui without close relatives elsewhere. Instead, analyses of two mitochondrial gene fragments evolving at different rates (16S rDNA and ND1 mtDNA; see Supplemental information) indicate that populations of a given species on individual summits are often closely related to those on other summits (e.g., *Oreophrynella*), or to those from the surrounding uplands (e.g., *Tepuihyla*). Uncorrected pairwise distances in both genes indicate unexpectedly low genetic divergence–as low as zero–among multiple tepui summit species or populations in five of the six groups (*Stefania* being the only exception), as well as among some summit species or populations and uplands populations described as distinct species (Fig. 1B, Supplemental information). Some of the lowest genetic distances are observed for populations that are currently recognized as distinct species and show striking phenotypic differences. For instance, the inconspicuously black ventral coloration in the toad *Oreophrynella nigra* (Yuruani-tepui and Kukenan-tepui) differs markedly from the potentially aposematic yellow–orange–black color contrasts in *O. quelchii* (Mt. Roraima and Wei Assipu-tepui), despite pairwise distances of 0.63–0.95% in ND1 and zero in 16S between both taxa.

The absence of genetic uniqueness suggests that the majority of these summit populations were only recently isolated. To provide an approximate estimate of the timing of their isolation, we used a nonlinear regression analysis that corrects for substitutional saturation and the systematic underestimation of evolutionary rates in recent divergences (Supplemental information). Our analyses suggest that 10 of the 11 most inaccessible tepuis studied show evidence for one or multiple instances of gene flow with other summits or with surrounding areas as recent as the late Pleistocene-Holocene (< 1.8 myr; Fig. 1B).

If the tepuis are indeed as ancient as often stated, the young age of extant summit fauna can only be explained by active dispersal among summits with subsequent extinction in the intervening uplands, e.g., during ice ages, or by passive dispersal, e.g., by birds or storms. The highly specific ecological niche preferences of some taxa restricted to tepui summits are likely to have limited active dispersal. Most *Oreophrynella* species for example exclusively occupy rocky habitats with extremely impoverished flora, which are absent in the intervening areas. Time estimates for the isolation of individual tepuis range from the Cretaceous [7, 8] to the Quaternary [2, 9]. The youngest estimates, although widely neglected in biological studies, could be compatible with the low genetic diversity and leave vicariance as a possible mechanism for speciation.

Regardless of the mechanism, our study shows that, even in small vertebrates restricted to summit-specific habitats, gene flow has been maintained until recently, making single-tepui endemism an exception rather than a rule. Nevertheless, as several of the taxa studied here (e.g., *Oreophrynella* and *Stefania*; Supplemental information) represent phylogenetically distinct lineages restricted to the Pantepui region, this area as a whole may still act as a reservoir of high-level endemism.



	Tepui summit	% div ND1	Time (myr)
1	Maringma	0.79	0.32
2	Wei Assipu	0.00	0.00
3	Roraima	0.00	0.00
4	Kukenan	0.32	0.13
5	Yuruani	0.32	0.13
6	Ilu	0.00	0.00
7	Tramen	0.00	0.00
8	Uei	0.00	0.00
9	Abakapa	0.16	0.63
10	Churi	9.53	5.10
11	Angasima	0.16	0.63

Figure **1. (A)** Mount Roraima, an emblematic tepui. **(B)** Map showing part of the Eastern Pantepui region, highlighting the highest and most isolated tepuis sampled in this study (numbered from 1 to 11), and table indicating estimates of divergence time among these tepuis, or between these tepuis and the surrounding uplands, based on genetic divergences in ND1 [see Supplemental Information for details].

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SUPPLEMENTAL INFORMATION

Supplemental Materials and Methods

Area of study and taxon sampling. Many tepui summit taxa are apparently rare, or at least difficult to collect, and many summit species are known only from very few specimens, often only the type series. Technical (most of these flat-topped mountains are only reachable by helicopter) and financial aspects have always seriously hindered extensive sampling for detailed and in-depth phylogenetic analyses of large datasets.

Over the past years, we managed to visit a total of 17 tepui summits/massifs and numerous uplands/lowlands localities in the Eastern Pantepui region and in other areas within the Guiana Shield, and obtained specimens and tissue samples of a considerable number of tepui taxa of almost all families represented on tepui tops. Some additional material was obtained from colleagues (see Acknowledgments). All specimens collected during our field surveys are housed in the collections of the Royal Belgian Institute of Natural Sciences, Belgium, the Royal Ontario Museum, Canada, and the National Museum of Natural History, USA. Tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel and in the Royal Ontario Museum. Additionally, we included useful sequences from GenBank in our phylogenetic analyses. A list of taxa and GenBank accession numbers is given in Supplemental Table 1.

Choice of markers. The mitochondrial 16S rDNA gene was first selected because it is reported as performing well for DNA barcoding in amphibians and to detect candidate species [S2, S3, S4, S5]. Because genetic divergences were surprisingly low among summit species/populations and among summit/uplands species/populations we also sequenced a faster protein-coding gene. Protein-coding genes are powerful markers for inferring evolutionary history in lower taxonomic categories such as families, genera and species [S6] and the subunit 1 of the NADH gene, shown to evolve at least 4 times faster than 16S, was therefore convenient for our purpose.

DNA extraction, PCR, sequencing and sequence alignment. Tissue samples (thigh muscle or liver) were taken in the field and stored in 95% ethanol. Total genomic DNA was extracted and purified using the Qiagen DNeasy® Tissue Kit following manufacturer's instructions. Fragments of the mitochondrial ribosomal gene 16S (*ca.* 550 bp) and of the protein-coding gene NADH subunit 1 (ND1, *ca.* 650-730 bp) were amplified and sequenced using the primers listed in Supplemental Table 2 under previously described PCR conditions [S7]. PCR products were checked on a 1% agarose gel and purified with the Qiagen PCR purification kit following manufacturer's instructions. PCR fragments were sequenced on both strands using the BigDye cycle sequencing kit (Applied Biosystems) on an ABI 3100 automated sequencer. Chromatograms were read using the Staden package [S8] and a consensus sequence was assembled from the forward and reverse primer sequences. ClustalX 2.0.11 [S9] was used to perform preliminary alignment using default parameters. Minor alignment corrections were made using MacClade 4.06 [S10] and the protein-coding gene ND1 was translated into amino-acid sequences to check for unexpected stop codons that would indicate the presence of pseudogenes. When present, ambiguous regions were excluded from subsequent analyses.

Phylogenetic Analyses. Uncorrected pairwise distances were estimated using PAUP* 4.0b10 [S11] (Supplemental Tables 3–10). For each of the six taxa studied, their closest known relatives according to previous phylogenetic studies were selected as outgroup taxa: *Rheobates* and *Dendrobates* for *Anomaloglossus* [S12], *Atelopus* for *Oreophrynella* [S7], *Eleutherodactylus* and *Stefania* for *Pristimantis* [S13], *Pristimantis* and *Gastrotheca* for *Stefania* [S14], *Osteocephalus* for *Tepuihyla* [S15], and *Ameiva* for the Gymnophthalmidae [S16]. Maximum Parsimony (MP) analyses of the concatenated 16S+ND1 dataset were performed in PAUP* as a heuristic search with TBR branch swapping and 1,000 random addition sequence replicates; bootstrap support was estimated with full heuristic search and 10,000 replicates. Maximum Likelihood (ML) analyses were conducted in PAUP* for the 16S+ND1 dataset under the model of nucleotide substitution selected by jModelTest 0.1.1 [S17]; bootstrap support was estimated with "fast" stepwise-addition and 500 replicates. Clade credibility was also estimated by Bayesian posterior probabilities (BPP) in MrBayes 3.2.1 [S18]. The Bayesian analyses implemented a mixed general time-reversible model (GTR + G + I) partitioned over the different gene fragments, flat Dirichlet priors for base frequencies and substitution rate matrices and uniform priors for among-site rate parameters. Two parallel Markov chain Monte Carlo (MCMC) runs of four incrementally heated (temperature parameter = 0.2) chains were performed, with a length of 6,000,000 generations, a sampling frequency of 1 per 1,000 generations, and a burn-in corresponding to the first 1,000,000 generations. Convergence of the parallel runs was confirmed by split frequency SDs (<0.01) and potential scale reduction factors (~1.0) for all model parameters, as reported by MrBayes. Adequate posterior sampling was verified using Tracer 1.4 [S19] if the runs had reached effective sampling sizes >200 for all model parameters. MrBayes trees are provided in Supplemental Figure 2.

Estimation of divergence times. Recent phylogenetic studies have indicated that some taxa endemic to the Pantepui region originated in the Tertiary [e.g. S7, S20, S21]. However, the dynamics of faunal interchange among tepui summits has never been studied with molecular data. Molecular clock estimation of recent divergence times poses certain problems that are not addressed by the dating methods implemented in any of the frequently used computer programs like R8s [S22], Multidivtime [S23], and BEAST [S24]. Mitochondrial gene fragments that are commonly used to estimate divergence ages for ancient nodes may fail to provide accurate age estimates for very recent divergences due to an apparent time-dependency of evolutionary rates [S25–S27]. Moreover, fast-evolving genes are likely to show substitutional saturation towards the past [S28], resulting in a nonlinear relationship between sequence divergence and the actual time since divergence. The likelihood models implemented in the commonly used molecular clock methods [S22–24] are supposed to partially correct for substitutional saturation (by being capable to detect more "hidden" homoplasy than e.g. the maximum parsimony method). However, in the absence of recent calibration points, these molecular clock methods may still lead to considerable overestimation of recent divergence times as a result of saturation [S29].

The lack of a linear correlation between sequence divergence and time since divergence can be corrected by using correction curves [e.g. S25]. We used a saturation curve to correct substitutional saturation in the NADH-subunit 1 (ND1) fragment. This curve is described by the following function:

$d(t) = D_{sat} \times (1 - e^{-t/T})$, where d is the uncorrected genetic distance between a pair of sequences, t is the divergence time between these sequences, D_{sat} is the sequence divergence at substitutional saturation (i.e. the maximum expected divergence between two DNA sequences), and T is the time required to reach a sequence divergence of $D_{sat} \times (1 - e^{-1}) = 63.2\%$ of D_{sat}. In other words, the shape of the saturation curve is determined by a parameter describing the expected sequence divergence at saturation (D_{sat}) and a parameter determining the rate at which the curve approaches saturation through time (T). This is analogous to saturation curves used in e.g. Michaelis-Menten enzyme kinetics. A saturation function allows us to obtain divergence time estimates for very recent nodes based on a fast-evolving gene by using divergence time estimates for older nodes that were based on slowly evolving genes. We proceeded through the following steps to obtain divergence times:

First, we plotted uncorrected pairwise distances for the ND1 gene fragment of 260 Hyloidea representatives (in this case bufonid taxa) against their divergence times inferred from relaxed clock analyses of two nuclear and nine mitochondrial genes in a previous study [S7]. The resulting scatter plot clearly indicates substitutional saturation in the ND1 gene, with genetic distances levelling out at approximately 20% divergence (Supplemental Figure 3).

Second, we used nonlinear regression based on the abovementioned function to estimate the best-fitting saturation curve through this scatter plot. This was done by searching the optimal values for D_{sat} and T using the Solver add-in in MS Excel (Microsoft, 2008). The best fitting saturation curve ($R^2 = 0.641$) corresponds to $D_{sat} = 19.67\%$ and $T = 7.732$ myr. Because the abovementioned time dependency of mitochondrial evolutionary rates may have also affected most recent divergence times in Van Bocxlaer *et al.* [S7] we additionally estimated a saturation curve on a scatter plot excluding all bufonid sequence divergences below 10%. Although this resulted in a reduced fit ($R^2 = 0.256$), the resulting curve was nearly identical to the original one, with $D_{sat} = 19.71\%$ and $T = 7.867$ myr.

Third, we used the obtained saturation curve and optimized parameters to convert uncorrected pairwise distances between two sequences from different tepui summits (we selected the highest and most isolated ones from which we have samples) and between a sequence from a tepui summit and the nearest sequence from upland into approximate divergence times. For each of the observed distances, the approximate divergence time using our saturation function corresponds to: $t = T \times -\ln[1-(d/D_{sat})]$.

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Next 5 pages: Supplemental Table **1.** List of taxa used in this study and GenBank accession numbers. Sequences newly generated are in **boldface**. * These taxa are swapped in the GenBank database.

