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Hand and foot musculature of Sooglossoidea: synapomorphies, convergences and hind limb digging behaviour in anurans

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We describe the hand and foot musculature of the fossorial Indian purple frog, *Nasikabatrachus sahyadrensis*, and compare it to other members of Sooglossoidea: the Seychellean sooglossid genera *Sechellophryne* and *Sooglossus*. Due to the key phylogenetic position of Sooglossoidea, we compare its members with the diversity of Anura and define 52 characters from the hand and foot musculature, among which 26 are novel hypotheses of homology. We found several synapomorphies for *Sooglossus*, Sooglossidae, Nasikabatrachidae and Sooglossoidea. Additionally, we (1) propose synapomorphies for diverse anuran clades at different taxonomic levels, (2) re-evaluate the identity of some conflicting plantar and palmar muscles in the context of Batrachia and (3) discuss putative adaptations to hind limb digging behaviour resulting from morphological convergences. The lack of a clear pattern of convergences among hind limb digging species suggests the occurrence of a phenomenon of many-to-one mapping from form to function.

ADDITIONAL KEYWORDS: adaptation – burrowing – function – homology – morphological convergence – Nasikabatrachidae – Sooglossidae – terminology.

INTRODUCTION

Sooglossoidea (Nasikabatrachidae + Sooglossidae) is a small clade composed of six species divided among three genera of two species each: *Nasikabatrachus* and the sooglossids *Sechellophryne* and *Sooglossus*. This clade has a puzzling biogeographical history, with Nasikabatrachidae distributed in the Western Ghats of India and Sooglossidae in the Seychelles (Biju & Bossuyt, 2003; Labisko *et al.*, 2019). Their morphological and natural history diversity is also remarkable: while *Nasikabatrachus* is a fossorial burrower with free-living larvae and no parental care, *Sechellophryne* and *Sooglossus* are terrestrial or arboreal with direct development and parental care (Gerlach & Willi, 2002; Gerlach, 2007; Nussbaum & Wu, 2007; Raj *et al.*, 2012; Zachariah *et al.*, 2012; Senevirathne *et al.*, 2016; Janani *et al.*, 2017).

The elusive *Nasikabatrachus* is a morphologically bizarre frog and carries with it one of the most

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*Corresponding author. E-mail: borisblotto@gmail.com curious stories of discovery in herpetology. The tadpole was described more than 80 years earlier than the adult, leading to alternative speculations about its phylogenetic relationships (Annandale & Rao, 1917; Ramaswami, 1944). Adults were discovered and formally described as the first species of Nasikabatrachidae only 18 years ago by Biju & Bossuyt (2003), who recovered Nasikabatrachidae as the sister taxon of Sooglossidae in a molecular phylogenetic analysis.

Although Nasikabatrachidae + Sooglossidae is well supported and has been consistently recovered (e.g. Biju & Bossuyt, 2003; Pyron & Wiens, 2011; Hime *et al.*, 2021), its phylogenetic position is not. It has been placed in alternative positions in relation to the major clades of Neobatrachia, being sister to either (1) the remainder of Neobatrachia (Biju & Bossuyt, 2003), (2) Notogaeanura (Frost *et al.*, 2006), (3) Phthanobatrachia (i.e. Neobatrachia to the exclusion of Heleophrynidae; Pyron & Wiens, 2011) or (4) Ranoides (Pyron, 2014; Frazão *et al.*, 2015; Jetz & Pyron, 2018; Hime *et al.*, 2021).

The more recent discovery of Nasikabatrachidae in 2003 imposed limits on the level of generality of the synapomorphies for Sooglossidae proposed previously by Nussbaum (1982) and Ford & Cannatella (1993). Additionally, neither Nussbaum & Wu (2007) nor Blotto *et al.* (2020) included *Nasikabatrachus* in their studies, which precluded them from determining the level of generality of some synapomorphies possibly attributable to either Sooglossidae or Sooglossoidea. Currently, the single synapomorphy proposed for Sooglossoidea is the absence of a columella, although this element was lost multiple times during the evolutionary history of anurans (Pereyra *et al.*, 2016).

The two known species of *Nasikabatrachus* are fossorial, with only a short period of activity above ground for breeding. They possess several features related to burrowing, such as a stout body, small head, sturdy and short limbs, small eyes, well-developed prehallux, and shovel-shaped metatarsal tubercle (Biju & Bossuyt, 2003; Senevirathne *et al.*, 2016).

Nasikabatrachus has been reported to use primarily the hind limbs for digging, although it also employs other digging modes (Biju & Bossuyt, 2003; Dutta *et al.*, 2004; Radhakrishnan *et al.*, 2007; Senevirathne *et al.*, 2016; Janani *et al.*, 2017). The genus is characterized by a well-ossified prehallux that reinforces a spade-like metatarsal tubercle, presumably used to shift soil during digging (Senevirathne *et al.*, 2016), as described in other species (e.g. Emerson, 1976; Trueb & Gans, 1983). Although *Nasikabatrachus* employs the hind limbs to initiate burrowing, individuals might also move through the soil using the head and forelimbs, as suggested by their wedge-shaped skull with an epidermal knob and well-ossified prepollex (Senevirathne *et al.*, 2016).

Considering the key phylogenetic position of Sooglossoidea, the lack of phenotypic studies including representatives of all three genera and major related clades, the contrasting natural history among their species and the morphological features associated with the digging behaviour of *Nasikabatrachus*, the aims of this study are to: (1) describe the hand and foot musculature of *Nasikabatrachus sahyadrensis* Biju & Bossuyt, 2003 (for taxonomic species authorities see Table 1) and compare it to that of Sooglossidae; (2) analyse the phenotypic variation of these character systems, define transformation series, and propose synapomorphies for Sooglossoidea, its internal clades and other major anuran clades; (3) evaluate, discuss and delimit hypotheses of homology for hand and foot muscles with controversial identities and correspondences within Anura and between Anura and Caudata; and (4) identify traits in foot musculature that are potentially related to hind limb digging behaviour.

MATERIAL AND METHODS

Taxon and character sampling

Except for a few additions (see below), we studied the same species and specimens reported by Blotto *et al.* (2020), which represent all major anuran clades (including representatives of 48 of the 56 recognized families; Frost, 2021), thereby enabling us to infer the ancestral character states for Sooglossoidea and internal clades and compare sooglossoids to species with diverse natural histories (e.g. different digging mechanisms). We also included the odontophrynids studied by Blotto *et al.* (2017) to enhance comparisons among fossorial and hind limb digging clades, as well as the following specimens: *Limnomedusa macroglossa* (male): MACN 49261: Argentina: Misiones: Oberá: Campo Ramón, Villa Bonita; *Nasikabatrachus sahyadrensis*: SDBDU 2009.06.01 (male): India: Kerala: Idukki district: Kattappana; SDBDU 2012.05.02 (female): India: Kerala: Idukki district: Methooty; and *Sechellophryne gardineri*: UMMZ 144551 (unknown sex): Seychelles: Island of Mahe: junction of Grand Bois River and Foret Noire road.

Within Sooglossoidea, we included one of the two species of the monotypic Nasikabatrachidae (*Nasikabatrachus sahyadrensis*) and three of the four known species of the two genera of Sooglossidae: both species of *Sooglossus* (*Sooglossus sechellensis* and *Sooglossus thomasseti*) and *Sechellophryne gardineri*. From this last species, our original data are limited to the plantar musculature, with a few characters from the palmar musculature taken from Burton (1998a).

Table 1. List of species included in the main text with their respective taxonomic authorities.

Anura
Alsodidae
Alsodes neuquensis Cei, 1976
Limnomedusa macroglossa (Duméril & Bibron, 1841)
Alytidae
Alytes obstetricans (Laurenti, 1768)
Discoglossus galganoi Capula, Nascetti, Lanza, Bullini, & Crespo, 1985
Discoglossus pictus Otth, 1837
Arthroleptidae
Arthroleptis variabilis Matschie, 1893
Ascaphidae
Ascaphus truei Stejneger, 1899
Batrachylidae
Atelognathus patagonicus (Gallardo, 1962)
Atelognathus praebasalticus (Cei & Roig, 1968)
Bombinatoridae
Barbourula busuangensis Taylor & Noble, 1924
Bombina bombina (Linnaeus, 1761)
Bombina orientalis (Boulenger, 1890)
Bombina variegata (Linnaeus, 1758)
Brevicipitidae
Breviceps adspersus Peters, 1882
Bufonidae
Anaxyrus woodhousii (Girard, 1854)
Atelopus pastuso Coloma, Duellman, Almendáriz, Ron, Terán-Valdez, & Guayasamin, 2010
Melanophryniscus klappenbachi Prigioni & Langone, 2000
Rhinella dorbignyi (Duméril & Bibron, 1841)
Ceratophryidae
Ceratophrys cranwelli Barrio, 1980
Lepidobatrachus laevis Budgett, 1899
Lepidobatrachus llanensis Reig & Cei, 1963
Dicroglossidae
Fejervarya vittigera (Wiegmann, 1834)
Hoplobatrachus rugulosus (Wiegmann, 1834)
Sphaerotheca breviceps (Schneider, 1799)
Eleutherodactylidae
Eleutherodactylus coqui Thomas, 1966
Heleophrynidae
Hadromophryne natalensis (Hewitt, 1913)
Heleophryne orientalis FitzSimons, 1946
Hemiphractidae
Hemiphractus proboscideus (Jiménez de la Espada, 1870)
Stefania evansi (Boulenger, 1904)
Hemisotidae
Hemisus marmoratus (Peters, 1854)
Hylidae
Dendropsophus luddeckei Guarnizo, Escallón, Cannatella, & Amézquita, 2012
Triprion petasatus (Cope, 1865)
Trachycephalus typhonius (Linnaeus, 1758)
Pseudis minuta Günther, 1858

Table 1. Continued

Scinax granulatus (Peters, 1871)
Hylodidae
Crossodactylus gaudichaudii Duméril & Bibron, 1841
Crossodactylus schmidti Gallardo, 1961
Hylodes dactylocinus Pavan, Narvaes, & Rodrigues, 2001
Hylodes japi de Sá, Canedo, Lyra, & Haddad, 2015
Hylodes phyllodes Heyer & Cocroft, 1986
Hyperoliidae
Hyperolius semidiscus Hewitt, 1927
Leiopelmatidae
Leiopelma hochstetteri Fitzinger, 1861
Leptodactylidae
Physalaemus biligonigerus (Cope, 1861)
Pleurodema kriegi (Müller, 1926)
Pseudopaludicola falcipes (Hensel, 1867)
Leptodactylus latinasus Jiménez de la Espada, 1875
Limnodynastidae
Adelotus brevis (Günther, 1863)
Heleioporus albopunctatus Gray, 1841
Limnodynastes peronii (Duméril & Bibron, 1841)
Limnodynastes tasmaniensis Günther, 1858
Neobatrachus aquilonius Tyler, Davies, & Martin, 1981
Notaden bennettii Günther, 1873
Philoria frosti Spencer, 1901
Platyplectrum ornatum (Gray, 1842)
Megophryidae
Leptobrachella ventripunctata (Fei, Ye, & Li, 1990)
Leptobrachium lumadorum Brown, Siler, Diesmos, & Alcala, 2010
Scutiger mammatus (Günther, 1896)
Pelobatrachus edwardinae (Inger, 1989)
Xenophrys aceras (Boulenger, 1903)
Microhylidae
Chaperina fusca Mocquard, 1892
Glyphoglossus guttulatus (Blyth, 1856)
Kaloula pulchra Gray, 1831
Microhyla heymonsi Vogt, 1911
Micryletta inornata (Boulenger, 1890)
Uperodon systoma (Schneider, 1799)
Phrynomantis bifasciatus (Smith, 1847)
Myobatrachidae
Crinia signifera Girard, 1853
Pseudophryne coriacea Keferstein, 1868
Rheobatrachus silus Liem, 1973
Taudactylus diurnus Straughan & Lee, 1966
Uperoleia laevigata Keferstein, 1867
Nasikabatrachidae
Nasikabatrachus bhupathi Janani, Vasudevan, Prendini, Dutta, & Aggarwal, 2017
Nasikabatrachus sahyadrensis Biju & Bossuyt, 2003
Odontophrynidae
Macrogenioglottus alipioi Carvalho, 1946
Odontophrynus achalensis di Tada, Barla, Martori, & Cei, 1984
Odontophrynus americanus (Duméril & Bibron, 1841)

Table 1. Continued

Odontophrynus barrioi Cei, Ruiz, & Beçak, 1982
Odontophrynus carvalhoi Savage & Cei, 1965
Odontophrynus cultripes Reinhardt & Lütken, 1862
Odontophrynus occidentalis (Berg, 1896)
Proceratophrys appendiculata (Günther, 1873)
Proceratophrys avelinoi Mercadal de Barrio & Barrio, 1993
Proceratophrys boiei (Wied-Neuwied, 1824)
Proceratophrys concavitympanum Giaretta, Bernarde, & Kokubum, 2000
Proceratophrys laticeps Izecksohn & Peixoto, 1981
Pelobatidae
Pelobates cultripes (Cuvier, 1829)
Pelobates fuscus (Laurenti, 1768)
Pelobates varaldii Pasteur & Bons, 1959
Pipidae
Hymenochirus boettgeri (Tornier, 1896)
Hymenochirus curtipes Noble, 1924
Pseudhymenochirus merlini Chabanaud, 1920
Xenopus borealis Parker, 1936
Xenopus epitropicalis Fischberg, Colombelli, & Picard, 1982
Xenopus laevis (Daudin, 1802)
Xenopus muelleri (Peters, 1844)
Xenopus tropicalis (Gray, 1864)
Xenopus victorianus Ahl, 1924
Pipa carvalhoi (Miranda-Ribeiro, 1937)
Pipa parva Ruthven & Gaige, 1923
Pyxicephalidae
Tomopterna delalandii (Tschudi, 1838)
Rhacophoridae
Polypedates leucomystax (Gravenhorst, 1829)
Rhacophorus pardalis Günther, 1858
Rhinophrynidae
Rhinophrynus dorsalis Duméril & Bibron, 1841
Scaphiopodidae
Scaphiopus couchii Baird, 1854
Scaphiopus hurterii Strecker, 1910
Spea bombifrons (Cope, 1863)
Spea hammondii (Baird, 1859)
Spea intermontana (Cope, 1883)
Sooglossidae
Sechellophryne gardineri (Boulenger, 1911)
Sooglossus sechellensis (Boettger, 1896)
Sooglossus thomasseti (Boulenger, 1909)
Caudata
Ambystomatidae
Ambystoma mexicanum (Shaw & Nodder, 1798)
Cryptobranchidae
Andrias japonicus (Temminck, 1836)
Cryptobranchus alleganiensis (Sonnini de Manoncourt & Latreille, 1801)
Proteidae
Necturus maculosus (Rafinesque, 1818)
Salamandridae
Lissotriton vulgaris (Linnaeus, 1758)

Although we studied all the muscles of the hand and foot, we restricted character sampling to (1) characters from muscles that vary within Sooglossoidea, (2) characters potentially associated with hind limb digging behaviour (e.g. see Burton, 2001; Blotto *et al.*, 2017) and (3) characters from Blotto *et al.* (2020). The inclusion of the characters defined by Blotto *et al.* (2020) is justified based on the key phylogenetic position of Sooglossoidea among major anuran clades (see Introduction for a summary); consequently, the inclusion of *Nasikabatrachus* and *Sechellophryne* in this study might affect some of the ancestral character state reconstructions reported in Blotto *et al.* (2020).

Dissection procedure and terminology

We studied specimens with the aid of a stereomicroscope following the procedure detailed by Blotto *et al.* (2020). We built the data matrix using the software Mesquite v.3.03 (Maddison & Maddison, 2015).

We follow Blotto *et al.* (2020) for the definition of the musculature layers and the edition of the images with three exceptions. First, we consider the forearm and hand m. flexor digitorum communis, m. flexor accessorius and flexor plate as belonging to the first musculature layer. Second, we redefined some muscles from the palmar surface of digit V (see Discussion). Third, we edited the m. adductor praehallucis (not figured by Blotto *et al.*, 2020) with the same colour as the mm. intermetatarsales and considered it to be a muscle of the fourth layer of the plantar surface of the foot. We use the same colour for these muscles because the m. adductor praehallucis was defined as a 'transversus-like' muscle (m. intermetatarsalis of our terminology) by Burton (2001) since it connects the prehallux to metatarsal I, similar to the mm. intermetatarsales, which connect the adjacent metatarsals.

The terminology for the carpus and tarsus follows Fabrezi (1992, 1993) and Fabrezi & Alberch (1996), while phalanx terminology follows Blotto *et al.* (2020). The terminology for hand and foot musculature follows Blotto *et al.* (2020), with a few modifications related to the palmar surface of digit V (see Discussion). The taxonomy follows Frost (2021), except for Hylidae, which follows Faivovich *et al.* (2018). See Supporting Information Appendix S1 for taxonomic comments on some specimens included in this study.

For descriptive expediency, we extrapolate the condition observed in *Nasikabatrachus sahyadrensis* to the genus, even though we did not observe *N. bhupathi*, and describe the differences between the two exemplars of *N. sahyadrensis* as differences between the male and female (although this does not necessarily imply that they are sexually dimorphic traits). The following abbreviations are used throughout the text and figures: abd, abductor; ACSR(s), ancestral character state reconstruction(s); add, adductor; contr/contrs, contrahentis/contrahentes; dc, distal carpal; dt, distal tarsal; HLD, hind limb digging; fi, fibulare; flex(s), flexor(es); m1–m5, metacarpals II–V/metatarsals I–V; ph, prehallux; pp, prepollex; ra, radiale; ru, radioulna; ti-fi, fused distal portions of the tibiale and fibulare; ti, tibiale; ul, ulnare; and Y, element Y.

ANCESTRAL CHARACTER STATE RECONSTRUCTIONS

We employed the phylogenetic hypothesis of Jetz & Pyron (2018) pruned to include only our sample of species for the ACSRs; however, when relevant, we also discuss the implications of alternative character optimizations derived from competing phylogenetic hypotheses. The ACSRs were done using Fitch's (1971) optimization in the software TNT v.1.5 (Goloboff & Catalano, 2016). Following the definition of the characters (Appendix 1), we indicate putative synapomorphies for major anuran clades recovered from the ACSRs. The placement of *Atelopus pastuso* (Bufonidae), *Leptobrachium lumadorum* and *Pelobatrachus edwardinae* (both Megophryidae) in the phylogenetic hypothesis of Jetz & Pyron (2018) is based on the justification of Blotto *et al.* (2020).

RESULTS

DESCRIPTION OF THE HAND AND FOOT MUSCULATURE OF *NASIKABATRACHUS SAHYADRENSIS*

Palmar surface of the forearm and hand: first layer (Fig. 1A, C)

M. flexor digitorum communis: This is a single, undivided muscle that originates from the medial epicondyle of the humerus. It shares a common insertion with the m. flexor accessorius, forming the flexor plate, which is a well-developed tendon of insertion.

M. flexor accessorius: This muscle originates from the laterodistal end of the radioulna via a short tendon (not visible in figures). It has an additional head with a fleshy origin from the palmar surface of the ulnare (Fig. 1C). The m. flexor accessorius inserts widely on the dorsal surface of the flexor plate.

Flexor plate: The flexor plate is well developed and constitutes the tendon of insertion of the m. flexor digitorum communis and m. flexor accessorius. It forms a thick connective tissue attached to the lateropalmar surface of the ulnare and distal carpal 3-4-5. The palmar sesamoid (a sesamoid embedded in the flexor plate) is absent. Burton's ligament is short and cylindrical, joining the mediodistal end of distal carpal 3-4-5 and the flexor plate at the level of the origin of the tendo superficialis digiti V.

Tendines superficiales: The tendo superficialis indicis and the tendines superficiales digitorum III–V originate from the flexor plate and insert on the palmar surface of the distal phalanx of their respective digits. The insertion of the tendines superficiales indicis and digiti III is via a common tendon with the m. flexor indicis superficialis proprius and m. caput profundum digiti III, respectively.

M. flexor indicis superficialis proprius: This is a well-developed muscle that originates from distal carpal 3-4-5. It inserts broadly along the dorsolateral surface of the tendo superficialis indicis. Distal to this broad insertion, the m. flexor indicis superficialis proprius and the tendo superficialis indicis fuse into a single tendon that attaches to the palmar surface of the distal phalanx of digit II.

M. caput profundum digiti III: This is a moderately developed muscle that originates from distal carpal 3-4-5. It inserts broadly along the dorsolateral surface of the tendo superficialis digiti III. Distal to this broad insertion, the m. caput profundum digiti III and the tendo superficialis digiti III fuse into a single tendon that attaches to the palmar surface of the distal phalanx of digit III.

Mm. lumbricales longi: The m. lumbricalis longus digiti IV is composed of medial and lateral slips of the same size. They originate from the flexor plate and the adjacent dorsal and proximal surface of the tendon superficialis digiti IV. Each slip inserts via a single, independent tendon that runs medially and laterally to the tendo superficialis digiti IV, respectively, and attaches to the proximal interphalangeal joint of digit IV. The female differs in that the m. lumbricalis longus digiti IV is not divided into slips and inserts via a single, wide tendon.

The m. lumbricalis longus digiti V is a single, undivided muscle located dorsally and laterally to the tendo superficialis digiti V. It has a fleshy origin from the flexor plate and inserts via a single, wide tendon on the proximal interphalangeal joint of digit V.

