



Contents lists available at ScienceDirect

Zoologischer Anzeiger

journal homepage: [www.elsevier.com/locate/jcz](http://www.elsevier.com/locate/jcz)

# The role of hand, feet, and digits during landing in anurans

Virginia Abdala<sup>a, b, \*</sup>, María Laura Ponssa<sup>c</sup>, Jessica Fratani<sup>c</sup>, Adriana Manzano<sup>d, e</sup>



<sup>a</sup> Cátedra de Biología General, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, 4000, Tucumán, Argentina

<sup>b</sup> Instituto de Biodiversidad Neotropical, UNT-CONICET, 4107, Yerba Buena, Tucumán, Argentina

<sup>c</sup> Área Herpetología, Unidad Ejecutora Lillo (UEL), CONICET-Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina

<sup>d</sup> CCYTTP. Centro de Investigaciones Científicas y Transferencia de Tecnología a La Producción, CONICET, Diamante, Entre Ríos, Argentina

<sup>e</sup> Cátedra de Embriología y Anatomía Comparadas, FCyT, Universidad Autónoma de Entre Ríos, Oro Verde, Entre Ríos, Argentina

## ARTICLE INFO

### Article history:

Received 2 April 2021

Received in revised form

5 January 2022

Accepted 7 January 2022

Available online 12 January 2022

Corresponding Editor: Janine M Ziermann

### Keywords:

Locomotion

Jump

Walk

Phalanges

Tendons

Character evolution

## ABSTRACT

Jumping consists of a series of complex movements with more variability in landing than in take-off. Different modes have been described concerning the landing phase, which seems to be linked to the general phylogenetic relationships of anuran groups. For example, the belly hit has been recorded in the basal-most living frog family Leiopelmatidae. Here we used high-speed videography to observe the role of hand and foot digits in landing behavior in ten species of neotropical anurans exhibiting different locomotor modes. We also calculated the time-lapse of each jump. We hypothesize that the role of digits can be pivotal to many anuran species during terrestrial landing. We also present data on the comparative anatomy of digits and those parts of the hands and feet involved in landing. Our video records show that landing through hand hit among anurans is performed with the distal curved phalanges of the hand digits. The morphological results show that all species surveyed, even the walker ones, exhibit distally curved phalanges, in lateral view. Movements of the distal phalanges of the hand are a key to understanding landing in anurans. All digits must be resistant to compression, since all the weight of the body falls on them. Digit hit seems to be action-driven by an elastic mechanism, which could indicate the activation, for example, of the flexor digitorum communis muscle. Landing in terrestrial frogs like *Rhinella arenarum* and *Leptodactylus chaquensis* follows a highly coordinated and synchronic pattern, with a longer time-lapse to complete each jump. Arboreal jumping frogs like *Scinax fuscovarius* and *Boana riojana* and semiaquatic hoppers like *Pleurodema borellii* and *Physalaemus biligonigerus* tend to be asynchronous and uncoordinated, but with a shorter time-lapse to complete each jump.

© 2022 Elsevier GmbH. All rights reserved.

## 1. Introduction

The most widespread mode of locomotion in Anura is jumping; however, the musculoskeletal system of the hind limbs, pelvis, and vertebral column allows them to use two or more locomotor modes with different performance (Emerson & De Jongh, 1980). This system is equally appropriate for functionally complex synchronic movements of the limb muscles, such as those used in swimming and jumping (Kargo et al. 2002), whereas walking involves other asynchronous muscle movements (Fabrezi et al. 2014). Prikryl et al. (2009) suggested that jumping is the primary locomotion activity

among anurans, whereas swimming (except in pseudines) and walking are derived specializations (Fabrezi et al. 2014).

Jumping is a locomotor mode, which consists of several movements developed in a cycle involving four phases: propulsion, flight, landing, and recovery (Nauwelaerts & Aerts 2006; Li et al. 2021). Akella & Gillis (2011) also recognized four phases, but from a kinematic perspective; take-off phase one, take-off phase two, aerial phase, and landing phase. Take-off is usually considered as tending to be much more conservative than landing. In general terms, only one way of take-off has been described (Emerson & De Jongh 1980; Zug 1985; Essner et al., 2010; Soliz et al. 2019). As anurans take off, they extend their hind limbs, using the forelimbs for landing. The forelimbs act as a pivot around which body rotation occurs (Nauwelaerts & Aerts 2006).

At least two different modes of hitting the substrate have been described among anurans: a touchdown with the body and a controlled touchdown with the forelimbs (Bijma et al. 2016).

\* Corresponding author. Cátedra de Biología General, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, 4000, Tucumán, Argentina.

E-mail address: [virginia@webmail.unt.edu.ar](mailto:virginia@webmail.unt.edu.ar) (V. Abdala).

Posteriorly, more landing modes were distinguished, such as belly hit, digit hit, and hand hit (Reilly et al. 2016; Soliz et al. 2019). These different landing modes at some point seem to be related to the general phylogenetic relationships of anuran groups, since, for example, the basal-most living frog family Leiopelmatidae exhibits the belly hit (Essner et al. 2010).

Several works have been published on the morphology of the distal phalanges of anurans, showing their high variability. Most of those papers associate the differences in the shape of anuran distal phalanges with phylogenetic relatedness (e.g., Liem 1970; Lynch 1971; Clarke 1981; Drewes 1984; Laurent 1986; Fabrezi 1996). Manzano et al. (2007) analyzed not only the skeletal differences of distal phalanges concerning the intercalary elements of arboreal anurans, but also the tendinous and muscular elements as an integrated system, considering also their evolution. The take-home messages of these studies are that the digits in anurans seem fundamental in the context of phylogenetic relatedness and that morphological variation of digits provides frogs with the functional flexibility to safely land on different substrates.

Although many studies have addressed landing in anurans and the comparative morphology of their digits, the role of digits in landing has been little explored. To date, the only reported description about the activity of digits during landing is that arboreal frogs tend to land with their digits (Bijma et al., 2016; Soliz et al., 2019).

Here we used high-speed videography to observe the role of hand and foot digits in landing behavior in ten species of neotropical anurans, and to calculate the time-lapse needed to perform each jump. We hypothesize that the role of digits can be pivotal to many anuran species during terrestrial landing. If this is the case, we expect to find morphologies associated with the behavior of digit hit, considering the high impact that digits tolerate in landing. Thus, we also present data on the comparative anatomy of digits and those parts of the hands and feet involved in landing, as observed in the video records. We selected those characters that seem crucial in performing landing and optimized them in a reduced phylogeny including the taxa analyzed. We hypothesize that our optimizations will show that digit landing is the ancestral landing mode among the analyzed taxa.

## 2. Material and methods

### 2.1. Video record

This study involved 40 individuals of 10 anuran species. The selected species included some with great ability to jump (terrestrial hopper: *Rhinella arenarum* Hensel, 1867, and terrestrial jumpers: *Leptodactylus latinasus* Jiménez de la Espada, 1875, *L. bufonius* Boulenger, 1894), some semiaquatic hoppers (*Physalaemus biligonigerus* Cope, 1861 and *Pleurodema borellii* Peracca, 1895), some that jump between tree branches (arboreal jumpers: *Boana riojana* (Koslowsky, 1895) and *Scinax fuscovarius* Lutz, 1925), some that do not jump and walk on the ground (terrestrial walker: *Melanophryniscus rubriventris* (Vellard, 1947)), and some that walk on tree branches (arboreal walkers: *Phyllomedusa sauvagii* Boulenger, 1882 and *Ph. boliviana* Boulenger, 1902) (Table 1).

Frogs were induced to jump on a surface by approaching the observer's hand or by gently tapping the posterior part of their body. Jumps were recorded with a high-speed video camera (FAST-TEC IMAGING, Model: TS5; Fastec Imaging Corp. San Diego, USA) at 250 frames per second (fps) in lateral view. Walker species, characterized by slow movements, were recorded with a full HD video camera JVC GZEX210BU at 50 fps in lateral view. Selected videos of landing in the studied species are included as Appendix A.

Based on the total of 431 video records, we estimated the time-lapse required to jump according to the different locomotor modes and species. The raw data of the hand first hit and the feet hit (or belly hit) are included in the Appendix A (Time-table). Differences between these values were considered as a proxy of the jumping time. We recorded the time-lapse between the first hit of the forelimbs and the hind limbs on the substrate during landing. We also classified individual lands in synchronic (both forelimbs hit the substrate simultaneously), asynchronous (right or left forelimb hit the substrate first), and body hit (any other body part impacts first on the substrate). We analyzed the difference in time-lapse among the selected species including the weight, habitat-locomotion categories, and developmental stage as factors in Analysis of Variance (ANOVA) models. The analysis and graphs were attained using packages nlme 3.1–153 (Pinheiro et al. 2021) and ggplot2 3.3.5 (Wickham, 2016) in R 4.4.1 (R Core Team, 2021).

This research was approved by the committee of care and use of laboratory animals of the Universidad Nacional de Tucumán (CICUAL-UNT), under the resolution n° 032/2021.