Tissue sample n°	Museum n°	16S	ND1	Order	Genus	Species	Locality	Country	Coordinates	Elevation (m)
VUB3321	IRSNB15863	**JQ742236**	**JQ742403**	Amphibia	"*Hyla*"	*warreni*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3735	Uncatalogued	**JQ742102**	**JQ742283**	Amphibia	*Anomaloglossus*	"*verbeeksnyderorum*"	Tobogán de la Selva	Venezuela	N 5°23' W 67°34'	56
VUB3568	IRSNB15849	**JQ742125**	**JQ742302**	Amphibia	*Anomaloglossus*	aff. *degranvillei*	Kaw Mountain	French Guiana	N 4°32'41" W 52°09'09"	221
VUB3570	IRSNB15848	**JQ742126**	**JQ742303**	Amphibia	*Anomaloglossus*	*baeobatrachus*	Angoulême	French Guiana	N 5°24'38" W 53°39'23"	22
VUB3730	IRSNB13741	**JQ742107**	#####	Amphibia	*Anomaloglossus*	*beebei*	Kaieteur National Park	Guyana	N 5°10' W 59°29'	440
VUB3731	IRSNB13752	**JQ742108**	#####	Amphibia	*Anomaloglossus*	*beebei*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
VUB3732	ROM39635	**JQ742109**	**JQ742287**	Amphibia	*Anomaloglossus*	*beebei*	Mt Ayanganna	Guyana	N 5°24' W 59°57'	1490-1550
VUB3054	IRSNB14454	**JQ742110**	#####	Amphibia	*Anomaloglossus*	*kaiei*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
VUB3106	ROM43327	**JQ742116**	**JQ742293**	Amphibia	*Anomaloglossus*	*kaiei*	Wokomung Massif	Guyana	N 5°06'35" W 59°48'37"	700
VUB3107	ROM43333	**JQ742117**	**JQ742294**	Amphibia	*Anomaloglossus*	*kaiei*	Wokomung Massif	Guyana	N 5°06'35" W 59°48'37"	700
VUB3530	ROM44102	**JQ742123**	**JQ742300**	Amphibia	*Anomaloglossus*	*kaiei*	Meamu River	Guyana	N 6°16'21" W 60°29'59"	664
VUB3531	ROM44104	**JQ742124**	**JQ742301**	Amphibia	*Anomaloglossus*	*kaiei*	Meamu River	Guyana	N 6°11'44" W 60°28'48"	781
VUB3055	IRSNB1986	#####	**JQ742285**	Amphibia	*Anomaloglossus*	*megacephalus*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3056	IRSNB14410	#####	**JQ742286**	Amphibia	*Anomaloglossus*	*praderioi*	Maringma Tepui	Guyana	N 5°12'16" W 60°34'39"	1376
Genbank	CPI10198	DQ502255	#####	Amphibia	*Anomaloglossus*	*praderioi*	Roraima Tepui	Guyana	N 5°16'30" W 60°43'00"	1310
Genbank	CPI10208	DQ502256	#####	Amphibia	*Anomaloglossus*	*praderioi*	Roraima Tepui	Guyana	N 5°16'30" W 60°43'00"	1310
VUB3057	IRSNB15864	#####	**JQ742288**	Amphibia	*Anomaloglossus*	*roraima*	Maringma Tepui	Guyana	N 5°12'59" W 60°35'05"	2147
VUB3086	IRSNB15865	#####	**JQ742289**	Amphibia	*Anomaloglossus*	*roraima*	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
VUB3087	IRSNB15851	#####	**JQ742290**	Amphibia	*Anomaloglossus*	*roraima*	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
Genbank	CPI10216	DQ502258	#####	Amphibia	*Anomaloglossus*	*roraima*	Roraima Tepui	Guyana	N 5°15'30" W 60°43'30"	1860-2350
Genbank	CPI10217	DQ502259	#####	Amphibia	*Anomaloglossus*	*roraima*	Roraima Tepui	Guyana	N 5°15'30" W 60°43'30"	1860-2350
Genbank	Untagged tadpoles	DQ502260	#####	Amphibia	*Anomaloglossus*	*roraima*	Roraima Tepui	Guyana	N 5°15'30" W 60°43'30"	1860-2350
VUB3733	Uncatalogued	**JQ742101**	#####	Amphibia	*Anomaloglossus*	*rufulus*	Churi Tepui	Venezuela	N 5°16' W 62°00'	ca. 2325
GenBank	UTAA56469	DQ502249	#####	Amphibia	*Anomaloglossus*	sp "Brownsberg"	Brownsberg	Suriname	N 5°04' W 54°58'	80
GenBank	UTAA56710	DQ502254	#####	Amphibia	*Anomaloglossus*	sp "Tomasing"	Mt Tomasing	Guyana	N 5°44'22" W 60°17'51"	550
VUB3128	ROM43892	**JQ742119**	**JQ742296**	Amphibia	*Anomaloglossus*	sp A	Wokomung Massif	Guyana	N 5°06'35" W 59°48'37"	700
VUB3126	ROM43902	**JQ742118**	**JQ742295**	Amphibia	*Anomaloglossus*	sp A	Wokomung Massif	Guyana	N 5°05'33" W 59°50'35"	1411
VUB3092	ROM43320	#####	**JQ742291**	Amphibia	*Anomaloglossus*	sp B	Wokomung Massif	Guyana	N 5°07'46" W 59°49'16"	1234
VUB3093	ROM43323	**JQ742115**	**JQ742292**	Amphibia	*Anomaloglossus*	sp B	Wokomung Massif	Guyana	N 5°05'33" W 59°50'35"	1400
VUB3527	ROM44110	**JQ742122**	**JQ742299**	Amphibia	*Anomaloglossus*	sp C	Seroun River	Guyana	N 6°08'11" W 60°22'46"	695
VUB3525	ROM44112	**JQ742120**	**JQ742297**	Amphibia	*Anomaloglossus*	sp C	Merume Mountain	Guyana	N 5°56'03" W 60°09'24"	950
VUB3526	ROM44113	**JQ742121**	**JQ742298**	Amphibia	*Anomaloglossus*	sp C	Meamu River	Guyana	N 6°11'44" W 60°28'48"	781
GenBank	MJH3950	DQ502108	#####	Amphibia	*Anomaloglossus*	*stepheni*	Manaus	Brazil	S 2°57' W 59°55'	100
VUB3734	Uncatalogued	**JQ742104**	#####	Amphibia	*Anomaloglossus*	*tepuyensis*	Auyantepui	Venezuela	N 5°46' W 62°33'	ca. 2100
VUB3736	Uncatalogued	**JQ742103**	**JQ742284**	Amphibia	*Anomaloglossus*	*wothuja*	Cerro Sipapo	Venezuela	N 5°05' W 67°27'	150
VUB3737	IRSNB15781	**JQ742148**	**JQ742324**	Amphibia	*Atelopus*	aff. *hoogmoedi*	Iwokrama Forest	Guyana	N 4°19'60" W 58°48'00"	67
VUB3573	PK3306	**JQ742150**	#####	Amphibia	*Atelopus*	*franciscus*	Angoulême	French Guiana	N 5°24'38" W 53°39'23"	22
VUB3132	IRSNB14477	**JQ742149**	#####	Amphibia	*Atelopus*	*hoogmoedi*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
GenBank	TNHC64416	HQ290991	HQ290991	Amphibia	*Dendrobates*	*tinctorius*	Sipaliwini	Suriname	N 2°00' W 56°04'	300
VUB1624	Uncatalogued	FJ882750	FJ882750	Amphibia	*Eleutherodactylus*	*coqui*	El Verde	Puerto Rico	no data	350
VUB1036	Uncatalogued	FJ882745	FJ882745	Amphibia	*Eleutherodactylus*	*marnockii*	no data	USA	no data	no data
Genbank	JLG09	AY843592	#####	Amphibia	*Gastrotheca*	*fissipes*	Guarapari, ES	Brazil	N 20°39' W 40°30'	24

Tissue sample n°	Museum n°	16S	ND1	Order	Genus	Species	Locality	Country	Coordinates	Elevation (m)
VUB985	Uncatalogued	AY948744	AY948744	Amphibia	*Melanophryniscus*	*stelzneri*	no data (pet trade)	"South America"	no data	no data
VUB3372	IRSNB15870	**JQ742239**	**JQ742406**	Amphibia	*Myersiohyla*	*kanaima*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3532	ROM39651	**JQ742139**	**JQ742316**	Amphibia	*Oreophrynella*	*“dendronastes”*	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3533	ROM46402	**JQ742140**	**JQ742317**	Amphibia	*Oreophrynella*	*macconnelli*	Wokomung Massif	Guyana	N 5°06' W 59°51'	1400
VUB3065	IRSNB14364	**JQ742141**	#####	Amphibia	*Oreophrynella*	*macconnelli*	Roraima Tepui	Guyana	N 5°15'30" W 60°43'30"	1830
VUB3067	IRSNB14366	**JQ742142**	**JQ742318**	Amphibia	*Oreophrynella*	*macconnelli*	Mt Kopinang	Guyana	N 5°00'08" W 59°52'47"	1524
VUB3142	IRSNB14334	**JQ742143**	**JQ742319**	Amphibia	*Oreophrynella*	*macconnelli*	Maringma Tepui	Guyana	N 5°12'16" W 60°34'39"	1376
VUB3534	ROM46405	**JQ742144**	**JQ742320**	Amphibia	*Oreophrynella*	*macconnelli*	Wokomung Massif	Guyana	N 5°05' W 59°50'	1700
VUB3535	ROM46413	**JQ742145**	**JQ742321**	Amphibia	*Oreophrynella*	*macconnelli*	Wokomung Massif	Guyana	N 5°08' W 59°49'	1234
VUB3537	ROM46429	**JQ742147**	**JQ742323**	Amphibia	*Oreophrynella*	*macconnelli*	Merume Mountain	Guyana	N 5°56' W 60°09'	950
VUB3536	ROM46432	**JQ742146**	**JQ742322**	Amphibia	*Oreophrynella*	*macconnelli*	Wokomung Massif	Guyana	N 6°19' W 60°32'	700
VUB3635	CPI10594	**JQ742135**	**JQ742312**	Amphibia	*Oreophrynella*	*“nigra”*	Kukenan Tepui	Venezuela	N 5°13'28" W 60°49'43"	2600
VUB3068	IRSNB14389	**JQ742136**	**JQ742313**	Amphibia	*Oreophrynella*	*“nigra”*	Kukenan Tepui	Venezuela	N 5°13'28" W 60°49'43"	2600
VUB3698	IRSNB15704	**JQ742137**	**JQ742314**	Amphibia	*Oreophrynella*	*“nigra”*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3713	IRSNB15732	**JQ742138**	**JQ742315**	Amphibia	*Oreophrynella*	*“nigra”*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3061	IRSNB14347	**JQ742133**	**JQ742310**	Amphibia	*Oreophrynella*	*quelchii*	Roraima Tepui	Guyana	N 5°12'00" W 60°44'00"	2590
VUB3145	IRSNB15866	**JQ742134**	**JQ742311**	Amphibia	*Oreophrynella*	*quelchii*	Wei Assipu Tepui	Guyana	N 5°13'03" W 60°42'23"	2207
VUB3146	IRSNB1979	**JQ742132**	**JQ742309**	Amphibia	*Oreophrynella*	*seegobini*	Maringma Tepui	Guyana	N 5°12'59" W 60°35'05"	2088
VUB3058	IRSNB1980	**JQ742131**	**JQ742308**	Amphibia	*Oreophrynella*	*seegobini*	Maringma Tepui	Guyana	N 5°12'59" W 60°35'05"	2088
VUB3069	IRSNB14398	**JQ742130**	**JQ742307**	Amphibia	*Oreophrynella*	*vasquezi*	Ilu Tepui	Venezuela	N 5°24'20" W 61°00'23"	2680
VUB3738	IRSNB15760	**JQ742128**	**JQ742305**	Amphibia	*Oreophrynella*	*vasquezi*	Tramen Tepui	Venezuela	N 5°26'40" W 61°01'20"	2371
VUB3739	IRSNB15761	**JQ742129**	**JQ742306**	Amphibia	*Oreophrynella*	*vasquezi*	Tramen Tepui	Venezuela	N 5°26'40" W 61°01'20"	2371
VUB3740	Uncatalogued	**JQ742127**	**JQ742304**	Amphibia	*Oreophrynella*	*vasquezi*	Ilu Tepui	Venezuela	N 5°24' W 61°00'	ca. 2600
VUB3387	IRSNB14673	**JQ742235**	**JQ742402**	Amphibia	*“Osteocephalus”*	*exophthalmus*	Kaieteur National Park	Guyana	N 5°10' W 59°30'	430
VUB3380	IRSNB14656	**JQ742237**	**JQ742404**	Amphibia	*Osteocephalus*	*leprieurii*	Kaieteur National Park	Guyana	N 5°10' W 59°30'	430
VUB3382	IRSNB14657	**JQ742238**	**JQ742405**	Amphibia	*Osteocephalus*	*oophagus*	Kaieteur National Park	Guyana	N 5°08' W 59°25'	540
VUB3674	IRSNB15634	**JQ742165**	#####	Amphibia	*Pristimantis*	aff. *pulvinatus*	La Escalera	Venezuela	N 5°54'57" W 61°26'05"	1416
VUB3751	IRSNB15786	**JQ742164**	**JQ742338**	Amphibia	*Pristimantis*	aff. *pulvinatus*	Iwokrama Forest	Guyana	N 4°20'11" W 58°46'54"	950
VUB3485	IRSNB14471	**JQ742166**	#####	Amphibia	*Pristimantis*	aff. *pulvinatus*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
VUB3491	IRSNB12862	**JQ742167**	**JQ742339**	Amphibia	*Pristimantis*	aff. *pulvinatus*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3741	IRSNB15643	**JQ742151**	**JQ742325**	Amphibia	*Pristimantis*	*aureoventris*	Roraima Tepui	Guyana	N 5°15' W 60°43'	2305
VUB3742	IRSNB15820	**JQ742153**	**JQ742327**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'04" W 60°42'21"	2196
VUB3743	IRSNB15821	**JQ742158**	**JQ742332**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'03" W 60°42'21"	2219
VUB3744	IRSNB15824	**JQ742155**	**JQ742329**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'04" W 60°42'21"	2196
VUB3745	IRSNB15825	**JQ742156**	**JQ742330**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'04" W 60°42'21"	2196
VUB3746	IRSNB4152	**JQ742157**	**JQ742331**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'15"	2210
VUB3499	IRSNB4153	**JQ742159**	**JQ742333**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'15"	2210
VUB3747	IRSNB4154	**JQ742154**	**JQ742328**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'04" W 60°42'21"	2196
VUB3748	Uncatalogued (egg)	**JQ742152**	**JQ742326**	Amphibia	*Pristimantis*	*aureoventris*	Wei Assipu Tepui	Guyana	N 5°13'04" W 60°42'21"	2196
VUB3626	Uncatalogued	**JQ742170**	**JQ742342**	Amphibia	*Pristimantis*	cf. *marmoratus*	Cacao Mountain	French Guiana	N 4°33'42" W 52°27'09"	107
VUB3493	IRSNB15867	**JQ742169**	**JQ742341**	Amphibia	*Pristimantis*	*jester*	Maringma Tepui	Guyana	N 5°12'16" W 60°34'39"	1376
GenBank	KU181015	EU186723	#####	Amphibia	*Pristimantis*	*pulvinatus*	La Escalera	Venezuela	N 5°59' W 61°24'	1250
VUB3490	IRSNB12859	**JQ742168**	**JQ742340**	Amphibia	*Pristimantis*	*saltissimus*	Maringma Tepui	Guyana	N 5°12'38" W 60°33'60"	1060

Tissue sample n°	Museum n°	16S	ND1	Order	Genus	Species	Locality	Country	Coordinates	Elevation (m)
VUB3749	IRSNB15868	**JQ742162**	**JQ742336**	Amphibia	*Pristimantis*	sp "Abakapa"	Abakapa Tepui	Venezuela	N 5°11'21" W 62°17'40"	2160
VUB3750	IRSNB15869	**JQ742163**	**JQ742337**	Amphibia	*Pristimantis*	sp "Angasima"	Angasima Tepui	Venezuela	N 5°02'35" W 62°04'51"	2121
GenBank	SBH268110	EU186721	#####	Amphibia	*Pristimantis*	sp "Aprada"	Aprada Tepui	Venezuela	N 5°24' W 62°26'	2540
VUB3717	IRSNB15640	**JQ742160**	**JQ742334**	Amphibia	*Pristimantis*	*yuruaniensis*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3720	IRSNB15641	**JQ742161**	**JQ742335**	Amphibia	*Pristimantis*	*yuruaniensis*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3624	IRSNB15850	**JQ742171**	#####	Amphibia	*Pristimantis*	*zeuctotylus*	Cacao Mountain	French Guiana	N 4°33'42" W 52°27'09"	107
GenBank	TNHCFS4955	HQ290967	HQ290967	Amphibia	*Rheobates*	*palmatus*	Boyaca	Colombia	N 5°38'16" W 73°32'08"	2118
VUB3538	ROM39475	**JQ742208**	**JQ742376**	Amphibia	*Stefania*	"*ackawaio*"	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3539	ROM42811	**JQ742209**	**JQ742377**	Amphibia	*Stefania*	"*ackawaio*"	Wokomung Massif	Guyana	N 5°08' W 59°49'	1234
VUB3558	ROM39470	**JQ742190**	**JQ742361**	Amphibia	*Stefania*	"*scalae*"	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1550
VUB3299	PK1846	**JQ742194**	**JQ742365**	Amphibia	*Stefania*	aff. *evansi*	Wayalayeng	Guyana	N 5°14'11" W 60°31'04"	678
VUB3555	ROM44254	**JQ742195**	**JQ742366**	Amphibia	*Stefania*	aff. *evansi*	Kurupung River	Guyana	N 6°02' W 60°16'	614
VUB3557	ROM44264	#####	**JQ742367**	Amphibia	*Stefania*	aff. *evansi*	Merume Mountain	Guyana	N 5°56' W 60°09'	950
VUB3302	IRSNB15871	**JQ742199**	**JQ742371**	Amphibia	*Stefania*	aff. *evansi*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3540	ROM39640	**JQ742210**	**JQ742378**	Amphibia	*Stefania*	*ayangannae*	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3542	ROM42906	**JQ742212**	**JQ742380**	Amphibia	*Stefania*	*ayangannae*	Wokomung Massif	Guyana	N 5°06' W 59°51'	1400
VUB3541	ROM42925	**JQ742211**	**JQ742379**	Amphibia	*Stefania*	*ayangannae*	Wokomung Massif	Guyana	N 5°05' W 59°50'	1700
VUB3543	ROM39478	**JQ742179**	**JQ742350**	Amphibia	*Stefania*	*coxi*	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3544	ROM42856	**JQ742180**	**JQ742351**	Amphibia	*Stefania*	*coxi*	Wokomung Massif	Guyana	N 5°05' W 59°50'	1700
VUB3277	IRSNB14588	**JQ742192**	**JQ742363**	Amphibia	*Stefania*	*evansi*	Kaieteur National Park	Guyana	N 5°10' W 59°29'	440
VUB3294	IRSNB14595	**JQ742193**	**JQ742364**	Amphibia	*Stefania*	*evansi*	Kaieteur National Park	Guyana	N 5°08' W 59°25'	530
VUB3551	ROM39450	**JQ742196**	**JQ742368**	Amphibia	*Stefania*	*evansi*	Mt Ayanganna	Guyana	N 5°25' W 59°58'	870
VUB3553	ROM42862	**JQ742198**	**JQ742370**	Amphibia	*Stefania*	*evansi*	Mt Ayanganna	Guyana	N 5°18' W 59°50'	676
VUB3552	ROM42882	**JQ742197**	**JQ742369**	Amphibia	*Stefania*	*evansi*	Wokomung Massif	Guyana	N 5°07' W 59°49'	700
VUB3752	PK3566	**JQ742173**	**JQ742344**	Amphibia	*Stefania*	*ginesi*	Abakapa Tepui	Venezuela	N 5°11'23" W 62°17'52"	2137
VUB3753	PK3580	**JQ742174**	**JQ742345**	Amphibia	*Stefania*	*ginesi*	Abakapa Tepui	Venezuela	N 5°11'07" W 62°17'21"	2209
VUB3754	Uncatalogued	**JQ742172**	**JQ742343**	Amphibia	*Stefania*	*riae*	Sarisarinama Tepui	Venezuela	N 4°41' W 64°13'	ca. 1100
VUB3697	IRSNB15703	**JQ742177**	**JQ742348**	Amphibia	*Stefania*	*riveroi*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3705	IRSNB15716	**JQ742178**	**JQ742349**	Amphibia	*Stefania*	*riveroi*	Yuruani Tepui	Venezuela	N 5°18'50" W 60°51'50"	2303
VUB3545	ROM39469	**JQ742213**	**JQ742381**	Amphibia	*Stefania*	*roraimae*	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3546	ROM42843	**JQ742214**	**JQ742276**	Amphibia	*Stefania*	*roraimae*	Wokomung Massif	Guyana	N 5°08' W 59°49'	1234
VUB3309	IRSNB15872	**JQ742203**	**JQ742372**	Amphibia	*Stefania*	*roraimae*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3310	IRSNB15873	**JQ742204**	**JQ742373**	Amphibia	*Stefania*	*roraimae*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3311	IRSNB15874	**JQ742205**	**JQ742374**	Amphibia	*Stefania*	*roraimae*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3312	IRSNB15875	**JQ742206**	**JQ742375**	Amphibia	*Stefania*	*roraimae*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3315	IRSNB15876	**JQ742207**	**JQ742275**	Amphibia	*Stefania*	*roraimae*	Maringma Tepui	Guyana	N 5°12'15" W 60°34'38"	1376
VUB3549	ROM44271	**JQ742202**	**JQ742274**	Amphibia	*Stefania*	*roraimae*	Seroun River	Guyana	N 6°08' W 60°23'	700
VUB3633	ROM44277	**JQ742200**	**JQ742272**	Amphibia	*Stefania*	*roraimae*	Partang	Guyana	N 5°49'07" W 60°13'26"	728
VUB3548	ROM44279	**JQ742201**	**JQ742273**	Amphibia	*Stefania*	*roraimae*	Apakai River	Guyana	N 5°54' W 60°07'	984
VUB3755	IRSNB15839	**JQ742175**	**JQ742346**	Amphibia	*Stefania*	*satelles*	Angasima Tepui	Venezuela	N 5°02'36" W 62°04'51"	2122
VUB3756	IRSNB15844	**JQ742176**	**JQ742347**	Amphibia	*Stefania*	*satelles*	Angasima Tepui	Venezuela	N 5°02'36" W 62°04'51"	2122
VUB3280	PK2060V	**JQ742191**	**JQ742362**	Amphibia	*Stefania*	*scalae*	El Danto	Venezuela	N 5°57'52" W 61°23'31"	1208
Genbank	MNHN2002.692	AY843768	#####	Amphibia	*Stefania*	*schuberti*	Auyantepui	Venezuela	N 5°46' W 62°33'	2325