Palmar surface of the hand: second layer (Fig. 1B)

Mm. lumbricales breves: The m. lumbricalis brevis indicis is divided into a medial and lateral slip, each with its own tendon of origin from the mediodistal surface of distal carpal 3-4-5. Both slips have a fleshy insertion on the palmar surface of the metacarpophalangeal joint of digit II: the medial slip inserts on its intermediate

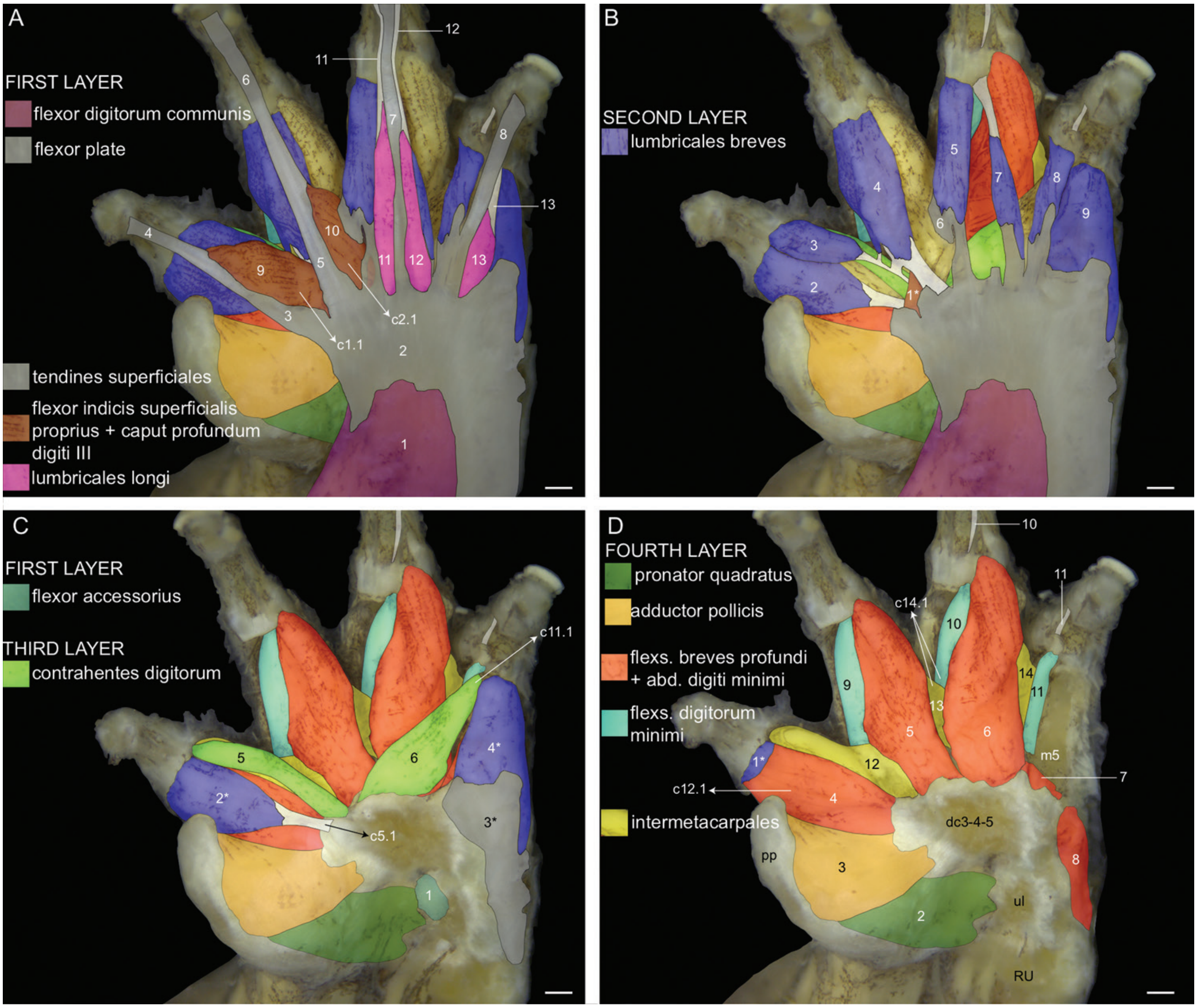

Figure 1. Palmar surface of the hand of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01; male). A, first layer of muscles. Labelled elements: **1,** m. flexor digitorum communis. **2,** flexor plate (a connective tissue that covers the lateropalmar region is fused to the flexor plate and it is also gray shaded; the m. flexor accessorius is hidden by this connective tissue). **3,** tendo superficialis indicis. **4,** tendo superficialis indicis and m. flexor indicis superficialis proprius: common tendon of insertion. **5,** tendo superficialis digiti III. **6,** tendo superficialis digiti III and m. caput profundum digiti III: common tendon of insertion. **7–8,** tendines superficiales digitorum IV–V. **9,** m. flexor indicis superficialis proprius. **10,** m. caput profundum digiti III. **11,** m. lumbricalis longus digiti IV: medial slip. **12,** m. lumbricalis longus digiti IV: lateral slip. **13,** m. lumbricalis longus digiti V. B, Second layer of muscles. Labelled elements: **1*,** m. flexor indicis superficialis proprius: proximal unremoved portion. **2,** m. lumbricalis brevis indicis: medial slip. **3,** m. lumbricalis brevis indicis: lateral slip. **4,** m. lumbricalis brevis digiti III. **5,** medial m. lumbricalis brevis digiti IV. **6,** medial m. lumbricalis brevis digiti IV: tendon of origin from connective tissue associated with the integument. **7,** lateral m. lumbricalis brevis digiti IV. **8,** medial m. lumbricalis brevis digiti V. **9,** lateral m. lumbricalis brevis digiti V. C, third layer of muscles. Labelled elements: **1,** m. flexor accessorius: unremoved portion with origin on the ulnare. **2*,** m. lumbricalis brevis indicis: medial slip. **3*,** heavy tendinous strip of the flexor plate at its insertion point on the laterodistal surface of the distal carpal 3-4-5 and ulnare (serves as origin for the lateral m. lumbricalis brevis digiti V). **4*,** lateral m. lumbricalis brevis digiti V. **5,** m. contrahentis indicis. **6,** m. contrahentis digiti V. D, fourth layer of muscles. Labelled elements: **1*,** m. lumbricalis brevis indicis: medial slip: distal unremoved portion. **2,** pronator quadratus. **3,** m. adductor pollicis. **4,** medial m. flexor indicis brevis profundus. **5,** m. flexor brevis profundus digiti III. **6,** m. flexor brevis profundus digiti IV. **7,** m. flexor brevis profundus digiti V (only the proximal portion remained unremoved). **8,** m. abductor digiti minimi. **9–11,** mm. flexores minimi digitorum III–V, respectively (the tendon of insertion of the muscle of digit III is covered by connective tissue and it is not visible or shaded). **12–14,** mm. intermetacarpales I–III, respectively. Asterisks (*)

and mediopalmar region (see also Fig. 1C), while the lateral slip inserts on its lateropalmar surface. Distinctly, the female has a single, well-developed m. lumbricalis brevis indicis, with a single tendon of origin and a wide, fleshy insertion on the complete palmar surface of the metacarpophalangeal joint.

The m. lumbricalis brevis digiti III originates from the mediodistal surface of distal carpal 3-4-5; the male has an additional origin from the tendon of origin of the lateral slip of the m. lumbricalis brevis indicis. This muscle has a fleshy insertion on the complete palmar surface of the metacarpophalangeal joint of digit III.

The mm. lumbricales breves of digit IV consist of a medial and lateral muscle, the former being larger. The medial m. lumbricalis brevis digiti IV originates via a tendon from the flexor plate and additionally from connective tissue associated with the integument; it has a fleshy insertion on the mediopalmar surface of the metacarpophalangeal joint of digit IV. The lateral m. lumbricalis brevis digiti IV has a tendinous origin from the flexor plate, partially in common with the tendon of origin of the m. lumbricalis longus digiti IV. It inserts via a long tendon on the middle portion of the palmar surface of the metacarpophalangeal joint of digit IV. The female differs in that the long tendon of insertion of the lateral m. lumbricalis brevis digiti IV inserts on the ventral and distal fascia of the m. flexor brevis profundus digiti IV; both muscles attach to the lateropalmar surface of the metacarpophalangeal joint of digit IV.

The medial m. lumbricalis brevis digiti V has a tendinous origin from the flexor plate and a fleshy insertion on the mediopalmar surface of the metacarpophalangeal joint of digit V. The lateral m. lumbricalis brevis digiti V is interpreted as the massive muscle originating from a heavy tendinous strip of the flexor plate attached to the laterodistal surface of distal carpal 3-4-5 and ulnare; it inserts on the lateropalmar surface of metacarpal V and the metacarpophalangeal joint of digit V. The lateral m. lumbricalis brevis digiti V and m. flexor brevis profundus digiti V are only discrete at their origins; distally, both muscles have a contiguous, fleshy insertion on metacarpal V (the former inserting lateral to the m. flexor brevis profundus digiti V).

In contrast to the male, the lateral m. lumbricalis brevis digiti V and the m. flexor brevis profundus digiti V are discrete muscles in the female (Fig. 2). Furthermore, the lateral m. lumbricalis brevis digiti V has partially differentiated medial and lateral portions: the medial portion inserts on the metacarpophalangeal joint of digit V and the lateral portion on the lateropalmar surface of metacarpal V, lateral to the insertion of the m. flexor brevis profundus digiti V.

Palmar surface of the hand: third layer (Figs 1C, 2A)

Mm. contrahentes digitorum: The m. contrahentis indicis has a fleshy origin from the mediodistal surface of distal carpal 3-4-5; it inserts via a tendon that passes through an internal channel of the metacarpophalangeal joint and attaches to the lateropalmar surface of the basal phalanx of digit II (not visible in figures due to the presence of a thick connective tissue covering it). The m. contrahentis digiti V has a short, wide tendon of origin on the distal surface of distal carpal 3-4-5 and a fleshy insertion on the distal palmar surface of metacarpal V, lateral to the m. flexor minimus digiti V. The mm. contrahentes digitorum III–IV and the m. opponens digiti V (which also belongs to the third layer; see Discussion) are absent.

Palmar surface of the hand: fourth layer (Figs 1D, 2B)

M. pronator quadratus: This muscle originates from the ulnare and the adjoining distal end of the radioulna via a short tendon (the origins from the ulnare and radioulna are proximally discrete as two independent slips in the female; not shown). It has a fleshy insertion on the prepollex, proximal and dorsal to the m. adductor pollicis.

M. contrahentis caput longus distalis: This is a short, oblique muscle that originates from the ulnare and

indicate unremoved muscles from more superficial muscle layers other than the one being exposed. Some tendons of origin without well-defined limits were not shaded to avoid the arbitrary definition of discrete limits. The limits of the m. adductor pollicis and m. pronator quadratus are approximate since they are partially covered by a dense connective tissue sheath. Labelled characters: c1.1: presence of m. flexor indicis superficialis proprius (A). c2.1: presence of m. caput profundum digiti III (A). c5.1: origin of the m. lumbricalis brevis indicis from distal carpal 3-4-5 (C). c11.1: presence of the insertion of the m. contrahentis digiti V on the distal end of the metacarpal V, laterally to the m. flexor minimus digiti V (C). c12.1: presence of the medial m. flexor indicis brevis profundus (D). c14.1: m. flexor minimus digiti IV dorsal to the m. intermetacarpalis II (D). Characters referring to absence not labelled in the figure: c3.0: absence of m. lumbricalis longus digiti III (A). c16.0: absence of intermediate slip of m. interphalangeus digiti V (D). c17.0: absence of m. contrahentis caput longus distalis (D). Scale bars = 0.5 mm.

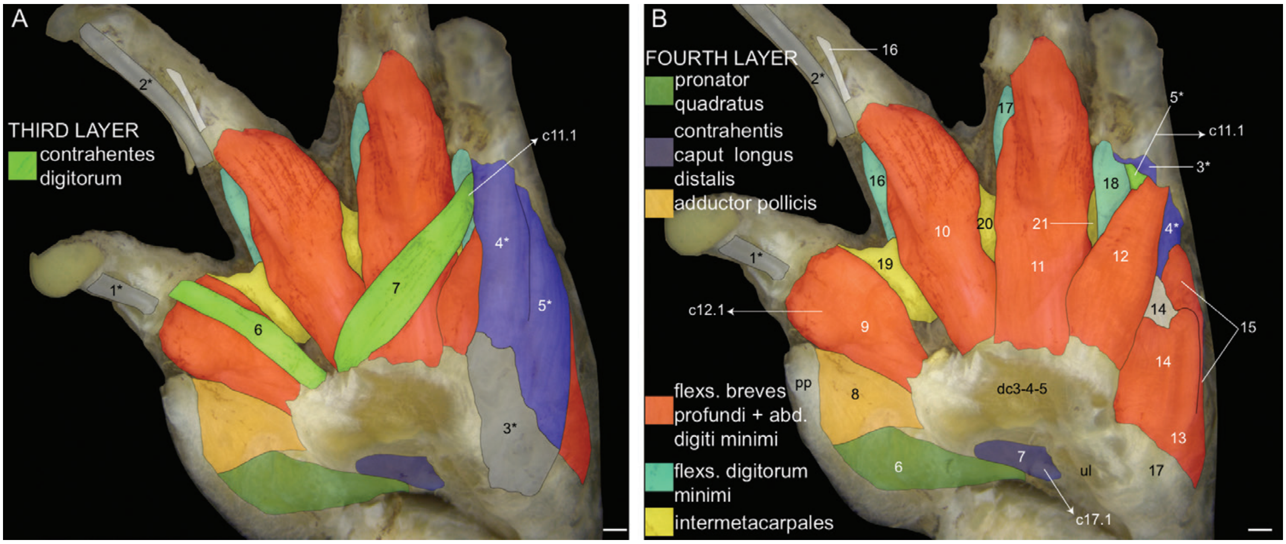

Figure 2. Palmar surface of the hand of *Nasikabatrachus sahyadrensis* (SDBDU 2012.05.02; female). Most relevant differences in comparison with the male shown in Figure 1 are the presence of the m. contrahentis caput longus distalis (absent in the male) and some muscles of digit V clearly differentiated (see text). A, third layer of muscles. Labelled elements: **1*,** tendo superficialis indicis and m. flexor indicis superficialis proprius: common tendon of insertion: distal unremoved portion. **2*,** tendo superficialis digiti III and m. caput profundum digiti III: common tendon of insertion: distal unremoved portion. **3*,** heavy tendinous strip of the flexor plate at its insertion point on the laterodistal surface of the distal carpal 3-4-5 and ulnare (serves as origin for the lateral m. lumbricalis brevis digiti V). **4*,** lateral m. lumbricalis brevis digiti V: portion inserting on the metacarpophalangeal joint. **5*,** lateral m. lumbricalis brevis digiti V: portion inserting on metacarpal V. **6,** m. contrahentis indicis. **7,** m. contrahentis digiti V. B, fourth layer of muscles. The lateral m. lumbricalis brevis digiti V was removed (with the exception of its distal portion), exposing the m. flexor brevis profundus digiti V and the m. abductor digiti minimi. Labelled elements: **1*,** tendo superficialis indicis and m. flexor indicis superficialis proprius: common tendon of insertion: distal unremoved portion. **2*,** tendo superficialis digiti III and m. caput profundum digiti III: common tendon of insertion: distal unremoved portion. **3*,** lateral m. lumbricalis brevis digiti V: portion inserting on the metacarpophalangeal joint: distal unremoved portion. **4*,** lateral m. lumbricalis brevis digiti V: portion inserting on metacarpal V: distal unremoved portion. **5*,** m. contrahentis digiti V: distal unremoved portion. **6,** m. pronator quadratus. **7,** m. contrahentis caput longus distalis. **8,** m. adductor pollicis. **9,** medial m. flexor indicis brevis profundus. **10–12,** mm. flexores breves profundi digitorum III–V, respectively. **13,** m. abductor digiti minimi. **14,** m. abductor digiti minimi: portion with tendinous insertion. **15,** m. abductor digiti minimi: portion with fleshy insertion. **16–18,** mm. flexores minimi digitorum III–V, respectively (only the tendon of insertion of the muscle of digit III is visible and shaded). **19–21,** mm. intermetacarpales I–III, respectively. Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. Some tendons of origin without well-defined limits were not shaded to avoid the arbitrary definition of discrete limits. The limits of the m. adductor pollicis and m. pronator quadratus are approximate since they are partially covered by a dense connective tissue. Labelled characters: c11.1: presence of the insertion of the m. contrahentis digiti V on the distal end of the metacarpal V, laterally to the m. flexor minimus digiti V (A, B). c12.1: presence of medial m. flexor indicis brevis profundus (B). c17.1: presence of m. contrahentis caput longus distalis (B). Characters referring to absence not labelled in the figure: c16.0: absence of intermediate slip of m. interphalangeus digiti V (B). Scale bars = 0.5 mm.

inserts on distal carpal 3-4-5. It is absent in the male.

M. adductor pollicis: This muscle has a wide, tendinous origin from the medial region of distal carpal 3-4-5. Its origin is proximally undifferentiated from the medial m. flexor indicis brevis profundus. Both muscles are distally discrete, as their fibres diverge to insert on the palmar surface of the prepollex and metacarpal II, respectively.

Mm. flexores breves profundi: The medial m. flexor indicis brevis profundus (the lateral muscle is absent) originates via a short tendon from the mediopalmar surface of distal carpal 3-4-5. It has a fleshy insertion along the mediopalmar surface of metacarpal II.

The mm. flexores breves profundi digitorum III and IV have each a single tendinous origin from the distal surface of distal carpal 3-4-5. They have a fleshy insertion on the lateropalmar surface of metacarpals III and IV and the metacarpophalangeal joints of digits III and IV, respectively. The insertions of the mm. flexores breves profundi digitorum III and IV are ventral to the mm. intermetacarpales II and III, respectively.

The m. flexor brevis profundus digiti V originates from the laterodistal end of distal carpal 3-4-5 and has a fleshy insertion on the palmar surface of metacarpal V, lateral to the m. flexor minimus digiti V. In the female, the m. flexor brevis profundus digiti V is completely differentiated from the lateral m. lumbricalis brevis digiti V.

M. abductor digiti minimi: This muscle has a fleshy origin from the ulnare and an insertion on the proximolateral surface of metacarpal V. In the female, the m. abductor digiti minimi distally has two partially differentiated portions, both of which insert on metacarpal V, one with a tendinous insertion and the other with a fleshy insertion.

Mm. flexores digitorum minimi: The mm. flexores minimi digitorum III and IV have a fleshy origin on the mediopalmar surface of metacarpals III and IV, dorsal to the origins of the mm. intermetacarpales I and II, respectively. The m. flexor minimus digiti V has a fleshy origin on metacarpal V, ventral to the origin of the m. intermetacarpalis III. Their tendons of insertion pass through an internal channel of their respective metacarpophalangeal joint and insert on the palmar surface of their respective basal phalanx.

Mm. intermetacarpales: These are transversal muscles that connect the metacarpals, with their origins located more proximally than their respective insertions. The mm. intermetacarpales I, II and III originate from metacarpals III, IV and V, respectively, and insert on metacarpals II, III and IV, respectively.

Dorsal surface of the hand: first layer (Fig. 3A)

M. extensor digitorum: This large extensor originates from the epicondyle of the humerus and extends distad along the radioulna. It is weakly differentiated distally into slips that insert on: (1) the metacarpophalangeal joint of digit III, in common with the m. extensor brevis superficialis digiti III; (2) the metacarpophalangeal joint of digit IV, in common with the m. extensor brevis superficialis digiti IV; (3) the metacarpophalangeal joint of digit V, in common with the m. extensor brevis superficialis digiti V; and (4) the dorsolateral surface of metacarpal V, distal to the insertion of the m. abductor brevis digiti V, via a tendon.

Dorsal surface of the hand: second layer (Fig. 3B)

M. abductor pollicis longus: This well-developed muscle is composed of two slips, one with a tendinous origin from the epicondyle of the humerus, and the other with a fleshy origin from the dorsal surface of the radioulna. Both slips converge distally and insert via a medial tendon on metacarpal II and a lateral tendon on the metacarpophalangeal joint of digit II, in common with the m. extensor indicis brevis superficialis. The slip from the humerus and the insertion on the metacarpophalangeal joint of digit II are absent in the female.

Mm. extensores digitorum breves superficiales: The m. extensor indicis brevis superficialis originates via a very short tendon from the ulnare and inserts on the metacarpophalangeal joint of digit II. The m. extensor brevis superficialis digiti III has a fleshy origin from the ulnare and inserts on the metacarpophalangeal joint of digit III.

The m. extensor brevis superficialis digiti IV consists of two slips with fleshy origins: a medial slip from the ulnare and a lateral slip from distal carpal 3-4-5. They converge into a single tendon of insertion that attaches to the metacarpophalangeal joint of digit IV. The m. extensor brevis superficialis digiti V has a fleshy origin from distal carpal 3-4-5 and inserts on the metacarpophalangeal joint of digit V.

Dorsal surface of the hand: third layer (Fig. 3C)

Mm. extensores digitorum breves medii: The m. extensor indicis brevis medius has a fleshy origin from element Y and inserts via a common tendon with the medial m. dorsometacarpalis indicis proximalis on the interphalangeal joint/distal phalanx of digit II. The mm. extensores breves medii digitorum III and IV originate via a very short tendon from the radiale; they insert via an independent tendon on the metacarpophalangeal joint of digits III and IV, respectively.

Dorsal surface of the hand: fourth layer (Fig. 3D)

M. abductor indicis brevis dorsalis: This muscle has a fleshy origin from element Y and a fleshy insertion on the prepollex and metacarpal II.

M. abductor brevis digiti V: This muscle has as a fleshy origin from distal carpal 3-4-5 and a fleshy insertion on the dorsolateral surface of metacarpal V.

Mm. dorsometacarpales proximales: The medial and lateral m. dorsometacarpalis indicis proximalis have a fleshy origin from the dorsal and proximal surface of metacarpal II and insert on the dorsomedial and dorsolateral surface of the interphalangeal joint/distal phalanx of digit II, respectively. The medial m. dorsometacarpalis proximalis digiti III consists of a medial slip with tendinous origin from metacarpal II and a lateral slip with fleshy origin from the dorsomedial surface of metacarpal III; they converge

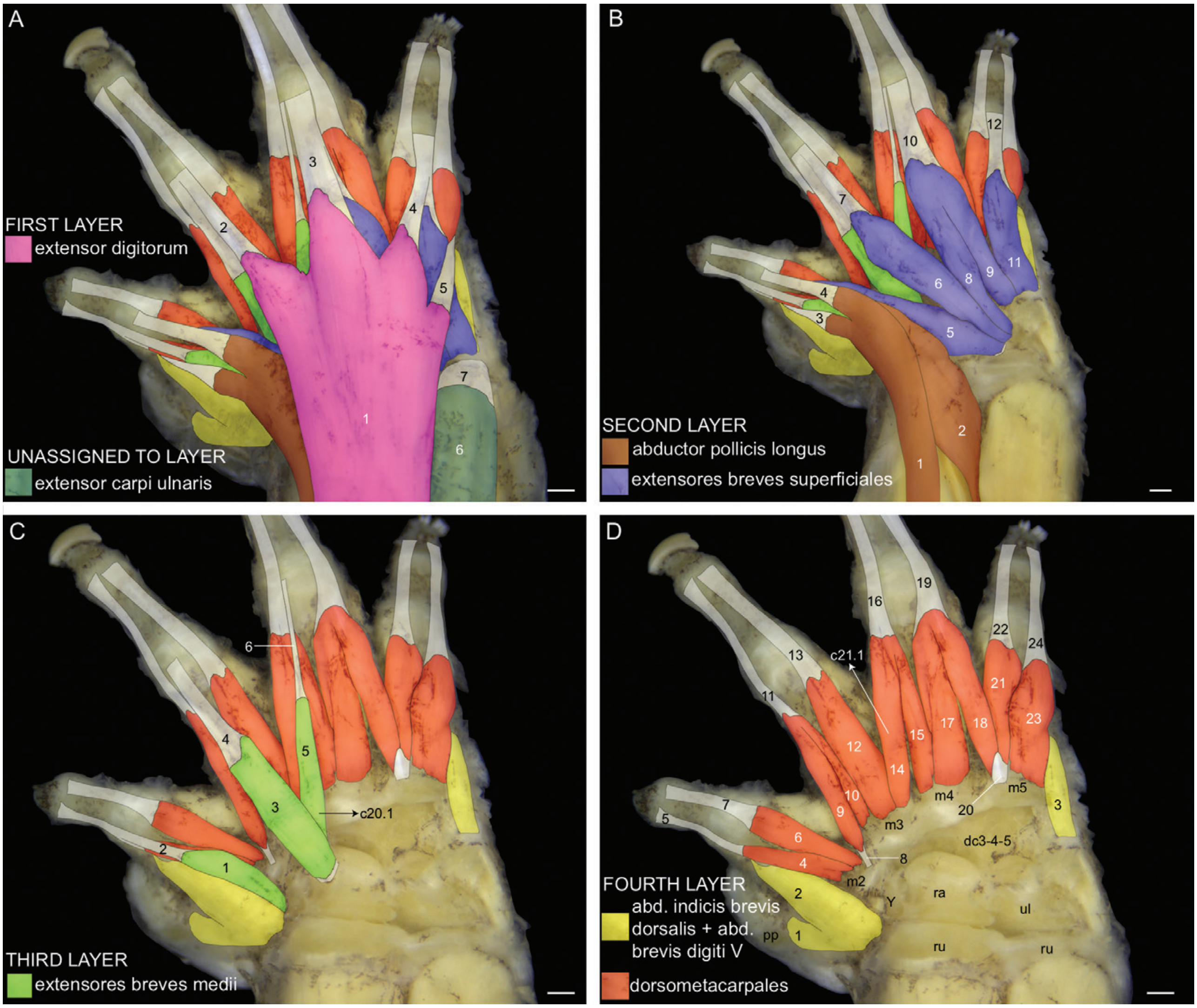

Figure 3. Dorsal surface of the hand of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01; male). A, first layer of muscles. Labelled elements: **1,** m. extensor digitorum. **2–4,** m. extensor digitorum: tendons of insertion on metacarpophalangeal joints of digits III–V, respectively. **5,** m. extensor digitorum: tendon of insertion on metacarpal V. **6–7,** m. extensor carpi ulnaris. B, second layer of muscles. Labelled elements: **1,** m. abductor pollicis longus: slip from humerus. **2,** m. abductor pollicis longus: slip from radioulna. **3,** m. abductor pollicis longus: tendon of insertion on metacarpal II. **4,** m. abductor pollicis longus: tendon of insertion on the metacarpophalangeal joint of digit II. **5,** m. extensor indicis brevis superficialis. **6–7,** m. extensor brevis superficialis digiti III. **8–9,** m. extensor brevis superficialis digiti IV: slips from ulnare and distal carpal 3-4-5, respectively. **10,** m. extensor brevis superficialis digiti IV: slips from ulnare and distal carpal 3-4-5: common tendon of insertion on metacarpophalangeal joint of digit IV. **11–12,** m. extensor brevis superficialis digiti V. C, third layer of muscles. Labelled elements: **1–2,** m. extensor indicis brevis medius. **3–4,** m. extensor brevis medius digiti III. **5–6,** m. extensor brevis medius digiti IV. D, fourth layer of muscles. Labelled elements: **1,** m. abductor indicis brevis dorsalis: slip inserting on prepollex. **2,** m. abductor indicis brevis dorsalis: slip inserting on metacarpal II. **3,** m. abductor brevis digiti V. **4–5,** medial m. dorsometacarpalis indicis proximalis. **6–7,** lateral m. dorsometacarpalis indicis proximalis. **8–9,** medial m. dorsometacarpalis proximalis digiti III: slip from metacarpal II. **10,** medial m. dorsometacarpalis proximalis digiti III: slip from metacarpal III. **11,** medial m. dorsometacarpalis proximalis digiti III: slips from metacarpals II and III: common tendon of insertion. **12–13,** lateral m. dorsometacarpalis proximalis digiti III. **14,** medial m. dorsometacarpalis proximalis digiti IV: slip from metacarpal III. **15,** medial m. dorsometacarpalis proximalis digiti IV: slip from metacarpal IV. **16,** medial m. dorsometacarpalis proximalis digiti IV: slips from metacarpals III and IV: common tendon of insertion. **17,** lateral m. dorsometacarpalis proximalis digiti IV: slip from metacarpal IV. **18,** lateral m. dorsometacarpalis proximalis digiti IV: slip from metacarpal V. **19,** lateral m. dorsometacarpalis proximalis digiti IV: slips from metacarpals IV and V:

into a single tendon that attaches to the dorsomedial surface of the interphalangeal joint/distal phalanx of digit III. The lateral m. dorsometacarpalis proximalis digiti III has a fleshy origin from the dorsolateral surface of metacarpal III and inserts via a tendon on the dorsolateral surface of the interphalangeal joint/ distal phalanx of digit III.