### 2.2. Morphology

Since the video records show that frogs tend to use the terminal part of the digits for landing, we focused on the general morphology of the distal phalanges. Sixty-one dried skeletons and cleared and stained (see Wassersug 1976) specimens of all selected species were examined (Appendix B). All the specimens belong to the Herpetological collection of Fundación Miguel Lillo (FML), Tucumán, Argentina, and the Laboratorio de Genética Evolutiva (LGE), Misiones, Argentina. Material from one morphological database was also reviewed: Morphosource <http://to.morphosource.org>. As the palmar and plantar sesamoids are closely related to hand and foot movements (Sustaita et al. 2013; Manzano et al. 2017), we also considered data on their presence from our material and those presented in Ponssa et al. (2010). Data on the patterns of the mm. extensor digitorum and flexor digitorum communis from 14 anuran specimens were also included, because they are fundamental structures driving the movement of hand and foot digits (Appendix B). Descriptions and figures are based on features observed in digit IV. We adopted the terminology of Fabrezi (1996) and Manzano et al. (2007) for the terminal phalanges. Names of muscles and tendons follow Manzano et al. (2007, 2008), Abdala & Diogo (2010), and Blotto et al. (2020).

### 2.3. Character evolution

To construct our data set, we coded the primary locomotor mode exhibited for each taxon. This main mode is what the species most frequently do, although we know that animals use more than one locomotor mode. We did not consider additional behavioral abilities that could make us lose the focus of our work.

For reconstruction of character evolution, data from the video records and morphology were included in a matrix (Appendix C) and optimized onto a pruned version of the anuran phylogeny of Jetz & Pyron (2018). We pruned the selected phylogeny to contain only the 10 species used in this analysis. The tree was drawn with TNT software (Goloboff et al. 2008) and the optimization was performed under parsimony, with Winclada software (Nixon, 1999). Some ambiguous optimizations were solved using a delayed transformation (DELTRAN) (for a methodological justification, see Agnarsson & Coddington, 2008).

We consider that the characters included in the matrix hold the primary homology criterion, i.e., the untested proposal that two parts are the same by inheritance (de Pinna, 1991). The proposed primary homology is based on reasonable assessment, in this case,

**Table 1**

Habitat and primary locomotion type of the selected species for this study. The respective literature reference, and number of recorded individuals are included. We analyzed an average of ten recordings per specimen and a total of 431 jumps or walking cycles.

Species	Habitat/locomotion	Literature reference	N Juvenile	N Adult
<i>Boana riojana</i>	Arboreal/jumper	Soliz et al. (2019)	2	1
<i>Leptodactylus bufonius</i>	Terrestrial/jumper	Reilly & Jorgensen (2011), Fratani et al. (2018)	3	4
<i>Leptodactylus latinasus</i>	Terrestrial/jumper	Gallardo (1958), Fratani et al. (2018)	2	3
<i>Melanophryniscus rubriventris</i>	Terrestrial/walker	McDiarmid (1971)	-	2
<i>Phyllomedusa boliviana</i>	Arboreal/walker	Vaira (2001), Wells (2007)	-	2
<i>Phyllomedusa sauvagii</i>	Arboreal/walker	Cei (1980), Wells (2007)	-	6
<i>Physalaemus biligonigerus</i>	Semiaquatic/hopper	Reilly & Jorgensen (2011), Fratani et al. (2018)	5	-
<i>Pleurodema borellii</i>	Semiaquatic/hopper	Reilly & Jorgensen (2011), Crump (2015)	-	1
<i>Rhinella arenarum</i>	Terrestrial/hopper	Reilly & Jorgensen (2011)	4	2
<i>Scinax fuscovarius</i>	Arboreal/jumper	Cei (1980), Soliz et al. (2019)	3	3

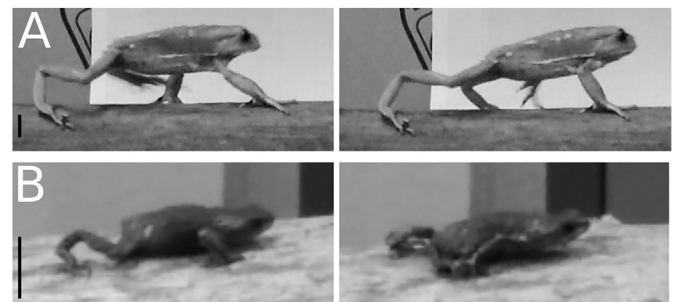
topology and function (Agnarsson & Coddington 2008). If the proposed primary homology passes the test, the character will constitute a synapomorphy (de Pinna 1991). Characters 5, 9, 10, and 11 are uninformative of the phylogenetic relationships since they do not present interspecific variations; however, we included them in the dataset because they show general morphological characteristics that shape the body plan of the studied species.

### 3. Results

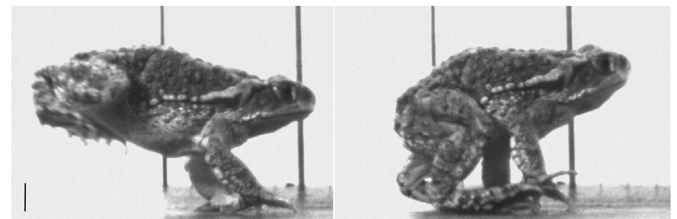
#### 3.1. Video record

The analyzed species exhibited two types of locomotion, jumping (character 0, state 0; *Leptodactylus latinasus*, *L. bufonius*, *Rhinella arenarum*, *Boana riojana*, *Scinax nasicus*, *Physalaemus biligonigerus*, *Pleurodema borellii*; Fig. 1) and walking (character 0, state 1; *Phyllomedusa sauvagii*, *Ph. boliviana*, *Melanophryniscus rubriventris*; Fig. 2). We consider a proper jump when it is performed following the commonly described phases (see, e.g., Nauwelaerts & Aerts 2006; Reilly et al. 2015; Akella & Gillis (2011); Li et al. 2021), and in which the specimen takes off and lands without sliding on the substrate. In a proper jump, landing is performed as follows:

The frog extends its forelimbs, landing with the digits of both hands synchronically and coordinated, while the hind limbs are flexed against the body (Fig. 3). In the recovery phase, the hind limbs move forward, describing a semicircular trajectory, until the feet, still suspended, are placed in the proper position to contact the substrate in the landing phase; after the foot contact, the toes touch the ground with their curved extremes (character 1, state 0; *Leptodactylus latinasus*, *L. bufonius*, *Rhinella arenarum*; Fig. 1A), and propel the body in a new take-off. In a proper jump, the movements of hands, forelimbs, feet, and hind limbs are all coordinated and synchronic. Three of the selected species do not follow the coordinated, synchronic sequence (character 1, state 1; *Boana riojana*,

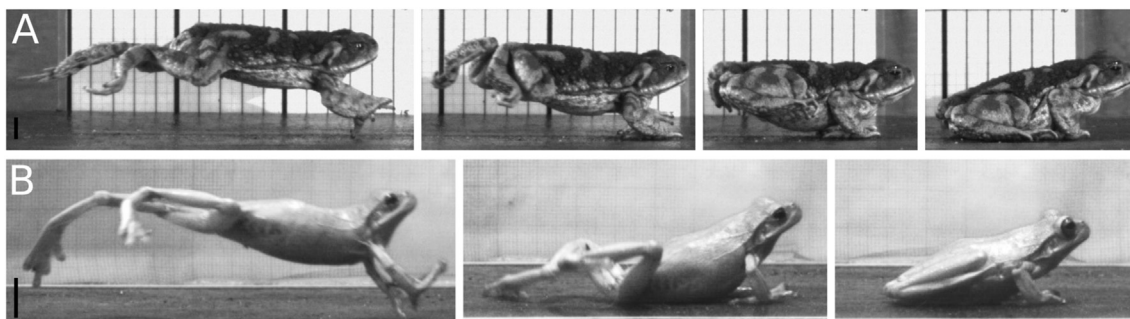


**Fig. 2.** Still images from two sequences of walking (A) *Phyllomedusa sauvagii*: the body is carried by the hand digits and toes, which are also supported by the curved distal phalanges (B) *Melanophryniscus rubriventris*: the body is nearly attached to the ground, the elbow is directed upwards, whereas the hind limbs are flattened against the floor, with the knee directed forward. Scale bars = 10 mm.



**Fig. 3.** Still images from the landing sequence of *Rhinella arenarum* showing the tibiale-fibulare hit. Scale bar = 10 mm.

*Scinax fuscovarius*; *Physalaemus biligonigerus*; *Pleurodema borellii*; Fig. 1B). In these cases, several alterations of the proper jump occur. One of the most frequent is a belly hit after the hand digits hit.



**Fig. 1.** Still images from two sequences of jumping during the landing phase (A) *Rhinella arenarum* extends its forelimbs synchronically and lands with the digits; the hind limbs are flexed against the body (B) *Boana riojana* landing on its belly, without synchronic or sequential movement of forelimbs. Scale bars = 10 mm.