Tissue sample n°	Museum n°	16S	ND1	Order	Genus	Species	Locality	Country	Coordinates	Elevation (m)
VUB3266	IRSNB15853	**JQ742181**	**JQ742352**	Amphibia	*Stefania*	sp "Wei-Assipu"	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
VUB3269	IRSNB15854	**JQ742182**	**JQ742353**	Amphibia	*Stefania*	sp "Wei-Assipu"	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
VUB3274	IRSNB15855	**JQ742183**	**JQ742354**	Amphibia	*Stefania*	sp "Wei-Assipu"	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
VUB3282	IRSNB13799	**JQ742185**	**JQ742356**	Amphibia	*Stefania*	*woodleyi*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
VUB3307	IRSNB15877	**JQ742186**	**JQ742357**	Amphibia	*Stefania*	*woodleyi*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3308	IRSNB15878	**JQ742187**	**JQ742358**	Amphibia	*Stefania*	*woodleyi*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3550	ROM20570	**JQ742189**	**JQ742360**	Amphibia	*Stefania*	*woodleyi*	Tukeit, KNP	Guyana	N 5°12' W 59°27'	205
VUB3547	ROM39465	**JQ742188**	**JQ742359**	Amphibia	*Stefania*	*woodleyi*	Mt Ayanganna	Guyana	N 5°25' W 59°58'	870
VUB3757	ROM42833	**JQ742184**	**JQ742355**	Amphibia	*Stefania*	*woodleyi*	Wokomung Massif	Guyana	N 5°07' W 59°49'	700
VUB3401	IRSNB15856	**JQ742218**	**JQ742385**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°12'58" W 60°42'16"	2216
VUB3402	IRSNB15857	**JQ742219**	**JQ742386**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'23"	2244
VUB3403	IRSNB15858	**JQ742220**	**JQ742387**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'23"	2244
VUB3405	IRSNB15859	**JQ742221**	**JQ742388**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'23"	2244
VUB3406	IRSNB15860	**JQ742222**	**JQ742389**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'23"	2244
VUB3407	IRSNB15861	**JQ742223**	**JQ742390**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°12'52" W 60°42'13"	2184
VUB3408	IRSNB15862	**JQ742224**	**JQ742391**	Amphibia	*Tepuihyla*	"*galani*"	Wei Assipu Tepui	Guyana	N 5°13'05" W 60°42'23"	2244
VUB3761	IRSNB15765	**JQ742215**	**JQ742382**	Amphibia	*Tepuihyla*	"*galani*"	Uei Tepui	Venezuela	N 5°01' 01" W 60°36'59"	2065
VUB3762	IRSNB15769	**JQ742216**	**JQ742383**	Amphibia	*Tepuihyla*	"*galani*"	Uei Tepui	Venezuela	N 5°01' 01" W 60°36'59"	2065
VUB3763	IRSNB15770	**JQ742217**	**JQ742384**	Amphibia	*Tepuihyla*	"*galani*"	Uei Tepui	Venezuela	N 5°01' 01" W 60°36'59"	2065
VUB3695	IRSNB15701	**JQ742225**	**JQ742392**	Amphibia	*Tepuihyla*	"*galani*"	Guadacapiapu Tepui	Venezuela	N 5°17'24" W 60°55'06"	1242
VUB3696	IRSNB15702	**JQ742226**	**JQ742393**	Amphibia	*Tepuihyla*	"*galani*"	Guadacapiapu Tepui	Venezuela	N 5°17'24" W 60°55'06"	1242
VUB3417	IRSNB14752	**JQ742227**	**JQ742394**	Amphibia	*Tepuihyla*	"*talbergae*"	Kaieteur National Park	Guyana	N 5°10' W 59°29'	440
VUB3418	IRSNB14753	**JQ742228**	**JQ742395**	Amphibia	*Tepuihyla*	"*talbergae*"	Kaieteur National Park	Guyana	N 5°10' W 59°29'	440
VUB3758	IRSNB15879	**JQ742232**	**JQ742399**	Amphibia	*Tepuihyla*	aff. *edelcae*	Abakapa Tepui	Venezuela	N 5°11'24" W 62°17'49"	2172
VUB3759	IRSNB15880	**JQ742233**	**JQ742400**	Amphibia	*Tepuihyla*	aff. *edelcae*	Abakapa Tepui	Venezuela	N 5°11'24" W 62°17'49"	2172
VUB3760	IRSNB15881	**JQ742234**	**JQ742401**	Amphibia	*Tepuihyla*	aff. *edelcae*	Abakapa Tepui	Venezuela	N 5°11'17" W 62°17'30"	2193
GenBank	MNHN1998.311	AY843770	#####	Amphibia	*Tepuihyla*	*edelcae*	Auyantepui	Venezuela	N 5°52' W 62°34'	2015
VUB3651	IRSNB15655	**JQ742230**	**JQ742397**	Amphibia	*Tepuihyla*	*rodriguezi*	Gran Sabana	Venezuela	N 5°49'21" W 61°25'42"	1330
VUB3653	IRSNB15658	**JQ742231**	**JQ742398**	Amphibia	*Tepuihyla*	*rodriguezi*	Gran Sabana	Venezuela	N 5°49'21" W 61°25'42"	1330
VUB3634	ROM44135	**JQ742229**	**JQ742396**	Amphibia	*Tepuihyla*	sp	Ayangaik	Guyana	N 6°04'54" W 60°36'30"	1310
GenBank	LSUMZH13856	AF420746	#####	Reptilia	*Alopoglossus*	*atriventris*	Porto Walter	Brazil	no data	no data
GenBank	LG1026	AF420744	#####	Reptilia	*Alopoglossus*	*carinicaudatus*	Guajara Mirim	Brazil	no data	no data
GenBank	LSUMZH12692	AF420745	#####	Reptilia	*Alopoglossus*	*copii*	RPF Cuyabeno	Ecuador	no data	no data
GenBank	ENS10011	HM012699	#####	Reptilia	*Ameiva*	*undulata*	Chamela-Cuixmala BR	Mexico	no data	no data
VUB3764	IRSNB2674	**JQ742263**	**JQ742425**	Reptilia	*Anadia*	*mcdiarmidi*	Abakapa Tepui	Venezuela	N 5°10'50" W 62°17'50"	2242
VUB3222	PK2066V	**JQ742259**	#####	Reptilia	*Arthrosaura*	aff. *reticulata*	Puerto Ayacucho	Venezuela	N 5°37' W 67°28'	200
VUB3224	ROM42976	**JQ742261**	**JQ742279**	Reptilia	*Arthrosaura*	aff. *reticulata*	Wokomung Massif	Guyana	N 5°05'33" W 59°50'35"	1411
VUB3218	IRSNB17342	**JQ742258**	**JQ742422**	Reptilia	*Arthrosaura*	*guianensis*	Kaieteur National Park	Guyana	N 5°11' W 59°28'	480
VUB3220	ROM39471	#####	**JQ742423**	Reptilia	*Arthrosaura*	*guianensis*	Mt Ayanganna	Guyana	N 5°21' W 59°57'	1490
VUB3221	IRSNB2653	**JQ742257**	**JQ742421**	Reptilia	*Arthrosaura*	*hoogmoedi*	Maringma Tepui	Guyana	N 5°12'60" W 60°35'06"	2112
VUB3591	PK3272	**JQ742262**	**JQ742280**	Reptilia	*Arthrosaura*	*kockii*	Kaw Mountain	French Guiana	N 4°32'41" W 52°09'09"	221
GenBank	MRT978011	AF420721	#####	Reptilia	*Arthrosaura*	*kockii*	Vila Rica	Brazil	no data	no data
GenBank	MRT976977	AF420722	#####	Reptilia	*Arthrosaura*	*reticulata*	Juruena	Brazil	no data	no data

Tissue sample n°	Museum n°	16S	ND1	Order	Genus	Species	Locality	Country	Coordinates	Elevation (m)
VUB3223	PK2068V	**JQ742260**	**JQ742424**	Reptilia	*Arthrosaura*	sp "Chimanta"	Churi Tepui	Venezuela	N 5°16' W 62°00'	ca. 2300
VUB3592	PK3261	**JQ742271**	**JQ742282**	Reptilia	*Bachia*	*flavescens*	Kaw Mountain	French Guiana	N 4°32'41" W 52°09'09"	221
VUB3226	ROM28532	**JQ742264**	**JQ742426**	Reptilia	*Cercosaura*	*ocellata*	Paramakatoi	Guyana	N 4°43'00" W 59°42'00"	970
GenBank	ROM22892	AF206584	#####	Reptilia	*Echinosaura*	*sulcarostrum*	Baramita	Guyana	N 7°22' W 60°29'	100
GenBank	LG1356	AF420738	#####	Reptilia	*Ecpleopus*	*gaudichaudii*	Boissucanga	Brazil	no data	no data
GenBank	LSUMZH12697	AF101370	#####	Reptilia	*Iphisa*	*elegans*	RPF Cuyabeno	Ecuador	S 0°0' W 76°10'	250
VUB3232	IRSNB17322	**JQ742265**	**JQ742281**	Reptilia	*Kaieteurosaurus*	*hindsi*	Kaieteur National Park	Guyana	N 5°11' W 59°28'	480
VUB3594	PK3264	**JQ742269**	**JQ742430**	Reptilia	*Leposoma*	*guianensis*	Kaw Mountain	French Guiana	N 4°32'41" W 52°09'09"	221
VUB3233	PK2065V	**JQ742270**	**JQ742431**	Reptilia	*Leposoma*	*hexalepis*	Puerto Ayacucho	Venezuela	N 5°37' W 67°28'	200
GenBank	MRT977435	AF420723	#####	Reptilia	*Leposoma*	*oswaldoi*	Aripuana	Brazil	no data	no data
VUB3234	IRSNB17840	**JQ742267**	**JQ742428**	Reptilia	*Leposoma*	*percarinatum*	Kaieteur National Park	Guyana	N 5°11' W 59°28'	480
VUB3236	IRSNB17853	**JQ742268**	**JQ742429**	Reptilia	*Leposoma*	*percarinatum*	Kaieteur National Park	Guyana	N 5°08' W 59°25'	530
GenBank	USNM531665	AF420735	#####	Reptilia	*Leposoma*	*percarinatum*	Iwokrama Forest	Guyana	no data	no data
GenBank	LG1409	AY217954	#####	Reptilia	*Leposoma*	*scincoides*	Una	Brazil	no data	no data
VUB3238	IRSNB17344	**JQ742242**	**JQ742409**	Reptilia	*Neusticurus*	aff. *rudis*	Kaieteur National Park	Guyana	N 5°08'44" W 59°25'31"	515
VUB3239	IRSNB17345	**JQ742243**	#####	Reptilia	*Neusticurus*	aff. *rudis*	Kaieteur National Park	Guyana	N 5°08' W 59°24'	580
VUB3243	IRSNB18146	**JQ742244**	**JQ742410**	Reptilia	*Neusticurus*	aff. *rudis*	Maringma Tepui	Guyana	N 5°12'37" W 60°33'59"	1060
VUB3245	IRSNB18147	**JQ742245**	**JQ742411**	Reptilia	*Neusticurus*	aff. *rudis*	Maringma Tepui	Guyana	N 5°12'16" W 60°34'39"	1376
VUB3247	PK2058V	**JQ742246**	**JQ742412**	Reptilia	*Neusticurus*	aff. *rudis*	Chivaton	Venezuela	N 5°35'15" W 61°40'50"	1400
VUB3598	IRSNB18149	**JQ742250**	**JQ742278**	Reptilia	*Neusticurus*	aff. *rudis*	Kaw Mountain	French Guiana	N 4°32'41" W 52°09'09"	221
VUB3249	ROM20514	**JQ742247**	**JQ742277**	Reptilia	*Neusticurus*	aff. *rudis*	Tukeit, KNP	Guyana	N 5°12' W 59°27'	205
VUB3250	ROM39498	**JQ742248**	**JQ742413**	Reptilia	*Neusticurus*	aff. *rudis*	Mt Ayanganna	Guyana	N 5°21'06" W 59°57'24"	1490
VUB3251	ROM42644	**JQ742249**	**JQ742414**	Reptilia	*Neusticurus*	aff. *rudis*	Wokomung Massif	Guyana	N 5°07'46" W 59°49'16"	1234
VUB3666	IRSNB18109	**JQ742251**	**JQ742415**	Reptilia	*Neusticurus*	aff. *rudis*	El Danto	Venezuela	N 5°57'52" W 61°23'31"	1208
VUB3667	IRSNB18110	**JQ742252**	**JQ742416**	Reptilia	*Neusticurus*	aff. *rudis*	La Escalera	Venezuela	N 5°57' W 61°23'	1100
VUB3668	IRSNB18111	**JQ742253**	**JQ742417**	Reptilia	*Neusticurus*	aff. *rudis*	La Escalera	Venezuela	N 5°57' W 61°23'	1100
GenBank	MRT926008	AF420709	#####	Reptilia	*Neusticurus*	aff. *rudis*	Serra do Navio	Brazil	no data	no data
VUB3765	IRSNB18150	**JQ742240**	**JQ742407**	Reptilia	*Neusticurus*	aff. *rudis*	Abakapa Tepui	Venezuela	N 5°11'06" W 62°17'28"	2156
VUB3766	IRSNB18151	**JQ742241**	**JQ742408**	Reptilia	*Neusticurus*	aff. *rudis*	Angasima Tepui	Venezuela	N 5°02'30" W 62°04'54"	2162
GenBank	MRT968462	AF420708	#####	Reptilia	*Neusticurus*	*bicarinatus*	Apiacas	Brazil	no data	no data
VUB3253	IRSNB2650	**JQ742266**	**JQ742427**	Reptilia	*Pantepuisaurus*	*rodriguesi*	Maringma Tepui	Guyana	N 5°12'57" W 60°35'07"	2080
GenBank	LG1006	AF420734	#####	Reptilia	*Placosoma*	*cordylinum*	Teresopolis	Brazil	no data	no data
GenBank	MRT0472	AF420748	#####	Reptilia	*Potamites*	*ecpleopus*	Apiacas	Brazil	no data	no data
GenBank	LSUMZH13823	AF420757*	#####	Reptilia	*Potamites*	*juruazensis*	Porto Walter	Brazil	no data	no data
GenBank	KU21677	AY507866	#####	Reptilia	*Potamites*	*strangulatus*	no data	no data	no data	no data
GenBank	LSUMZH13603	AF420758*	#####	Reptilia	*Ptychoglossus*	*brevifrontalis*	Porto Walter	Brazil	no data	no data
GenBank	MRT887336	AF420737	#####	Reptilia	*Rachisaurus*	*brachylepis*	Serra do Cipo	Brazil	no data	no data
VUB3263	IRSNB18152	**JQ742256**	**JQ742420**	Reptilia	*Riolama*	*leucosticta*	Maringma Tepui	Guyana	N 5°12'39" W 60°35'30"	1942
VUB3254	IRSNB18153	**JQ742255**	**JQ742419**	Reptilia	*Riolama*	*leucosticta*	Wei Assipu Tepui	Guyana	N 5°13'03" W 60°42'21"	2219
VUB3767	Uncatalogued	**JQ742254**	**JQ742418**	Reptilia	*Riolama*	*leucosticta*	Yuruani Tepui	Venezuela	N 5°18'54" W 60°51'44"	2346