The medial m. dorsometacarpalis proximalis digiti IV is composed of a medial and lateral slip, both with a fleshy origin on metacarpals III and IV, respectively. They insert via a single common tendon on the dorsomedial surface of the distal interphalangeal joint/distal phalanx of digit IV.

The lateral m. dorsometacarpalis proximalis digiti IV consists of a medial slip with a fleshy origin on metacarpal IV and a lateral slip with tendinous origin on metacarpal V, partially shared with the medial m. dorsometacarpalis proximalis digiti V. They insert via a single common tendon on the dorsolateral surface of the distal interphalangeal joint/distal phalanx of digit IV.

The medial m. dorsometacarpalis proximalis digiti V has a tendinous origin proximally (in common with the slip from metacarpal V of the lateral m. dorsometacarpalis proximalis digiti IV) and a fleshy origin distally on the dorsomedial surface of metacarpal V; it inserts via a tendon on the dorsomedial surface of the distal interphalangeal joint/distal phalanx of digit V. The lateral m. dorsometacarpalis proximalis digiti V has a fleshy origin from the dorsal surface of metacarpal V and inserts via a tendon on the dorsolateral surface of the distal interphalangeal joint/distal phalanx of digit V.

Dorsal surface of the forearm: muscles unassigned to layer (Fig. 3A)

M. extensor carpi ulnaris: This forearm muscle originates from the epicondyle of the humerus and runs lateral to the m. extensor digitorum. It inserts via a short tendon on the dorsolateral surface of the ulnare and the proximolateral and dorsal surfaces of distal carpal 3-4-5.

Plantar surface of the foot: first layer (Fig. 4A)

Superficial cutaneous tendons: (The intersexual variation reported in relation to the presence and extension of each cutaneous tendon might be due to the accidental removal of portions of these delicate tendons during the deflection of the skin. Consequently, the following description should be interpreted with caution.) These tendons are present in digits II–IV (not shown in the figures). Those of digits II and III originate from the proximal surface of the respective tendines superficiales. They insert on the connective tissue joining the integument to the lateral region of the metatarsophalangeal joints of digits II and III, respectively.

Digit IV has a lateral and medial superficial cutaneous tendon, both originating from the proximal surface of the tendo superficialis digiti IV. The medial tendon attaches to the connective tissue joining the integument to the medial portion of the metatarsophalangeal joint of digit IV; the lateral tendon attaches to the connective tissue joining the integument to the lateral portion of the metatarsophalangeal and on the integument associated with the interphalangeal joints.

The female is similar, only differing partially in digit IV. This digit has two main cutaneous tendons, both originating in common from the proximal surface of the tendo superficialis digiti IV. One of these two cutaneous tendons splits into (1) a medial tendon attaching to the integument associated with the proximal and second interphalangeal joints of digit IV, and (2) a lateral tendon attaching to the integument associated with the lateral region of the metatarsophalangeal joint and the lateral region of the proximal and second interphalangeal joints of digit IV. The other main superficial cutaneous tendon attaches to the integument associated with the lateral regions of the metatarsophalangeal joint plus the proximal and second interphalangeal joints.

Tendines superficiales: The tendo superficialis praehallucis is wide and short, being thicker distally. It is formed by the insertion of the aponeurosis plantaris on the prehallux and a tendon that splits proximally from the tendo superficialis hallucis (which inserts on the dorsal surface of the portion originating from the aponeurosis plantaris).

The tendo superficialis hallucis has multiple origins: (1) from the connective tissue located medially to the prehallux, passing dorsad to the

common tendon of insertion. **20,** lateral m. dorsometacarpalis proximalis digiti IV (slip from metacarpal V) and medial m. dorsometacarpalis proximalis digiti V: common tendon of origin. **21–22,** medial m. dorsometacarpalis proximalis digiti V. **23–24,** lateral m. dorsometacarpalis proximalis digiti V. Labelled characters: c20.1: presence of the origin from the radiale of the m. extensor brevis medius digiti IV (C). c21.1: presence of the slip from metacarpal III of the medial m. dorsometacarpalis proximalis digiti IV (D). Characters referring to absence not labelled in the figure: c19.0: absence of the slip of the m. extensor brevis medius digiti III originating from element Y (C). Scale bars = 0.5 mm.

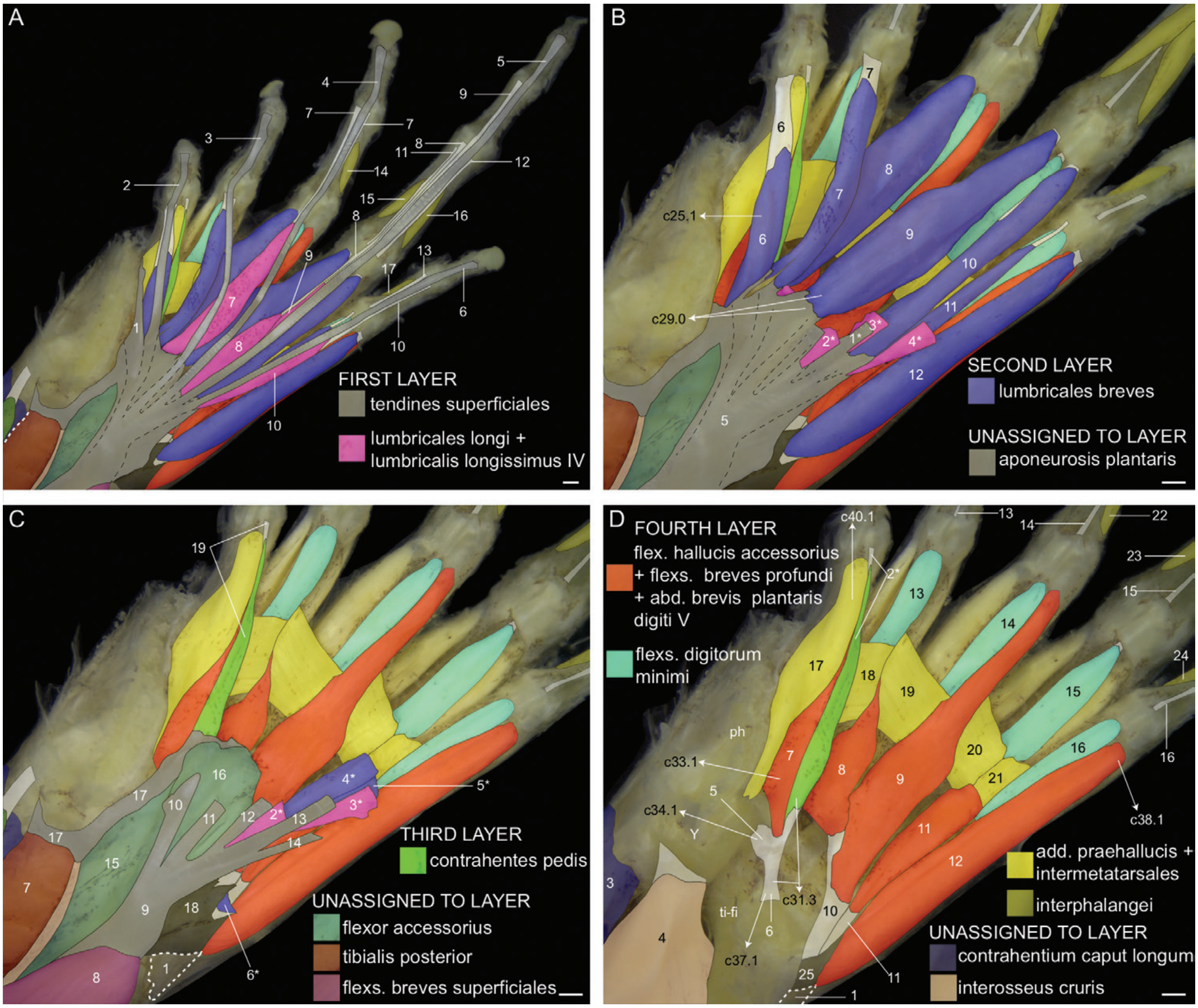

Figure 4. Plantar surface of the foot of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01; male). A, first layer of muscles. The mm. interphalangei (fourth layer) and ligaments are also labelled in this figure; we edited the thicker portion of the aponeurosis plantaris with the predefined grey shading, and with a white dashed line its approximate limits (which includes the medial and lateral thinner portions; see also element number 5 in B and a complete view of the tarsal region in Figs 5A, 14C). Labelled elements: **1–6,** tendo superficialis praehallucis, tendo superficialis hallucis and tendines superficiales digitorum II–V, respectively. **7–8,** mm. lumbricales longi digitorum III–IV. **9,** m. lumbricalis longissimus digiti IV. **10,** m. lumbricalis longus digiti V. **11,** ligament joining the medioplantar portion of the metatarsophalangeal joint and the medioplantar portion of the proximal interphalangeal joint of digit IV. **12,** ligament joining the lateroplantar portion of the metatarsophalangeal joint and the lateroplantar portion of the proximal interphalangeal joint of digit IV. **13,** ligament joining the medioplantar portion of the metatarsophalangeal joint and medioplantar portion of the proximal interphalangeal joint of digit V. **14,** m. interphalangeus digiti III: lateral slip. **15–16,** m. interphalangeus proximalis digiti IV: medial and lateral slips, respectively. **17,** m. interphalangeus proximalis digiti V: medial slip. The dark dashed line represents the tendon of insertion of the mm. flexores breves superficiales and proximal ends of the tendines superficiales, partially visible through the aponeurosis plantaris. B, second layer of muscles. Labelled elements: **1*,** tendo superficialis digiti IV: proximal unremoved portion. **2*,** m. lumbricalis longus digiti IV: proximal unremoved portion. **3*,** m. lumbricalis longissimus digiti IV: proximal unremoved portion. **4*,** m. lumbricalis longus digiti V: proximal unremoved portion. **5,** aponeurosis plantaris (the thicker portion of the aponeurosis plantaris was edited with the predefined grey shading; the white dashed line indicates its approximate limits, which include the medial and lateral thinner portions; see text). **6,** m. lumbricalis brevis hallucis. **7–8,** mm. lumbricales breves digitorum II–III, respectively. **9,** medial m. lumbricalis brevis digiti IV. **10,** lateral m. lumbricalis brevis digiti IV. **11,** medial m. lumbricalis brevis digiti V. **12,** lateral m. lumbricalis brevis

tendo superficialis praehallucis (not shown); (2) from the aponeurosis plantaris; and (3) from the multifurcation of the tendon of insertion of the mm. flexores breves superficiales – this portion converges with the dorsal surface of the portion of the tendo superficialis hallucis originating from the aponeurosis plantaris. These three portions of the tendo superficialis hallucis converge very proximally, forming a single tendo superficialis hallucis that inserts on the plantar surface of the distal phalanx of digit I.

The tendines superficiales digitorum II–III have two origins, ventrally from the aponeurosis plantaris and dorsally from the multifurcation of the tendon of insertion of the mm. flexores breves superficiales. The tendines superficiales digitorum IV and V originate from the multifurcation of the tendon of insertion of the mm. flexores breves superficiales; the tendo superficialis digiti IV also originates from the aponeurosis plantaris in the female. The tendines superficiales digitorum II–V insert on the plantar surface of the distal phalanx of digits II–V, respectively.

Mm. lumbricales longi and m. lumbricalis longissimus digiti IV: The m. lumbricalis longus digiti III originates from the aponeurosis plantaris and inserts via a single tendon, which splits into a medial and lateral one (relative to the tendo superficialis digiti III) at the level of the proximal region of the basal phalanx; the lateral tendon is thinner and it is partially joined to the medial by a sheet of connective tissue. The medial and lateral tendons insert on the medio- and lateroplantar surface of the proximal interphalangeal joint of digit III, respectively. The lateral tendon of insertion is missing in the female.

The m. lumbricalis longus digiti IV originates via a short tendon from the tendon of insertion of the mm. flexores breves superficiales at its splitting point into the tendines superficiales digitorum III and IV. It inserts via a medial tendon (relative to the tendo superficialis digiti IV) that attaches to the proximal interphalangeal joint of digit IV. A partial fusion between the tendons of insertion of the m. lumbricalis longus digiti IV and the m. lumbricalis longissimus digiti IV (or the medial tendon of the m. lumbricalis

digiti V. The dark dashed line delimits the tendon of insertion of the mm. flexores breves superficiales and proximal ends of the tendines superficiales, partially visible through the aponeurosis plantaris. C, third layer of muscles. Labelled elements: **1,** aponeurosis plantaris: distal unremoved portion inserting on the plantar cartilage. **2*,** m. lumbricalis longus digiti IV: proximal unremoved portion. **3*,** m. lumbricalis longus digiti V: proximal unremoved portion. **4*,** lateral m. lumbricalis brevis digiti IV: proximal unremoved portion. **5*,** medial m. lumbricalis brevis digiti V: proximal unremoved portion. **6*,** lateral m. lumbricalis brevis digiti V: proximal unremoved portion. **7,** m. tibialis posterior. **8,** mm. flexores breves superficiales. **9,** mm. flexores breves superficiales: tendon of insertion. **10,** mm. flexores breves superficiales: portion of the tendon of insertion that connects with the tendo superficialis praehallucis and tendo superficialis hallucis. **11–14,** mm. flexores breves superficiales: portions of the tendon of insertion that connects with the tendines superficiales digitorum II–V, respectively. **15,** m. flexor accessorius proximalis. **16,** m. flexor accessorius distalis. **17,** connective tissue attaching to the prehallux that serves as insertion point for the m. tibialis posterior and m. flexor accessorius (proximalis and distalis); see text for further comments about its identity. **18,** plantar cartilage. **19,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: portion that topologically corresponds to the former (see text). D, fourth layer of muscles. Labelled elements: **1,** aponeurosis plantaris: distal unremoved portion inserting on the plantar cartilage. **2*,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: portion that topologically corresponds to the former (see text). **3,** m. contrahentium caput longum. **4,** m. interosseus cruris. **5,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: tendon of origin from the element Y (but see text). **6,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: tendon of origin from the distal fused end of tibiale and fibulare. **7,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: portion that topologically corresponds to the latter (see main text). **8–9,** mm. flexores breves profundi digitorum II and III, respectively. **10,** mm. flexores breves profundi digitorum II and III: common tendon of origin. **11,** m. flexor brevis profundus digiti IV. **12,** m. abductor brevis plantaris digiti V. **13–16,** mm. flexores minimi digitorum II–V (their tendons of insertion pass through an internal channel of the metatarsophalangeal joints and are not visible, resulting in this apparent discontinuity). **17,** m. adductor praehallucis. **18–21,** mm. intermetatarsales I–IV. **22,** m. interphalangeus digiti III: lateral slip. **23,** m. interphalangeus proximalis digiti IV: medial slip. **24,** m. interphalangeus proximalis digiti V: medial slip. **25,** plantar cartilage, unremoved portion. Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. Labelled characters: c25.1: presence of m. lumbricalis brevis hallucis (B). c29.0: origin of the medial m. lumbricalis brevis digiti IV from the aponeurosis plantaris (B). c31.3: origin of the m. contrahentis pedis hallucis from the fused distal portions of the tibiale and fibulare (D). c33.1: presence of m. flexor hallucis accessorius (D). c34.1: presence of the origin from element Y of the m. flexor hallucis accessorius (D). c37.1: presence of the origin from the fused distal portions of the tibiale and fibulare of the m. flexor hallucis accessorius (D). c38.1: insertion of the m. abductor brevis plantaris digiti V reaching the proximal 3/4 or more of metatarsal V (D). c40.1: presence of m. adductor praehallucis (D). Scale bars = 0.5 mm.

longissimus in the female; see below) occurs at the level of the basal phalanx of digit IV.

The m. lumbricalis longus digiti V arises from the plantar cartilage (in common with the lateral m. lumbricalis brevis digiti IV and medial m. lumbricalis brevis digiti V; see Fig. 5B) and from the aponeurosis plantaris (at the level of the proximal portion of the tendo superficialis digiti V). It inserts via a lateral tendon (relative to the tendo superficialis digiti V) that attaches to the lateroplantar surface of the proximal interphalangeal joint of digit V.

The m. lumbricalis longissimus digiti IV has a tendinous origin from the same region as the m. lumbricalis longus digiti IV. It inserts via a medial tendon (relative to the tendo superficialis digiti IV) that attaches to the medioplantar surface of the second interphalangeal joint of digit IV. The female differs in that the insertion is via a wide tendon that splits into a medial and lateral one (relative to the tendo superficialis digiti IV) at the level of the basal phalanx; they attach to the medio- and lateroplantar surface of the second interphalangeal joint of digit IV, respectively.

Plantar surface: second layer (Fig. 4B)

Mm. lumbricales breves: The m. lumbricalis brevis hallucis originates from the mediodistal end of the aponeurosis plantaris via a thick common tendon with a dorsal portion of mm. lumbricales breves digitorum II and III. It inserts via a flat, wide and long tendon (medially thicker) on the medioplantar surface of the metatarsophalangeal joint of digit I (the tendon of insertion is shorter in the female).

The m. lumbricalis brevis digiti II has two origins from the aponeurosis plantaris, medially via a common tendon with the mm. lumbricales breves hallucis and digiti III and laterally via a common tendon with the m. lumbricalis brevis digiti III. It inserts on the medioplantar surface of the metatarsophalangeal joint of digit II via a short to medium-sized tendon. The female differs in that mm. lumbricales breves hallucis and digitorum II–III have a single common tendon of origin.

The m. lumbricalis brevis digiti III is well developed. It originates as described above for the mm. lumbricales breves hallucis and digiti II and attaches to the medioplantar surface of the metatarsophalangeal joint of digit III via a fleshy insertion.

The medial m. lumbricalis brevis digiti IV is more developed than the lateral one. It originates from the aponeurosis plantaris and inserts on the medioplantar surface of the metatarsophalangeal joint of digit IV via a short tendon. The lateral m. lumbricalis brevis digiti IV originates from the plantar cartilage via a common tendon with the m. lumbricalis longus digiti V and the medial m. lumbricalis brevis digiti V (see Fig. 5B). It inserts via a short tendon on the lateroplantar surface of the metatarsophalangeal joint of digit IV.

The medial m. lumbricalis brevis digiti V originates as described above for the lateral m. lumbricalis brevis digiti IV and inserts on the medioplantar surface of the metatarsophalangeal joint of digit V via a long tendon (this tendon is shorter in the female). The lateral m. lumbricalis brevis digiti V originates from the plantar cartilage and inserts on the lateroplantar surface of the metatarsophalangeal joint of digit V via a short tendon.

Plantar surface: third layer (Fig. 4C)

Mm. contrahentes pedis: This layer is composed only of the m. contrahentis pedis hallucis. This muscle is hypothesized to be fused with the m. flexor hallucis accessorius in the male. This fused muscle has two tendinous origins, one from element Y and the other from the fused distal portions of the tibiale and fibulare.

The m. contrahentis pedis hallucis is only distinguishable from the m. flexor hallucis accessorius distally. The lateral portion attaching to the lateroplantar surface of the metatarsophalangeal joint and proximal end of the basal phalanx of digit I is tentatively considered to be the m. contrahentis pedis hallucis and is labelled as such in Figures 4C, D and 5C. The medial portion with a fleshy insertion on metatarsal I corresponds topologically to the m. flexor hallucis accessorius.

In the female, the mm. contrahentis pedis hallucis and flexor hallucis accessorius share only a common tendon of origin from the fused distal portions of the tibiale and fibulare (the origin from element Y is absent) and are independent muscles distally to that point. The m. contrahentis pedis hallucis inserts via a long tendon on the same region as described for the male.

Plantar surface: fourth layer (Fig. 4D).

M. flexor hallucis accessorius: See description above for the m. contrahentis pedis hallucis.

Mm. flexores breves profundi: The mm. flexores breves profundi digitorum II and III have a common tendon of origin from the distal and lateroplantar surface of the fibulare, just medially to the origin of the m. flexor brevis profundus digiti IV. The m. flexor brevis profundus digiti II has a fleshy insertion on the lateroplantar surface of the proximal half of metatarsal II, while the insertion of the m. flexor brevis profundus digiti III is fleshy on the complete lateroplantar surface of metatarsal III.