Three of the selected species present a quadrupedal walking gait (character 2; *Phyllomedusa boliviana*, *Ph. sauvagii*, and *Melanophryniscus rubriventris*). On occasions, these three species jump, hitting with their bellies after the hands, without the typical take-off and landing body postures. We detected two types of quadrupedal gaits. One of them exhibits semi-erected limbs that move in alternating, diagonal pairs (Ahn et al. 2004; Reynaga et al. 2018); the elbow is flexed backward, while the knee is flexed forwards. The body is carried by the hand digits and toes, which are also supported by the curved distal phalanges (character 2, state 0; *Phyllomedusa* species; Fig. 2A). In the other gait, the frog maintains its body nearly attached to the floor, the elbow is directed upwards, while the hind limbs are flattened against the floor, with the knee directed forward. While walking, the toad hardly lifts its body off the ground (character 2, state 1; *Melanophryniscus rubriventris*; Fig. 2B). In both gaits, the tips of the digits remain curved.

Among the species that do jump, we distinguished two different hind quarter hits: foot sole hit (tarsal and metatarsal) (character 3, state 0; *Leptodactylus latinasus*, and *L. bufonius*, *Rhinella arenarum*, *Physalaemus biligonigerus*, *Pleurodema borellii*; Fig. 1A), and tibiale-fibulare hit (character 3, state 1; *Rhinella arenarum*; Fig. 3). Some species can occasionally also hit with the belly, always after the hand digit hit (character 3, state 2; *Boana riojana*, *Scinax fuscovarius*; Fig. 1B). In the landing of *Leptodactylus latinasus*, *L. bufonius*, *Rhinella arenarum*, and *Physalaemus biligonigerus*, and occasionally *Boana riojana*, the hand first hits the substrate with the digit of both hands simultaneously touching the floor in a conservative sequence, digit 2 followed by digit 3, then digit 4 and the last one is always digit 5 (character 4, state 0; Fig. 4). Another hand hit was recorded, without the already described coordinated, synchronic sequence. In this case, the frog tends to reach the walls of the terrarium instead of the floor, using the adhesive pads of its hand digits, performs a circular movement with its hind limbs, and surrounds the stuck hand digits, until it attaches the hind limbs to the wall. Either the digit pads of the forelimbs or of the hind limbs are used to attach to the substrate (see also Bijma et al. 2016) (character 4, state 1; *Boana riojana*, *Scinax fuscovarius*; Fig. 5).



**Fig. 4.** Still images from hand hit sequence during landing in *Rhinella arenarum*. The hand hits the substrate first, with the digit synchronically touching the ground in a conservative sequence, digit 1 followed by digit 2, then digit 3 and the last one is always digit 4. Scale bar = 10 mm.

The time-lapse between fore- and hind limb is significantly related to the body mass of the sampled species ( $R^2 = 0.1654$ ;  $P < 0.01$ ). There is a marked tendency to a shorter time-lapse and a higher frequency of asynchronous digits hit of both hands, and body hits in semiaquatic hoppers and arboreal jumpers species compared to terrestrial hoppers and jumpers (Fig. 6). The ANOVA model comparing time-lapse among habitat-locomotion categories showed that semiaquatic hoppers differ significantly from terrestrial jumpers, and arboreal jumpers differ significantly from terrestrial hoppers and jumpers (Table 2). The ANOVA model comparing time-lapse among species showed that *Leptodactylus bufonius*, a terrestrial jumper, significantly differs from *Boana riojana*, *Scinax fuscovarius*, and *Physalaemus biligonigerus*, two arboreal jumpers, and a semiaquatic hopper, respectively (Table 3). *Rhinella arenarum*, a terrestrial hopper, significantly differs from *P. biligonigerus* and *S. fuscovarius*. Although there is a trend to a shorter time-lapse in juvenile stages, when compared to adults, there was no significant difference between developmental stages within each category.

## 3.2. Morphology

### 3.2.1. Digit position at rest

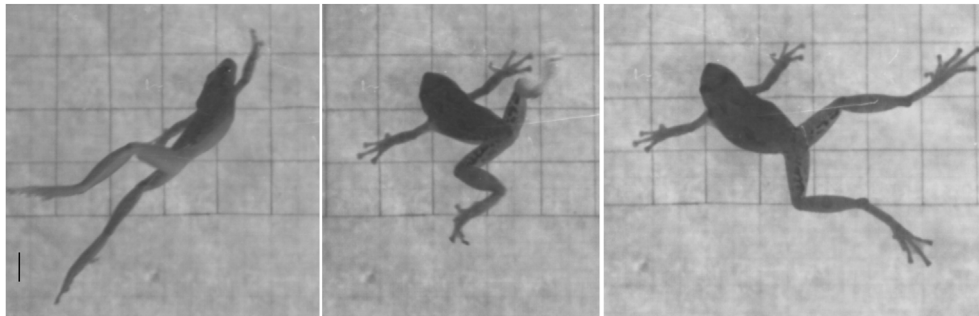
Video records and photographs of all the studied anuran species show the tips of the digits curved on the substrate at rest (character 5, state 0; Figs. 1–3).

### 3.2.2. Terminal phalanx skeleton

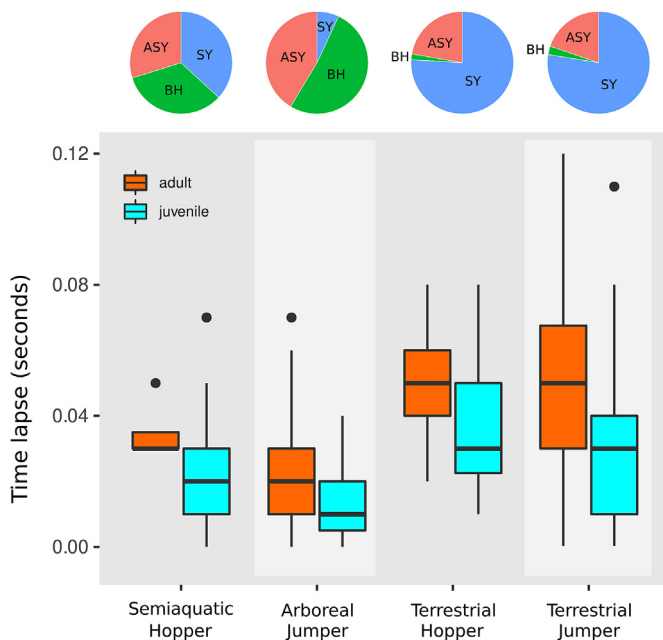
The studied skeletons showed that the distal phalanges of hands and feet tend to be morphologically similar. Two general morphological patterns of distal phalanges in lateral view were observed: simple distal phalanges with an undivided extreme, and distal phalanges with a divided, bifurcated extreme (Fig. 7). Among the simple terminal phalanges, there is a pointed, curved type, slightly displaced from the digit axis because of the intercalary cartilage element located between the last and the penultimate phalanx (see Manzano et al. 2007). This morphology corresponds to the “clawlike” of Drewes (1984) and Fabrezi (1996) (character 6, state 0; *Boana riojana*, *Phyllomedusa sauvagii*, *Ph. boliviana*, *Scinax fuscovarius*; Fig. 7A). Among the digits lacking intercalary elements, we recorded a curved tip of the distal phalanx elements (character 6, state 1; *Physalaemus biligonigerus* and *Pleurodema borellii*). We also recognized a truncated, blunt phalanx, curved or slightly curved (character 6, state 2; *Rhinella arenarum*; Fig. 7B). We recorded a truncated mostly curved distal phalanx (character 6, state 3; *Scinax fuscovarius*; Fig. 7C; *L. latinasus*). We found another type of simple phalanx tip, with a dilated and irregular phalanx, and with cylindrical protuberances towards the ventral area (character 6, state 4; *Melanophryniscus rubriventris*; Fig. 7E). We also found terminal phalanges with a T-shaped divided extreme (character 6, state 5; *L. bufonius* and *L. latinasus*; Fig. 7F, see also Fabrezi 1996; Manzano et al. 2007).

### 3.2.3. Sesamoids

Two sesamoids were identified in these species: a palmar (character 7, state 0; *Leptodactylus* species, *Rhinella arenarum*, *Physalaemus biligonigerus*, *Pleurodema borellii*) and a plantar one (character 8, state 0; *Leptodactylus* species, *Rhinella arenarum*, *Physalaemus biligonigerus*, *Pleurodema borellii*, and *Melanophryniscus rubriventris*). The palmar sesamoid (character 7, state 1; *Boana riojana*, *Phyllomedusa sauvagii*, *Ph. boliviana*, *Scinax fuscovarius*, *Melanophryniscus rubriventris*), and the plantar sesamoid (character 8, state 1; *Boana riojana*, *Phyllomedusa sauvagii*, *Ph. boliviana*, *Scinax fuscovarius*) were absent in the arboreal species and in one walker species.