Supplemental Table **2.** Primers used in this study.

Name	Gene	Sequence 5’-3’	Reference
16S-A	16S	CGCCTGTTTAYCAAAAACAT	Simon *et al.* (1994)
16S-B	16S	CCGGTYTGAACTCAGATCAYGT	Simon *et al.* (1994)
NDH-AA	ND1	TACATACAACTACGNAARGGYCC	This study
NDH-AB	ND1	AAGGTGTATTAGTTGRTCRTANCG	This study
NDH-J	ND1	TTTACGACCTCGATGTTGGA	Roelants & Bossuyt (2005)
NDH-L	ND1	AAACTATTTAYYAAAGARCC	Roelants & Bossuyt (2005)
NDH-M	ND1	GGGTATGANGCTCGNACTCA	Roelants & Bossuyt (2005)
NDH-Q	ND1	TAAAACTATTCATNAARGAACC	Roelants & Bossuyt (2005)
NDH-R	ND1	TAAAACTATTCATNAARGAGCC	Roelants & Bossuyt (2005)
NDH-S	ND1	GGGTATGANGCTCGNATCCA	Roelants & Bossuyt (2005)
NDH-W	ND1	GGGTATGANGCTCGNATTCA	Roelants & Bossuyt (2005)

Supplemental Table **3.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Oreophrynella* species/populations from tepui summits and uplands in the Eastern Pantepui Region.

	Maringma	Wei Assipu	Roraima	Kukenan	Yuruani	Ilu	Tramen	Uplands
Maringma		0.1054	0.1054	0.1054	0.1054	0.1134	0.1134	0.1615
Wei Assipu	0.0250		0.0000	0.0063	0.0095	0.0649	0.0649	0.1472
Roraima	0.0250	0.0000		0.0063	0.0095	0.0649	0.0649	0.1472
Kukenan	0.0250	0.0000	0.0000		0.0032	0.0665	0.0665	0.1487
Yuruani	0.0250	0.0000	0.0000	0.0000		0.0665	0.0665	0.1519
Ilu	0.0192	0.0153	0.0153	0.0153	0.0153		0.000	0.1424
Tramen	0.0196	0.0156	0.0156	0.0156	0.0156	0.0000		0.1424
Uplands	0.0556	0.0421	0.0421	0.0421	0.0421	0.0487	0.0487	

Supplemental Table **4.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Tepuihyla* species/populations from tepui summits and uplands in the Eastern Pantepui Region; n.d. = no data.

	Wei Assipu	Uei	Auyantepui	Abakapa	Uplands
Wei Assipu		0.0000	n.d.	0.0491	0.0000
Uei	0.0018		n.d.	0.0506	0.0000
Auyantepui	0.0089	0.0125		n.d.	n.d.
Abakapa	0.0054	0.0089	0.0071		0.0459
Uplands	0.0000	0.0018	0.0106	0.0071	

Supplemental Table **5.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Pristimantis* species/populations from tepui summits and uplands in the Eastern Pantepui Region; n.d. = no data.

	Wei Assipu	Yuruani	Aprada	Abakapa	Angasima	Uplands
Wei Assipu		0.0812	n.d.	0.1204	0.1189	0.0114
Yuruani	0.0082		n.d.	0.1402	0.1386	0.1202
Aprada	0.0329	0.0329		n.d.	n.d.	n.d.
Abakapa	0.0309	0.0350	0.0165		0.0016	0.1315
Angasima	0.0288	0.0463	0.0144	0.0062		0.1300
Uplands	0.0036	0.0268	0.0498	0.0391	0.0517	

Supplemental Table **6.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Stefania* species/populations from tepui summits and uplands in the Eastern Pantepui Region; n.d. = no data.

	Wei Assipu	Yuruani	Auyantepui	Abakapa	Angasima	Uplands
Wei Assipu		0.1669	n.d.	0.2422	0.2163	0.1434
Yuruani	0.0409		n.d.	0.2532	0.2159	0.1645
Auyantepui	0.0702	0.0682		n.d.	n.d.	n.d.
Abakapa	0.0916	0.0955	0.0682		0.1833	0.2305
Angasima	0.0838	0.0838	0.0663	0.0721		0.2021
Uplands	0.0391	0.0234	0.0604	0.0858	0.0731	

Supplemental Table **7.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Anomaloglossus* species/populations from tepui summits and uplands in the Eastern Pantepui Region; n.d. = no data.

	Maringma	Wei Assipu	Auyantepui	Churi	Uplands
Maringma		0.0079	n.d.	n.d.	n.d.
Wei Assipu	0.0019		n.d.	n.d.	n.d.
Auyantepui	0.0478	0.0459		n.d.	n.d.
Churi	0.0344	0.0325	0.0363		n.d.
Uplands	0.0019	0.00000	n.d.	n.d.	

Supplemental Table **8.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Riolama* species/populations from tepui summits in the Eastern Pantepui Region.

	Maringma	Wei Assipu	Yuruani
Maringma		0.0075	0.1045
Wei Assipu	0.0000		0.1003
Yuruani	0.0096	0.0096	

Supplemental Table **9.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Arthrosaura* species/populations from tepui summits and uplands in the Eastern Pantepui Region.

	Maringma	Churi	Uplands
Maringma		0.1024	0.0057
Churi	0.0120		0.0953
Uplands	0.0000	0.0416	

Supplemental Table **10.** Lowest uncorrected pairwise distances in 16S (below diagonal) and in ND1 (above diagonal) between *Neusticurus* species/populations from tepui summits and uplands in the Eastern Pantepui Region.

	Abakapa	Angasima	Uplands
Abakapa		0.0469	0.0129
Angasima	0.0162		0.0433
Uplands	0.0022	0.0198	

Supplemental Figure **1.** [Next page] Typical tepui landscapes showing vertical cliffs and tepui summit isolation. Numbers above tepuis correspond to those provided in Fig. 1B (main text). A: Mount Roraima, photographed from Wei Assipu-tepui (photo by PJR Kok). B: Spectacular vertical cliffs of Mount Roraima, photographed from the air (photo by DB Means). C: Kukenan-tepui, Yuruani-tepui and Ilu-tepui, photographed from the air flying over Mount Roraima (photo by DB Means). D: Ilu-tepui and Tramen-tepui, photographed from the air (photo by DB Means). E: Aprada-tepui above the clouds, photographed from the air (photo by PJR Kok). F: Angasima-tepui (left) and Akopan-tepui (right), photographed from Upuigma-tepui (photo by PJR Kok). G. Part of the Eastern Tepui Chain rising above the Gran Sabana, photographed from the air (photo by PJR Kok). H: Upuigma-tepui, photographed from Angasima-tepui (photo by PJR Kok).


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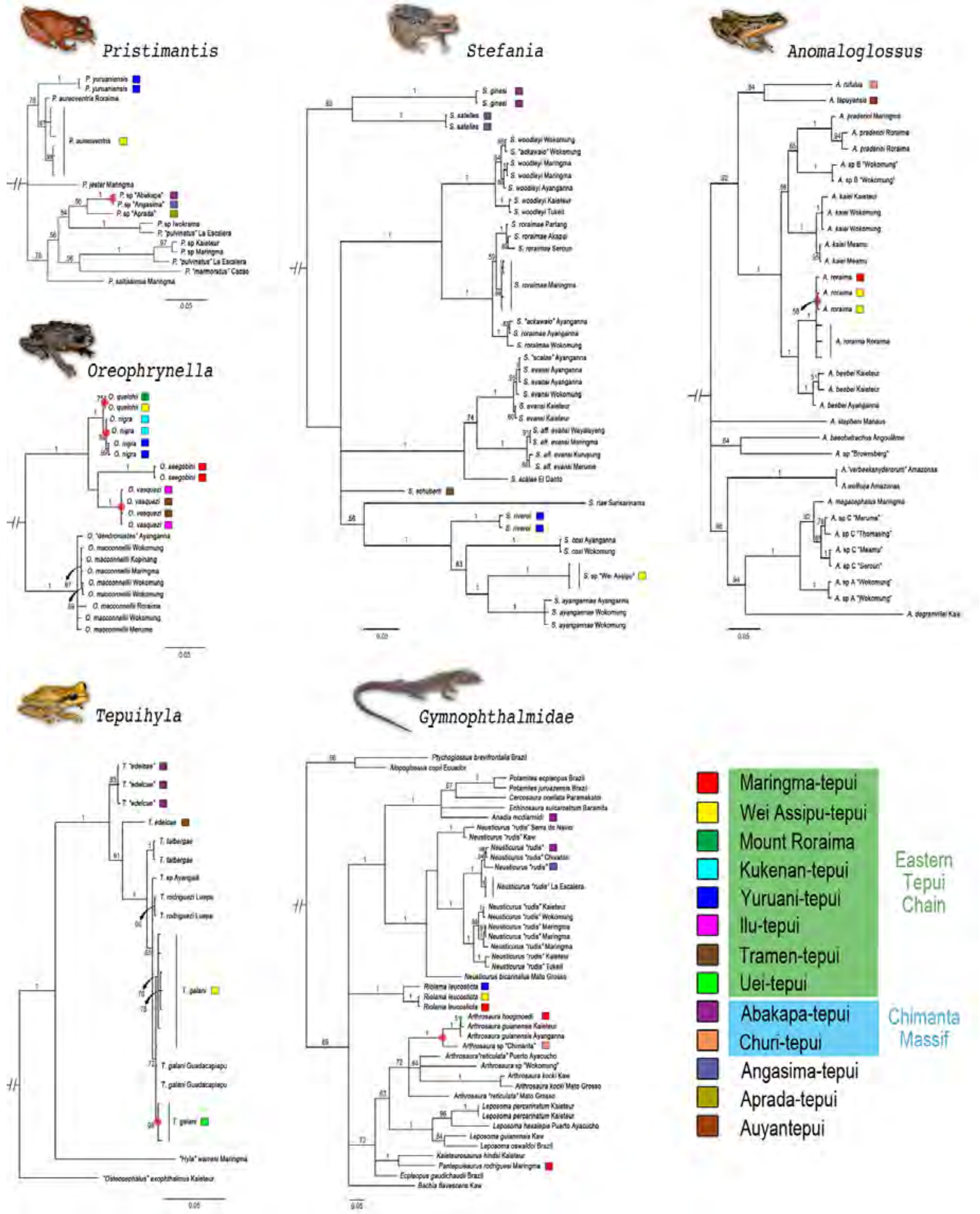
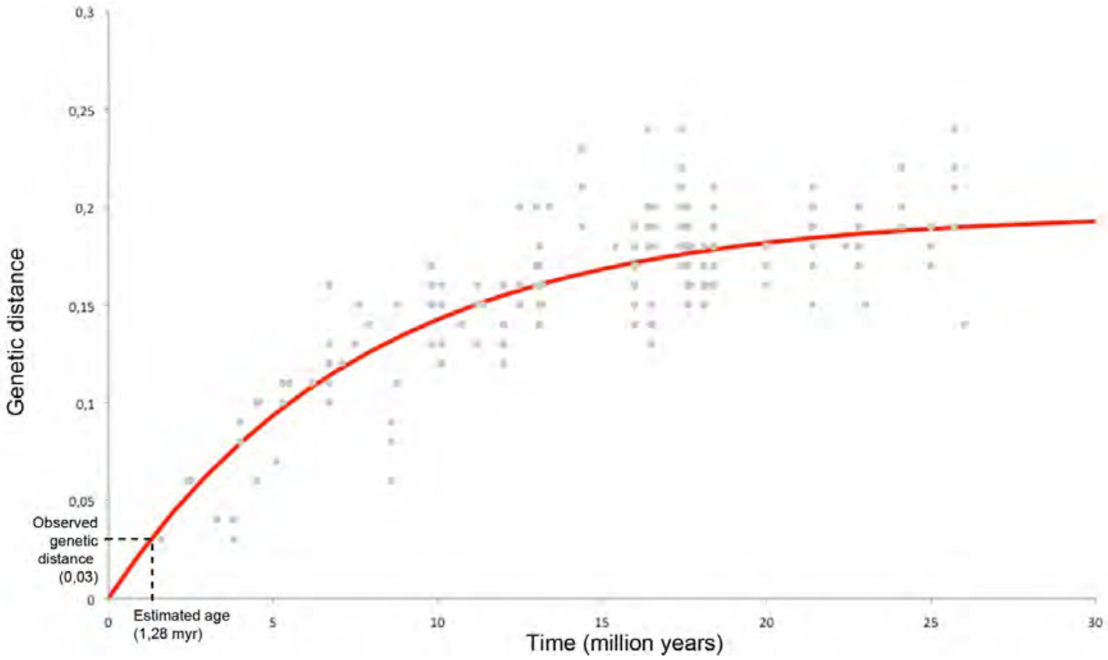
Supplemental Figure **2.** Phylogenetic relationships among tepui summit populations and their upland-lowland relatives in six typical Pantepui taxa. Taxa labelled by colored blocks represent summit populations, with differently colored blocks indicating different tepuis, as listed in the legend. Taxa without labels represent upland/lowland populations. The trees represent Bayesian consensus phylograms based on the analysis of the concatenated data set of 16S and ND1. Numbers above branches are Bayesian posterior probabilities. Internal nodes labelled by red dots represent divergences between tepui populations and their closest sampled relatives (either from another tepui or from the upland/lowland) for which approximate divergence times were inferred (see supplemental text). Outgroups (see supplemental text) were removed for presentation purposes.



Supplemental Figure **3.** Saturation curve (red line) obtained by nonlinear regression to estimate approximate divergence times based on observed pairwise sequence divergences in the ND1 fragment (dotted lines). The curve is based on a scatter plot (grey circles) of ND1 sequence divergences against reported divergence ages in the toad family Bufonidae [S7]. See supplemental text for full details.