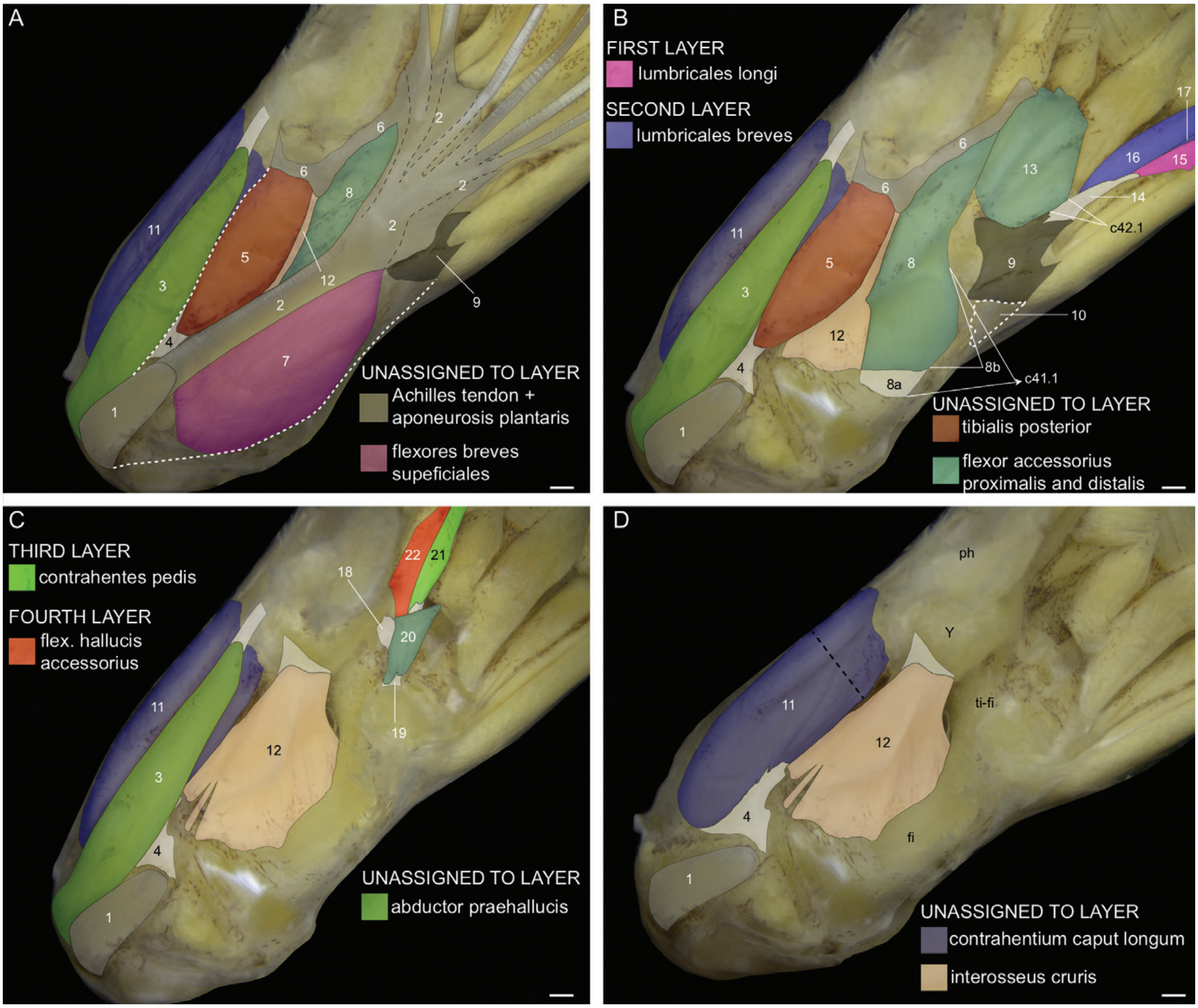

Figure 5. Plantar surface of the tarsal region of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01; male). Since the involved muscles of this region of the leg are fewer in number than the foot, we enumerate all the muscles following a single sequential numbering in A–D. A, labelled elements: **1,** Achilles tendon (note the cartilaginous structure within it). **2,** aponeurosis plantaris (the thicker portion of the aponeurosis plantaris was edited with the predefined grey shading; the white dashed line indicates its approximate limits, which include the medial and lateral thinner portions; see text). **3,** m. abductor praehallucis. **4,** m. contrahentium caput longum and m. tibialis posterior: common tendon of origin. **5,** m. tibialis posterior. **6,** connective tissue attaching to the prehallux that serves as insertion point for the m. tibialis posterior and m. flexor accessorius (proximalis and distalis); for further comments about its identity see main text. **7,** mm. flexores breves superficiales. **8,** m. flexor accessorius proximalis. **8a,** m. flexor accessorius proximalis: portion with tendinous origin. **8b,** m. flexor accessorius proximalis: portion with fleshy origin. **9,** plantar cartilage. **10,** aponeurosis plantaris: distal unremoved portion inserting on the plantar cartilage. **11,** m. contrahentium caput longum (the black dashed line in D indicates the most proximal region of its insertion on the tibiale). **12,** m. interosseus cruris. **13,** m. flexor accessorius distalis. **14,** m. lumbricalis longus digiti V, lateral m. lumbricalis brevis digiti IV, and medial m. lumbricalis brevis digiti V: common tendon of origin (note a distal portion of the m. flexor accessorius distalis originating from it). **15,** m. lumbricalis longus digiti V. **16,** lateral m. lumbricalis brevis digiti IV. **17,** medial m. lumbricalis brevis digiti V. **18,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: tendon of origin from element Y (but see text). **19,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: tendon of origin from the fused distal portions of the tibiale and fibulare. **20,** m. flexor accessorius (see text for comments on its identity as the proximalis or distalis portion of the muscle): portion originating on the tendon of origin of the fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius. **21,** fused m. contrahentis pedis hallucis and m. flexor hallucis accessorius: portion that topologically corresponds to the former (see text). **22,** fused

The m. flexor brevis profundus digiti IV originates via a tendon from the distal end of the fibulare. It has a fleshy insertion on the proximal half of the lateroplantar surface of metatarsal IV, dorsally to the insertion of the m. intermetatarsalis IV.

M. abductor brevis plantaris digiti V: This is a well-developed muscle that originates from the distal end of the fibulare via a tendon and attaches to the entire lateroplantar surface of metatarsal V via a fleshy insertion.

M. adductor praehallucis: This is a well-developed muscle with a fleshy origin from the lateral surface of the prehallux and from the adjoining connective tissue laterally located to the prehallux. The insertion is fleshy and divided into two portions, which are separated by a small gap. The proximal portion inserts on the distal third of the medioplantar surface of metatarsal I, not reaching its distal extreme. The distal portion inserts on the distal plantar surface of metatarsal I, almost reaching the metatarsophalangeal joint of digit I.

Mm. intermetatarsales: The mm. intermetatarsales I–IV are flat transversal muscles that join the metatarsals. They originate from metatarsals II, III, IV and V and insert on metatarsals I, II, III and IV, respectively. Additionally, there is a thin raphe separating the mm. intermetatarsales III and IV along their mutual contact zone, giving the appearance of being fused into a single m. intermetatarsalis connecting the metatarsals III and V.

Mm. flexores digitorum minimi: The mm. flexores minimi digitorum II–V have a fleshy origin from the metatarsals II–V, respectively. The proximal portions of the origin of the mm. flexores minimi digitorum II–IV are dorsally located with respect to the origin of the mm. intermetatarsales I–III, respectively, while the origin of the m. flexor minimus digiti V is ventral with respect to origin of the m. intermetatarsalis IV. Their tendons of insertion pass through an internal channel in their respective metatarsophalangeal joints and attach to the plantar surface of their respective basal phalanges. In the female, the m. flexor minimus digiti IV inserts via two well-defined parallel tendons on the basal phalanx of digit IV (not shown).

Mm. interphalangei: The m. interphalangeus digiti III is represented by the lateral slip; it originates from the lateroplantar surface of the basal phalanx and inserts on the proximal end of the second phalanx of digit III. The m. interphalangeus proximalis digiti IV is composed of a medial and lateral equally developed slip; they originate on the medio- and lateroplantar surface of the basal phalanx and insert via a common tendon on the proximal end of the second phalanx of digit IV. The m. interphalangeus distalis digiti IV is absent.

The m. interphalangeus proximalis digiti V is represented by the medial slip in the male; it originates on the medioplantar surface of the basal phalanx and inserts on the proximal end of the second phalanx of digit V. The female has the three slips of the m. interphalangeus proximalis digiti V: medial, intermediate and lateral. They originate from the medioplantar surface of the basal phalanx, metatarsophalangeal joint and lateroplantar surface of the basal phalanx of digit V, respectively. The lateral slip is reduced and distally located in relation to the medial one, while the intermediate slip is well developed. They insert on the proximal end of the second phalanx of digit V and the intermediate slip has an additional fleshy insertion on the distal end of the plantar surface of the basal phalanx of digit V (not shown). The m. interphalangeus distalis digiti V is absent.

Plantar surface of the foot: muscles unassigned to layer (Figs 4C, D, 5)

Aponeurosis plantaris: The Achilles tendon and the aponeurosis plantaris are portions of the tendon of insertion of the m. flexor digitorum communis, the aponeurosis plantaris being its distal expansion. The aponeurosis plantaris is poorly developed medially and laterally, being thicker on the middle and distal region of the tarsal surface. It serves as the point of origin for several muscles (see above). The os sesamoides tarsale (located in the Achilles tendon; see Nussbaum, 1982) is absent or uncalcified (see Discussion).

M. tibialis posterior: This muscle is not well developed; it originates from the medial side of the ligamentum calcanei via a tendon (partially shared with the m. contrahentium caput longum); its fibres extend distad on the medioplantar side of the tarsal region

m. contrahentis pedis hallucis and m. flexor hallucis accessorius: portion that topologically corresponds to the latter. The dark dashed line delimits the tendon of insertion of the mm. flexores breves superficiales and proximal ends of the tendines superficiales, partially visible through the aponeurosis plantaris (see Fig. 4C where the aponeurosis plantaris is removed and these tendons are exposed). The plantar cartilage was removed in C and D. Labelled characters: c41.1: broad origin of m. flexor accessorius proximalis, occupying more than the distal 1/3 of the fibulare (B). c42.1: presence of the origin of the m. flexor accessorius distalis from the proximal portion of the tendon of origin of mm. lumbricales of digits IV and V (B). Scale bars = 0.5 mm.

and insert on the connective tissue that is proximal to the prehallux; this connective tissue can be interpreted as a tendon of insertion of the m. tibialis posterior and/or as a thicker portion of the aponeurosis plantaris attaching to the prehallux. The fleshy insertion of the m. tibialis posterior on the dorsal surface of the aponeurosis plantaris is absent.

Mm. flexores breves superficiales: This muscle is composed of a single body. It originates from the lateral side of the ligamentum calcanei, runs distad on the lateroplantar surface of the tarsal region, and inserts via a single strong tendon, with no sesamoid embedded within it. This single tendon splits distally into five tendons (described above also as a multifurcation) that are the proximal ends of the tendines superficiales I–V (the tendo superficialis praehallucis originates from the tendo superficialis hallucis distally to this multifurcation).

M. flexor accessorius: This muscle is composed of a proximal and distal portion. The m. flexor accessorius proximalis is well developed, with its origin covering more than the distal half of the fibulare. The origin is tendinous proximally and fleshy distally, and the insertion is on the connective tissue medial to the prehallux; this connective tissue can also be interpreted as a thicker portion of the aponeurosis plantaris attaching to the prehallux. The m. flexor accessorius distalis originates from the plantar cartilage and from the proximal portion of the common tendon of origin of the m. lumbricalis longus digiti V, lateral m. lumbricalis brevis digiti IV and medial m. lumbricalis brevis digiti V. There is a portion with origin from the distal end of the fibulare that does not have a discrete gap with respect to the portion originating from the plantar cartilage; this portion is tentatively considered as part of the m. flexor accessorius distalis.

Additionally, there is a distal and medial portion of the m. flexor accessorius with origin on the common tendon of origin of the m. contrahentis pedis hallucis and m. flexor hallucis accessorius from the fused distal portions of the tibiale and fibulare. It is unclear whether this portion corresponds to the m. flexor accessorius proximalis or distalis because there is a spatial gap between this supplementary portion and those muscles.

M. abductor praehallucis: This well-developed muscle has a fleshy origin from the medial surface of the Achilles tendon, runs medially to the m. tibialis posterior and inserts via a tendon on the proximal end of the prehallux.

M. contrahentium caput longum: This muscle has a tendinous origin from the medial side of the ligamentum calcanei, partially shared with the origin of the m. tibialis posterior, and inserts on the distal end of the tibiale.

M. interosseus cruris: This muscle originates from the tibiale and fibulare (including the fused proximal portions of these bones) and tapers into a very short, wide and strong tendon that attaches to element Y.

Dorsal surface of the foot: first layer (Fig. 6A)

M. extensor digitorum longus: This muscle originates from the distal end of the tibiofibula and is distally differentiated into a medial and lateral slip. The former attaches to the metatarsophalangeal joint of digit I, in common with the m. extensor brevis medius hallucis. The lateral slip attaches to the metatarsophalangeal joint of digit II, in common with the insertion of the mm. extensores breves medius digiti II and superficialis digiti II.

Dorsal surface of the foot: second layer (Fig. 6B)

Mm. extensores digitorum breves superficiales: The m. extensor brevis superficialis hallucis is well developed. It has a fleshy origin on the dorsal surface of the fibulare, proximally to the origin of the remaining mm. extensores breves superficiales. It inserts on the prehallux via a wide and short tendon.

The mm. extensores breves superficiales digitorum II and III are reduced and originate via a common tendon from the fibulare. The m. extensor brevis superficialis digiti II inserts via a common tendon with the m. extensor digitorum longus and m. extensor brevis medius digiti II on the metatarsophalangeal joint of digit II.

The m. extensor brevis superficialis digiti III is composed of a medial and lateral slip. The former diverges from the proximal portion of the m. extensor brevis superficialis digiti II and inserts via a common tendon with the m. extensor brevis medius digiti III on the metatarsophalangeal joint of digit III. The lateral slip is more developed than the medial; it inserts via an independent tendon on the dorsal surface of the proximal interphalangeal joint of digit III. The m. extensor brevis superficialis digiti III is absent in the female.

The m. extensor brevis superficialis digiti IV is composed of medial and lateral muscles that are proximally undifferentiated; their common origin is fleshy from the dorsodistal surface of the fibulare. The medial muscle is larger than its lateral counterpart and inserts via a tendon on the metatarsophalangeal joint of digit IV. The lateral m. extensor brevis superficialis digiti IV inserts via a single, long tendon on the proximal interphalangeal joint of digit IV. The

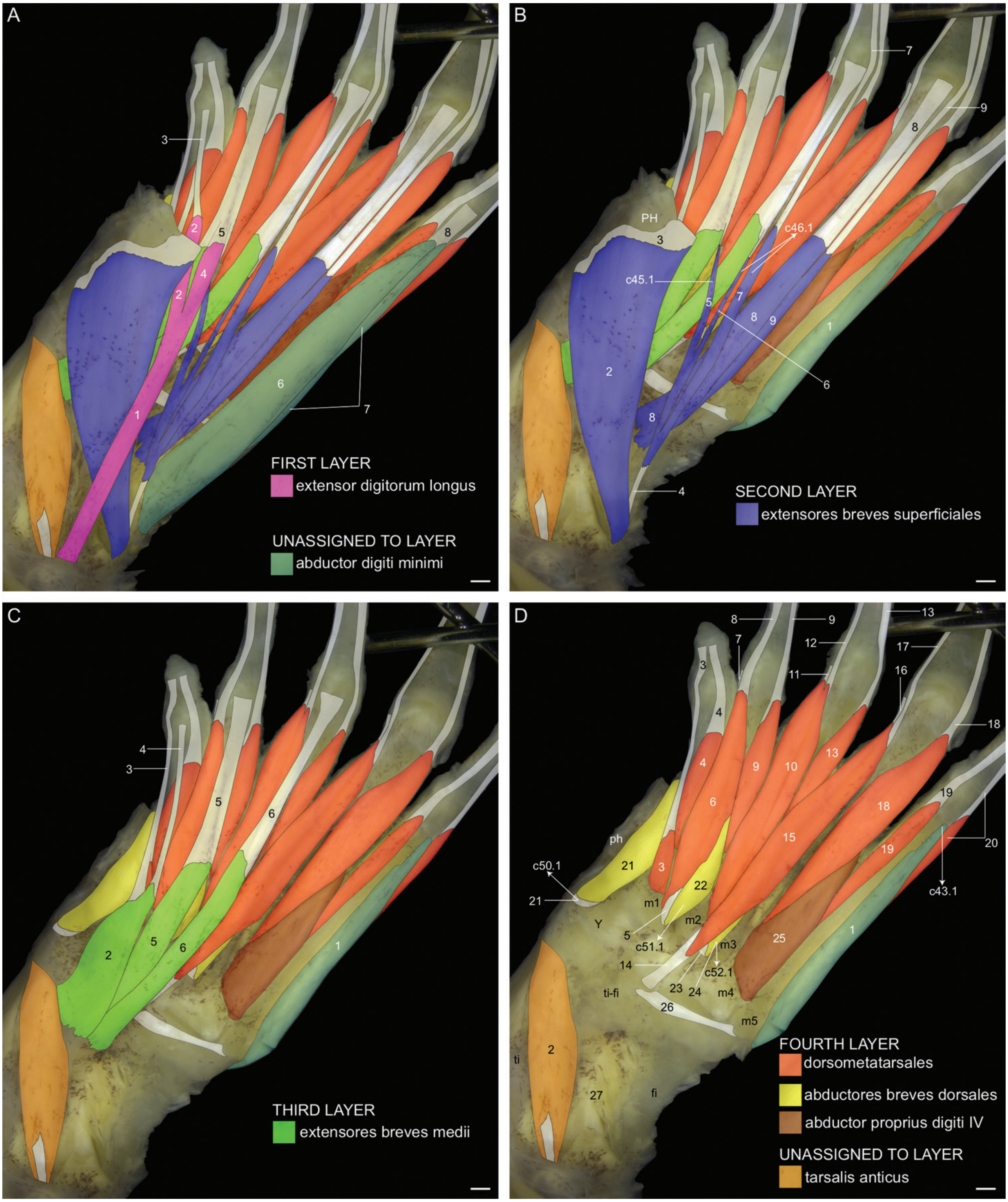

Figure 6. Dorsal surface of the foot of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01; male). A, first layer of muscles. Labelled elements: **1,** m. extensor digitorum longus. **2,** m. extensor digitorum longus: slip to digit I. **3,** m. extensor digitorum longus: tendon of insertion attaching to the metatarsophalangeal joint of digit I (in common with the m. extensor brevis medius hallucis). **4,** m. extensor digitorum longus: slip to digit II. **5,** m. extensor digitorum longus: tendon of insertion

m. extensor brevis superficialis digiti V is tentatively considered to be present, although undifferentiated from the m. abductor digiti minimi (see below).

Dorsal surface of the foot: third layer (Fig. 6C)

Mm. extensores digitorum breves medii: The mm. extensores breves medii digitorum I–III have a fleshy origin from the fused distal portions of the tibiale and fibulare. The m. extensor brevis medius hallucis inserts via a medial and lateral tendon. The medial tendon converges into a common tendon with the medial m. dorsometatarsalis hallucis proximalis and attaches to the interphalangeal joint/distal phalanx of digit I; the lateral tendon attaches to the metatarsophalangeal joint of digit I. The mm. extensores breves medii digitorum II and III insert each via a single tendon on the metatarsophalangeal joint of digits II and III, respectively.

Dorsal surface of the foot: fourth layer (Figs 6D, 7)

Mm. dorsometatarsales proximales: The medial m. dorsometatarsalis hallucis proximalis has a fleshy origin from the proximodorsal surface of metatarsal I and inserts via a long tendon on the dorsomedial surface of the interphalangeal joint/distal phalanx of digit I. The lateral m. dorsometatarsalis hallucis proximalis is more developed and distally located with respect to the medial muscle; it originates from the dorsolateral surface of metatarsal I and inserts via a tendon on the dorsolateral surface of the interphalangeal joint/distal phalanx of digit I.

The medial m. dorsometatarsalis proximalis digiti II originates from the base of metatarsal I; its origin is proximally tendinous (in common with the m. abductor brevis dorsalis digiti II) and distally fleshy. It inserts via a short tendon on the medial surface of the metatarsophalangeal joint of digit II

attaching to the metatarsophalangeal joint of digit II (in common with the m. extensor brevis superficialis digiti II and m. extensor brevis medius digiti II). **6,** m. abductor digiti minimi: main portion. **7,** m. abductor digiti minimi: partially differentiated lateral portion. **8,** m. abductor digiti minimi and/or m. extensor brevis superficialis digiti V: tendon of insertion on metatarsophalangeal joint of digit V (see text for discussion). B, second layer of muscles. Labelled elements: **1,** m. abductor digiti minimi: partially differentiated lateral portion. **2,** m. extensor brevis superficialis hallucis. **3,** m. extensor brevis superficialis hallucis: tendon of insertion on prehallux. **4,** mm. extensores breves superficiales digitorum II and III: common tendon of origin. **5,** m. extensor brevis superficialis digiti II (note the common insertion with the m. extensor brevis medius digiti II). **6,** m. extensor brevis superficialis digiti III: medial slip (note the common insertion with the m. extensor brevis medius digiti III). **7,** m. extensor brevis superficialis digiti III: lateral slip (note the independent insertion on the interphalangeal joint). **8,** medial m. extensor brevis superficialis digiti IV. **9,** lateral m. extensor brevis superficialis digiti IV. C, third layer of muscles. A dorsal and distal portion of the prehallux was removed to expose some underlying muscles. Labelled elements: **1,** m. abductor digiti minimi: partially differentiated lateral portion. **2,** m. extensor brevis medius hallucis. **3,** m. extensor brevis medius hallucis: common tendon of insertion with the medial m. dorsometatarsalis hallucis proximalis. **4,** m. extensor brevis medius hallucis: tendon of insertion attaching the metatarsophalangeal joint. **5–6,** mm. extensores breves medii digitorum II and III, respectively. D, fourth layer of muscles. The m. tarsalis anticus and a ligament attaching to the metatarsal V are also shown. Labelled elements: **1,** m. abductor digiti minimi: partially differentiated lateral portion. **2,** m. tarsalis anticus. **3,** medial m. dorsometatarsalis hallucis proximalis. **4,** lateral m. dorsometatarsalis hallucis proximalis. **5,** medial m. dorsometatarsalis proximalis digiti II and m. abductor brevis dorsalis digiti II: common tendon of origin. **6,** medial m. dorsometatarsalis proximalis digiti II. **7,** medial m. dorsometatarsalis proximalis digiti II: tendon of insertion on the metatarsophalangeal joint. **8,** medial m. dorsometatarsalis proximalis digiti II: tendon of insertion on the interphalangeal joint/distal phalanx. **9,** lateral m. dorsometatarsalis proximalis digiti II. **10,** medial m. dorsometatarsalis proximalis digiti III. **11,** medial m. dorsometatarsalis proximalis digiti III: tendon of insertion on the metatarsophalangeal joint. **12,** medial m. dorsometatarsalis proximalis digiti III: tendon of insertion on the distal interphalangeal joint/distal phalanx. **13,** lateral m. dorsometatarsalis proximalis digiti III. **14,** medial m. dorsometatarsalis proximalis digiti IV: tendon of origin. **15,** medial m. dorsometatarsalis proximalis digiti IV. **16,** medial m. dorsometatarsalis proximalis digiti IV: tendon of insertion on the metatarsophalangeal joint. **17,** medial m. dorsometatarsalis proximalis digiti IV: tendon of insertion on the distal interphalangeal joint/distal phalanx. **18,** lateral m. dorsometatarsalis proximalis digiti IV. **19,** m. medial dorsometatarsalis proximalis digiti V. **20,** lateral m. dorsometatarsalis proximalis digiti V. **21,** m. abductor brevis dorsalis hallucis. **22,** m. abductor brevis dorsalis digiti II. **23,** m. abductor brevis dorsalis digiti III and medial m. dorsometatarsalis proximalis digiti III: common tendon of origin. **24,** m. abductor brevis dorsalis digiti III. **25,** m. abductor proprius digiti IV. **26,** ligament joining the fused distal portions of the tibiale and fibulare to the proximal end of metatarsal V. **27,** m. interosseus cruris (a ventral muscle; not shaded, but visible as a muscular mass occupying the gap between the tibiale and fibulare; see Figs 4, 5 for ventral views). Labelled characters: c43.1: insertion of m. abductor digiti minimi broad, reaching at least the proximal half of metatarsal V (D). c45.1: presence of m. extensor brevis superficialis digiti II (B). c46.1: presence of m. extensor brevis superficialis digiti III (B). c50.1: origin of the m. abductor brevis dorsalis hallucis tendinous (D). c51.1: presence of m. abductor brevis dorsalis digiti II (D). c52.1: presence of m. abductor brevis dorsalis digiti III (D). Characters referring to absence not labelled in the figure: c47.0: absence of m. extensor brevis medius digiti IV (C). Scale bars = 0.5 mm.

and a second tendon on the dorsomedial surface of the interphalangeal joint/distal phalanx of digit II. The lateral m. dorsometatarsalis proximalis digiti II is smaller than the medial muscle; it has a fleshy origin from the dorsolateral surface of metatarsal II and inserts via a tendon on the dorsolateral surface of the interphalangeal joint/distal phalanx of digit II.