**Fig. 5.** Still images from the landing sequence of *Scinax fuscovarius* showing hand hit without the stereotyped sequence. The frog reaches the walls of the terrarium using the adhesive pads of its hand digits, performing a circular movement with its hind limbs, surrounding the stuck hand digits, until it attaches the hind limbs to the wall. Scale bar = 10 mm.



**Fig. 6.** Time-lapse between fore- and hind limb hit during landing from 431 video records. Species are grouped according to habitat and locomotion mode, and colored according to developmental stage (adult/juvenile). The piecharts depict the proportion of synchronous (SY) and asynchronous (ASY) hind limb hit, or body hits (BH) during final stages of landing.

3.2.4. Selected tendons and muscles

We recognized one pattern of the m. extensor digitorum, which is common to all studied species. This muscle originates from the humerus distal condyle, inserting through three branches onto the base of metacarpals III, IV, and V (character 9; Fig. 8A). We also recognized one pattern of dorsometacarpalis proximalis and distalis tendons and muscles to each digit (character 10; Fig. 8B).

The ventral surface of the hand presents a flexor plate (Haines 1950; Abdala et al. 2009; Ponssa et al. 2010), from which the flexor tendons originate (tendo superficialis of Manzano et al. 2007). These tendons insert into the distal extreme of the distal phalanges of digits 3 to 5, with the tendon of digit 2 being independent of the flexor plate (Fig. 8C). A different pattern is observed, e.g., in *Phyllomedusa sauvagii*, in which each flexor tendon is inserted independently to each digit, without flexor plate (see also Manzano et al. 2008) (Fig. 8D). We consider that these different morphologies of the flexor surface of the hand are correlated with the presence or absence of sesamoids. Therefore, we did not code them as new characters.

In the hind limb, the m. flexor digitorum communis (plantaris longus of Dunlap 1960) communicates with the Achilles tendon. This tendon is continuous with the plantar aponeurosis, currently with an embedded plantar sesamoid (Fig. 9A), which ends in the flexor tendons inserted in the distal phalanges. This is a common pattern in the studied specimens (Character 11, state 0). In most species, the flexor tendons of toes III-V arise from the m. flexor digitorum brevis superficialis (character 12, state 0; Fig. 9B), except for *Phyllomedusa* and *Melanophryniscus rubriventris*, in which only the tendons of toes IV-V arise from m. flexor digitorum brevis superficialis (character 12, state 1; Fig. 9C).

3.3. Ancestral state reconstruction

Our optimizations (Figs. 10 and 11) show that coordinated synchronic landing with sequential digits hit and the foot sole and is the ancestral state in the studied group (Character 0 and 1). There was a switch from jumping to walking as the dominant locomotor mode as a derived state independently acquired in *Phyllomedusa* species and *Melanophryniscus rubriventris*. Synchronic jumping also gave rise to another derived state, the asynchronous and uncoordinated jump without a sequence of digit hit present in the arboreal species, and in the semiaquatic hoppers *Physalaemus biligonigerus* and *Pleurodema borellii*. The quadrupedal gait, as exhibited by

**Table 2**

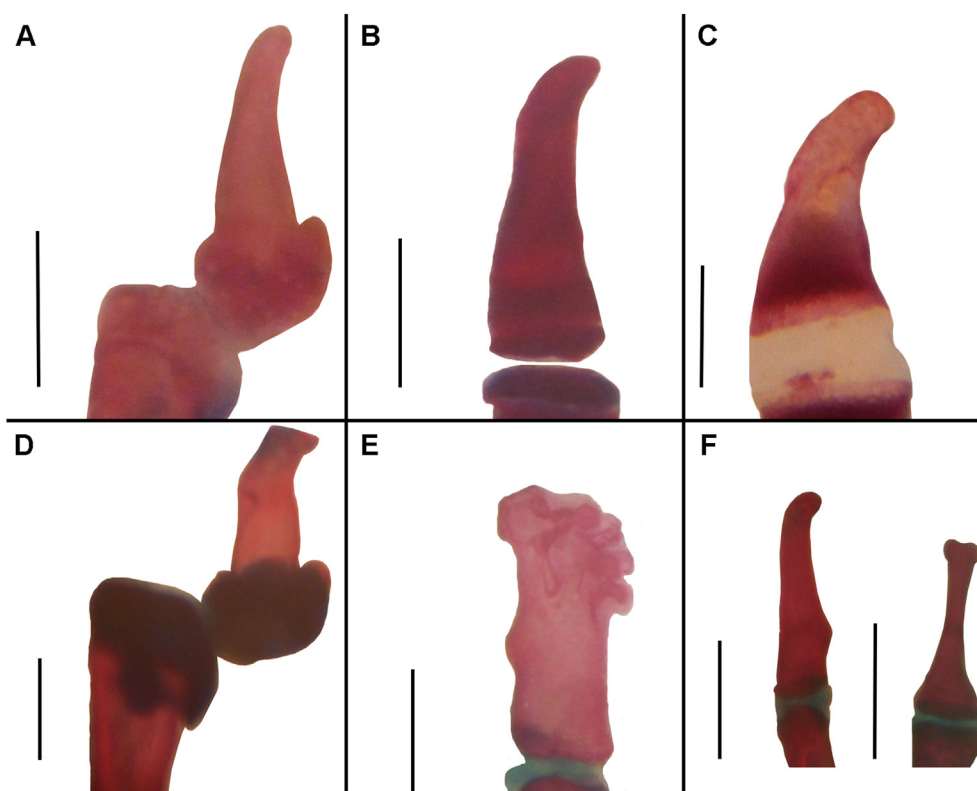
Post hoc comparisons for time-lapse among habitat-locomotion mode from 431 video records. Significant results are highlighted in bold.

habitat-locomotion mode		SE	t	p
Aquatic-hopper	Arboreal-jumper	0.01330	-1050	0.7202
Semiaquatic-hopper	Terrestrial-hopper	0.01416	-2425	0.0746
Semiaquatic-hopper	Terrestrial-jumper	0.01282	-3418	<b>0.0040</b>
Arboreal-jumper	Terrestrial-hopper	0.00776	-2626	<b>0.0447</b>
Arboreal-jumper	Terrestrial-jumper	0.00491	-6083	<b>&lt;.0001</b>
Terrestrial-hopper	Terrestrial-jumper	0.00689	-1377	0.5147

**Table 3**

Post hoc comparisons for time-lapse among species from 431 video records. Significant results are highlighted in bold.

Species		SE	t	p
<i>B. riojana</i>	<i>L. bufonius</i>	0.00542	−5152	<.0001
<i>B. riojana</i>	<i>L. latinasus</i>	0.01423	340	0.9994
<i>B. riojana</i>	<i>P. biligonigerus</i>	0.01664	2486	0.1316
<i>B. riojana</i>	<i>R. arenarum</i>	0.00794	−2100	0.2903
<i>B. riojana</i>	<i>S. fuscovarius</i>	0.00968	1518	0.6533
<i>L. bufonius</i>	<i>L. latinasus</i>	0.01358	2412	0.1555
<i>L. bufonius</i>	<i>P. biligonigerus</i>	0.01609	4306	<b>0.0003</b>
<i>L. bufonius</i>	<i>R. arenarum</i>	0.00671	1676	0.5487
<i>L. bufonius</i>	<i>S. fuscovarius</i>	0.00871	4893	<.0001
<i>L. latinasus</i>	<i>P. biligonigerus</i>	0.02078	1757	0.4952
<i>L. latinasus</i>	<i>R. arenarum</i>	0.01477	−1456	0.6925
<i>L. latinasus</i>	<i>S. fuscovarius</i>	0.01578	625	0.9892
<i>P. biligonigerus</i>	<i>R. arenarum</i>	0.01710	−3393	<b>0.0102</b>
<i>P. biligonigerus</i>	<i>S. fuscovarius</i>	0.01798	−1483	0.6754
<i>R. arenarum</i>	<i>S. fuscovarius</i>	0.01046	2997	<b>0.0348</b>