11

GENERAL CONCLUSION: THE "LOST WORLD" CONUNDRUM, INSIGHTS FROM PANTEPUI AMPHIBIANS AND REPTILES

"*Imagination is more important than knowledge*"
A. Einstein

"*Se non è vero, è ben trovato*"

Italian proverb

Neotropical diversification, timing and evolutionary causes

Timing of the origin and evolutionary causes of the high species diversity of many taxonomic groups in the Amazon Basin and adjacent Guiana Shield lowlands remain highly controversial (*e.g.* Hoorn *et al*. 2010, Rull 2011, Hoorn *et al*. 2011). Most explanations of diversification mechanisms have focused on the role of geographic isolation through vicariance to produce phenotypic divergence (allopatric speciation). The causes of isolation of populations have been explained by several hypotheses (briefly reviewed in Antonelli *et al.* 2010), the major ones being the Riverine Barrier hypothesis (Ayres & Clutton-Brock 1992), the Marine Transgression hypothesis (Frailey *et al.* 1988), the Disturbance-Vicariance hypothesis (Colinvaux 1993, expanded by Bush 1994), the Vanishing Refuge hypothesis (Vanzolini & Williams 1981), the Taxon Pulses hypothesis (Erwin 1979), and the Refuge hypothesis (*i.a.* Haffer 1969, Mayr & O'Hara 1986, Haffer & Prance 2001). The latter, for a long time treated as the definitive driver of the rich Amazonian biodiversity, has recently been strongly criticized on the basis of recent paleoecological and paleobotanical data (*i.a.* Bush 1994, Rull 2004a, b, Bush & de Oliveira 2006, Hoorn *et al.* 2011), tending to confirm that the high Neotropical biodiversity has been shaped by complex and more varied mechanisms (*i.a.* Bush 1994, Colinvaux 1998, Rull 2005, Rull 2011).

The so-called Refuge hypothesis argues that a series of climatic changes during the Pleistocene resulted in a drastic reduction in tropical rainforest cover of lowland South America due to aridification. Some tropical rainforest taxa would thus have been restricted to isolated, usually small areas wet enough to support evergreen forest (like hilltops, where orographic precipitation was sufficient to maintain such an ecosystem, or riverine forests). This isolation would have led to increased allopatric speciation among forest species (Haffer & Prance 2001). According to this assumption, Quaternary climatic fluctuations would have been the main factor producing the Neotropical species richness. However, as reported by several authors (*i.a.* Bush & de Oliveira 2006), paleoecological data do not support the predominance of savannah in the Amazon Basin during the Pleistocene. Another compelling argument against the Refuge hypothesis is that many Amazonian species divergence events seem to predate the Quaternary (*e.g.* Heyer & Maxson 1982, Moritz *et al.* 2000, Bush 2005, Ribas *et al.* 2005, Gamble *et al.* 2008). Rheindt *et al.* (2008), for instance, in their recent study of the evolutionary history of *Elaenia* flycatchers (Neotropical birds) highlighted the importance of savannah habitat during the Neotropical Pliocene and late Miocene biogeography, thus before the Pleistocene. Despite these criticisms, the results provided by some authors (*i.a.* Wüster *et al.* 2005a, Quijada-Mascareñas *et al.* 2007) still argue in favour of the Refuge hypothesis, whereas in particular the extent of Pleistocene tropical rainforest fragmentation remains unclear. Interpretation of data and phylogeographic analyses were sometimes subject to vibrant discussions (*i.a.* Gosling & Bush 2005, Wüster *et al*. 2005b). Complicating the matter further is the fact that some authors (*i.a.* Schneider *et al.* 1999) presented results indicating that isolation through vicariance may be insufficient to produce phenotypic divergence among populations. Habitat and elevation shifts may occur frequently and likely constitute an important diversification mechanism.

An alternative hypothesis to the geographical models, the Gradient hypothesis, was suggested by Endler (1977). This model does not necessarily require an isolating barrier (*i.e.* parapatric speciation) and postulates that geographic differentiation and speciation may develop with or without gene flow.

More recently, Santos *et al.* (2009) studying Amazonian poison frogs suggested that instead of being a key source of diversity (from which species dispersed to other areas), the Amazon Basin diversity stemmed from repeated dispersals from adjacent areas, especially from the Andes—but also from the Guiana Shield (from where the oldest dispersal would have occurred)—and is primarily derived from late Miocene lineages. Likewise, Hoorn *et al.* (2010) showed that the Andean uplift played a major role in Neotropical diversification and that "*current biodiversity patterns are rooted deep in the pre-Quaternary*" (Hoorn *et al.* 2010, 2011) arguing that Andean mountain building primarily shaped the remarkable Neotropical species richness, not Quaternary climatic fluctuations.

Diversification in the Pantepui region, current hypotheses

On a smaller geographic scale, there is still much debate about the origin and the diversification of the Pantepui biota (Myers & Donnelly 1996). According to Rull (2004b) and based on the latest palynological data, tepui summits likely did not serve as a biotic refuge during the Pleistocene glaciations simply because the climate on tepui tops during the Last Glacial Maximum (LGM) seems to have been unfavourable to the subsistence of extensive summit communities (although the existence of microrefugia has been postulated, *e.g.* Rull *et al.* 1988, Rull 2009a, 2010b). On the contrary, it has been hypothesized that glacial maxima would have allowed spreading of highland organisms via ecological connections between tepuis (*e.g.* Cook 1974, Rull 2004b).

Rull (2009b) considered the origin of the "*amazing levels of biodiversity and endemism*" in the Pantepui region as a still-unresolved evolutionary enigma.

Although the palaeoecologist Rull produced many publications on the subject (not without redundancy, *e.g.* Rull 2004a vs. 2004b), the same author (Rull 2010a) pointed out that very few recent contributions shed any fresh insight on this hot topic, and that all the current hypotheses are still those formulated by earlier scientists (mainly Tate 1930, 1938, 1939, Chapman 1931, Mayr & Phelps 1967, Maguire 1970, Haffer 1970, 1974, Cook 1974). Pérez-Hernandez & Lew (2001), for instance, proposed a review of six hypotheses of diversification in Pantepui (the Mountain Bridge theory, the Plateau theory, the Cool Climate theory, the Distance Dispersal theory, the Modified Cool Climate theory, and the Habitat Shift theory), but their contribution does not bring any new or additional information compared to the discussion already provided by Hoogmoed more than twenty years before (Hoogmoed 1979). In their comprehensive review of the herpetofauna of the Guiana Highlands and in the light of their compiled distributional data McDiarmid & Donnelly (2005) examined in detail four main hypotheses (Distance Dispersal, Cool Climate, Habitat Shift, and Plateau Hypothesis) that, they say, could explain the Pantepui herpetofauna origin. Concomitantly, Rull (2004a, b, 2005) rekindled the debate based on observations from the latest palaeoclimatic and palynological data. Désamoré *et al.* (2010) summarized the main hypotheses (old vicariance vs. recent dispersal) accounting for the evolution of the Pantepui biota, and documented patterns of diversity and endemism in bryophytes in the region. Marín (2010) listed the main biogeographic hypotheses and discussed the origin and diversification of Pantepui birds, providing new interpretations of previously existing information. A critical shortcoming of all these biogeographical analyses is that they only use limited sampling (and thus likely incomplete distributional data), and lack any molecular phylogenetic evidence.

Nevertheless, a few molecular phylogenetic analyses tackled, at least partly, the processes of diversification of some Pantepui organisms (*e.g.* Bromeliaceae and Rapateaceae by Givnish *et al.* 1997, 2000, 2004, 2011, and the frog genus *Tepuihyla* by Salerno *et al*. 2012), but once more sampling was limited and samples were mostly gathered from few and usually "easily" accessible tepuis (this mainly for the reasons mentioned in Chapters 1 and 10).

Below I propose a tentative reappraisal of the suggested hypotheses in the light of new molecular phylogenetic evidence based on a thorough sampling of tepui summit vertebrates including both Pantepui endemics and more widespread taxa.

Biogeographical hypotheses proposed to account for the origin and unique patterns of biotic diversification in the Pantepui region belong to two mechanisms: "old" vicariance, which invokes landscape evolution and fragmentation as the main drivers of speciation, and "recent" dispersal, which invokes migratory events leading to genetic isolation.

1) Vicariant theory:

Plateau theory

Author: Although the name was first coined by Mayr & Phelps (1967), this theory was originally formulated for birds by Tate (1930, 1938), and Chapman (1931).

Synonyms: Panbiogeography theory [in part] (Croizat 1976), Lost World hypothesis (Rull 2004a).

Assumption: The Plateau theory states that extant tepui summit species are derived from highland ancestors that occupied a large continuous plateau that was gradually eroded and dissected into several isolated tepuis. Because the tepui dissection is often reported as being very old (tepui isolation dating back to the Cretaceous, but see Chapters 1 and 10), this theory implies that tepui summit species remained isolated for millions of years, and therefore would currently harbour "relict" organisms. This model would explain the observed current high level of endemism on tepui summits and the apparent similarities between tepui top populations. The condition of "long isolation" led Rull (2004a) to rename this hypothesis the "Lost World hypothesis", based on the famous novel by Sir Arthur Conan Doyle (1912). Rivero (1970) suggested a modified version of the Plateau theory to explain the distribution of frogs of the genus *Stefania* (Hemiphractidae) in Pantepui. Rivero's modified theory implies that the Roraima Formation was a mountain range with valleys, watersheds, and depressions instead of a "*smooth and unindented plateau*" (Rivero 1970: 471).

2) Dispersal theories:

Cool Climate theory

Author: Although the name was first coined by Mayr & Phelps (1967), this theory was originally formulated by Chapman (1931) and Tate (1938).

Synonyms: Vertical Displacement hypothesis [in part] (Rull 2004a, b), Vertical

Migration hypothesis [in part] (Rull 2010a).
Assumption: This model, first suggested for Pantepui birds (Chapman 1931), then for Pantepui mammals (Tate 1939), assumes that a more or less important decrease in temperature in the lowlands between the Andes and the Guiana Shield (thus within the Amazon Basin) during glacial periods (ice ages) would have shifted the habitat and thus facilitated migration of cold-adapted Andean organisms. This habitat shift (or habitat expansion) would also have allowed the existence of ecological corridors between tepuis previously isolated by the warmer, environmentally distinct intervening areas. Rull lengthily discussed this theory for plants (*i.a.* 2004a, b, 2005, 2006) renaming it the "Vertical Displacement hypothesis", and revisited the model based on observations from new palaeoclimatic and palynological data. The author hypothesized that both vicariance and dispersal (biotic mixing) account for the origin and diversification of the Pantepui biota (Rull 2004a, b), a scenario already postulated by Cook (1974) and Steyermark & Dunsterville (1980). Repeated speciation and dispersal events (notably vertical displacements) instigated by numerous climatic oscillations in the Guiana Highlands throughout the Pleistocene would have caused the Pantepui region to act as a "biodiversity pump" for the lowlands (Rull 2005). This scenario is also similar to the Disturbance-Vicariance hypothesis for Amazonian lowland biodiversity (Colinvaux 1993, Bush 1994).

Distance Dispersal theory

Author: Although the name was first coined by Mayr & Phelps (1967), the ideas behind this theory were originally discussed and formally rejected by Chapman (1931).
Synonyms: "Island-Hopping" (Salerno *et al.* 2012).
Assumption: This theory was initially invoked to explain the distribution of the Pantepui avifauna. Western tepuis would have been colonized by Andean bird species (or their ancestors) flying across the intervening lowlands, and subsequently dispersing eastward by "island hopping" from a tepui to another.

Modified Cool Climate theory

Author: Haffer (1970).
Synonyms: Vertical Displacement hypothesis [in part] (Rull 2004a, b), Vertical Migration hypothesis [in part] (Rull 2010a).
Assumption: This model combines aspects of the Cool Climate theory with those of the Distance Dispersal theory (Haffer 1970, 1974, Cook 1974) and assumes that the cooling of the climate in the Amazon Basin was not sufficient to make these lowlands subtropical instead of tropical, but may have facilitated dispersal in some organisms (like birds) thanks to the shift of mountain life zones to lower altitudes. It suggests that organisms were able to disperse through "sub-optimal" habitats, using small mountains harbouring optimal habitat as "steppingstones".

Habitat Shift theory

Author: Mayr & Phelps (1967).
Synonyms: None.
Assumption: The Habitat Shift theory states that some Pantepui organisms are derived from lowland ancestors that shifted their habitat preference (Hoogmoed 1979). Some species would thus have locally diversified after invasion of the highlands by lowland ancestors, or have sufficient ecological plasticity to survive in the lowlands/uplands and on tepui summits.

Specialized Habitat theory

Author: Mayr & Phelps (1967).
Synonyms: None.
Assumption: This model has been proposed for birds living on tepui cliffs and in tepui crevices and suggests that some tepui organisms are found in the Pantepui region only because their specialized requirements are not met in the intervening lowlands or uplands.

Mountain Bridge theory

Author: Although the name was first coined by Haffer (1974), this theory was originally formulated for birds by Chapman (1917) and Todd & Carriker (1922) to explain the origin and the distribution of some Colombian birds.
Synonym: None.
Assumption: This hypothesis was invoked to explain the apparent affinities between the Andean and the Tepuian avifauna and assumes the past existence of a physical connection (a “bridge”) between the Andes and the tepuis that would have allowed the bird faunas to disperse in their respective life zone.

Lessons from Pantepui amphibians and reptiles

Before examining the hypotheses outlined above, the following observations can be made, all inferred from phylogeny reconstructions and molecular dating (see Chapter 10), taxonomic study of museum specimens obtained during the course of this study (see Chapters 2–9), and review of pertinent literature. See previous chapters for material and methods.

(1) When known, divergence between each amphibian or reptile genus endemic to Pantepui—or that has multiple representatives on tepui summits—and its known sister group predates the Neogene. In all cases studied the divergence dates back to the Paleogene: Eocene/Oligocene (*ca.* 25–45 mya) for the taxa studied here (this work, Heinicke *et al.* 2007, Santos *et al.* 2009, Van Bocxlaer *et al.* 2010, Salerno *et al.* 2012), and up to the Paleocene for *Ceuthomantis* (*ca.* 60 mya according to Heinicke *et al.* 2009).

(2) When known, “basalmost” members of clades sister to Pantepui amphibian endemics are generally (i) found outside the Guiana Shield, (ii) not Amazonian,

(iii) currently geographically separated from Pantepui endemics by lowland areas that have potentially been impacted by periodic marine incursions, possibly since the Late Cretaceous (see Lovejoy *et al.* 1998, Hernández *et al.* 2005, Antonelli *et al.* 2009, Bloom & Lovejoy 2011).

(3) Although most genera endemic to Pantepui are early-branching lineages, they are always more recent than the oldest supposed age of tepui dissection, which is stated to date back to the Cretaceous, *ca.* 70–90 mya in some recent biological studies (*e.g.* Salerno *et al.* 2012).

(4) Several extant species or populations from individual tepui summits were only recently isolated (isolation as recent as the Holocene/Pleistocene; see Chapter 10), including species in genera that diverged from their known sister group in the Eocene (*e.g. Oreophrynella*).

(5) Pantepui currently harbours one endemic amphibian family (Ceuthomantidae), eight endemic amphibian genera (*Ceuthomantis*, *Dischidodactylus*, *Metaphryniscus*, *Minyobates*, *Myersiohyla*, *Oreophrynella*, *Stefania*, and *Tepuihyla*) and four endemic reptile genera (*Adercosaurus*, *Kaieteurosaurus*, *Pantepuisaurus*, and *Riolama*). This does not include some still undescribed putative genera of frogs and lizards (McDiarmid & Donnelly 2005, R. McDiarmid, pers. comm.).

(6) Among the genera endemic to Pantepui studied here, the highest genetic divergences between species and oldest diversification events are found in the genus *Stefania* and date back to the late Eocene/Oligocene (see Chapter 10, Salerno *et al.* 2012).

(7) Some populations from different summits form monophyletic clades (see Chapter 10).

(8) Genera having representatives both in the Andes and on tepui summits are scarce.