The medial m. dorsometatarsalis proximalis digiti III originates from the base of metatarsal II; its origin is proximally tendinous (in common with the m. abductor brevis dorsalis digiti III) and distally fleshy. It inserts via a short tendon on the medial surface of the metatarsophalangeal joint of digit III and a second tendon on the dorsomedial surface of the distal interphalangeal joint/distal phalanx of digit III. The lateral m. dorsometatarsalis proximalis digiti III is more distally located and smaller than the medial muscle; it has a fleshy origin from the dorsal and laterodistal half of metatarsal III and inserts via a tendon on the dorsolateral surface of the distal interphalangeal joint/distal phalanx of digit III.

The medial m. dorsometatarsalis proximalis digiti IV originates via a tendon from the fused distal portions of the tibiale and fibulare. It has two tendons of insertion, one attached to the medial surface of the metatarsophalangeal joint of digit IV and the other to the dorsomedial surface of the distal interphalangeal joint/distal phalanx of digit IV.

The medial m. dorsometatarsalis proximalis digiti IV has a supplementary dorsal slip in the male (Fig. 7). It has a fleshy origin from the dorsolateral surface of metatarsal III and inserts via a short tendon on the medial portion of the metatarsophalangeal joint of digit IV.

The lateral m. dorsometatarsalis proximalis digiti IV has a fleshy origin from the dorsolateral surface of metatarsal IV and inserts via a tendon on the dorsolateral surface of the distal interphalangeal joint/distal phalanx of digit IV. The medial and lateral m. dorsometatarsalis proximalis digiti V are quite small, with a fleshy origin on the dorsomedial and dorsolateral surface of metatarsal V, respectively; each insert on the dorsomedial and dorsolateral surface of the distal interphalangeal joint/distal phalanx of digit V, respectively.

Mm. abductores breves dorsales: The m. abductor brevis dorsalis hallucis has a tendinous origin from the lateral surface of element Y and a fleshy insertion on the proximomedial surface of metatarsal I. The mm. abductores breves dorsales digitorum II and III originate from metatarsals I and II, respectively, in common with the medial mm. dorsometatarsales proximales digitorum II and III, respectively. Their insertion is fleshy on the dorsomedial surface of metatarsals II and III, respectively.

M. abductor proprius digiti IV: This well-developed muscle originates from the proximomedial end of metatarsal V and inserts along the entire lateral surface of metatarsal IV.

Dorsal surface of the foot: muscles unassigned to layer (Figs 6A, D)

M. abductor digiti minimi: This well-developed muscle has a fleshy origin from the dorsolateral surface of the fibulare and a fleshy insertion on almost the entire dorsolateral surface of metatarsal V; the male has a partially differentiated lateral portion. This massive muscle also attaches via a short tendon to the metatarsophalangeal joint of digit V; this portion might correspond to the m. extensor brevis superficialis digiti V.

M. tarsalis anticus: This muscle originates from the distal end of the tibiofibula via a discrete tendon. It has a fleshy insertion on the dorsodistal surface of the tibiale.

Characters and data matrix

We defined 52 transformation series, among which 26 were taken from the literature (Burton, 1998a, 1998b, 2004; Blotto *et al.*, 2017, 2020) and 26 represent novel hypotheses either first proposed here or significantly modified from previous authors (see Appendix 1). The resulting data matrix has 8684 cells (167 terminals and 52 characters) with 2.0% missing data, 1.8% inapplicable data and 0.3% polymorphisms (treated as ambiguous). The data matrix and ACSRs for the 52 characters are provided in Supporting Information Appendices S2 and S3, respectively.

DISCUSSION

Systematic implications

The character sampling of this study was designed to identify synapomorphies and autapomorphies within Sooglossoidea and characters potentially associated with digging behaviour. However, due to the diverse taxon sample and abundant homoplasy, we also identified several synapomorphies for taxa of different taxonomic levels (those at the family level or above are summarized in Fig. 11; see Appendix 1 for less inclusive clades). We discuss in this section the systematic implications of some of these newly proposed synapomorphies. Except for Sooglossoidea, which is treated in more detail, the account below does not address synapomorphies that are highly tentative or restricted to small clades (listed in Appendix 1; Supporting Information Appendix S3) or those discussed below in the section ‘Foot

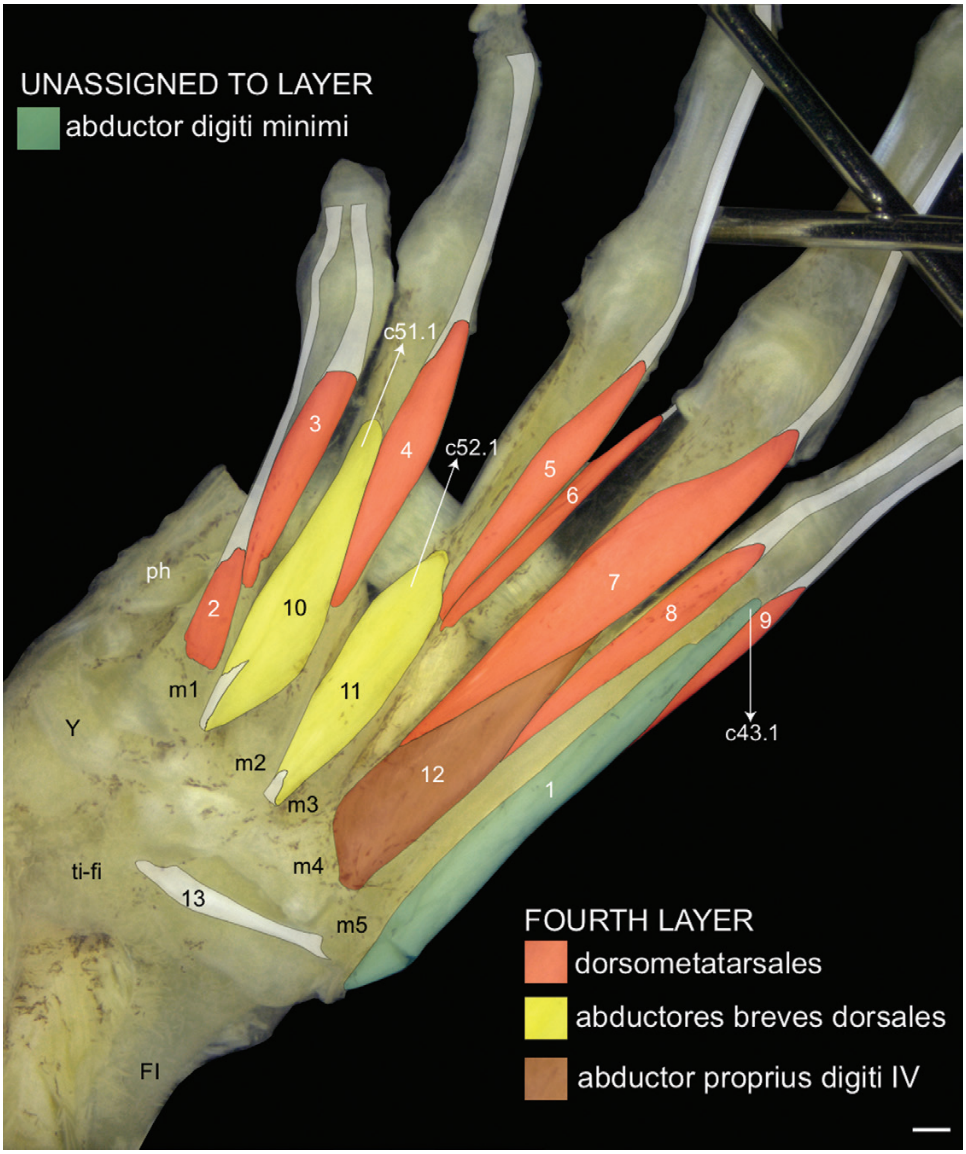

Figure 7. Fourth layer of muscles from the dorsal surface of the foot of *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01). In comparison with Figure 6D, some muscles (medial mm. dorsometatarsales proximales digitorum II and III, and the slip originating from the fused distal portions of the tibiale and fibulare of the medial m. dorsometatarsalis proximalis digiti IV) were removed to expose the mm. abductores breves dorsales digitorum II and III, and the dorsal slip from metatarsal III of the medial m. dorsometatarsalis proximalis digiti IV. The m. abductor brevis dorsalis hallucis was also removed. A dorsal and distal portion of the prehallux was removed to expose some underlying muscles. Labelled elements: **1,** m. abductor digiti minimi: partially differentiated lateral portion. **2,** medial m. dorsometatarsalis hallucis proximalis. **3,** lateral m. dorsometatarsalis hallucis proximalis. **4,** lateral m. dorsometatarsalis proximalis digiti II. **5,** lateral m. dorsometatarsalis proximalis digiti III. **6,** media m. dorsometatarsalis proximalis digiti II: slip originating from the metatarsal III. **7,** lateral m. dorsometatarsalis proximalis digiti IV. **8,** medial m. dorsometatarsalis proximalis digiti V. **9,** lateral m. dorsometatarsalis proximalis digiti V. **10–11,** mm. abductores breves dorsales digitorum II and III, respectively. **12,** m. abductor proprius digiti IV. **13,** ligament joining the fused distal portions of the tibiale and fibulare to the proximal end of metatarsal V. Labelled characters: c43.1: insertion of m. abductor digiti minimi broad, reaching at least the proximal half of metatarsal V. c51.1: presence of m. abductor brevis dorsalis digiti II. c52.1: presence of m. abductor brevis dorsalis digiti III. Scale bar = 0.5 mm.

musculature, convergence and hind limb digging behaviour'.

Sooglossoidea

None of the novel characters incorporated into this study optimize as synapomorphies of Sooglossoidea. Nevertheless, knowledge of the foot musculature of Nasikabatrachidae allows more precise determination of the level of generality of two character states previously defined by Blotto *et al.* (2020). These are Characters 51.1 and 52.1: presence of the mm. abductores breves dorsales digitorum II and III, respectively (Figs 6D, 7), which Blotto *et al.* (2020) hypothesized to be synapomorphies of Sooglossidae or Sooglossoidea, pending confirmation of the condition in Nasikabatrachidae and *Sechellophryne*.

The mm. abductores breves dorsales digitorum II and III are present in *Nasikabatrachus* and might be synapomorphies of Sooglossoidea; however, if these muscles are found to be absent in *Sechellophryne* (condition unknown), then the optimization will be ambiguous in this region of the tree (i.e. it would be equally parsimonious to be gained in Sooglossoidea and lost in *Sechellophryne* or gained independently in *Nasikabatrachus* and *Sooglossus*). If confirmed to be present in *Sechellophryne*, their presence will provide the first two myological synapomorphies for this major clade (the other known phenotypic synapomorphy is the absence of the columella; Pereyra *et al.*, 2016).

The other two character states hypothesized by Blotto *et al.* (2020) to be synapomorphies of Sooglossidae or Sooglossoidea are Characters 13.1 (presence of m. flexor minimus indicis) and 42.0 (absence of the foot m. extensor brevis superficialis digiti III). The former is restricted here to Sooglossidae or *Sooglossus*, due to the absence in *Nasikabatrachus* and the unknown condition in *Sechellophryne* (see below). Character 46.0 is ambiguous for Sooglossoidea due to its polymorphism in *Nasikabatrachus* (only present in the male; Fig. 6B).

Sooglossidae: new synapomorphies and future research

The condition of most previous non-molecular synapomorphies (e.g. Ford & Cannatella, 1993; Nussbaum & Wu, 2007; Blotto *et al.*, 2020) or specific phenotypic traits (Tyler, 1985) suggested for Sooglossidae is unknown in *Nasikabatrachus*. Among the exceptions, in which the condition of *Nasikabatrachus* was considered, are direct development and female parental care (Blotto *et al.*, 2020). Among the several putative synapomorphies from the hand and foot musculature suggested here for Sooglossidae, the condition in *Sechellophryne* must be determined for Characters 10, 11, 12, 13, 15, 16, 38, 48 and 49. Knowledge of the condition of these characters in *Sechellophryne* is necessary to determine their level of generality (i.e. synapomorphies of Sooglossidae or *Sooglossus*).

The os sesamoides tarsale, described by Nussbaum (1982; see also Scott, 2005: char. 109) for Sooglossidae and a few additional taxa, is absent or unossified in *Nasikabatrachus*. Interestingly, Nussbaum (1982: 315) described a dense cartilaginous structure in the same region where the os sesamoides tarsale occurs in some species of Pyxicephalidae, similar to the condition observed in *Nasikabatrachus* (see Fig. 5, labelled as 1). As such, this cartilaginous structure might be homologous with the os sesamoides tarsale, although in an unossified state [as previously suggested by Nussbaum (1982) for some species of Pyxicephalidae]. Considering this hypothesis, the occurrence of the structure (ossified or not) in the Achilles tendon might be a synapomorphy of Sooglossoidea, with the os sesamoides tarsale (the ossified condition) being a synapomorphy of Sooglossidae, as previously suggested by Nussbaum (1982) and Ford & Cannatella (1993).

Finally, the study of Nussbaum & Wu (2007) requires some comments. They performed a phylogenetic analysis (see their fig. 1) of phenotypic characters from adult external morphology, myology (excluding characters from hand and foot musculature) and osteology. They recovered Sooglossidae in a polytomy with (1) Dendrobatoidea, (2) part of Brachycephaloidea and (3) part of Myobatrachidae. The inclusive clade was recovered as the sister of their ranoid samples.

This heterodox topology is probably due to the limited character and taxon sampling for what was known and available at that time (e.g. DNA sequence data from Biju & Bossuyt, 2003, and Frost *et al.*, 2006). On the basis of this this topology, Nussbaum & Wu (2007) proposed 24 phenotypic synapomorphies for Sooglossidae, ten for *Sechellophryne* and seven for *Sooglossus*. However, these synapomorphies must be re-evaluated in light of the topologies recovered in the more densely sampled phylogenetic analyses (e.g. Biju & Bossuyt, 2003; Frost *et al.*, 2006; Pyron & Wiens, 2011; Pyron, 2014; Jetz & Pyron, 2018; Hime *et al.*, 2021).

Nasikabatrachidae: putative sexual dimorphism and autapomorphies

We recovered ten autapomorphies from the hand (Char. 19.0) and foot musculature (Chars. 22.1, 23.1, 24.1, 31.3, 40.1, 41.1, 42.1, 43.1 and 50.1) of *Nasikabatrachus*. Characters 31, 40–43 and 50 are discussed below in the section 'Foot musculature, convergence and hind limb digging behaviour'. We discuss next an additional possible character from the forearm and hand that appears to be sexually dimorphic and the foot characters 22–24.

The potential sexually dimorphic muscle refers to the slip originating from the humerus of the m. abductor pollicis longus, which is absent in the female (see Fig. 3B for its presence in the male, labelled as 1). This hypothesis is tentative because we only studied a single specimen of each sex of *Nasikabatrachus*. Similarly, we only studied this muscle in one or more specimens of each sex in a few species (*Limnomedusa macroglossa*, *Pseudis minuta* and *Trachycephalus typhonius*) with no sexual dimorphism regarding the presence of these slips.

Burton (1998b: char. 24) stated that, for the few species in which he studied the m. abductor pollicis longus in sexes (namely *Atelognathus patagonicus*, *A. praebasalticus* and *Limnodynastes tasmaniensis*), he only observed variation in its size, being thicker in males, as also described by Hoyos & Salgar (2016) in males of *Dendropsophus luddeckei*. Similarly, Pinheiro *et al*. (In press), in an extensive taxon sampling of the hylid tribe Cophomantini, found that some species were sexually dimorphic, with the m. abductor pollicis longus (in reference to the slip from the radioulna; the slip from humerus is absent in those species) being larger in males.

Although our hypothesis of sexual dimorphism in the m. abductor pollicis longus is tentative, two aspects regarding the presence of the slip from the humerus remain to be discussed: whether its presence in the male is a novelty of *Nasikabatrachus*, and what its biological significance might be. Concerning the first point, the slip from humerus is absent in the two species of *Sooglossus* and unknown in *Sechellophryne* (we studied a male of *Sooglossus thomasseti*, and the sex of our specimen of *Sooglossus sechellensis* is unknown). Considering the relevant taxa that might affect the ACSR for the presence of the slip from the humerus in Sooglossoidea or internal clades, it is absent in Allodapanura (i.e. Afrobatrachia + Microhylidae) and Heleophrynidae, present in Calyptocephalellidae and most Anomocoela, and variable in Natatanura and Nobleobatrachia (Burton, 1998b; this study). Although a detailed study of the occurrence of the slip from the humerus across Anura and quantitative ACSR are required, its presence in the male of *Nasikabatrachus* is possibly apomorphic at this level of generality.

With respect to its biological significance, the presumed function of the slip from the humerus is to contribute to the reinforcement of the abduction of the wrist and digit II. The m. abductor pollicis longus of the male has, in addition to the slip from the humerus, a supplementary insertion on the metacarpophalangeal joint of digit II, which is another novelty of *Nasikabatrachus* (see Fig. 3B, labelled as 4). The notable size difference between sexes, combined with the round body and short extremities, result in a peculiar amplexus in which the male tightly digs his fists into the female beside the vertebral column (Zachariah *et al.*, 2012: 55, fig. 3A–B). The characteristics of the m. abductor pollicis longus of the male might reinforce the abductor component of the force for the strong clasping required in this amplexus. In contrast to some brevicipitids and microhylids (e.g. Visser *et al.*, 1982; Siegel *et al.*, 2008; Pombal & Cruz, 2016), the male lacks adhesive glands on the belly or chest (Zachariah *et al.*, 2012: 55), which would assist in maintaining amplexus. Further studies with more specimens of *Nasikabatrachus*, Sooglossidae, both sexes of other relevant species (representing the phylogenetic and behavioural diversity), and the several relevant aspects (e.g. functional measurements of the forearm associated with biomechanical models) discussed by Emerson (1991) in relation to the biomechanics of amplexus are required to test this hypothesis.

A set of striking autapomorphies of *Nasikabatrachus* comes from the mm. flexores breves superficiales (Chars. 22.1, 23.1 and 24.1; Figs 4C, 5A). In Anura, this muscle is usually composed of a single muscular body; it originates from the ligamentum calcanei and usually inserts via a single tendon, which splits distally into the tendines superficiales digitorum III–V (or, which is the same, the tendines superficiales digitorum III–V originate from the mm. flexores breves superficiales). Exceptions to this condition occur within some arboreal clades, in which there is a partial or complete subdivision of the muscular body into two or three slips. In this last case, each slip inserts via its own tendon that distally forms the tendines superficiales digitorum III–V (Dunlap, 1960; Burton, 2004; Blotto *et al.*, 2020).

The origin of the tendines superficiales of the prehallux and digits I–II from the tendon of insertion of the mm. flexores breves superficiales, in addition to the typical origin from the aponeurosis plantaris, are novelties restricted to *Nasikabatrachus*. As discussed below (see section 'Foot musculature, convergence and hind limb digging behaviour'), these supplementary insertions on the preaxial region of the foot by the mm. flexores breves superficiales, and particularly on the prehallux via the tendo superficialis praehallucis, are probably related to hind limb digging behaviour. These novelties might represent an additional example of the multiple, interrelated modifications associated with reinforcing the prehallux and preaxial region of the foot via supplementary and fortified insertions for enhancing digging action. Functional studies are required to test the functional hypothesis and establish the role of these novelties.

Impact of Nasikabatrachus *on non-sooglossoid synapomorphies*

Considering the key phylogenetic position of Sooglossoidea among the major anuran clades, knowledge of the character states of *Nasikabatrachus* might affect the status of some previously suggested synapomorphies for other major lineages. Considering this, we re-evaluated the ACSRs of Blotto *et al.* (2020) and found that the ACSR of Character 14 (char. 9 of Blotto *et al.*, 2020) was modified.

Blotto *et al.* (2020) suggested the presence of a dorsal origin of the m. flexor minimus digiti IV with respect to the m. intermetacarpalis II as a synapomorphy of Nobleobatrachia (our Char. 14.1). However, the dorsal origin of the m. flexor minimus digiti IV with respect to the m. intermetacarpalis II in *Nasikabatrachus* turns the ACSR ambiguous for Nobleobatrachia. Unfortunately, this character state was considered the single unambiguous known phenotypic synapomorphy for this major clade (Blotto *et al.*, 2020).

Caudata, Ascaphidae + Leiopelmatidae, and Lalagobatrachia: homology and polarity problems

We identified two putative synapomorphies from the foot musculature for Ascaphidae + Leiopelmatidae (Chars. 34.1 and 38.0) or for its sister clade Lalagobatrachia (Chars. 34.0 and 38.1). Since these are the earliest diverging clades of Anura, knowledge of the caudate condition is required to establish the character polarity at this level of universality. We identify below the putatively homologous muscles in Anura and Caudata to discuss the optimization of these characters. To avoid repeating references to alternative names of other authors for caudate musculature, we present a list of synonyms for the muscles discussed here in Table 2.

Studies of foot musculature are scarce in Caudata, but data are available from at least one representative of *Ambystoma* (Ambystomatidae), *Andrias* and *Cryptobranchus* (Cryptobranchidae), *Lissotriton*, *Salamandra*, *Taricha* and *Triturus* (Salamandridae), and *Necturus* (Proteidae; Humphry, 1871; Perrin, 1892, 1899; Ribbing, 1907, 1909; Francis, 1934; Walthall & Ashley-Ross, 2006; Diogo & Tanaka, 2012, 2014; Diogo *et al.*, 2018). Although Restrepo & Hoyos (1998) described the foot musculature for *Bolitoglossa* (Plethodontidae), they did not describe the muscles discussed below. Importantly, data are unavailable for Hynobiidae, which is highly relevant because it forms with Cryptobranchidae the sister group of all remaining caudates (Frost *et al.*, 2006; Pyron & Wiens, 2011; Pyron, 2014; Jetz & Pyron, 2018; Hime *et al.*, 2021).

One of the two putative synapomorphies for Ascaphidae + Leiopelmatidae or Lalagobatrachia involves the origin of the m. flexor hallucis accessorius from element Y, being either absent (Char. 34.0, Lalagobatrachia) or present (Char. 34.1, Ascaphidae + Leiopelmatidae). The identity of the homologous muscle of the m. flexor hallucis accessorius (a muscle so far defined for Anura) in Caudata, if it exists, is unclear.

Some evidence suggests that the m. flexor hallucis accessorius is a differentiated portion of the

Table 2. Homology and correspondence of the foot muscles discussed in the text between Anura and Caudata, and their synonyms from the caudate literature. Note that Humphry (1871) considered our m. contrahentis pedis hallucis and m. contrahentium caput longum under the same name, his m. flexor profundus digitorum. The correspondence of the m. flexor hallucis accessorius with a portion of the caudate contrahentis pedis hallucis is tentative (see Discussion)

Terminology used in this study		Synonyms from literature
Anura	Caudata	Caudata
Contrahentis pedis hallucis Flexor hallucis accessorius	Contrahentis pedis hallucis	**Same** (Ribbing, 1907; Francis, 1934; Walthall & Ashley-Ross, 2006; Diogo & Tanaka 2014; Diogo *et al.*, 2018); **flexor profundus digitorum** (Humphry, 1871); **fléchisseurs profond de la première phalange** (Perrin, 1892)
Contrahentium caput longum	Contrahentium caput longum	**Same** (Diogo *et al.*, 2018); **flexor profundus digitorum** (Humphry, 1871); **fléchisseur commun profond des phalanges** (Perrin, 1892); **caput longum musculorum contrahentium** (Ribbing, 1909; Francis, 1934; Walthall & Ashley-Ross, 2006)
Abductor brevis plantaris digiti V	Flexor brevis profundus digiti V	**Same** (Ribbing, 1909; Francis, 1934; Walthall & Ashley-Ross, 2006; Diogo & Molnar, 2014; Diogo *et al.*, 2018); **tarso-metatarsalis** (Humphry, 1871); **fléchisseurs primitif du cinquième métatarsien** (Perrin, 1892)

m. contrahentis pedis hallucis. This hypothesis was proposed by Dunlap (1960: 41) and corroborated by Blotto *et al.* (2020: 52; see also Diogo *et al.*, 2018: 507, 579), and it is based on the fact that both muscles are incompletely differentiated in some anuran species. Data from the present study also support this hypothesis, since both muscles are almost completely undifferentiated in the male *Nasikabatrachus* (they are distinct only distally at the insertion point of each muscle; see description in Results and Fig. 4D) and only partially differentiated in the female (they share a common tendon of origin).