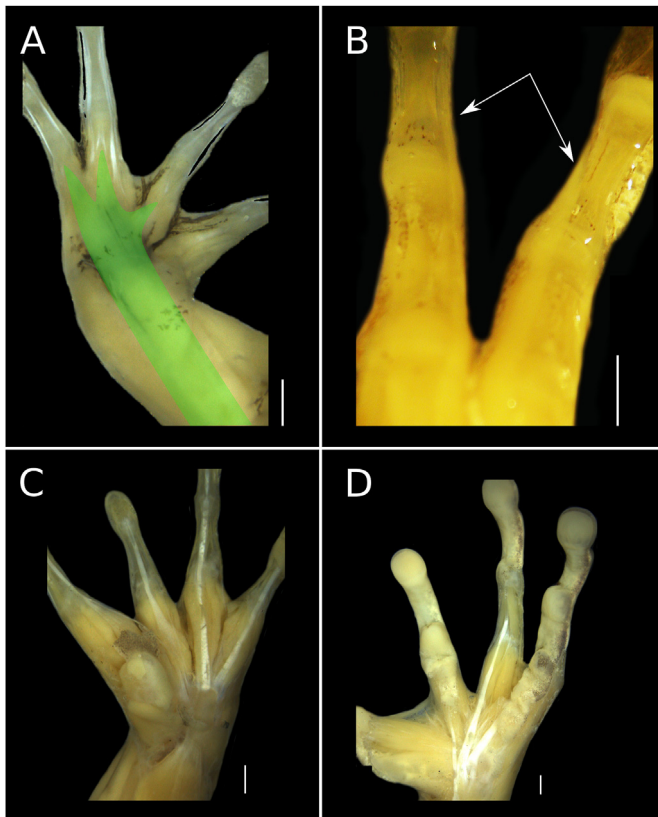
**Fig. 7.** Terminal phalanx skeleton shapes (Character 6) (A) State 0: simple, pointed, curved, with intercalary element (*Boana riojana*, FML 16882) (B) State 1: simple, curved, without intercalary element (*Physalaemus biligonigerus*, LGE 346) (C) State 2: truncated, blunt phalanx, curved or slightly curved (*Rhinella arenarum*, FML 29863) (D) State 3: truncated mostly curved last phalanx (*Scinax fuscovarius*, FML 28134) (E) State 4: simple, with a dilated and irregular phalanx, with cylindrical protuberances towards the ventral area (*Melanophryniscus rubriventris*, FML 00816) (F) State 5: Terminal phalanges with a T-shaped divided extreme (*Leptodactylus latinasus*, FML 29512 and 29515). Terminal phalanx correspond to finger IV, in lateral view (A–E); left, lateral view and right, dorsal view (F). Scale bars = 0.5 mm.

*Phyllomedusa* species, is the ancestral character state, which gives rise to the gait of *Melanophryniscus rubriventris* (Character 2).

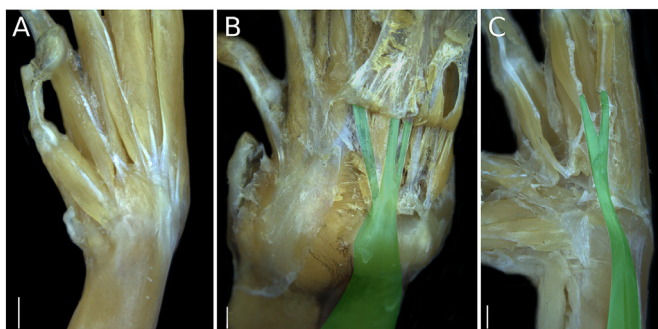
As for the terminal phalanx morphology, the pattern of the terminal phalanges of hylids, all with intercalary elements and a simple distal skeleton, is the ancestral state from which all other types of phalanges derive (Character 6). Absence of the palmar sesamoid (Character 7) appears linked to the asynchronous jumping of arboreal frogs, except for *Melanophryniscus rubriventris*. The presence of the palmar sesamoid is an ancestral state, with its absence optimizing as a putative synapomorphy of hylids and phyllomedusids. This loss appears independently in

*Melanophryniscus rubriventris*. The plantar sesamoid (Character 8) is ancestrally present in anurans, and is secondarily lost in the species belonging to the hylid and phyllomedusid families (Ponssa et al. 2010). The flexor tendons of toes III to V, originated from m. flexor digitorum brevis superficialis, are the ancestral pattern (Character 12); the derived state of only the flexor tendons of toes IV and V being originated from this muscle was independently acquired by the species exhibiting a quadrupedal gait.

Four characters are not variable in the species surveyed and show a common morphology associated with the anuran bauplan: the tip of the digit curved on the substrate at rest (Character 5); the



**Fig. 8.** Morphological characters of the hand (A) *m. extensor digitorum* highlighted in green, inserting through three branches onto the base of the metacarpals III, IV, and V. Digit 1 to the right (B) *m. dorsometacarpalis distalis* and its tendons, and the *m. dorsometacarpalis proximalis* and its tendons, between digits 5, to the left, and 4 to the right (C) Flexor tendons of digits 3 to 5 and flexor plate. Digit 1 to the left (D) Independent flexor tendons (absence of flexor plate). Digit 1 to the left. Scale bar = 1 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 9.** Morphological characters of the feet (A) Aponeurosis plantaris of *Scinax fuscovarius* (L 1424). *m. flexor digitorum brevis superficialis* gives rise to the flexor tendons of toes III-V in (B) *Rhinella arenarum* (L 1427), and to the tendons of toes IV-V in (C) *Phyllomedusa boliviana* (L 1531). Digit 1 to the left. Scale bars = 1 mm.

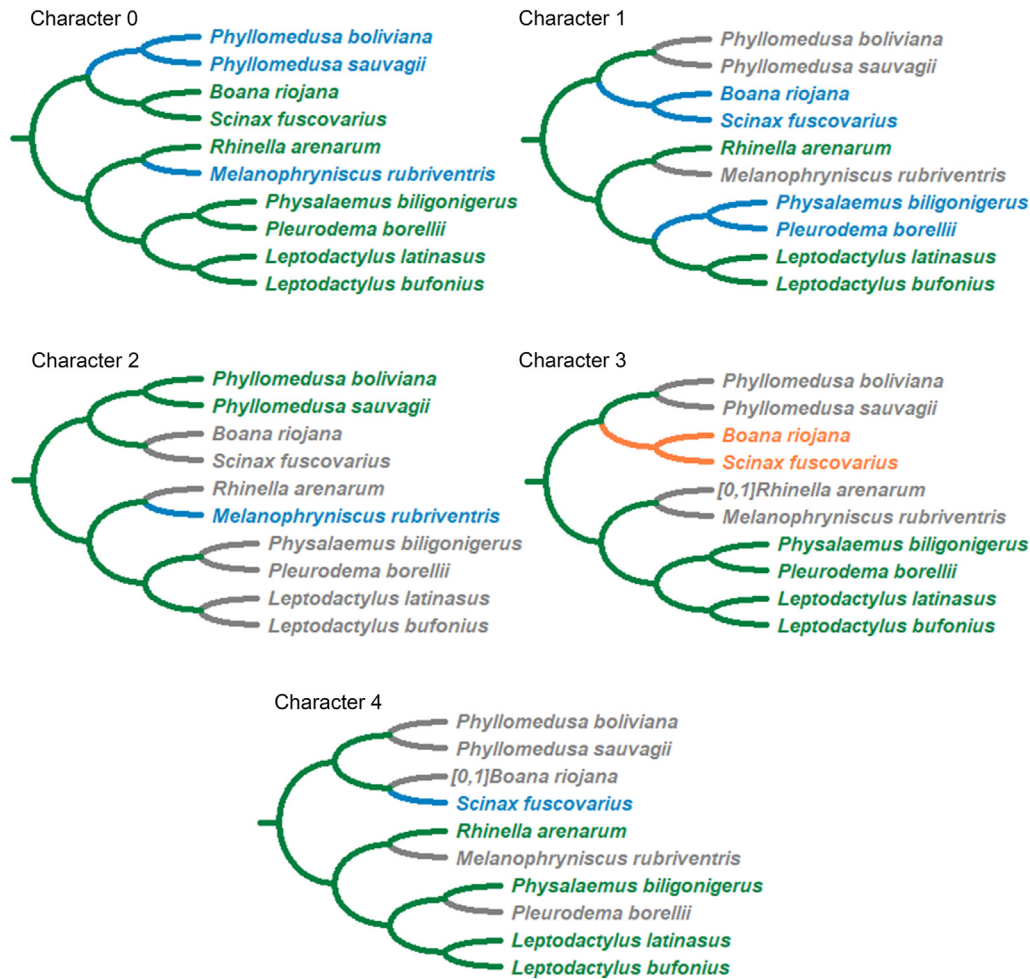
extensor digitorum muscle that originates from the humerus distal condyle (Character 9), inserting through three branches onto the base of the metacarpals III, IV, and V; digits served by dorsometacarpalis and their tendons (Character 10); the Achilles tendon continuous with the plantar aponeurosis, with or without an embedded plantar sesamoid, which ends in the flexor tendons inserted in the distal phalanges (Character 11).

#### 4. Discussion

Our video records clearly show that landing through hand hit among anurans in this analysis is mostly performed with the distal curved phalanges of the hand digits. The morphological results show that all species surveyed exhibit the distal phalanges curved, in lateral view, even the walker ones. Our optimization analysis shows that jumping is the ancestral locomotor mode of the studied group, which is consistent with the previous proposal for anurans (see also Jenkins & Shubin 1998; Prikryl et al. 2009). The curved distal phalanges are also ancestrally present in the studied group. Indeed, movements of the hand distal phalanges are a key aspect to understanding landing in anurans. All digits must be resistant to compression, since all the weight of the body falls on them. Furthermore, sometimes the body is supported only by one digit, as can be seen in the Fig. 1A. The skeletal anatomy does not show signs of bone reinforcement; therefore, the extra resistance is probably achieved by the position of the digits and the angles formed between them. Our character reconstruction shows that digits hit following a stereotyped sequence is the ancestral state from which the other, less standardized jumping, derives. The curvature of the distal phalanges can also be thought of in another functional context. Most vertebrates have claws, which are probably their most common biological mechanism of adhesion (Tulli et al., 2009; Zani, 2000). Anurans lack claws; it could be inferred that their adhesion to the substrate could be less efficient. Curved distal phalanges could alleviate this handicap, helping to anchor the frog to the substrate avoiding slipping. Unfortunately, this line of research has seldomly been studied in depth.