(9) In the region investigated (which represents only a fraction of Pantepui), single-tepui endemism does not seem as common as previously suggested. Some tepui summit species described as being single-tepui endemics turned out to be synonyms of more widespread taxa (*e.g.* in the genera *Anomaloglossus* and *Tepuihyla*, see also Chapters 8–9). On the one hand, species reported as highly restricted often also occur on nearby tepuis, or in some cases in the surrounding uplands. On the other hand, some populations occurring on different tepui summits and identified as a single species turned out to be a complex of distinct taxa (*e.g.* in the genus *Stefania*).

(10) In spite of very low genetic distances arguing in favour of conspecificity, some tepui summit populations recognized as distinct species show striking phenotypic differences (Fig. 1). Conversely, some tepui summit populations show identical morphology in spite of high genetic divergences (Fig. 2).

(11) The “astonishing” biodiversity and endemism reported by some authors (*e.g.* Rull 2009b) on tepui summits are not observed in amphibians and reptiles, at least not at the species level and in the area studied. Tepui summit herpetofaunas are typically depauperate (Myers & Donnelly 2001, MacCulloch *et al.* 2007), and as noted earlier, single-tepui endemism has probably been overestimated. Likewise, the postulate of the Pantepui region acting as a Pleistocene “biodiversity pump” for the lowlands (Rull 2005) cannot be demonstrated for amphibians and reptiles.

Figure **1.** Striking example of phenotypic differences between currently isolated tepui summit populations in absence of significant genetic divergence (0.0% in 16S and max. 0.4% in ND1). All specimens of *Oreophrynella quelchii* (left; found only on the summits of Wei-Assipu-tepui and Mount Roraima) have a possibly aposematic ventral colouration consisting of large yellow to orangish red markings on a black background, while all specimens of *O. nigra* (right; found only on the summits of Kukenan-tepui and Yuruani-tepui) have a completely black ventral face. See Fig. 10 in Chapter 1 for location of these tepuis (#7, 8 and #9, 10, respectively). Photos by the author.

Figure **2.** Striking example of morphological stasis between currently isolated tepui summit populations in presence of significant genetic divergence (4.0% in 16S and 16.7% in ND1). Left: a still undescribed *Stefania* species endemic to the summit of Wei-Assipu-tepui. Right: *Stefania riveroi* found only on the summit of Yuruani-tepui. Both species are intraspecifically variable in colour pattern and morphology and no morphological character has been found to discriminate between them, although molecular phylogenies indicate that they are not sister species (see Suppl. Fig. 2 in Chapter 10). See Fig. 10 in Chapter 1 for location of these tepuis (#7 and #10, respectively). Photos by the author.

Test of hypotheses: towards a phylogenetically supported diversification model?

Current hypotheses aiming at explaining the origin and diversification of the Pantepui biota are mostly based on “mobile” organisms that are able to disperse through the air (*e.g.* birds, flying insects, plants). Because of their assumed better dispersal abilities, these organisms are perhaps not the best models to resolve the Pantepui conundrum. Small terrestrial vertebrates with narrow elevational limits, like amphibians and reptiles, should be, unless proved otherwise, much more reliable models for phylogeographic studies in such highly dissected landscapes. In any case, as pointed out by Hoogmoed (1979) and Duellman & Hoogmoed (1984), it is not surprising that differences in dispersal abilities and in geological ages of these groups led to different conclusions.

Although this work provides new insights on the origin and the diversification of Pantepui amphibians and reptiles (see previous chapters), we are still far from a complete understanding of all the mechanisms involved in the diversification of the Pantepui biota, which will probably require additional sampling outside the region studied here (*i.e.* west of the Río Caroní), and additional meta-analyses.

Plateau theory

Phylogenetic and temporal predictions: (1) early lineage splits are linked with geological events; (2) the origins of Pantepui endemic genera are rooted in the Paleogene; (3) multiple phylogenetic lineages are restricted to Pantepui and endemism at higher ranks than species; (4) Pantepui distributions are shared by taxa having different ecology.

Discussion: It is generally accepted that the tepuis are remnants of an enormous sedimentary landmass dating from the Precambrian that remained buried for millions of years before being sporadically uplifted, possibly since the early break-up of Gondwana. That landmass was broken up by tectonic forces; wind and weathering gradually led to the present-day appearance of the tepuis (see Chapter 1).

The Plateau theory gives rise to two fundamental questions (1) are extant Pantepui endemic species “relict” organisms derived from highland ancestors that once occupied that large plateau (in other words, is the “Lost World hypothesis” sustainable?); (2) was the magnitude of the Plateau uplift(s) sufficient to cause vicariance between the Plateau and the surrounding areas?

According to Hoogmoed (1979) and McDiarmid & Donnelly (2005) (based on morphological data), some herpetofauna distribution patterns seem to support the Plateau theory. Discussing the genus *Stefania*, Hoogmoed (1979) and Duellman & Hoogmoed (1984) invoked the Plateau theory as an explanation of the distribution pattern of the genus, and Duellman & Hoogmoed (1984) argued that

> “*Some aspects of the phylogenetic arrangements of the species of* Stefania *are consistent with the hypothesis that the tepuis are erosional remnants of a former plateau that eroded more rapidly in the west than in the east*” (1984: 34).

As suggested by McDiarmid & Donnelly (2005), the genera *Oreophrynella* and *Metaphryniscus* (Anura, Bufonidae), and *Riolama* (Squamata, Gymnophthalmidae) are other serious candidates for such a “relict hypothesis”.

The Plateau theory has also been more or less implicitly invoked in the evolution of some other groups, as shown in the following selected examples:

- Maguire (1970) discussing some families of the flora of the Guiana Highlands suggested that a highly autochthonous flora had evolved in the Guiana Highlands region before a Miocene uplift.
- Berry & Riina (2005), studying the flora of the Guiana Shield, suggested an important role of the Pantepui region in the early evolution of a number of plant families, and pointed out the need of dating the evolution of Pantepui lineages.
- De Marmels *et al.* (2003) studying the butterfly genera *Pereute* and *Pseudopieris*, and De Marmels (2007) studying the endemic Guianan damselfly genus *Tepuibasis* argued that prior to Andean orogeny, the ancient Guiana Shield region was populated by their ancestors. The authors postulated that local ancestral populations were raised to considerable height as a result of the Andean uplift, which would have triggered a simultaneous isostatic rise of large parts of the Guiana Shield. That population hence became vicariant from the surrounding lowland populations and progressively adapted to high elevation conditions. Further dissection by erosion of the Guiana Shield Plateau would have caused secondary vicariance and speciation events explaining the current distribution of the genera in Pantepui.
- Brumfield & Edwards (2007) studying two thamnophilid bird species, one from the Andes and the other from the Pantepui region, suggested that *Thamnophilus divisorius* (currently restricted to a small area in the Peruvian Andes) could represent a relict of the avifauna having inhabited an extensive ancient sandstone system that produced the present-day Pantepui region.

Until very recently, the Plateau theory had never been empirically tested owing to a lack of phylogenetic studies. Based on phylogenetic analyses and estimations of divergence time of an endemic Pantepui frog genus (*Tepuihyla*), Salerno *et al.* (2012) suggested the rejection of the Plateau hypothesis. Salerno *et al.* (2012) reinforced their point by stating that the “Lost World hypothesis” (another name for the Plateau theory, see above) was not satisfied by data for the Pantepui frog genus *Stefania* either, because *Stefania*, like *Tepuihyla*, radiated more recently than the dissection of the plateau in isolated tepuis, which according to these authors (although not based on unequivocal geological evidence) occurred in the Cretaceous, 70–90 mya. A truism since all frogs currently having stable populations on tepui summits belong to the superfamily Hyloidea, which only began to diversify in the Paleogene (Roelants *et al.* 2007), thus well after the hypothetical tepui isolation suggested by Salerno *et al.* (2012). The sampling of Salerno *et al.* (2012) only covers a single Pantepui genus, including only four (of seven known) species from three tepui summits only, and is therefore probably too limited to draw far-reaching conclusions. In addition, the Cretaceous age of tepui isolation assumed by Salerno *et al.* has not been demonstrated satisfactorily and is not widely accepted (as earlier discussed in Chapter 1). Interestingly, none of the three references given by Salerno *et al.* (2012) for a Cretaceous age of tepui isolation contains such a statement (see Chapter 1).

Although my results show a similar pattern of recent isolation in many extant tepui summit species (see Chapter 10), they do not necessarily refute the Plateau hypothesis. On the contrary several elements seem to support that hypothesis for the early origin of the Pantepui fauna. Many lineages of amphibians and reptiles, but also in other zoological groups such as birds (*e.g.* Mayr & Phelps 1967), invertebrates (*e.g.* Breure 2009), and in plants (*e.g.* Steyermark 1986, Berry & Riina 2005) are currently endemic to the remnant of that ancient plateau. As highlighted in Chapter 10, several of the taxa studied here (*Oreophrynella*, *Stefania*, *Tepuihyla*, *Riolama*) represent phylogenetically distinct lineages restricted to the Pantepui region, and the area as a whole seems to act as a reservoir of endemism at the genus and species levels, but also at the family level (*e.g.* the recently discovered frog family Ceuthomantidae), which is remarkable given the current relatively reduced size of the region.

Endemic taxa are more likely to develop in isolated areas (oceanic islands being probably the most iconic example), and areas of endemism are often assumed to be the result of non-stochastic processes, such as vicariance caused by geological or climatologic events (Evans *et al.* 2004). A concordant pattern of distribution and endemism observed in other Pantepui groups than amphibians and reptiles (both in plants and animals) seems to further support the Plateau hypothesis. However, what actually caused the isolation of Pantepui and what were, and probably still are, the barriers to dispersal (biotic and abiotic) of some Pantepui organisms remain puzzling.

As pointed out in Chapters 1 and 10, time estimates for the isolation of individual tepuis range roughly from the Cretaceous to the Quaternary. If we re-evaluate the age of tepui isolation assumed by Salerno *et al.* (2012) of *ca.* 45 million years downward (which does not disagree with time estimates for geological events suggested by *e.g.* Gansser 1954, Simpson 1979, Gómez *et al.* 2003, Orme 2007, and Hoorn & Wesselingh 2010), and thus remove the assumption of "very long" (*i.e.* Cretaceous) isolation of Pantepui, the Plateau theory appears to be congruent with phylogenetic data. Preliminary observations seem to indicate a link between early lineage splits and timing of possible uplift(s) (and/or subsidence of surrounding areas, *e.g.* the Takutu Rift), as well as timing of marine incursions (in which case the foothills of the Andes and Pantepui could have served as "ancient" refuges), but confirmation of this requires extensive additional analyses.

The occurrence of "young" taxa on tepui summits and the Plateau theory are thus not mutually exclusive and in my opinion the Plateau theory cannot be unequivocally refuted, most Pantepui amphibian and reptile endemics appearing to be the result of long-term survival and evolution on an isolated plateau since the Paleogene rather than "recent" founder dispersal from the surrounding areas. Despite probable extinction events (see below), some metapopulations of Pantepui organisms have preserved patterns of endemism and vicariance that seem to reflect the geological history of the region.

The following (still highly speculative) scenario could tentatively be deduced from phylogenetic results, estimates of divergence time, and literature data. The exact role of uplift(s) in Pantepui isolation still needs to be elucidated:

1) Pantepui, which was submerged until the Lower Triassic, experienced a (first?) epeirogenic uplift during the Lower Cretaceous, possibly contemporaneously with the break-up of Gondwana and the opening of the South Atlantic Ocean. The extent of this uplift is difficult to assess, but erosional denudation was probably extensive and could have substantially lowered the plateau, keeping it low and accessible to the paleofauna [according to geologists (H. Briceño pers. comm.), about 3,000 m of sediments would have been removed from the top of the present-day tepuis due to erosion, but no exact dating of this event is available (see Chapter 1)].
2) A second significant (?) epeirogenic uplift began in the Upper Cretaceous/Paleocene, close to the K-T boundary, as the first signs of the Amazon Basin became visible

(Haffer 1974, Duellman 1979, Simpson 1979); erosion was probably accelerated. That uplift slightly predates (and possibly promoted?) the split between the frog genus *Ceuthomantis* (Ceuthomantidae) and its sister taxon (all other Terraranans). Again, the extent of the uplift is difficult to appreciate, but vertical isolation from the surrounding areas of the—already partly eroded[1]—plateau would have likely reached its apogee in the Middle Eocene/Oligocene, with some major massifs (*e.g.* Chimantá and Auyantepui) disconnected from each other, but several tepuis and tepui massifs still linked to each other and to the uplands by more or less extensive ridges (remnants of which are still visible today, see Fig. 3). That epoch (Middle Eocene/Oligocene) roughly corresponds to the split between most known endemic Pantepui genera and their respective sister group, as well as to the earliest diversification in *Stefania*. That episode of high fragmentation and rapid vertical isolation corresponds in part to the Andean orogeny, but also to the Oligocene uplift of the Sierra de Perijá, an extension of the eastern Andean chain in northern Venezuela (*ca.* 25 mya according to Kellogg 1984).

3) Rate of erosion and weathering, although not constant, gradually led to the present-day appearance of the tepuis, but some connectivity between tepui summits within a same massif or “tepui chain” (like in the Eastern tepui chain) could have remained at least until a potential third uplift and its erosional response in the late Miocene/Pliocene, concomitant with the emergence of the Central American Isthmus and the climax of Andean tectonism (Hoorn & Wesselingh 2010). That period roughly corresponds to the earliest diversification of several Pantepui endemics (except *Stefania*). Valleys between some nearby tepuis could have been less deep than today, a topography maintained until fairly recently (*e.g.* Pleistocene/Holocene).

In summary, patterns of distribution and endemism of several Pantepui amphibians and reptiles seem to argue in favour of the Plateau theory. When the timing of the geomorphological evolution of the tepuis and the timing of amphibian and reptile species diversification inferred from molecular phylogeny reconstructions and estimates of divergence time are considered as a whole, the Plateau theory turns out to seem appropriate to explain the early origin of several Pantepui taxa (*e.g. Oreophrynella*, *Stefania*, *Tepuihyla*) and several diversification events. But vicariance alone fails to explain the distribution and diversification of all extant tepui summit taxa. As mentioned in Chapter 1, the Andean main uplift (starting *ca.* 25–30 mya, with a peak around 10 mya) and the emergence of the Central American Isthmus (final closure *ca.* 3 mya) are major regional mountain-building episodes that drastically modified the hydrologic regime and the climate in South America and probably played a major role during the following period, which is described below under the Disturbance-Vicariance theory.

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[1] Thus in agreement with Rivero’s (1970) postulate that the Roraima Formation could have been already partly broken by some valleys and watersheds instead of being each time uplifted as a totally smooth peneplane surface. Erosion and weathering are not sudden events, and there were probably long periods in the Pantepui history during which the tepuis, as we know them today, were better connected by shallow valleys.