Furthermore, the points of insertion and the morphology of the m. contrahentis pedis hallucis described for some caudates might also support the hypothesis that the m. flexor hallucis accessorius is a differentiated portion of the m. contrahentis pedis hallucis, as discussed in the previous paragraph for anurans. An additional insertion of the m. contrahentis pedis hallucis on metatarsal I (which is a characteristic of the m. flexor hallucis accessorius) was reported in some specimens of *Ambystoma* and *Salamandra*, while an independent portion of the m. contrahentis pedis hallucis inserting on metatarsal I was reported for *Cryptobatrachus* (Ribbing, 1909: 65). Considering this preliminary hypothesis for the correspondence between the anuran m. flexor hallucis accessorius and the caudate m. contrahentis pedis hallucis, we compare below both muscles.

The origin of the m. contrahentis pedis hallucis of caudates is restricted to the basale (commune I-II, or II if unfused) and the tendon of insertion of the m. contrahentium caput longum on that tarsal bone (*Ambystoma mexicanum*, *Andrias japonicus*, *Cryptobranchus alleganiensis*, *Lissotriton vulgaris*, *Necturus maculosus*, *Salamandra salamandra*; Humphry, 1871: 26; Perrin, 1892: 19; Ribbing, 1909: 65; Francis, 1934: 118; Diogo & Tanaka, 2014: 117), with no reports of an origin from element Y. Considering the caveats detailed above for the identity of the anuran m. flexor hallucis accessorius, the taxonomic distribution described for Caudata results in an ACSR in which the presence of the origin of the m. flexor hallucis accessorius from the element Y (Char. 34.1) is a synapomorphy of Ascaphidae + Leiopelmatidae.

The other putative synapomorphy for Ascaphidae + Leiopelmatidae or Lalagobatrachia involves the extension of the insertion of the m. abductor brevis plantaris digiti V on metatarsal V: on its proximal 2/3 or less (Char. 38.0, Ascaphidae + Leiopelmatidae) or reaching at least its proximal 3/4 (Char. 38.1, Lalagobatrachia). The m. abductor brevis plantaris digiti V is considered to correspond to the caudate m. flexor brevis profundus of digit V (Perrin, 1892: 67; Ribbing, 1909: 72, 1911: 20; Diogo & Molnar, 2014: 1063; Diogo *et al.*, 2018: 507, 571). Following some authors (Diogo & Molnar, 2014: 1063; Diogo *et al.*, 2018: 570), there are ten muscles of this group in caudates, comprising one medial and one lateral muscle in each digit. Other authors (Humphry, 1871; Perrin, 1892; Ribbing, 1909; Francis, 1934) describe these muscles as comprising only one muscle per digit, with differentiated portions inserting on their corresponding metatarsal: a medial, ventral or middle, and lateral portion (Humphry, 1871: 28; Francis, 1934: 119), or simply a medial and lateral portion (Perrin, 1892: 21–22; Ribbing, 1909: 71). These three (medial, ventral or middle, and lateral) or two (medial and lateral) portions are defined with respect to the position of their insertions on the respective metatarsal and, usually, relative to the mm. flexores digitorum minimi (i.e. the medial, ventral or middle, and lateral portions are those inserting medially, proximally and laterally to the mm. flexores digitorum minimi, respectively).

Perrin (1892: 67) considered that the m. abductor brevis plantaris digiti V corresponds to the lateral muscle (or portion, as described by him) of the m. flexor brevis profundus digiti V of caudates. Based on their similar topology, and following the suggestion of Perrin (1892), we compare the m. abductor brevis plantaris digiti V with the lateral muscle (or lateral portion) of the caudate m. flexor brevis profundus digiti V.

Descriptions and figures from most authors dealing with caudate musculature are not precise enough to determine the extension of the insertion of the lateral muscle (or portion) of the m. flexor brevis profundus digiti V on metatarsal V. From the caudate species with available descriptions for the foot musculature (see above), it is possible to infer that in at least *Andrias* (Humphry, 1871: 28, fig. 12), *Salamandra* (Perrin, 1892: 22, figs 1, 4; Francis 1934: 119), and *Taricha* (Walthall & Ashley-Ross, 2006: fig. 4; note that the foot mm. flexores breves profundi went undescribed in that study, so we base our inferences from their figure only) the insertion of the lateral muscle (or portion) reaches at least the proximal 3/4 of metatarsal V (Char. 38.1).

Keeping the limitations mentioned above in mind, the insertion of this muscle on the proximal 2/3 or less of metatarsal V (Char. 38.0) appears to be another synapomorphy of Ascaphidae + Leiopelmatidae. However, precise data are required to unambiguously determine the character state in *Andrias* (in order to confirm our interpretation of Humphry, 1871) and *Cryptobranchus* (the description of Ribbing, 1909: 71, is not sufficiently detailed), as well as data from Hynobiidae, which are lacking.

Costata

Frost *et al.* (2006: 184) recovered Costata as the sister clade of all remaining Lalagobatrachia except Xenoanura and identified five larval character states from Haas

(2003) as synapomorphies of this clade: chars. 52.1, 54.1, 88.0, 99.1 and 108.0. These character states also optimize as synapomorphies of Costata (this study; results not shown) in the phylogenetic hypotheses that recover Costata as the sister taxon of all the remaining lalagobatrachians (e.g. Pyron & Wiens, 2011; Pyron, 2014; Jetz & Pyron, 2018; Hime *et al.*, 2021). Frost *et al.* (2006) also indicated the opisthocoelous vertebrae as a characteristic of Costata, although an ambiguous synapomorphy (this type of vertebrae is also present in Xenoanura). Thus, the presence of the insertion of the m. contrahentis digiti V on the distal end of the metacarpal V, medially to the m. flexor minimus digiti V (Char. 9.1), represents the only unambiguous phenotypic synapomorphy reported for adults of Costata.

Xenoanura

The presence of the intermediate slip of the hand m. interphalangeus digiti V (Char. 16.1) is the second proposed synapomorphy from adult myology [the other being from foot musculature; see Blotto *et al.* (2020: char. 14), here as Char. 25] and the first from hand musculature. Although this character has several instances of homoplasy across Anura (see Supporting Information, Appendix S3 and section below), the taxon sampling of this study covers the diversity of the group. The single reversal occurs in *Xenopus* cf. *borealis* (Pipidae; intermediate slip absent).

Pelodytidae + Pelobatidae + Megophryidae

The presence of the intermediate slip of the hand m. interphalangeus digiti V (Char. 16.1) optimizes as the second reported synapomorphy from the hand musculature [the other being from Blotto *et al.* (2020: char. 11), here reported as Char. 18]. Despite several instances of homoplasy across Anura (see Supporting Information, Appendix S3 and the section of Xenoanura above), most genera of this clade were sampled and there are no reversals within the clade.

Myobatrachoidea

We recovered the presence of the origin of the m. flexor hallucis accessorius from the fused distal portions of the tibiale and fibulare (Char. 37.1) as a synapomorphy of this major clade. The ACSR of this character shows some instances of homoplasy in distantly related clades (Costata, Leiopelmatidae, *Nasikabatrachus* and Rhinophrynidae) and an internal reversion in the myobatrachid *Pseudophryne*. The relevance of this finding is that it constitutes the second known phenotypic synapomorphy for this superfamily and the first from foot musculature, the other being from hand musculature (Blotto *et al.*, 2020: char. 6; our Char. 7).

IDENTITY AND HOMOLOGY OF SOME PALMAR MUSCLES OF DIGIT V

This section addresses the homology of the lateral m. lumbricalis brevis digiti V, m. opponens digiti V, m. abductor primus digiti V and m. abductor secundus digiti V *sensu* Gaupp (1896), which are muscles with conflictive identities across the literature (see Blotto *et al.*, 2020). Below we review their descriptions from the literature and, in addition to our novel data, redefine their identities and homologies (see Appendix 2 for some re-identifications from Blotto *et al.*, 2020).

The m. abductor primus digiti V was described by Gaupp (1896: 166–167, figs 92–94) as a muscle originating from the flexor plate and ulnare and inserting on the lateropalmar surface of metacarpal V. We redefine the portion originating from the flexor plate as part of the lateral m. lumbricalis brevis digiti V and the portion from the ulnare as the m. flexor brevis profundus digiti V. This redefinition is mainly based on topology, since the portion of the m. abductor primus digiti V from the flexor plate is an independent portion positioned on the same layer as the mm. lumbricales breves, which is superficial with respect to the portion from the ulnare; this hypothesis is further justified below.

The lateral m. lumbricalis brevis digiti V originating from the flexor plate and the m. abductor primus digiti V originating from the flexor plate (both *sensu* Gaupp) are present as a single muscle in some species (e.g. Fig. 12A–C). This single muscle has a fleshy insertion on metacarpal V (portion attributed to the m. abductor primus digiti V *sensu* Gaupp) and on the lateropalmar portion of the metacarpophalangeal joint of digit V (attributed to the lateral m. lumbricalis brevis digiti V). In other species, the m. abductor primus digiti V originating from the flexor plate (*sensu* Gaupp) shares a common origin with the lateral m. lumbricalis brevis digiti V on the flexor plate (as described by Gaupp, 1896, and observed in several species from this study), while in some species both muscles are independent from origin to insertion (this study). Our proposal is that the portion of the m. abductor primus digiti V that originates on the flexor plate (*sensu* Gaupp) corresponds to the portion of the lateral m. lumbricalis brevis digiti V that inserts on metacarpal V. This hypothesis is partially in line with Ribbing (1907: 596), who considered the m. abductor primus digiti V of Gaupp (1896) as part of his mm. flexores breves superficiales (which mainly correspond to our mm. lumbricales; see Blotto *et al.*, 2020: 90).

The portion of the m. abductor primus digiti V originating from the ulnare is attributed here to the group of the mm. flexores breves profundi. This assignation is based on the fact that: (1) no other muscle of this group attaches to digit V and (2) it is topologically and morphologically very similar to the mm. flexores breves profundi of digits III and IV.

Interestingly, the situation is analogous to that of the homonymous muscle of the foot (see section 'Caudata, Ascaphidae + Leiopelmatidae, and Lalagobatrachia: homology and polarity problems'). Across our sampling, we observed that the m. flexor brevis profundus digiti V (*sensu* this study) originates from the distal carpals (the more common condition; Figs 1D, 2B, 8B, 12A, D), the distal carpals and ulnare, or the ulnare [as described for *Pelophylax* (Ranidae) by Gaupp, 1896].

Furthermore, we reject the hypothesis that our m. flexor brevis profundus digiti V (i.e. the portion of the m. abductor primus digiti V from the distal carpals and/or ulnare *sensu* Gaupp, 1896) corresponds to the m. abductor digiti minimi of other tetrapods, as previously considered by some authors (Abdala &Diogo, 2010: 12; Diogo & Abdala, 2010: 384; Diogo & Ziermann, 2014: table 2; Diogo *et al.*, 2018: 457; Blotto *et al.*, 2020: 9). We justify our proposal based on (1) the topological similarity discussed above between our m. flexor brevis profundus digiti V and the mm. flexores breves profundi digitorum III and IV, and (2) the fact that it co-occurs with another muscle that is more laterally located and has a clear abductor function, the m. abductor secundus digiti V *sensu* Gaupp (1896), Burton (1998b) and Blotto *et al.* (2020). The m. abductor secundus digiti V was only tentatively considered to be part of the mm. flexores breves profundi by Abdala & Diogo (2010: 33), Diogo & Abdala (2010: 382) and Diogo *et al.* (2018: 455), while Diogo & Ziermann (2014: table 2) stated that it is probably part of their m. abductor digiti minimi.

Considering the conflicting identity of the m. abductor secundus digiti V evidenced above, Blotto *et al.* (2020: 75) retained the name from Gaupp (1896). Based on our redefinition of the m. flexor brevis profundus digiti V and the notable similarity between the anuran m. abductor secundus digiti V and the caudate m. abductor digiti minimi (see Perrin, 1899: 255, fig. 11; Francis, 1934: 84; Walthall & Ashley-Ross, 2006: 54, fig. 7; Diogo *et al.*, 2018: fig. 16.3.F), we identify the m. abductor secundus digiti V *sensu* Gaupp (1896) as the m. abductor digiti minimi.

Gaupp (1896: 167) described the presence of superficial fibres of his m. abductor secundus digiti V with a flat tendinous insertion on the metacarpophalangeal joint of digit V in some specimens of *Pelophylax*. We consider this portion to be part of our m. abductor digiti minimi and corroborate its presence in several ranoids studied by us. Considering this assignation, the abductor muscle referred to by Blotto *et al.* (2020) in *Pipa carvalhoi* (Pipidae; fig. 9C, labelled as 7–8) and *Rheobatrachus silus* (p. 92) is identified here as the portion of our m. abductor digiti minimi attaching to the metacarpophalangeal joint, based on its similarity with the ranoid condition.

Finally, the m. opponens digiti V *sensu* Gaupp (1896) was considered to be part of the mm. flexores breves profundi by Abdala & Diogo (2010: 33), Diogo & Abdala (2010: 382), Diogo *et al.* (2018: 455) and Blotto *et al.* (2020: 75). However, as described by Burton (1998b: 54) and depicted in Figure 12A, B, the m. opponens digiti V belongs to the third layer of muscles, as do the mm. contrahentes digitorum, and not to the fourth layer where the mm. flexores breves profundi are located. Furthermore, the m. opponens digiti V co-occurs with the m. flexor brevis profundus digiti V (as redefined here), rejecting its homology via the conjunction test (Patterson, 1982).

The m. opponens digiti V is present in some clades (e.g. Burton, 1998b; this study) and always co-occurs with the m. contrahentis digiti V, whose identity is clear and requires no discussion. The question that arises at this point is whether the m. opponens digiti V is part of the group of the mm. contrahentes digitorum, based on its location in the same layer of muscles and their similar attachments. The m. opponens digiti V originates from the distal carpals, lateral to the m. contrahentis digiti V, and inserts on metacarpal V (laterally to the m. flexor minimus digiti V) and/or the metacarpophalangeal joint of digit V (Gaupp, 1896; Burton, 1998b; this study), as does the m. contrahentis digiti V (see Chars. 9–11). Due to the unclear relationship of the m. opponens digiti V with other groups of muscles, and to the fact that a muscle clearly identified as an m. contrahentis is present in digit V, we prefer to retain the name 'm. opponens digiti V' from Gaupp (1896) for the time being.

FOOT MUSCULATURE, CONVERGENCE AND HIND LIMB DIGGING BEHAVIOUR

Background, scope and limitations

The discussion in this section focuses mainly on the independent evolution in distantly related clades of primary homologue modifications of homologue muscles (i.e. characters about the nature of the muscles: Chars. 41.1, 42.1, 43.1, 50.1) and primary homologue muscles or slips (i.e. characters about their absence/presence: Chars. 40.1, 44.1). Additionally, and considering the possible occurrence of a many-to-one phenomenon (see below), we also discuss modifications in other muscles with similar attachments and putative function regarding HLD behaviour to those mentioned above.

A relevant approach to be undertaken in future complementary studies is the recording of the myoelectrical activity of the relevant muscles in digging (e.g. Manzano *et al.*, 2008). This approach will test and determine more precisely the presumed functions attributed to the muscles during HLD behaviour.

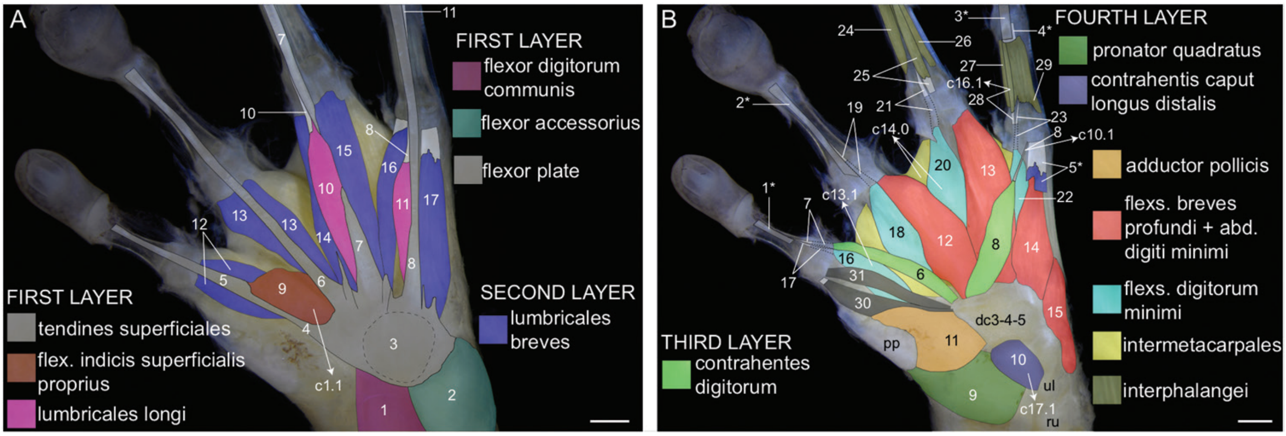

Figure 8. Palmar surface of the hand of *Sooglossus thomasseti* (UMMZ 144473). A, first and second layers of muscles. Labelled elements: **1,** m. flexor digitorum communis. **2,** m. flexor accessorius. **3,** flexor plate (the dashed line indicates the limits of a cartilaginous palmar sesamoid embedded within it). **4,** tendo superficialis indicis. **5,** tendo superficialis indicis and m. flexor indicis superficialis proprius: common tendon of insertion. **6–8,** tendines superficiales digitorum III–V, respectively. **9,** m. flexor indicis superficialis proprius. **10–11,** mm. lumbricales longi digitorum IV–V, respectively. **12,** m. lumbricalis brevis indicis. **13,** m. lumbricalis brevis digiti III. **14,** medial m. lumbricalis brevis digiti IV. **15,** lateral m. lumbricalis brevis digiti IV. **16,** medial m. lumbricalis brevis digiti V. **17,** lateral m. lumbricalis brevis digiti V. B, third and fourth layers of muscles. Labelled elements: **1*,** tendo superficialis indicis and m. flexor indicis superficialis proprius: common tendon of insertion: distal unremoved portion. **2*,** tendo superficialis digiti III: distal unremoved portion. **3*,** tendo superficialis digiti V: distal unremoved portion. **4*,** m. lumbricalis longus digiti V: tendon of insertion: distal unremoved portion. **5*,** lateral m. lumbricalis brevis digiti V: distal unremoved portion. **6,** m. contrahentis indicis. **7,** m. contrahentis indicis: tendon of insertion (the dashed line indicates the portion that pass through an internal channel of the metatarsophalangeal joint). **8,** m. contrahentis digiti V. **9,** m. pronator quadratus. **10,** m. contrahentis caput longus distalis. **11,** m. adductor pollicis. **12–14,** mm. flexores breves profundi digitorum III–V, respectively. **15,** m. abductor digiti minimi. **16,** m. flexor minimus indicis. **17,** m. flexor minimus indicis: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metacarpophalangeal joint). **18,** m. flexor minimus digit III. **19,** m. flexor minimus digiti III: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metacarpophalangeal joint). **20,** m. flexor minimus digit IV. **21,** m. flexor minimus digiti IV: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metacarpophalangeal joint). **22,** m. flexor minimus digit V. **23,** m. flexor minimus digiti V: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metacarpophalangeal joint). **24–26,** m. interphalangeus digiti IV: medial, intermediate and lateral slips, respectively. **27,** m. interphalangeus digiti V: portion that topologically corresponds to the medial slip (medial and lateral slip fused). **28,** m. interphalangeus digiti V: intermediate slip. **29,** m. interphalangeus digiti V: portion that topologically corresponds to the lateral slip (medial and lateral slip fused). **30–31,** unidentified muscles with origin from the distal carpal 3-4-5 and insertion on the metacarpophalangeal joint of digit II (see text for discussion). Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. The origin of the m. adductor pollicis, m. contrahentis digiti V and mm. flexores breves profundi are via very short tendons and are not shaded. Labelled characters: c1.1: presence of m. flexor indicis superficialis proprius (A). c10.1: presence of the insertion of the m. contrahentis digiti V on the metacarpophalangeal joint or basal phalanx of digit V (B). c13.1: presence of m. flexor minimus indicis (B). c14.0: origin of m. flexor minimus digiti IV ventral to the m. intermetacarpalis II (B). c16.1: presence of the intermediate slip of the m. interphalangeus digiti V (B). c17.1: presence of m. contrahentis caput longus distalis (B). Characters referring to absence and not labelled in the figure: c2.0: absence of m. caput profundum digiti III (A). c3.0: absence of m. lumbricalis longus digiti III (A). Scale bars = 0.5 mm.

The implications of this study in relation to the suggestion of hypotheses of adaptation also require comments. Although we refer to possible correlations or associations between character states, presumed functions and the occurrence of HLD behaviour, they should be considered cautiously in relation to adaptation. A formal quantitative study of convergences employing phylogenetic comparative methods, coupled with other methods from different fields (e.g. direct measurements of selection in populations and the study of the functional correlates of the traits), is required to infer natural selection and test hypotheses of adaptation (Kluge, 2005; Losos, 2011). Thus, the following discussion should be considered as a preliminary, exploratory step, with the aim of pointing to possible paths for future

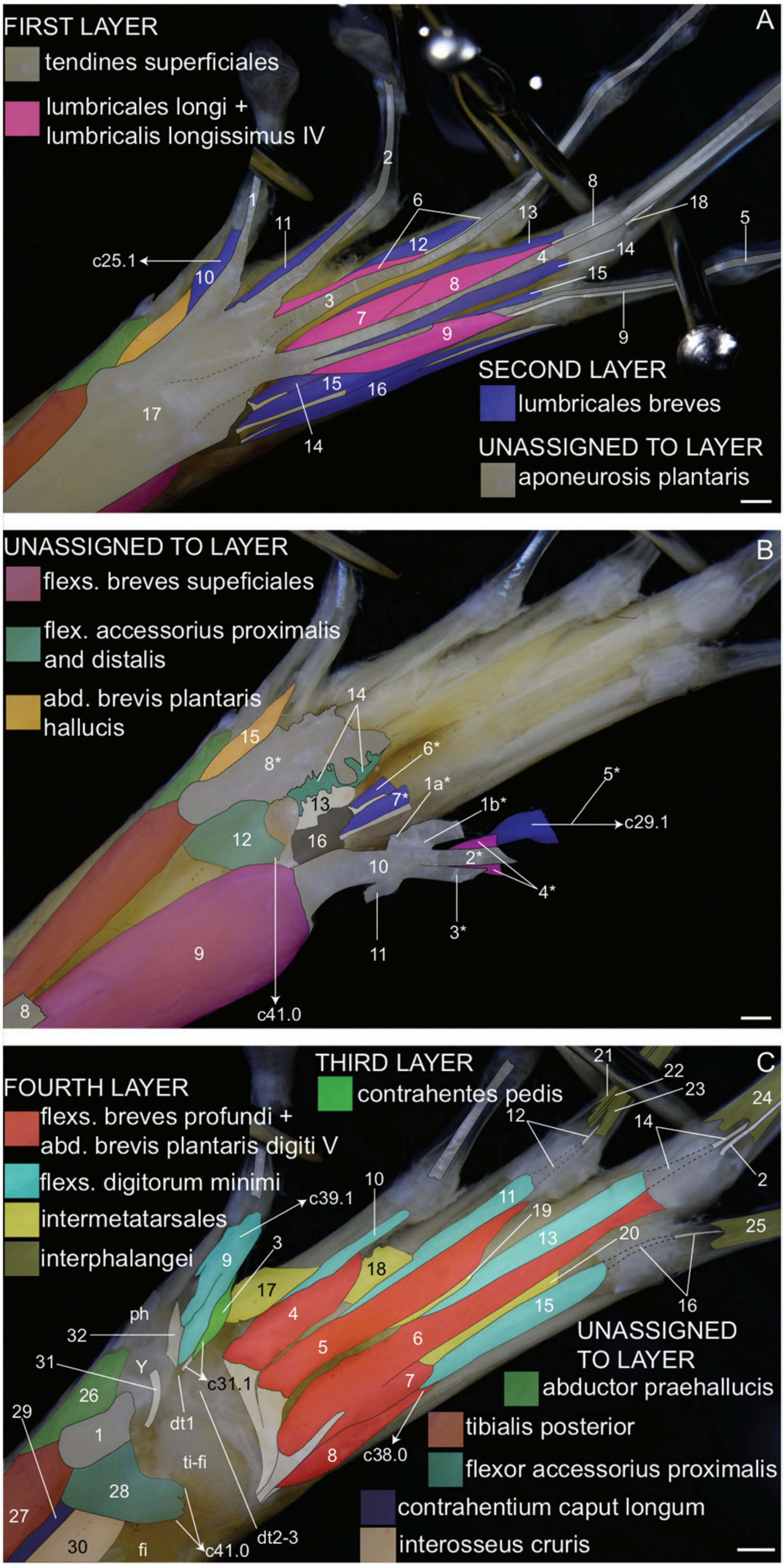

Figure 9. Plantar surface of the foot of *Sooglossus thomasseti* (UMMZ 144473). A, first and second layers of muscles. Labelled elements: **1,** tendo superficialis hallucis. **2–5,** tendines superficiales digitorum II–V, respectively. **6–7,** mm. lumbricales longi

studies focused on adaptations for HLD behaviour in Anura.