Hand distal phalanges are served by the flexor tendons, which are originated from the flexor plate (Haines 1950; Abdala et al. 2009) in the species of *Leptodactylus*, *Rhinella*, and *Physalaemus*. In all these cases, a palmar sesamoid is embedded in the tendon of the *m. flexor digitorum communis* (Ponssa et al. 2010). The presence of a palmar sesamoid is the ancestral state character. In the species of *Phyllomedusa*, *Boana*, and *Scinax*, the flexor tendons are originated from the *m. flexor digitorum communis*, without integrating a flexor plate (Manzano et al. 2008; Sustaita et al. 2013; De Oliveira-Lagôa et al. 2019); the absence of a palmar sesamoid is a state independently acquired by *Melanophryniscus rubriventris*. Thus, digit hit seems to be action-driven by an ancestral elastic mechanism, which could indicate the activation, for example, of the flexor digitorum communis muscle (Reynaga et al. 2019). This muscle plays a pivotal role in modulating performance, probably induced by the mechanical interactions of the limb and the substrate. Mendoza et al. (2020) concluded that much of the variation in anuran jumping power can be related to the effectiveness of using elastic mechanisms. Although the authors did not refer to the flexor tendons, the same rationale could be used to explain landing through digit hit. In this case, the palmar sesamoid probably keeps the distal phalanges in the correct position by maintaining the flexor tendons with adequate tension (see also Sustaita et al. 2013; Manzano et al. 2017). Loss of the palmar sesamoid plus the independence of the hand flexor tendons (Manzano et al. 2008) evolved to the pattern typical of arboreal species with an asynchronous jump, except for *Melanophryniscus*, a typically walker frog. In this last case, the absence of the palmar sesamoid is a convergence that can not be attributed to functionalist or ecological explanations.

The critical role of arm and forearm muscles in-air positioning of the manus and digits before landing was clearly established (Akella & Gillis 2011; Ekstrom & Gillis 2015). Ekstrom & Gillis (2015) analyzed the wrist muscle activation prior to landing in the *m. extensor carpi ulnaris*, *m. extensor digitorum* (which the authors refer to as *extensor digitorum communis longus*); the wrist flexors, *m. flexor carpi ulnaris*, and the *m. flexor digitorum communis*

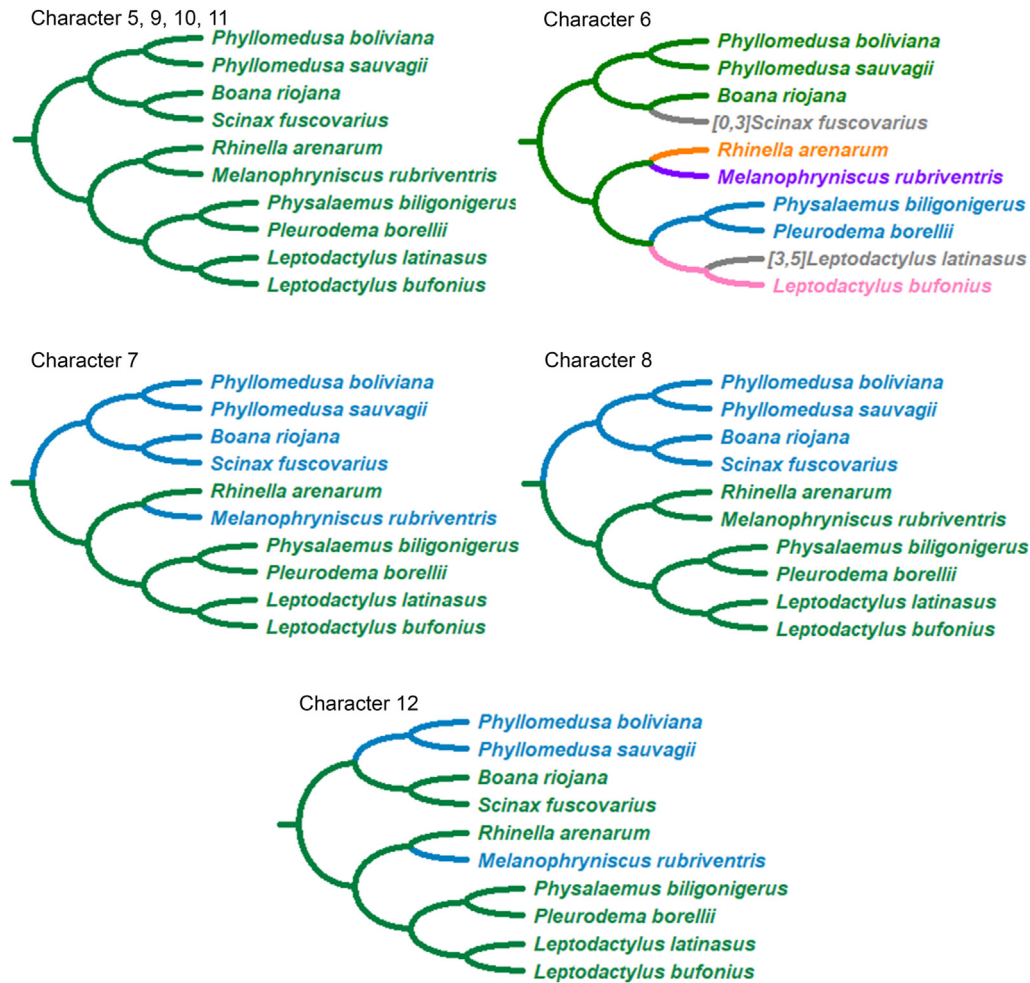


**Fig. 10.** Pruned phylogeny of Jetz & Pyron (2018), showing the relationships among the analyzed taxa. Mapping of the characters 0 to 4. Colors indicating states: green: state 0; blue: state 1; orange: state 2; red: state 3; violet: state 4; pink: state 5; gray: ambiguity. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(mentioned as *m. palmaris longus* in that work). The authors concluded that in all those muscles, activation intensity was greatest shortly before impact, indicating the importance of those muscles during landing. Thus, it could be safely inferred that the co-contraction of the *m. extensor digitorum* and *m. flexor digitorum communis* is the factor that stiffens not only the wrist joint but also the joint between the penultimate and ultimate phalanges of the hand digits. The earlier pre-landing activity of the *m. extensor digitorum* and the *m. flexor digitorum communis* (Ekstrom & Gillis 2015) added to the curvature of the distal phalanges - maintained by the flexor tendons-make up a complex device appropriate for a safe landing. It is also important to consider that the forelimbs are used as brakes when an excessive impulse during the take-off throws the body too far forward. To obtain the needed strength, both flexors and extensors should be activated and tuned simultaneously, not only prior to (Ekstrom & Gillis 2015) but also during landing, considering their importance in stabilizing the wrist joint at impact (Ekstrom & Gillis 2015). It is probably due to all these fundamental actions that these muscles tend to have a common general pattern in all the surveyed species. Another shared character among all the landing types is the curvature of the digit tip, which would be the optimal configuration to anchor the body to the substrate, counteracting the momentum of movement during locomotion.

In the hind limb, the *m. flexor digitorum communis* also plays a key role during landing. This muscle connects with the aponeurosis plantaris through the Achilles tendon. Astley & Roberts (2012) showed that early in the jump, the *m. flexor digitorum communis* (mentioned as *plantaris longus* in their work) is shortened without joint movement, stretching the associated tendons, and storing the work done by muscle contraction. This stretching of the tendons could also enhance the distal phalanges curve. As can be easily observed in the video records (Appendix A), the frogs hit the ground with the foot soles -tarsal and metatarsal-, as in the *Leptodactylus* species, or with the tibiale-fibulare or the foot soles, as in *Rhinella arenarum*. Landing with the tibialefibulare in *Rhinella* may facilitate a faster recovery to perform the bounding step described by Reilly et al. (2015, 2016). Once the tibiale-fibulare area touches the ground, the sole of the foot is elevated, ready to propel the body for the next take-off (Appendix A) through its hit with the ground. This jumping mode leaves the frog in the optimal position to perform the next jump. Thus, it does not need to allocate time to prepare for another jump. Interestingly, many anuran species, including *Rhinella*, present one or two sesamoids located in the hit area of the tibiale-fibulare, which would act analogously to the sesamoids of the knee joint – e.g., patella – as an anatomic pulley for the *m. flexor digitorum communis* (*plantaris longus*) (Ponssa et al. 2010). The same catapult-like mechanism (Astley & Roberts





**Fig. 11.** Pruned phylogeny of Jetz & Pyron (2018), showing the relationships among the analyzed taxa. Mapping of the characters 5 to 12. Code colors as in Fig. 10. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2012) can be obtained either by hitting with the foot sole or the tibiale-fibulare. Thus, hind limb landing of toads seems to be more versatile than the landing of the other jumper frogs such as *Leptodactylus* species, which always land with the foot soles. Interestingly, on rare occasions, arboreal frogs such as *Scinax* can also land with a tibialefibulare hit (Appendix A).