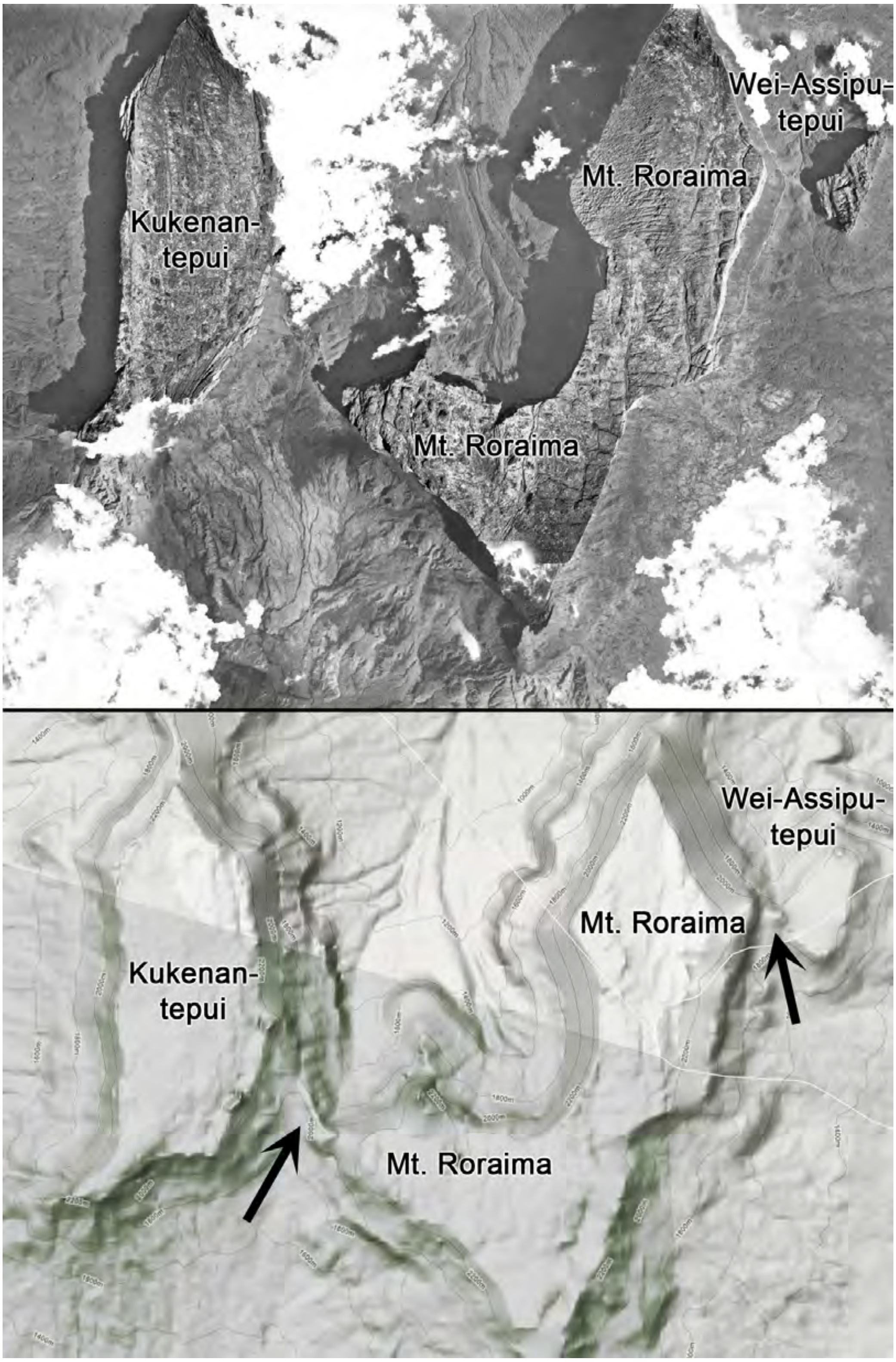

Figure **3.** Radar map (above) and relief map (below) showing examples of current tepui summits isolation and remnants of connective “bridges” (black arrows) that are barely visible on the radar map, but well noticeable on the relief map. These ridges frequently occur between tepuis. Radar map courtesy of C. Brewer-Carías, relief map © Google Maps.

Cool Climate and Modified Cool Climate theories

Phylogenetic and temporal predictions: (1) diversification events are linked to climatic instability, and (2) early lineage splits are linked to ice ages if the theory applies to the origin of the Pantepui biota (which *per se* implies Quaternary colonisation from the Andes).
Discussion: As we have seen before, early splits between Pantepui endemics and their sister taxa largely predate the Quaternary, therefore the "Cool Climate" and the "Modified Cool Climate" theories do not seem to fit the data for the early origin of the Pantepui amphibians and reptiles (which as seen earlier is probably the result of vicariance).

I reject the hypothesis of Pantepui endemic taxa being derived from "cold-adapted" Andean invaders because Andean colonisers would have had to reached Pantepui during the Paleogene by crossing large lowland areas that were (1) possibly submerged by marine incursions, (2) likely ecologically considerably different.

Climate-induced migrations could however explain diversification within Pantepui, but were probably not limited to "long" migrations caused by temperature fluctuations (as stated in the Cool Climate and the Modified Cool Climate hypotheses), or to vertical displacements (as suggested in the Vertical Displacement/Vertical Migration hypothesis). Although hypothesized migration events could have been promoted by climate, they are not necessarily linked to cooler temperatures, but could also be related to aridification, reduced atmospheric CO_2, and/or habitat modification. Similarly, migration events were likely not limited to the vertical plane. The "Disturbance-Vicariance" theory proposed by Colinvaux (1993) to account for the species richness and endemism in the Amazonian lowlands seems appropriate to describe the major processes involved in diversification within Pantepui. Under the name "Disturbance-Vicariance", I group part of the Cool Climate theory of Mayr & Phelps (1967), and the Modified Cool Climate theory of Haffer (1970, 1974), and thus the Vertical Displacement/Migration hypothesis of Rull (2004a, b, 2010a) that pertain to Pantepui local diversification.

Disturbance-Vicariance theory

Phylogenetic and temporal predictions: (1) diversification events are linked to climatic instability; (2) most species diversifications occurred in the Neogene.
Discussion: The Disturbance-Vicariance hypothesis was first formulated by Colinvaux (1993), who proposed that, under this model, speciation is triggered by temperature fluctuations, local changes in precipitation or seasonality, and habitat heterogeneity. Colinvaux (1993) underlined that the principle of Disturbance-Vicariance is also applicable on a smaller scale (thus *contra* the Cool Climate theory, which requires long distance dispersal).

My results mostly agree with Haffer (1970, 1974), Cook (1974), Steyermark (1986), and Rull (*i.a.* 2004a, b, 2005), showing that dispersal promoted by climate instability probably actively contributed to the diversification of most Pantepui amphibians and reptiles at a local scale (*i.e.* within Pantepui). Rull (2005) also stated that niche fragmentation and climatic instability are the main forces driving the timing and the extent of evolutionary processes in the Guiana Highlands.

However my analysis diverges from Rull's (2004a) model because, as explained below, my results seem to indicate that climate instability caused, in several cases, a depletion of ancestral Pantepui amphibian and reptile populations instead of promoting a so-called "biodiversity pump" for the surrounding areas.

Data strongly suggest that most herpetofaunal diversity patterns in Pantepui were shaped before the Pleistocene, probably in the Oligocene or even earlier (here hypothesized as pre-Neogene vicariance), but tend to indicate that species diversity was substantially reorganized during or shortly after periods of climate instability that occurred in the area from the late Miocene until today (as shown by the recent isolation of several extant species or populations from individual tepui summits). The data suggest that some genera that apparently originated in the Pantepui region (the best example being *Oreophrynella*) suffered significantly from climate change and its probable corollary habitat modification at those high elevations, forcing them to move (probably altitudinally) and find alternative suitable habitat. Climate change could have considerably reduced their populations causing local extinctions and bottlenecks. This could explain an early-lineage branching and a recent origin of most extant species.

I hypothesize that the causes of these extinctions and bottlenecks in several groups were the climate instability promoted by (1) the climax of the Andean orogeny, (2) the emergence of the Central American Isthmus, and (3) Quaternary climate oscillations. Climate change most likely was not an *opportunity* for all Pantepui organisms to locally disperse, but instead it was a *constraint* for most of them to move. Only reduced populations of these Pantepui taxa would have been able to survive in small "dispersal centres" (*sensu* Steyermark 1979), possibly at slightly lower elevations, and subsequently reinvaded their original range (theoretically tepui summits) constrained again by ecological factors induced by climate oscillations (implying that lower elevation populations went extinct). This scenario is still highly speculative, but could explain the observed low genetic diversity among many extant tepui summit populations.

Box 1 – Ecological preferences of Pantepui organisms

We should be cautious in our speculations about ecological preferences of Pantepui ancestors. A shift in ecological preferences may have taken place in the evolution of some taxa, and a putative good example in Pantepui is *Oreophrynella*. All *Oreophrynella* species have opposable toes, but only two known species (*O. macconnelli* from the Eastern Pantepui uplands, and *O. weiassipuensis* known only from a deep canyon on Wei-Assipu-tepui) are mainly arboreal (pers. obs., D.B. Means pers. comm.), whereas strict tepui summit species are terrestrial. Although the opposable toes condition is plesiomorphic in the genus, we do not know whether the *Oreophrynella* ancestor was arboreal or terrestrial (see also Chapter 4). It is tempting to assume the *Oreophrynella* ancestor as being arboreal, but opposable toes could also be an adaptation to rock climbing (or be involved in unknown functions), that was subsequently co-opted by two extant taxa for tree climbing ("exaptation" *sensu* Gould & Vrba 1982). It should be noted that among the many extant arboreal anuran taxa, only a very few have opposable toes (to my knowledge only species of the hylid genus *Phyllomedusa*), so the selective advantage of opposable toes for arboreality in anurans is not obvious.

Reinvasions of original ranges, supposedly tepui summits, were probably easier among tepuis that were still physically connected (though even poorly) to the Pantepui uplands and/or between each other, for instance by shallow valleys. Reinvasions were probably restrained by major watercourses. Tepuis and tepui massifs that were already strongly isolated from the relictual populations could not be reinvaded by some groups, which may

Box 2 – The case of *Stefania*

Under the Disturbance-Vicariance theory, the only taxon here studied that *seems* to have less significantly suffered from climatic instability is *Stefania*. Genetic divergences between *Stefania* species are relatively high and single-tepui endemism seems less uncommon in the genus (Chapter 10). Although this could be linked to the structure of the genome of ancestral species (*e.g.* ancestral polymorphism), a possible interpretation lies in a different response to environmental challenge compared to other tepui organisms. *Stefania* is the only taxon currently found on tepui summits that is not dependent on water or on at least semi-permanent moist places to deposit its eggs. Indeed, *Stefania* females carry eggs and metamorphs on their back until juveniles are fully formed and independent (Duellman & Hoogmoed 1984, Jungfer & Boehme 1991), and they can actively procure the right conditions for the eggs to successfully develop. Other tepui summit amphibians have either a biphasic life cycle (eggs being laid in water, *e.g. Tepuihyla*), or are direct-developers (*e.g. Oreophrynella*, *Pristimantis*) laying eggs in places remaining sufficiently moist for a minimal period of time (several months in some cases). Reptiles also are dependent on such relatively moist places to deposit their eggs. *Stefania* could have better survived on individual tepui summits by using *in situ* microrefugia like deep fractures and canyons, but on the other hand could have been extirpated when suitable microrefugia were absent (*e.g.* no *Stefania* are known to occur on the summits of Mt. Roraima, Kukenan-tepui, Ilu and Tramen-tepuis, Ptari-tepui, etc.).

explain why some taxa like *Oreophrynella* and *Riolama* are now absent from the Chimantá Massif and from its western satellite tepuis (*e.g.* Upuigma, Angasima, Aprada).

Interestingly, this scenario seems to be further supported by botanical studies suggesting that tepui summits had no or very limited organic soils, during the LGM. Environmental conditions were therefore probably too inhospitable for the maintenance of viable floral and faunal populations (*i.a.* Schubert *et al.* 1986, Huber 1995, Rull 2004b, H. Briceño pers. comm.).

Vertical migration promoted by recent climatic instability was reported as not realistic for plant taxa occurring on the highest tepuis (mountains having a base-summit difference exceeding 1,100 m) because, according to Rull (2005), the maximum downward vertical shift estimated for the last glaciation in the region was 1,100 m. This is not in contradiction with the available evidence for the herpetofauna in the studied area and could explain why (1) some populations in certain groups (*e.g. Stefania*) show higher genetic divergences between summit populations; (2) some typical Pantepui taxa are absent from some tepui tops (probably due to extinction). Nevertheless we must be aware that current tepui isolation does not necessarily reflect the situation in the area a few million years ago.

It is noteworthy that similar observations on migration and diversification promoted by climate instability were made by Noonan & Gaucher (2005, 2006) who examined phylogeographical structure of Guianan *Atelopus* (Anura, Bufonidae) and *Dendrobates tinctorius* (Anura, Dendrobatidae) [lowland/upland taxa distributed east of the Pantepui region] and also suggested the Disturbance-Vicariance hypothesis (*i.a.* Colinvaux 1993, 1998, Bush 1994, Bush *et al*. 2002, Mayle *et al.* 2004), which "*invokes changes in temperature and atmospheric* CO_2 *levels associated with precessional cycles as the dominant factor influencing the historical continuity of Amazonian communities*" to account for their diversification (Noonan & Gaucher 2006). Noonan & Gaucher (2005) suggest that the extant Guianan *Atelopus* species derive from a common ancestor that migrated from the Andes through the Amazon Basin thanks to the Pliocene cooling, and that local diversification was promoted by Quaternary climatic instability and alternating physical isolation on hilltops. The taxa involved show very low genetic divergences between populations due to secondary contacts. At a more local scale a similar statement can be made about Pantepui.

Although climate instability probably played a major role in the recent diversification of Pantepui amphibians and reptiles, a third model must perhaps be invoked to explain diversification in groups that are not Pantepui endemics, but that are found on tepui summits like the lizards *Neusticurus* and *Arthrosaura*. This third model is the Habitat Shift theory as developed below.

Habitat Shift theory

Phylogenetic and temporal predictions: (1) occurrence of conspecific populations on tepui summits and in intervening areas, (2) tepui summit populations are derived from widespread lowland/upland taxa (*e.g.* Pan-Amazonian).

Discussion: According to Hoogmoed (1979) and McDiarmid & Donnelly (2005) several species seem to fit the Habitat Shift hypothesis, and my results concur with their observations. As noted earlier by several authors (Mayr & Phelps 1967, Myers & Donnelly 2001, McDiarmid & Donnelly 2005), tepui summits have been for long (and probably still are) available to active colonizers from the surrounding lowlands/uplands. Although sometimes surprising, it appears that some organisms are able to reach tepui tops, including some of those that seem to be currently topographically strongly isolated (*e.g.* Angasima-tepui). Invasions of tepui tops have been suggested in such groups as ants (Jaffe *et al.* 1993) or plants (Givnish *et al.* 2004).

Phylogeny reconstructions (see Chapter 10) show that, in some taxa, tepui summit populations are conspecific with upland populations and that some extant populations are derived independently from much more widespread lowland/upland taxa (*e.g. Neusticurus* and *Arthrosaura*). In the lowlands/uplands, *Neusticurus* species are primarily riparian, but on tepui summits they have been found associated with very small puddles, or were even collected under rocks far from any body of water (pers. obs.). D. B. Means (pers. comm.) reported a female *Neusticurus* with eggs in a vegetated crack about 3 m up off the top of the talus slopes at the base of Mount Roraima’s cliffs. Likewise, a few species that are widespread in the surrounding uplands, or even lowlands, can be found on some tepui summits (*e.g.* the frog *Hypsiboas sibleszi*, and the snake *Leptodeira annulata*, which occurs from sea level to tepui tops). These species likely have relatively recently invaded the tepuis and have adapted to the tepui summits climate probably thanks to ecological plasticity. On the other hand, it is possible that the descendants of ancestors that could have secondarily invaded the uplands from the tepui summits are physiologically predisposed to reinvade tepui tops (*e.g. Anomaloglossus roraima*).

Distance Dispersal theory

Phylogenetic and temporal predictions: None for amphibians and reptiles since they are not able to disperse through the air.

Discussion: Although useful to explain the distribution of some flying organisms, long-distance dispersals does not appear credible for amphibians and reptiles (Hoogmoed 1979, McDiarmid & Donnelly 2005).

Specialized Habitat theory

Phylogenetic and temporal predictions: None for amphibians and reptiles.
Discussion: McDiarmid & Donnelly (2005) considered the Specialized Habitat theory of little relevance for amphibians and reptiles. As noted by these authors this hypothesis may explain the distribution of cavernicolous or "cliff dweller" birds that are more widespread in northern South America (*e.g.* the oilbird *Steatornis caripensis* a common inhabitant of tepui canyons), but it fails to explain the diversity of tepui summit amphibians and reptiles.