Modes, intensities and functions for HLD behaviour vary greatly across species. Digging behaviour occurs not only for refuge, as in fossorial species (e.g. Ceratophryidae, Scaphiopodidae, *Nasikabatrachus*; see sources in Supporting Information, Appendix S4), but also for the construction of holes and chambers for reproduction (e.g. the hylids *Aplastodiscus* and some *Boana*; several leptodactylines; Martins, 1993; Haddad *et al.*, 2005; de Sá *et al.*, 2014). Additionally, there is considerable variation in the digging mode, including the use of hind limbs, the forelimbs, the snout and head, or a combination of them (Emerson, 1976; Nomura *et al.*, 2009; Engelkes *et al.*, 2020; Keeffe & Blackburn, 2020), coupled with variation in the intensity and the sex involved in this

digitorum III–IV, respectively. **8,** m. lumbricalis longissimus digiti IV. **9,** m. lumbricalis longus digiti V. **10,** m. lumbricalis brevis hallucis. **11–12,** mm. lumbricalis breves digitorum II–III, respectively. **13,** medial m. lumbricalis brevis digiti IV. **14,** lateral m. lumbricalis brevis digiti IV. **15,** medial m. lumbricalis brevis digiti V. **16,** lateral m. lumbricalis brevis digiti V. **17,** aponeurosis plantaris. **18,** ligament joining the lateroplantar portion of the metatarsophalangeal joint and the lateroplantar portion of the proximal interphalangeal joint of digit IV. The dashed line delimits the tendon of insertion of the mm. flexores breves superficiales, visible through partial transparency of the aponeurosis plantaris. B, plantar surface of the tarsal region of the foot, showing mainly the mm. flexores breves superficiales, m. flexor accessorius and m. abductor brevis plantaris hallucis. The mm. flexores breves superficiales were deflected laterally to reveal the different points of origin of the mm. lumbricales; note the origin of the medial m. lumbricalis brevis digiti IV from the tendon of insertion of the mm. flexores breves superficiales. Labelled elements: **1a* and 1b*,** tendo superficialis digiti III: proximal unremoved portions with origin from the aponeurosis plantaris and the mm. flexores breves superficiales, respectively. **2*–3*,** tendines superficiales digitorum IV–V: proximal unremoved portions. **4*,** m. lumbricalis longus digiti IV: proximal unremoved portion. **5*,** medial m. lumbricalis brevis digiti IV: proximal unremoved portion. **6,** lateral m. lumbricalis brevis digiti IV: proximal unremoved portion. **7*,** medial m. lumbricalis brevis digiti V: proximal unremoved portion. **8,** aponeurosis plantaris: unremoved portions. **9,** mm. flexores breves superficiales. **10,** mm. flexores breves superficiales: tendon of insertion at its point of multifurcation into tendines superficiales digitorum III–V. **11,** tendinous portion joining the tendon of insertion of the mm. flexores breves superficiales, aponeurosis plantaris, and plantar cartilage. **12,** m. flexor accessorius proximalis. **13,** m. flexor accessorius distalis: tendon of origin. **14,** m. flexor accessorius distalis. **15,** m. abductor brevis plantaris hallucis. **16,** plantar cartilage. C, third and fourth layer of muscles. Labelled elements: **1,** aponeurosis plantaris: unremoved portion. **2,** ligament joining the lateroplantar portion of the metatarsophalangeal joint and the lateroplantar portion of the proximal interphalangeal joint of digit IV. **3,** m. contrahentis pedis hallucis. **4–5,** mm. flexores breves profundi digitorum II–III. **6–7,** m. flexor brevis profundus digiti IV: ventral and dorsal portions with respect to the m. intermetatarsalis IV, respectively. **8,** m. abductor brevis plantaris digiti V. **9,** m. flexor minimus hallucis (note its proximal portion originating from the ligament joining element Y and metatarsal I). **10–11,** mm. flexor minimi digitorum II–III, respectively. **12,** m. flexor minimus digiti III: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metatarsophalangeal joint). **13,** m. flexor minimus digiti IV. **14,** m. flexor minimus digiti IV: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metatarsophalangeal joint). **15,** m. flexor minimus digiti V. **16,** m. flexor minimus digiti V: tendon of insertion (the dashed line indicates the portion that passes through an internal channel of the metatarsophalangeal joint). **17–20,** mm. intermetatarsales I–IV, respectively. **21,** m. interphalangeus digiti III: portion that topologically corresponds to the medial slip. **22,** m. interphalangeus digiti III: intermediate slip. **23,** m. interphalangeus digiti III: portion that topologically corresponds to the lateral slip. **24,** m. interphalangeus proximalis digiti IV: fused medial and lateral slips. **25,** m. interphalangeus proximalis digiti V: fused medial and lateral slips. **26,** m. abductor praehallucis. **27,** m. tibialis posterior. **28,** m. flexor accessorius proximalis. **29,** m. contrahentium caput longum. **30,** m. interosseus cruris. **31,** m. interosseus cruris: tendon of insertion (the discontinuity is due to the fact that it passes through a groove in the condyle of the tibiale that hides it and reappears distally to insert on element Y). **32,** ligament joining element Y to metatarsal I. Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. The morphology and proportions of the following elements are approximated, since they were not completely distinguishable in the picture to allow accurate shadings (drawings and descriptions were employed as complementary): m. interphalangeus digiti III, m. interphalangeus proximalis digiti IV and m. intermetatarsalis III. The tendo superficialis praehallucis is scarcely developed and was not shaded. The tendons of insertion of the m. flexor minimus hallucis, m. contrahentis pedis hallucis and m. flexor minimus digiti II are hidden by unremoved portions of the tendines superficiales of digits I and II and were not shaded. Labelled characters: c25.1: presence of m. lumbricalis brevis hallucis (A). c29.1: origin of the medial m. lumbricalis brevis digiti IV from the tendon of insertion of the mm. flexores breves superficiales (B). c31.1: origin of the m. contrahentis pedis hallucis from the distal tarsals (C). c38.0: insertion of the m. abductor brevis plantaris digiti V reaching no more than the proximal 2/3 of metatarsal V (C). c39.1: presence of m. flexor minimus hallucis (C). c41.0: origin of the m. flexor accessorius proximalis distal, occupying no more than the distal 1/3 of the fibulare (B, C). Characters referring to absence and not labelled in the figure: c42.0: absence of the origin of the m. flexor accessorius distalis from the proximal portion of the tendon of origin of mm. lumbricales of digits IV and/or V (B). Scale bars = 0.5 mm.

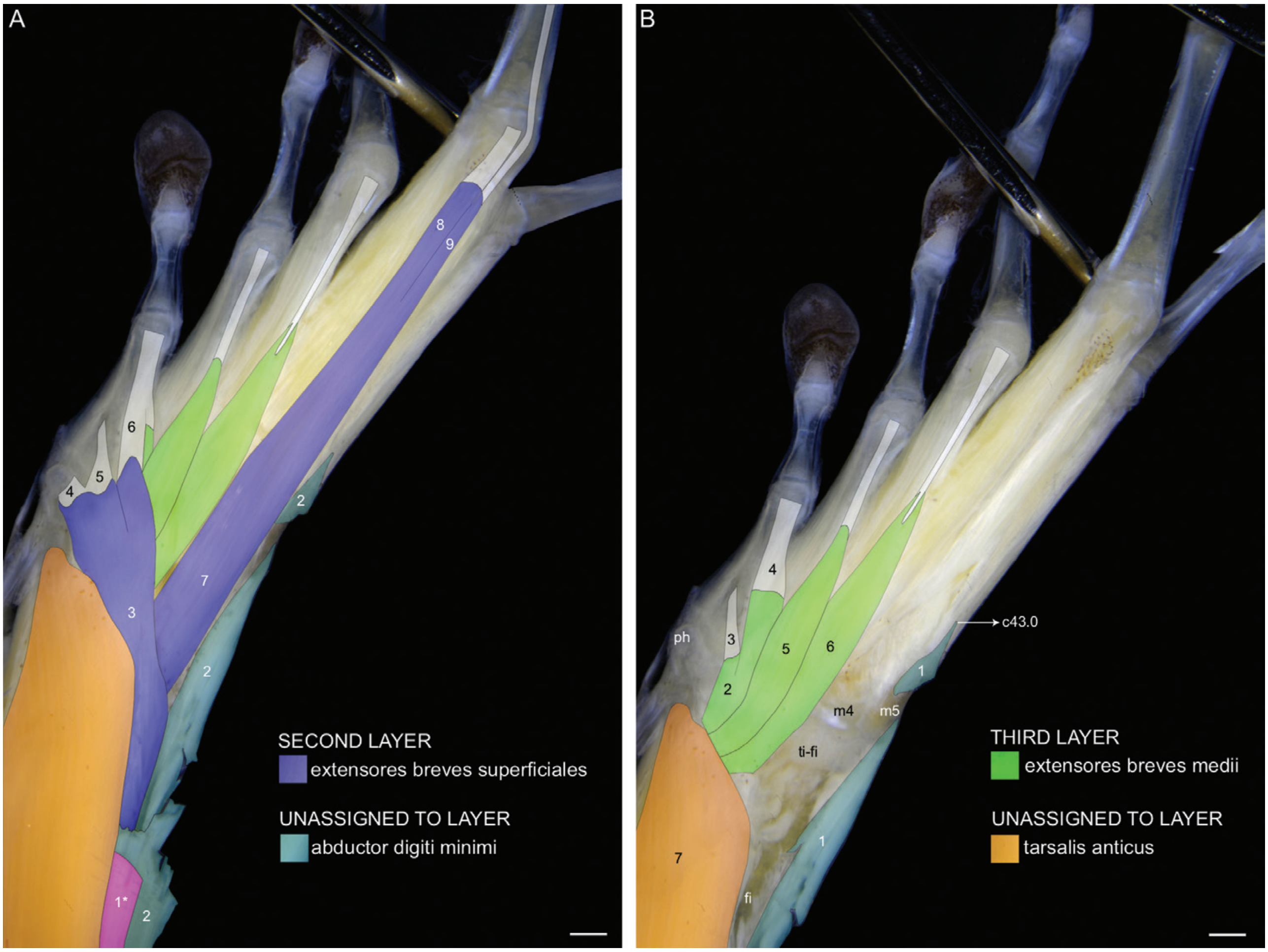

Figure 10. Dorsal surface of the foot of *Sooglossus thomasseti* (UMMZ 144473). A, second layer of muscles (except the m. extensor brevis superficialis digiti V, which was removed). Labelled elements: **1*,** m. extensor digitorum longus. **2,** m. abductor digiti minimi (partially removed). **3,** m. extensor brevis superficialis hallucis. **4,** m. extensor brevis superficialis hallucis: tendon of insertion on the prehallux. **5,** m. extensor brevis superficialis hallucis: tendon of insertion on metatarsal I. **6,** m. extensor brevis superficialis hallucis: tendon of insertion on the metatarsophalangeal joint (in common with the m. extensor brevis medius hallucis). **7,** medial and lateral m. extensor brevis superficialis digiti IV: proximal fused portion. **8,** medial m. extensor brevis superficialis digiti IV. **9,** lateral m. extensor brevis superficialis digiti IV. B, third layer of muscles. Labelled elements: **1,** m. abductor digiti minimi (partially removed). **2,** m. extensor brevis medius hallucis. **3,** m. extensor brevis medius hallucis: tendon of insertion on metatarsal I. **4,** m. extensor brevis medius hallucis: tendon of insertion on metatarsophalangeal joint. **5,** m. extensor brevis medius digiti II. **6,** m. extensor brevis medius digiti III. Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. The common tendon of insertion of the mm. extensores breves superficialis hallucis and medius hallucis, and the tendon of insertion of the m. extensor brevis medius digiti III were edited as inserting on the metatarsophalangeal joint of their respective digit; however, our data are not conclusive and the possibility of an additional insertion on the interphalangeal joints should be further evaluated. The limits and proportions of the tendons of insertion of the mm. extensores breves superficialis hallucis and medius hallucis are approximate. Labelled characters: c43.0: proximal insertion of the m. abductor digiti minimi, reaching less than the proximal half of metatarsal V (B). Characters referring to absence and not labelled in the figure: c45.0: absence of m. extensor brevis superficialis digiti II (A). c46.0: absence of m. extensor brevis superficialis digiti III (A). c47.0: absence of m. extensor brevis medius digiti IV (B). Scale bars = 0.5 mm.

behaviour (e.g. Martins, 1993; de Sá *et al.*, 2014; Ponssa & Barrionuevo, 2012; Ponssa & Medina, 2016).

From all this variation, we focus the following discussion on (1) a set of character states from the foot musculature that shows some degree of correlation with the occurrence of HLD behaviour (Fig. 13), (2) a set of muscles with phenotypic variation of continuous nature that was not formally delimited as a transformation

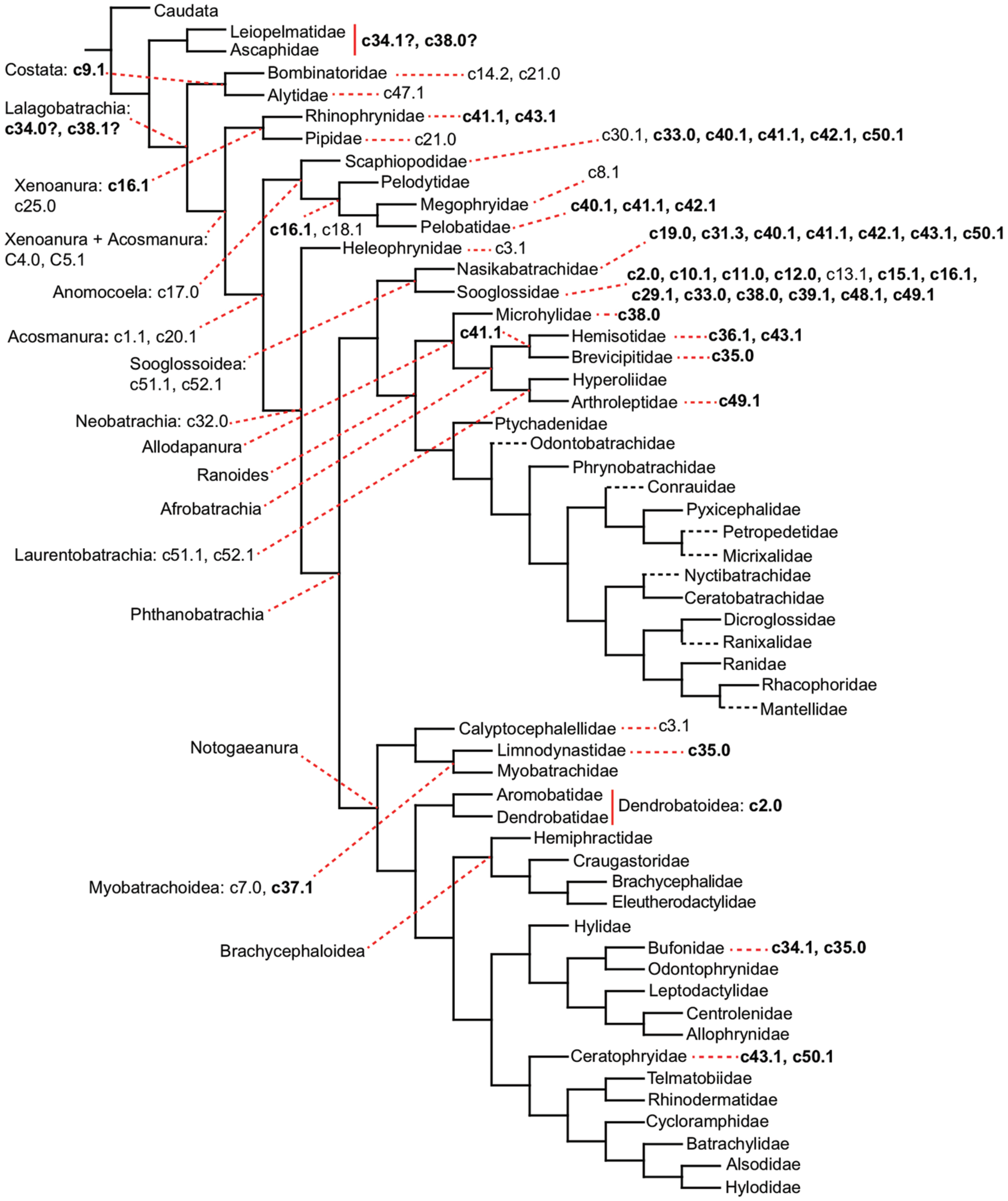

Figure 11. Reduced tree at the family level following the topology of Jetz & Pyron (2018). Some of the suggested synapomorphies, as obtained with the ACSR (see Supporting Information, Appendix S3), are indicated at each node (for synapomorphies below the family level see Appendix 1 and Appendix S3). Families represented by dotted branches in the phylogeny were not sampled in this study. Major clades addressed in the text are also indicated for guide, even if no synapomorphies are proposed in this paper. Character states in bold represent novel synapomorphies from this study.

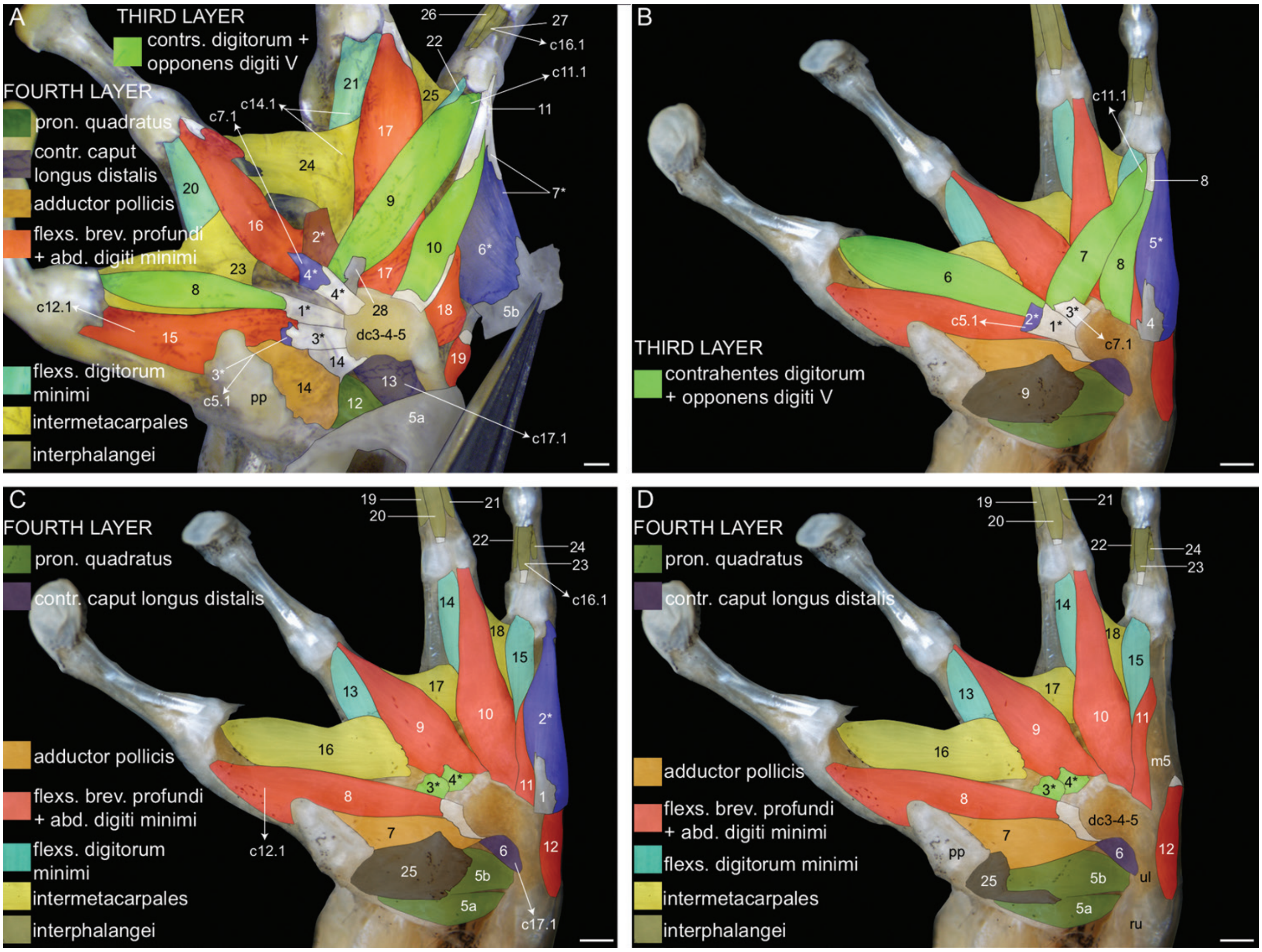

Figure 12. Palmar surface of the hand of *Odontophrynus cultripes* (MZUSP 141197; A) and *Limnomedusa macroglossa* (MACN 49261; B–D). Note the nature and topological relationships of the lateral m. lumbricalis brevis digiti V, m. opponens digiti V, m. flexor brevis profundus digiti V and m. abductor digit minimi, discussed in the section 'Identity and homology of some palmar muscles of digit V.' A, third and fourth layer of muscles. Note the lateral m. lumbricalis brevis digiti V (elements 6* and 7*) and the portion of the flexor plate that serves as its origin (element 5b), which are held with forceps and deflected laterally for exposing their dorsal side and its extended insertion on metacarpal V; compare it with the natural position as shown in B (as elements 4 and 5*). Labelled elements: **1*,** m. flexor indicis superficialis proprius: unremoved tendon of origin. **2*,** m. caput profundum digiti III: proximal unremoved portion. **3*,** m. lumbricalis brevis indicis: proximal unremoved portion. **4*,** m. lumbricalis brevis digiti III: slip from distal carpals: proximal unremoved portion. **5a,** flexor plate: folded in on itself to expose deeper muscles. **5b,** flexor plate: portion that serves as origin for the lateral m. lumbricalis brevis digiti V. **6*,** lateral m. lumbricalis brevis digiti V: portion inserting on metacarpal V. **7*,** lateral m. lumbricalis brevis digiti V: portion inserting on the metacarpophalangeal joint. **8,** m. contrahentis indicis. **9,** m. contrahentis digiti V. **10,** m. opponens digiti V. **11,** m. opponens digiti V and m. lumbricalis brevis digiti V: common tendon of insertion on the metacarpophalangeal joint. **12,** m. pronator quadratus (partially hidden by the flexor plate). **13,** m. contrahentis caput longus distalis (partially hidden by the flexor plate). **14,** m. adductor pollicis. **15,** medial m. flexor indicis brevis profundus. **16–18,** mm. flexores breves profundi digitorum III–V. **19,** m. abductor digiti minimi. **20–22,** mm. flexores minimi digitorum III–V. **23–25,** mm. intermetacarpales I–III. **26,** m. interphalangeus digiti V: medial slip. **27,** m. interphalangeus digiti V: intermediate slip. **28,** Burton's ligament: proximal unremoved portion. The lateral portion of the m. flexor brevis profundus digiti III and the medial portion of the m. intermetacarpalis II are partially torn and do not represent their natural morphology. B, third layer of muscles. Labelled elements: **1*,** m. flexor indicis superficialis proprius: unremoved tendon of origin. **2*,** m. lumbricalis brevis indicis: proximal unremoved portion. **3*,** m. lumbricalis brevis digiti III: slip from distal carpals: unremoved tendon of origin. **4,** flexor plate: portion that serves as origin for the lateral m. lumbricalis brevis digiti V. **5*,** lateral m. lumbricalis brevis digiti V. **6,** m. contrahentis indicis. **7,** m. contrahentis digiti V. **8,** m. opponens digiti V. **9,** unidentified muscle with origin from the flexor plate and insertion on the prepollex. C–D, fourth layer of muscles. Labelled elements: **1,** flexor plate:

series but that represents a promising line of future research in relation to adaptations for HLD behaviour (Figs 14–16), and (3) two muscles with a unique morphology which are restricted to a single species each (*Nasikabatrachus* and *Rhinophrynus*). It is also noteworthy that the discussion below considers species that are fossorial and specialist burrowers, those that are terrestrial and semifossorial but also dig with the hind limbs [e.g. *Kaloula pulchra* (Microhylidae); Emerson, 1976; Blackburn *et al.*, 2013], and those that use the hind limbs secondarily for specific tasks [e.g. *Leptodactylus latinasus* (Leptodactylidae); Gallardo, 1958], such as refuge, feeding or reproduction. However, it should be noted that specialist burrowers have conspicuous characteristics associated with digging, such as globular bodies, shorter hind limbs, a spade-like inner metatarsal tubercle and an enlarged prehallux (Laurent, 1964; Emerson, 1976; Fabrezi, 2001; Henrici, 2016; Moen, 2019). These modifications are expected to have a greater correlation with hind limb musculature than non-specialists or occasional burrowers. Thus, additional studies are needed to establish a more refined categorization to consider those differences.