Landing in arboreal jumper frogs like *Scinax fuscovarius* and *Boana riojana* or semiaquatic hoppers like *Pleurodema borellii* and *Physalaemus biligonigerus* does not show a consistent pattern. These species can perform a sequential hand digit hit, as *Rhinella arenarum* does, but it is often followed with a hit performed with any part of their body, frequently the bellies. Thus, one is tempted to consider that these frogs do not jump well. However, their jump is performed in a shorter time than in *Rhinella* and *Leptodactylus*, and they have managed to survive and are very successful in terms of both diversity and geographical distribution (Faivovich et al., 2005). It seems more accurate to interpret jumping in arboreal frogs in terms of trade-offs. Arboreal frogs jump on moving compliant substrates, usually branches that deform under loads, absorbing energy that can be returned or lost (Astley et al. 2013). Many arboreal frogs are capable of regaining the energy lost in the branches, making some behavioral adjustments necessary to avoid falling down (Astley et al. 2013; Vera et al. 2020). Thus, arboreal jumper frogs have grasping hands and feet, and present morphological devices such as the intercalary elements and adhesive pads

(Manzano et al. 2007), which also contribute to their stability in the arboreal niche of the narrow branches. The environmental compliance and energy regaining, apart from their lower weight, could explain the shorter time-lapse in performing jumping and the less stereotyped sequence of movements in arboreal and semiaquatic frogs than the terrestrial ones. Terrestrial frogs are heavier, and face a mostly non-compliant environment requiring more rigid behavior to sort out the obstacles without damage. When terrestrial animals land, they face considerable large ground reaction forces that could damage their musculoskeletal and tendinous systems. A good posture during jumping would prevent damage (Azizi et al. 2014). The preponderance of the synchronic and coordinated landing in terrestrial frogs can be understood as the proper posture achieved through the cooperative behavior and function of fore- and hind limbs (Li et al. 2021) resulting in a persistently similar pattern of landing. The synchronicity and coordination shown by terrestrial frogs could be thus explained as a way to protect themselves from injuries. In addition, our data suggest that meeting all phases of the terrestrial frogs' jump requires more time than a simple recovery without any sequence specification.

As for the walker frogs, although they can occasionally jump, having thus the abilities and general morphological bauplan of any anuran, most of the time they walk. *Phyllomedusa* species exhibit elongated hind limbs compared to the forelimbs; thus, as

specialized walkers, they deviate from the symmetry between fore and hind limbs typical of anurans (Reynaga et al. 2018). *Melanophryniscus*, which according to our records, moves very differently from *Phyllomedusa* species, does not exhibit remarkably different traits in limb length, and joint-angle patterns between fore- and hind limbs from those of *Phyllomedusa* (Reynaga et al. 2018). These authors also found that quadrupedal walking frogs use similar proportions for their fore- and hind limb lengths across a stride. Interestingly, despite the big differences in body postures used for walking, *Phyllomedusa* and *Melanophryniscus* do not exhibit concomitant differences, for example, in pitch angles (Reynaga et al. 2018). They seem to overcome the constraints of a jump-adjusted morphology by a fine-tuning of the vertical extension in the fore- and hind limbs, increasing their elevation angle during a stride (Reynaga et al. 2018). These results highlight that despite their very different postures, walker frogs exhibit a remarkably constant pattern in the solutions to the problem of walking with a jumper body.

In general terms, our ancestral character state reconstruction showed interesting historical evolutionary trends. Thus, for example, the loss of the simultaneity between both hand digit hits in the jumping locomotor mode, the loss of the sequence of digit hit, and the loss of the palmar and plantar sesamoids seem to be linked to the genesis of the asynchronous, uncoordinated jumping typical of the arboreal frogs. Furthermore, the loss of the digit III tendon of *m. flexor digitorum brevis superficialis* characterizes the walker species surveyed. Interestingly, the same trend is present in relation to the skeleton of the distal phalanges, because the intercalary elements typical of the asynchronous, uncoordinated arboreal jumper species constitute the ancestral state character. The intercalary elements are lost in all other species more derived in the phylogeny. Taken together, the evolutionary history of most of the selected characters indicates a general process that suggests a loss of functions and morphological structures; however, such loss was not a disadvantage but allowed the invasion of a new locomotor niche in the analyzed group.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgement

We are grateful to Matías Barrantes (Instituto de Biología Neotropical) for his continuous help in the use of the high-speed camera. We also thank Sonia Kretschmar and Marta Cánepa for the loan of the specimens housed at the Fundación Miguel Lillo Herpetological Collection, and Diego Baldo for the loan of the specimens housed at the Laboratorio de Genética Evolutiva. This study was founded with the PIP 0389 to VA, PICT 2016–2772 and 2018–0832 to VA, and PICT 2019–3520 to JF.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jcz.2022.01.002>.

### References

Abdala, V., Diogo, R., 2010. Comparative anatomy, homologies, and evolution of the pectoral and forelimb musculature of tetrapods with special attention to extant limbed amphibians and reptiles. *J. Anat.* 217, 536–573.

- Abdala, V., Manzano, A.S., Tulli, M.J., Herrel, A., 2009. The tendinous patterns in the palmar surface of the lizard manus: tests of functional consequences for grasping ability. *Anat. Rec.* 292, 842–853.
- Agnarsson, I., Coddington, J.A., 2008. Quantitative test of primary homology. *Cladistics* 24, 51–61.
- Ahn, A.N., Furrow, E., Biewener, A.A., 2004. Walking and running in the red-legged running frog, *Kassina maculata*. *J. Exp. Biol.* 207, 399–410. <https://doi.org/10.1242/jeb.00761>.
- Astley, H.C., Roberts, T.J., 2012. Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol. Lett.* 8, 386–389. <https://doi.org/10.1098/rsbl.2011.0982>.
- Akella, T., Gillis, G.B., 2011. Hopping isn't always about the legs: forelimb muscle activity patterns during toad locomotion. *J. Exp. Zool.* 315, 1–11.
- Astley, H.C., Abbott, E.M., Azizi, E., et al., 2013. Chasing maximal performance: a cautionary tale from the celebrated jumping frogs of Calaveras County. *J. Exp. Biol.* 216, 3947–3953. <https://doi.org/10.1242/jeb.090357>.
- Azizi, E., Larson, N.P., Abbott, E.M., Danos, N., 2014. Reduce torques and stick the landing: limb posture during landing in toads. *J. Exp. Biol.* 217, 3742–3747. <https://doi.org/10.1242/jeb.108506>.
- Bijma, N.N., Gorb, S.V., Kleinteich, T., 2016. Landing on branches in the frog *Tra-chycephalus resinifictrix* (Anura: Hylidae). *J. Comp. Physiol.* 202, 267–276.
- Blotto, B., Pereyra, M.O., Grant, T., Faivovich, J., 2020. Hand and foot musculature of Anura: structure, homology, terminology, and synapomorphies for major clades. *Bull. Am. Mus. Nat. Hist.* 443, 155. <https://doi.org/10.1206/0003-0090.443.1.1>.
- Boulenger, G.A., 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. Second Edition. Taylor & Francis, London.
- Boulenger, G.A., 1894. List of reptiles and batrachians collected by Dr. J. Bohls near Asuncion, Paraguay. *Ann. Mag. Nat. Hist.* 13 (Serie 6), 342–348.
- Boulenger, G.A., 1902. Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia. *Ann. Mag. Nat. Hist.* 10 (Serie 7), 394–402.
- Cei, J.M., 1980. Amphibians of Argentina. *Monit. zool. ital. Monografia* 2, 1–609.
- Clarke, B.T., 1981. Comparative osteology and evolutionary relationships in the African Raninae (Anura: Ranidae). *Monit. Zool. Ital. Suppl.* 15 (14), 285–331.
- Crump, M. L., 2015. Anuran reproductive modes: evolving perspectives. *J. Herpetol.* 49(1), 1–16.
- Cope, E.D., 1861. Descriptions of new species of the reptilian genera *Hyperolius*, *Liuperus* and *Tropidodipsas*. *Proc. Acad. Nat. Sci. Philadelphia* 12, 517–518.
- Crump, M.L., 2015. Anuran Reproductive Modes: Evolving Perspectives. *Journal of Herpetology* 49 (1), 1–16. <https://doi.org/10.1670/14-097>.
- De Oliveira-Lagôa, S., Cruz, F.B., Moreno Azócar, D.L., Lavilla, E.O., Abdala, V.A., 2019. Anuran forelimb muscle tendinous structures and their relationship with locomotor modes and habitat use. *Curr. Zool.* 65, 599–608. <https://doi.org/10.1093/cz/zoy086>.
- de Pinna, M.C.C., 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7, 367–394.
- Drewes, R.E., 1984. A phylogenetic analysis of the Hyperoliidae (Anura): tree-frogs of Africa, Madagascar, and the Seychelles Islands. *Pap. California Acad. Sci.* 139, 1–70.
- Dunlap, D.G., 1960. The comparative myology of the pelvic appendage in the Salientia. *J. Morphol.* 106, 1–76.
- Ekstrom, L., Gillis, G.B., 2015. Pre-landing wrist muscle activity in landing toads. *J. Exp. Biol.* 218, 2410–2415.
- Emerson, S.B., De Jongh, H.J., 1980. Muscle activity at the ilio-sacral articulation of frogs. *J. Morphol.* 166, 129–144.
- Essner, R.L., Suffan, D.J., Bishop, P.J., Reilly, S.M., 2010. Landing in basal frogs: evidence of saltational patterns in the evolution of anuran locomotion. *Naturwissenschaften* 97, 935–939.
- Fabrezi, M., 1996. Las falanges terminales en la clasificación de los anuros. *Cuad. Herpetol.* 10, 1–9.
- Fabrezi, M., Manzano, A.S., Abdala, V., Lobo, F., 2014. Anuran locomotion: ontogeny and morphological variation of a distinctive set of muscles. *Evol. Biol.* 41, 308–326. <https://doi.org/10.1007/s11692-014-9270-y>.
- Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W., 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. *Bull. Am. Mus. Nat.* 294, 1–240. [https://doi.org/10.1206/0003-0090\(2005\)294\[0001:SR0TFF\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2005)294[0001:SR0TFF]2.0.CO;2).
- Fratani, J., Ponssa, M.L., Abdala, V., 2018. Tendinous framework of anurans reveals an all-purpose morphology. *Zoology* 126, 172–184.
- Gallardo, J.M., 1958. Observaciones biológicas sobre *Leptodactylus prognathus* Boulenger. *Ciencia e Invest.* 14, 460–465.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24 (5), 774–786.
- Haines, R.W., 1950. The flexor muscles of the forearm and hand in lizards and mammals. *J. Anat.* 84, 13–29.
- Hensel, R., 1867. Beiträge zur Kenntnis der Wirbelthiere Südbrasilens. *Arch. Naturgesch.* 33, 120–162.
- Jenkins Jr., F.A., Shubin, N.H., 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *J. Vertebr. Paleontol.* 18, 495–510.
- Jetz, W., Pyron, R.A., 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat. Ecol. Evol.* 2, 850.
- Jiménez de la Espada, M., 1875. Vertebrados del Viaje al Pacífico Verificado de 1862 a 1865 por una Comisión de Naturalistas Enviada por el Gobierno Español. *Batracios*. A. Miguel Ginesta, Madrid.