Mountain Bridge theory

Phylogenetic and temporal predictions: Multiple co-occurrences of congeneric species in the Andes and in Pantepui.
Discussion: Hoogmoed (1979) and McDiarmid & Donnelly (2005) rejected this model for amphibians and reptiles because no geological evidence for such connection exists [although Galvis Vergara (1994) presented new elements reported as in favour of this possibility]. My results point in the same direction as that of Hoogmoed (1979) and McDiarmid & Donnelly (2005) mostly because if a mountain bridge would have existed between Pantepui and the Andes in some recent geological time we should probably observe more genera with species distributed in the two areas, which is not the case. There are very few affinities between the Andean and the Tepuian contemporary herpetofauna. The only primarily Andean genera found on tepui summits are the lizards *Anadia* [with one tepui summit species and one upland species described so far (Chapter 7, Myers *et al.* 2009)], and *Euspondylus* [with one tepui summit species recently described (Myers *et al.* 2009)]. These species are more likely relatively recent invaders from the highlands of northern Venezuela.

Conclusion

Paraphrasing Bush (1994), speciation in Pantepui is a necessarily complex model (see also Rull 2008). Multiple nonexclusive processes implying vicariance and dispersal probably promoted the origin and the diversification in Pantepui possibly according to the following sequence based on the Plateau, Disturbance-Vicariance, and Habitat Shift theories: (1) pre-Quaternary vicariance, (2) recent reorganization of species diversity constrained by climatic instability (climate oscillations), (3) recent invasions (post-Pleistocene) of widespread upland taxa.

The diversification model hypothesized here appears congruent with the biogeographical history of taxa other than amphibians and reptiles. It is consistent with most geological data, and does not support the postulate of the tepuis being formed and already isolated in the Cretaceous (70–90 mya) as claimed by Salerno *et al.* (2012), rather suggesting a period of accelerated uplift and high fragmentation during the Eocene/Oligocene (25–45 mya), and a more recent period for complete isolation of individual tepui summits (late Miocene to Holocene). Results suggest that connective "bridges" between some tepui summits could have existed until relatively recently. Remnants of these possible past connections are detectable on relief maps (Fig. 3). These ridges are now too low and ecologically too different from the summit habitats to allow contemporary dispersion between tepui tops, but they might have been higher until the Pleistocene and used by some summit organisms during possible diasporas caused by forced migrations due to climate instability.

It is interesting to note that early scientists (*i.a.* Mayr & Phelps 1967, Cook 1974, Haffer 1974) who had "only" their taxonomic knowledge at hand already drafted the main principles of the Pantepui biogeographical history, which are here at least partially supported by molecular evidence.

The antagonism between vicarianists and dispersalists is no longer legitimate because both mechanisms apparently shaped the Pantepui biodiversity. As explained above, the stumbling block has most likely been a probably erroneous estimation/interpretation of the timing of the Pantepui orogeny and geomorphology as recently exemplified in Salerno *et al.* (2012). The extent to which this preconception of Cretaceous tepui isolation has been influenced by Sir Arthur Conan Doyle's fiction novel " The Lost World" is quite fascinating.

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FUTURE PERSPECTIVES

> *"Your time is limited, so don't waste it living someone else's life. Don't be trapped by dogma - which is living with the results of other people's thinking. Don't let the noise of others' opinions drown out your own inner voice. And most important, have the courage to follow your heart and intuition"*
>
> S. Jobs

The results presented here hopefully shed some fresh light on the origin and diversification of the Pantepui biota, tending to reconcile geological hypotheses with molecular phylogenies. However, the molecular results should be considered as still incomplete (and to some extent speculative in Chapter 11) since they are based on a fraction of Pantepui only. Sampling in the western part of Pantepui is highly needed, and the elucidation of the phylogenetic position of some groups like *Metaphryniscus* and *Cryptobatrachus* are necessary to have a complete picture of the situation. Unfortunately the current political situation in Venezuela, and associated bureaucratic obstruction, make life of scientists (local and foreign) very hard, rendering sampling in the western Pantepui extremely challenging.

Phylogenetic and morphological analyses performed during the course of this work revealed several taxonomic issues that will be soon assessed in more details. The major ones being:

- Composition of the current species groups in *Stefania* is not congruent with the phylogenetic relationships of the species themselves (species of the *evansi* and *goini* groups are polyphyletic)
- *Stefania ackawaio* MacCulloch and Lathrop, 2002 should be synonymised with *S. roraimae* Duellman and Hoogmoed, 1984
- The occurrence of *Stefania scalae* in Guyana is not confirmed since specimens identified as *S. scalae* have been confused with *S. evansi*. The distribution of *S. scalae* is therefore still restricted to the eastern part of the Gran Sabana in Venezuela.
- Several new Pantepui taxa, at least in the genera *Anomaloglossus*, *Stefania* and *Pristimantis*, await description
- *Anomaloglossus verbeeksnyderorum* Barrio-Amorós, Santos, and Jovanovic, 2010 should be synonymised with *A. wothuja* (Barrio-Amorós, Fuentes-Ramos, and Rivas-Fuenmayor, 2004)
- *Oreophrynella dendronastes* Lathrop and MacCulloch, 2007 should be synonymised with *O. macconnelli* Boulenger, 1900
- The genus *Oreophrynella* needs to be thoroughly revised
- *Tepuihyla galani* Ayarzagüena, Señaris, and Gorzula, 1993 and *T. talbergae* Duellman and Yoshpa, 1996 should be synonymised with *T. rodriguezi* (Rivero, 1968)
- *Tepuihyla edelcae* is not monophyletic, specimens previously identified as *T. edelcae* from the Chimantá Massif (Bolívar, Venezuela) belong to a distinct, undescribed species
- *Osteocephalus exophthalmus* Smith and Noonan, 2001 and "*Hyla*" *warreni* Duellman and Hoogmoed, 1992 should be transferred to the genus *Tepuihyla*

- *Neusticurus rudis* is not monophyletic
- Close genetic relationship between *Arthrosaura guianensis* and *A. hoogmoedi* suggests reconsideration of the taxonomic status of the latter, but is in strong conflict with morphology-based analyses

Historical processes behind the isolation of Pantepui from the surrounding areas remain puzzling, and the possible role of marine incursions in the isolation of Pantepui endemics remains to be assessed. This should be done by using meta-analyses involving multiple unrelated groups.

While I was working on this thesis some more fundamental questions arose, like:

(1) What are the genetic adaptations to the tepui summit habitat? What is the genomic basis of adaptation to thermic (alternance of very low and very high temperatures), hypoxic, and oxidative (exerted by strong Ultra-Violet light irradiation) stress? Amphibians seem ideal models to study this since they need adaptation both in larval and adult stages. Why some lowland species seem to cope with these challenges, and is there any genomic differentiation between lowland and tepui top populations within a same species? Since a few taxa are found from the surrounding uplands to high tepui summits Pantepui seems the ideal region to study these exciting topics.

(2) How much of the morphological variation is truly genetic, and how much of it is merely environmentally induced?

(3) How much are patterns explained by vicariant events and how much by climate?

(4) Why do some taxa tend to actively disperse, while others remain philopatric? Does ecological plasticity have a genetic basis?

CURRICULUM VITAE | PHILIPPE JACQUES ROBERT KOK

PERSONALIA

Date of birth:	December 20, 1970
Place of birth:	Watsa (Democratic Republic of the Congo)
Nationality:	Belgian
E-mail:	philippe.kok@naturalsciences.be, pjrkok@gmail.com
Web:	www.philippekok.com

CURRICULUM

After having received his high school diploma (Athénée Royal Emile Bockstael, 1989), Philippe Kok enrolled at the Free University of Brussels (ULB) as a bachelor in Veterinary Medicine (1989), which he stopped after two years. He then spent a year at the Institut Paul Lambin (Brussels) studying Biotechnology. At the age of 22 he decided to leave Belgium for the tropics and spent several weeks in the rainforest of French Guiana, where he familiarized with field herpetology, and definitely fell in love with the tropical rainforests.

Back in Belgium in 1994 Philippe Kok was enrolled as a Research Associate at the Royal Belgian Institute of Natural Sciences (IRSNB) in Brussels, where he is still active.

Within the framework of an ongoing project on the systematics and biogeography of the Neotropical herpetofauna (with a focus on the Guiana Shield) he conducted numerous field trips mainly in French Guiana, Guyana, and Venezuela between 1996 and today (more than 20 expeditions, totalizing more than 500 days spent in the field).

In 1998 Kok and colleagues were sent one month to Thailand by the IRSNB within the framework of a project on the diversity of the reptiles and amphibians of Na Haeo, Loei Province, in collaboration with the Srinakharinwirot University, Bangkok.

In 1999 Philippe Kok started as CITES Expert (Amphibians and Reptiles) for the Belgian Government. Between 2003 and 2007 he worked as a freelance scientific consultant, notably for *Parc Paradisio* (now *Pairi Daiza*) in Brugelette, Belgium.

Between 2004 and 2008 he received substantial funding from the Belgian Directorate-General for Development Cooperation in the framework of a Global Taxonomy Initiative project on the herpetofaunal diversity of Kaieteur National Park in Guyana (and later extended to the Guiana Highlands) aiming at training local scientists in taxonomy and parataxonomy ("training through research" program).

Philippe Kok is associate editor for the journal *Phyllomedusa (Journal of Herpetology)* since 2007, subject editor for the online journal *Check List* since 2011, and member of the Scientific Board of the *Boletim do Museu Paraense Emílio Goeldi* since 2012; he has served as a reviewer for journals such as *Journal of Herpetology*, *Zootaxa*, *American Museum Novitates*, *Herpetologica*, *Journal of Biogeography*, *Contributions to Zoology*, etc. He is IUCN SSC Amphibian Specialist Group Regional Co-Chair for the Guiana Shield.

Since 2009 Kok is employed as a part-time researcher in the Amphibian Evolution Lab at the Vrije Universiteit Brussel, where he also teaches the Field Herpetology course to the second year students of Master in Herpetology.

Philippe Kok was enrolled as a PhD student in Leiden University, The Netherlands, in February 2011 under the supervision of Prof. Dr. E. Gittenberger and Prof. Dr. E. Smets.

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GLOSSARY OF GEOLOGICAL TERMS

Archean: Geologic eon before the Proterozoic, *ca.* 2,500–3,800 million years ago.

Cenozoic: Geologic era covering *ca.* 65.5 million years ago to present.

Craton: Old and stable portion of the continental lithosphere (lithosphere = rigid outermost shell of the planet).

Cretaceous: Geologic period, *ca.* 65.5–145.5 million years ago.

Denudation: The long-term sum of processes leading to a reduction of landscapes elevation.

Diabase: Subvolcanic rock.

Diagenesis (diagenetic processes): The process of chemical, physical or biological change (exclusive of weathering and metamorphism) undergone by sediments at relatively low temperatures and pressures after their initial deposition and during and after their conversion to rock (lithification).

Diastrophism: Deformation process of the earth's crust leading to the formation of continents, mountains, folds, faults, etc.

Dike (or dyke): Discordant intrusion of igneous rock cutting vertically (or almost) through and across strata (note: some dikes may be of sedimentary origin).

Edaphic: Related to soil.

Eocene: Geologic epoch, *ca.* 55.8–33.9 million years ago.

Epeirogeny (epeirogenic movements): Broad regional vertical movement (uplift or depression) of earth's crust exhibiting little folding and resulting in only mild deformation.

Erosion: Natural process by which soil and rock are removed from earth's surface by wind and water flow.

Holocene: Geologic epoch, covering *ca.* 11,700 years ago to present.

Igneous rocks: Rocks formed from the solidification of molten rock material. Igneous rock can be intrusive (solidifying below earth's surface) or extrusive (solidifying on or above earth's surface).

Intrusion: Any formation of intrusive igneous rock (*e.g.* magma cooling and solidifying within earth's crust).

Isostasy (isostatic rebound): Gravitational equilibrium between the earth's lithosphere (rigid outermost shell of the planet) and asthenosphere (highly viscous region of the upper mantel of earth lying below the lithosphere).

Jurassic: Geologic period, *ca.* 199.6–145.5 million years ago.

Kaolinite: A layered silicate mineral.

Karst: Topography largely shaped by the dissolving action of water on soluble bedrock.

K-T boundary: The Cretaceous (K)-Tertiary (T) boundary (now better known as the Cretaceous-Paleogene boundary) is a geological signature associated to a mass extinction and marks the end of the non-avian dinosaurs.

Mesoproterozoic: Geologic era, *ca.* 1,000–1,600 million years ago.

Mesozoic: Geologic era, *ca.* 251–65.5 million years ago.

Metamorphic (rock): Altered in texture, composition, or internal structure by extreme heat, pressure, and chemically active fluids.

Miocene: Geologic epoch, *ca.* 23.03–5.33 million years ago.

Mya: Million years ago.

Myr: Million years old.

Neogene: Geologic period, *ca.* 23.03–1.81 million years ago.

Oligocene: Geologic epoch, *ca.* 33.9–23.03 million years ago.

Orogeny: Processes of structural deformation of the earth’s lithosphere (rigid outermost shell of the planet) due to the engagement of tectonic plates; primary mechanism by which mountains are built.

Paleocene: Geologic epoch, *ca.* 65.5–55.8 million years ago.

Paleogene: Geologic period, *ca.* 65.5–23.03 million years ago.

Paleozoic: Geologic era, *ca.* 542–251 million years ago.

Pirophyllite (or Pyrophyllite): A layered silicate mineral.

Pleistocene: Geologic epoch, *ca.* 2.58 million years ago to 11,700 years ago.

Pliocene: Geologic epoch, *ca.* 5.33–2.58 million years ago.

Precambrian: Geologic time prior to *ca.* 542 million years ago.

Proterozoic: Geologic eon following the Archean, *ca.* 542–2,500 million years ago.

Quaternary: Geologic period, covering *ca.* 2.58 million years ago to present.

Sedimentation: Accumulation of sediment in layers.

Shale: Fine grained sedimentary rock that splits easily.

Sill: Tabular intrusion of igneous rock, usually fed by dikes.

Stratigraphic: Related to rock strata.

Subsidence: Opposite of uplift, sinking of earth’s surface in response to geologic or man-induced cause.

Tertiary: Deprecated geologic time, *ca.* 65.5–2.58 million years ago.

Triassic: Geologic period, *ca.* 251–199.6 million years ago.

Tuff: Relatively soft, porous rock composed of compacted volcanic ash or dust.

U-Pb analyses: Uranium-lead dating.

Weathering: Process that produces change in the surface of rock through contact with earth's atmosphere, biota and water. Weathering occurs *in situ* with no movement unlike erosion, which involves displacement of rocks and minerals by water, wind, etc.

STELLINGEN

Behorende bij het proefschrift
Islands in the Sky: Species Diversity, Evolutionary History, and Patterns of Endemism of the Pantepui Herpetofauna

door **Philippe Jacques Robert Kok**

1. Contrary to common belief, many extant species or populations from individual tepui summits were only recently isolated (Holocene/Pleistocene), including in genera that diverged from their known sister group in the Eocene (*this thesis*).
2. Isolation of individual tepuis most likely does not date back to the Cretaceous (*contra* Salerno *et al.* 2012), and likely did not occur before the Eocene, and not at the same pace for all tepuis (*this thesis*).
3. Endemism in Pantepui *sensu lato* most probably results from "non-stochastic" processes such as vicariance caused by geological and climatologic events (*this thesis*).
4. The antagonism between vicarianists and dispersalists is no longer legitimate because multiple nonexclusive processes implying vicariance and dispersal apparently shaped the Pantepui biodiversity (*this thesis*).
5. At the species level, faunal biodiversity and endemism on tepui summits are not "astonishing" (*contra* Rull 2009), but Pantepui could have been an ancient cradle of diversity for the surrounding lowlands (*this thesis*).
6. Morphology alone can sometimes be strongly misleading to distinguish among species in amphibians and reptiles, therefore, whenever possible, any morphological study should be performed in a molecular phylogenetic context.
7. Amphibians are ideal models to study genetic adaptation to highland habitat since they need adaptation to thermic, hypoxic, and oxidative stress both in larval and adult stages.
8. Species as we intuitively understand them are freezed frames in time. We ignore when they begin and when they end, but they are nevertheless recognized by humans since time immemorial, and are necessary components of cladogenesis.
9. Scientists always look for a pattern in observations or experimental data, a story, which sometimes confers to the quest of some sort of design. We should finally realize that there is not always a pattern and that our human brains can find patterns and stories in everything.
10. The discovery of the existence of God, or extraterrestrial life, is not worth to be published in high impact factor journals such as Science since this will only confirm widely spread believes.