- Kargo, W.J., Nelson, F.E., Rome, L., 2002. Jumping in frogs: assessing the design of the skeletal system by anatomically realistic modeling and forward dynamic simulation. *J. Exp. Biol.* 205, 1683–1702.
- Koslowsky, J.G., 1895. Batracios y reptiles de la Rioja y Catamarca, recogidos durante los meses de febrero a mayo de 1895. *Rev. Mus. La Plata* 6, 359–365.
- Laurent, R.F., 1986. Sous classe lissamphibiens (Lissamphibia). *Systématique. Tome XIV, Batraciens, Fasc. 1B*. Masson. In: Grassé, P.P., Delsol, M. (Eds.), *Traité de Zoologie. Anatomie, Systématique, Biologie*. Paris, pp. 594–798.
- Li, M., Gao, Z., Wang, J., et al., 2021. Cooperation behavior of fore- and hindlimbs during jumping in *Rana dybowskii* and *Xenopus laevis*. *Ecol. Evol.* 11, 7569–7578. <https://doi.org/10.1002/ece3.7589>.
- Liem, S.S., 1970. The morphology, systematics and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Field. Zool.* 57, 1–45.
- Lutz, A., 1925. Batraciens du Brésil. *C. R. Seances Soc. Biol. Fil.* 93, 211–214.
- Lynch, J.F., 1971. Evolutionary relationships, osteology and zoogeography of leptodactyloid frogs. *Univ. Kans. Publ. Mus. Nat. Hist.* 53, 1–238.
- Manzano, A.S., Fabrezi, M., Vences, M., 2007. Intercalary elements, treefrogs, and the early differentiation of a complex system in the neobatrachia. *Anat. Rec.* 290, 1551–1567.
- Manzano, A.S., Abdala, V., Herrel, A., 2008. Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? *J. Anat.* 213, 296–307.
- Manzano, A.S., Fontanarrosa, G., Abdala, V., 2017. Manual and pedal grasping among anurans: a review of relevant concepts with empirical approaches. *Biol. J. Linn. Soc.* 127, 598–610.
- McDiarmid, R.W., 1971. Comparative morphology and evolution of frogs of the Neotropical genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*. *Bull. Los Angeles County Museum Nat. Hist.* 12, 1–66.
- Mendoza, E., Azizi, E., Moen, D.S., 2020. What explains vast differences in jumping power within a clade? Diversity, ecology and evolution of anuran jumping power. *Funct. Ecol.* 34, 1053–1063.
- Nauwelaerts, S., Aerts, P., 2006. Take-off and landing forces in jumping frogs. *J. Exp. Biol.* 209, 66–77.
- Nixon, K.C., 1999. Winclada (BETA) ver. 0.9.9. PUBLISHED BY THE AUTHOR.
- Peracca, M.G., 1895. Viaggio del Dr. Borelli nella Rep. Argentina e nel Paraguay. Rettili e anfibi. *Boll. Mus. Zool. Anat. Comp., Torino* 10 (195), 1–32.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2021. *Linear and Nonlinear Mixed Effects Models*. R Package Version 3.1-153. <https://CRAN.R-project.org/package=nlme>.
- Ponssa, M.L., Goldberg, J., Abdala, V., 2010. Sesamoids in Anurans: new data, old issues. *Anat. Rec.* 293, 1646–1668.
- Přikryl, T., Aerts, P., Havelkova, P., Herrel, A., Roček, Z., 2009. Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. *J. Anat.* 214, 100–139.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. <https://www.R-project.org/>.
- Reilly, S.M., Jorgensen, M.E., 2011. The evolution of jumping in frogs: morphological evidence for the basal anuran locomotor condition and the radiation of locomotor systems in crown group anurans. *J. Morphol.* 272 (2), 149–168.
- Reilly, S.M., Montuelle, S.J., Schmidt, A., Naylor, E., Jorgensen, M.E., Halsey, L.G., Essner Jr., R.L., 2015. Conquering the world in leaps and bounds: hopping locomotion in toads is actually bounding. *Funct. Ecol.* <https://doi.org/10.1111/1365-2435.12414>.
- Reilly, S.M., Montuelle, S.J., Schmidt, A., Krause, C., Naylor, E., Essner Jr., R.L., 2016. Functional evolution of jumping in frogs: interspecific differences in take-off and landing. *J. Morphol.* 277, 379–393.
- Reynaga, C.M., Astley, H.C., Azizi, E., 2018. Morphological and kinematic specializations of walking frogs. *J. Exp. Zool.* 1–12, 2018.
- Reynaga, C.M., Eaton, C.E., Strong, G.A., Azizi, A., 2019. Compliant substrates disrupt elastic energy storage in jumping tree frogs. *Integr. Comp. Biol.* 59, 1535–1545.
- Soliz, M.C., Tulli, M.J., Abdala, V., 2019. Relationship between myological variables and different take-off and landing behaviors in frogs. *Acta Zool.* <https://doi.org/10.1111/azo.12292>.
- Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Hertel, F., et al., 2013. Getting a grip on tetrapod grasping: form, function, and evolution. *Biol. Rev.* 88, 380–405.
- Tulli, M.J., Cruz, F.B., Herrel, A., Vanhooydonck, B., Abdala, V., 2009. The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. *Zoology* 112, 379–392.
- Vaira, M., 2001. Breeding biology of the leaf frog, *Phyllomedusa boliviana* (Anura, Hylidae). *Amphibia-Reptilia* 22 (4), 421–429.
- Vellard, J., 1947. Un nuevo batracio del Norte Argentino. *Acta Zool. Lillo.* 4, 115.
- Vera, M.C., Ferreti, J.L., Abdala, V., Cointy, G., 2020. Biomechanical properties of anuran long bones: correlations with locomotor modes and habitat use. *J. Anat.* 236 (6), 1112–1125. <https://doi.org/10.1111/joa.13161>.
- Wassersug, R.J., 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. *Stain Technol.* 51, 131–134.
- Wells, K.D., 2007. *The Ecology and Behavior of Amphibians*. The University of Chicago Press, Chicago.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, ISBN 978-3-319-24277-4. <https://ggplot2.tidyverse.org>.
- Zani, P.A., 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. *J. Evol. Biol.* 13, 316–325.
- Zug, G., 1985. Anuran locomotion: fatigue and jumping performance. *Herpetologica* 4, 188–194.