Finally, due to the scarce direct observations on natural history, digging behaviour was historically inferred through the presence of specific characteristics in the external morphology (e.g. see comments in Keeffe & Blackburn, 2020), such as those mentioned above. Most of our analyses and conclusions in this section rest on species that are positively known to use the hind limbs for digging (see Supporting Information, Appendix S4), while in a few cases we also discuss species that are suspected to be HLD (although making explicit statements about this assumption).

Characters associated with HLD

Figure 13 depicts a set of characters from the foot musculature with a pattern of convergences possibly related to HLD behaviour. This pattern expresses two kinds of deviations for the correlation between the taxonomic distribution of the character states and the presence of HLD behaviour. First, not all the HLD species share all these character states (i.e. the convergences are restricted to different subgroups of HLD species). Second, several species use the hind limbs for digging but do not share any character state with the remaining HLD species: *Anaxyrus woodhousii*, *Rhinella dorbignyi* (both Bufonidae), *Arthroleptis variabilis* (Arthroleptidae), *Phrynomantis bifasciatus* (Microhylidae), *Platyplectrum ornatum* (Limnodynastidae), *Pleurodema kriegi* (Leptodactylidae), *Pseudophryne coriacea*, *Uperoleia laevigata* (both Myobatrachidae) and *Sphaerotheca breviceps* (Dicroglossidae). Besides these deviations, there are species in which digging behaviour is unknown, but share one character state with other HLD species: *Crossodactylus schmidti* (Hylodidae), *Leptobrachium lumadorum* (Megophryidae), *Limnodynastes peronii* (Limnodynastidae), *Microhyla heymonsi* (Microhylidae) and *Physalaemus biligonigerus* (Leptodactylidae); these species are discussed below in the section 'Predictive value?'.

Some of the character states shown in Figure 13 were previously related to HLD by Burton (2001; Chars. 40.1 and 41.1) and Blotto *et al.* (2017; Chars. 40.1, 42.1, 44.1). Furthermore, Blotto *et al.* (2017) tentatively associated the presence of the origin from the aponeurosis plantaris of the m. contrahentis pedis hallucis and m. flexor hallucis accessorius (Chars. 31.2 and 36.1, respectively) with HLD behaviour. However, the combination of inapplicable data for some species (due to the absence of these muscles) in addition to deviations due to the presence in a few non-HLD species (compare Fig. 13 with ACSRs of Chars. 31 and 36) precludes a conclusion; an increased taxon sampling is required to test these hypotheses.

There are other muscles with phenotypic variation possibly related to HLD behaviour, which were not formally delimited into transformation series here. In the sections below, we describe their variation and

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portion that serves as origin for the lateral m. lumbricalis brevis digiti V (removed in D). **2*,** lateral m. lumbricalis brevis digiti V (removed in D). **3*,** m. contrahentis indicis: proximal unremoved portion. **4*,** m. contrahentis digiti V: proximal unremoved portion. **5a,** m. pronator quadratus: slip from radioulna. **5b,** m. pronator quadratus: slip from ulnare. **6,** m. contrahentis caput longus distalis. **7,** m. adductor pollicis. **8,** medial m. flexor indicis brevis profundus. **9–11,** mm. flexores breves profundi digitorum III–V. **12,** m. abductor digiti minimi. **13–15,** mm. flexores minimi digitorum III–V. **16–18,** mm. intermetacarpales I–III. **19–21,** m. interphalangeus digiti IV: medial, intermediate, and lateral slips, respectively. **22–24,** m. interphalangeus digiti V: medial, intermediate and lateral slips, respectively. **25,** unidentified muscle with origin from the flexor plate and insertion on the prepollex (partially removed in D). Asterisks (*) indicate unremoved muscles from more superficial muscle layers other than the one being exposed. Labelled characters: c5.1: presence of the origin from the distal carpals of the m. lumbricalis brevis indicis (A, B). c7.1: presence of the slip of the m. lumbricalis brevis digiti III originating from the distal carpals (A, B). c11.1: presence of the insertion of the m. contrahentis digiti V on the distal end of metacarpal V, laterally to the m. flexor minimus digiti V (A, B). c12.1: presence of the medial m. flexor indicis brevis profundus (A, C). c14.1: m. flexor minimus digiti IV dorsal to the m. intermetacarpalis II (A). c16.1: presence of the intermediate slip of the m. interphalangeus digiti V (A, C). c17.1: presence of m. contrahentis caput longus distalis (A, C). Scale bars = 0.5 mm.

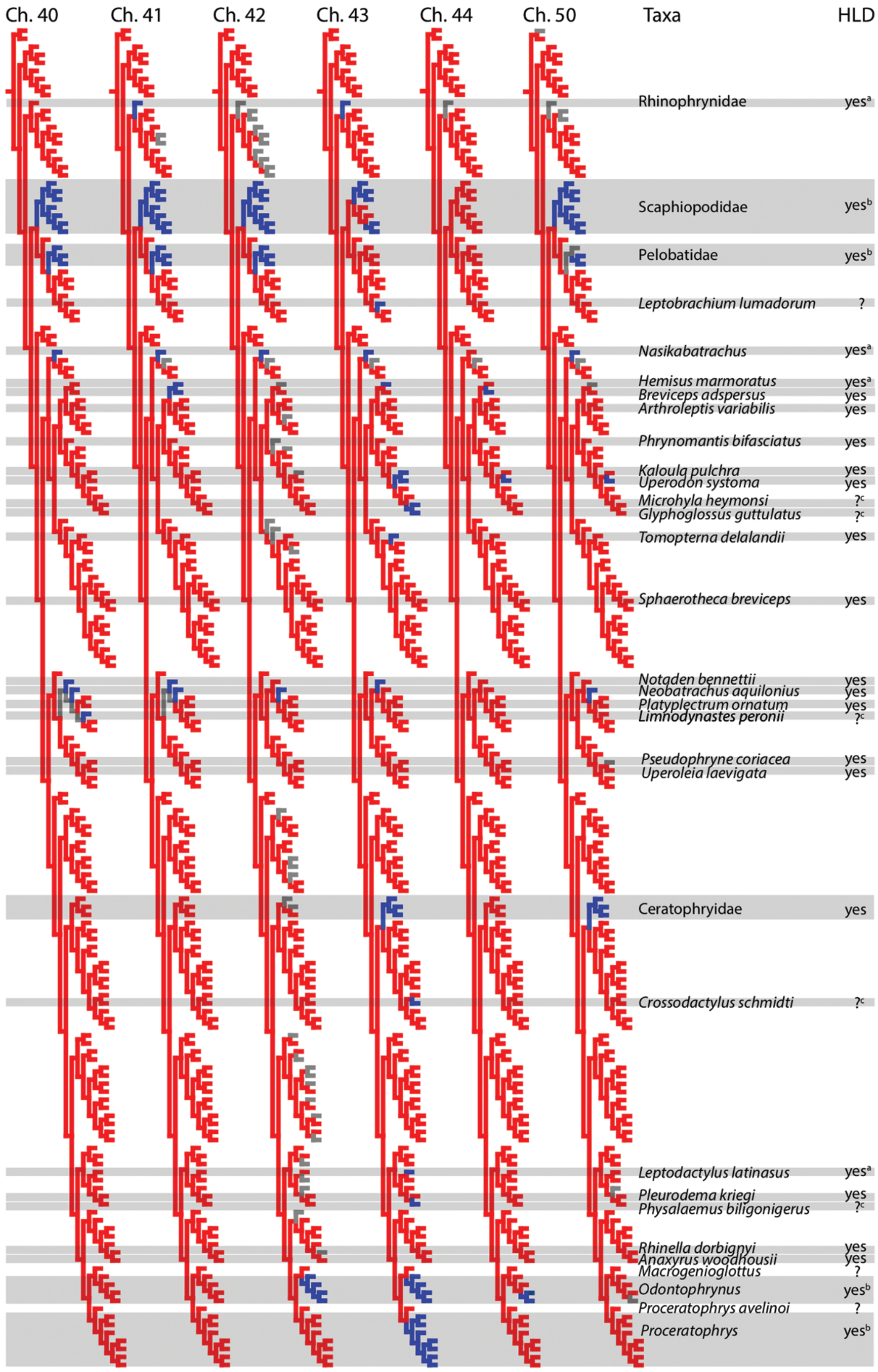

Figure 13. Ancestral character state reconstructions of selected characters with partial correlation with hind limb digging behaviour. Highlighted in grey are: (1) species or clades that are known to use the hind limbs for digging (see

discuss their presumed functions in relation to HLD behaviour.

Many-to-one mapping

The pattern of exceptions described above for the correlation between the character states shown in Figure 13 and the species that are positively known to use the hind limbs for digging defines an asymmetric scenario. Possessing one or more of these character states potentially associated with HLD behaviour implies that a species probably uses the hind limbs for digging, but not sharing any of these character states does not imply that a species does not use the hind limbs for digging. This fact, coupled with the absence of a unique morphology (i.e. a set of character states) related to HLD behaviour might indicate the occurrence of a many-to-one mapping of form to function phenomenon [Wainwright *et al.*, 2005; see also Moen (2019) and Engelkes *et al.* (2020) for discussion in the context habitat use, locomotion modes and burrowing specializations in Anura]. In this case, different morphologies (i.e. different morphological configurations from modifications in different non-homologous muscles) would serve for the same function, expressing the same or similar functional performance, leading to a partial decoupling of morphological characters and function (Wainwright *et al.*, 2005).

This scenario highlights the need for further studies dedicated to evaluating the occurrence and relevance of redundant mapping in influencing the diversity of this functional system. To contribute to that research line, we qualitatively describe and discuss the phenotypic variation (which is of continuous nature, related to development and topology) observed in some additional foot muscles: the m. abductor praehallucis, m. tibialis posterior and m. extensor brevis superficialis hallucis. These muscles have attachments to the prehallux and might have a similar functional value for digging activity as some of the muscles shown in Figure 13. Quantification of their phenotypic variation and its definition into transformation series will require morphometric approaches that were considered out of the scope of this study. Nevertheless, we describe their variation across diverse representatives of Anura from a qualitative and narrative perspective as a first step for a formal quantitative analysis.

The variations observed in these muscles potentially related to HLD behaviour are: (1) m. abductor praehallucis, usually more developed in HLD species (Figs 14, 15); (2) m. tibialis posterior, characterized by greater independence from the aponeurosis plantaris and an insertion (direct or indirect) on the prehallux in HLD species (Figs 14, 15); and (3) the portion of the m. extensor brevis superficialis hallucis inserting on the prehallux, which is more developed in HLD species (Fig. 16). This phenotypic variation, along with the character states shown in Figure 13, suggests that there are many potential combinations of traits that might result in a similar performance for digging.

Finally, there are two muscles with a unique morphology which are restricted to a single species each that can be added to the group of muscles with putative relation to HLD behaviour: the attachment to the prehallux of the mm. flexores breves superficiales via the tendo superficialis praehallucis in *Nasikabatrachus* (see Fig. 4C and Char. 22) and the presence of a massive m. extensor brevis medius hallucis with a strong insertion on the prehallux in *Rhinophrynus* (see Dunlap, 1960: 53, fig. 35; Blotto *et al.*, 2017: 435–436, fig. 4C). This muscle of *Rhinophrynus* is similar in morphology, topology and presumed function to the slip from the tibiale of the m. extensor brevis superficialis hallucis (Char. 44), and it has an atypical insertion on the prehallux (the m. extensor brevis medius hallucis usually attaches to the metatarsophalangeal joint or phalanges of digit I across Anura). Interestingly, and also suggestive of a many-to-one mapping scenario, *Rhinophrynus* is the only species in which the m. extensor brevis superficialis hallucis, which typically inserts on the prehallux, is known to be absent (Dunlap, 1960; Burton, 2001, 2004; Blotto *et al.*, 2017, 2020; Fig. 16).

Thus, the consequent redundancy of the many-to-one mapping can generate a decoupling of the morphology associated with specific functions (Wainwright *et al.*, 2005), some traits associated with HLD function being

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sources in Supporting Information, Appendix S4), indicated as 'yes' under the column of HLD; and (2) species that are unknown regarding this behaviour but share at least one character state with the HLD species, indicated as '?' under the column of HLD. Among the species highlighted in grey, superscripts denote: (a) clades in which the digging mode is still unknown in at least one of its members (see Appendix S4 for details), but it is extrapolated for the clade; (b) species that, besides the hind limbs, also use other digging modes (e.g. forelimbs); and (c) species with unknown digging behaviour, but with close relatives that are known to use the hind limbs for digging (see Discussion and Appendix S4). We tentatively exclude *Alytes obstetricans* from the group of species that use the hind limbs for digging because it is a forward burrowing species that only uses its hind limbs to kick posteriorly the soil brought to the surface by the forelimbs (Brown & Crespo, 2000).

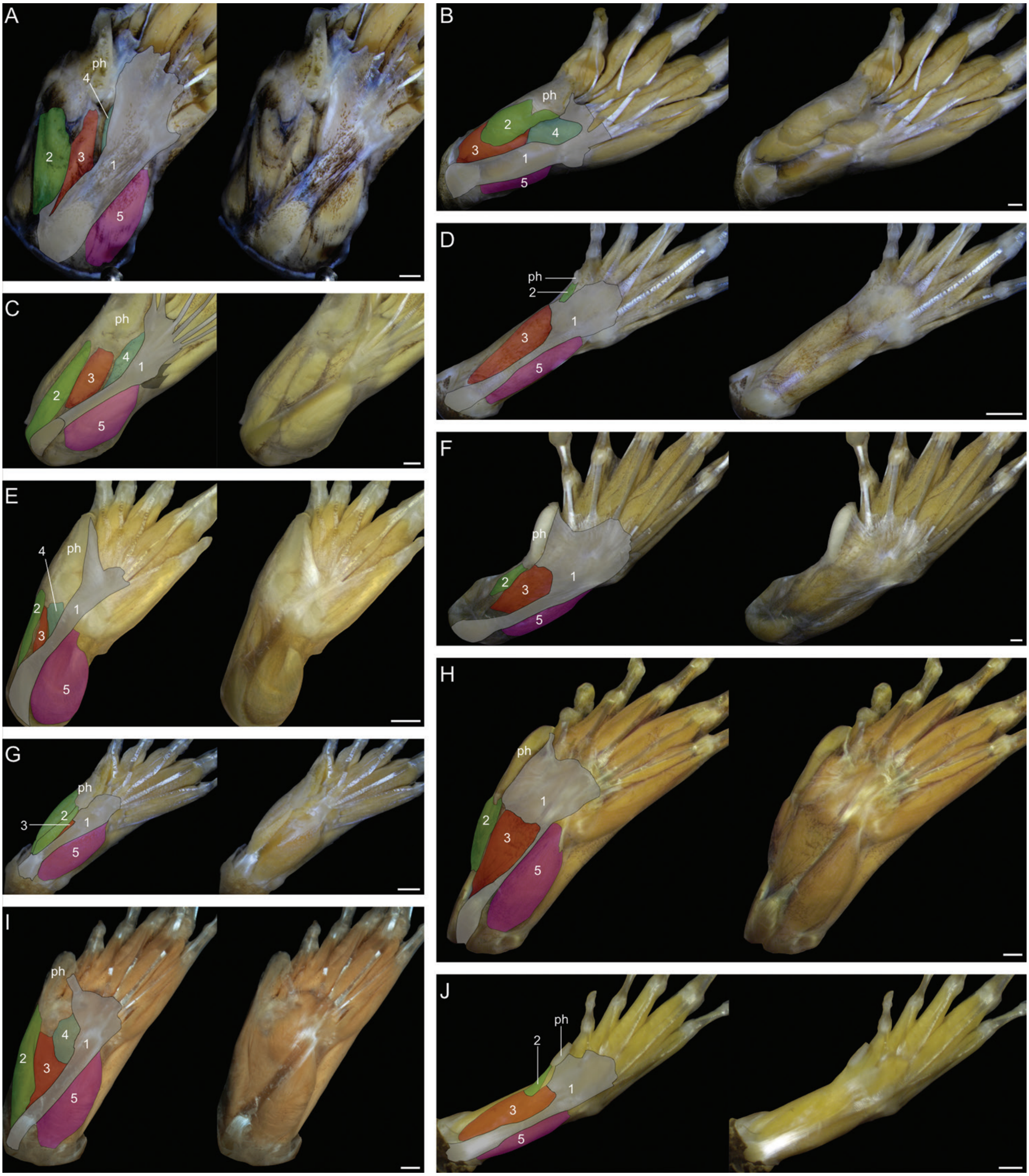

Figure 14. Plantar surface of the tarsal region of the foot from representatives of hind limb digging species (A–E, G, I) or suspected to be (F, H, J; see text for discussion), showing the development and relationships among the aponeurosis plantaris, m. abductor praehallucis, m. tibialis posterior, m. flexor accessorius and mm. flexores breves superficiales. A distal portion of the prehallux was removed in some specimens in order to expose some relevant aspects of the musculature. Although the aponeurosis plantaris covers most of the plantar surface of the foot except the mm. abductores praehallucis and hallucis, the thickness and distribution of the thicker portion of the aponeurosis plantaris varies among species. We coloured the thicker portion of the aponeurosis plantaris on the left image of each figure with the predefined grey shading; compare

absent, possibly explaining partially the deviations found in Figure 13. It should be emphasized at this point that the HLD species studied here have notable differences in several aspects of their natural history. This consideration is particularly relevant under an eventual scenario of a many-to-one mapping of form to function, where different configurations (i.e. combinations of character states) may produce the same or similar performance for digging, while it alleviates potential trade-offs between the performance required for different aspects of their natural history (Holzman *et al.*, 2011; Moen, 2019). Among these alternative natural history aspects found in the HLD species studied here are diverse habitat use (terrestrial, aquatic, saxicolous, fossorial) and locomotion modes (hopping, jumping, swimming and walking).

Presumed functions for digging

Emerson (1976), in her study on burrowing frogs, attempted to establish the specific region of the foot that concentrates the force during digging in relation to jumping. Emerson (1976: 440, fig. 2) concluded that the concentration of the force for the digging action is apparently located in the area associated with the inner metatarsal tubercle, rather than the distal heads of the metatarsals as in jumping. Burton (2001: 556) discussed the presumed function of the m. adductor praehallucis (mentioned by him as the 'direct slip' in the referred paragraph of p. 556) and suggested that this muscle provides HLD species with a greater mobility of the inner metatarsal tubercle, which is associated with the prehallux. This is in accordance with the reports for *Nasikabatrachus*, where recently metamorphosed frogs dig pushing against the substrate with their feet, concentrating the force in the region of the inner metatarsal tubercle, which is associated with the well-developed and ossified prehallux (Senevirathne *et al.*, 2016: 19). Thus, stronger and supplementary connections to the prehallux are somewhat expected in HLD species.

In this regard, the novelty of the attachment to the tendo superficialis praehallucis of the mm. flexores breves superficiales of *Nasikabatrachus* (see Char. 22 and section above 'Many-to-one mapping'), the peculiar m. extensor brevis medius hallucis of *Rhinophrynus*, the nature of the m. abductor praehallucis, m. tibialis posterior, and m. extensor brevis superficialis hallucis (discussed in section 'Many-to-one mapping'), and five (Chars. 40–42, 44, and 50) of the six characters shown in Figure 13 are characterized by modifications in the attachments associated with the region of the prehallux. The remaining character (Char. 43) is an abductor of metatarsal V.

While Characters 40 and 44 refer to the presence of a muscle and a supplementary slip, respectively, both with direct insertion on the dorsal surface of the prehallux, Characters 41 and 42 refer to the extension of the origin of the m. flexor accessorius. This plantar muscle attaches to the aponeurosis plantaris totally or partially at the level of its connection to the prehallux. Thus, a broad origin results in a greater development of the muscle, possibly reinforcing the digging via its indirect attachment to the prehallux.

The remaining character associated with the region of the prehallux is Character 50 and refers to the type of origin of the m. abductor brevis dorsalis hallucis. This muscle originates from the prehallux and/or the element Y and inserts on metatarsal I (Blotto *et al.*, 2020: 52). The taxonomic distribution of Character 50 shows that a tendinous origin (in contraposition to a fleshy origin) is restricted to a subgroup of HLD species. Further studies are required to evaluate the biomechanical aspects associated with this transformation as a possible reinforcement for the attachment to the prehallux and element Y in relation to the digging action.

Finally, as discussed above, the greater development of the m. abductor praehallucis and m. extensor brevis superficialis hallucis attaching to the prehallux, the direct or indirect insertion of the m. tibialis posterior on the prehallux, and the atypical well-developed m. extensor brevis medius hallucis with a wide insertion on the prehallux (observed only in *Rhinophrynus*) represent additional examples of supplementary and/or stronger attachments to the prehallux. These insertions, along with the attachments from muscles defined in Characters 22, 40–42, 44 and 50, might contribute to a greater and diversified mobility of the inner metatarsal tubercle, to which the prehallux is associated, combining different degrees of abduction (m. abductor praehallucis), flexion (tendo superficialis praehallucis originating from the mm. flexores breves superficiales, m. tibialis posterior, m. flexor

the edited image with the same unedited picture on the right of the figure. A, *Rhinophrynus dorsalis* (KU 171202). B, *Scaphiopus couchii* (KU 47023). C, *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01); note the alternative interpretation of the extension of the aponeurosis plantaris in comparison with Figures 4 and 5. D, *Uperoleia laevigata* (KU 180019). E, *Breviceps adspersus* (CAS 170339). F, *Macrogenioglottus alipioi* (MZUSP 126264). G, *Sphaerotheca breviceps* (KU 200460). H, *Odontophrynus carvalhoi* (MZUSP 98179). I, *Neobatrachus aquilonius* (KU 935762). J, *Proceratophrys appendiculata* (CFBH 32577). Labelled elements: 1, aponeurosis plantaris; 2, m. abductor praehallucis; 3, m. tibialis posterior; 4, m. flexor accessorius; 5, mm. flexores breves superficiales. Scale bars = 1 mm.

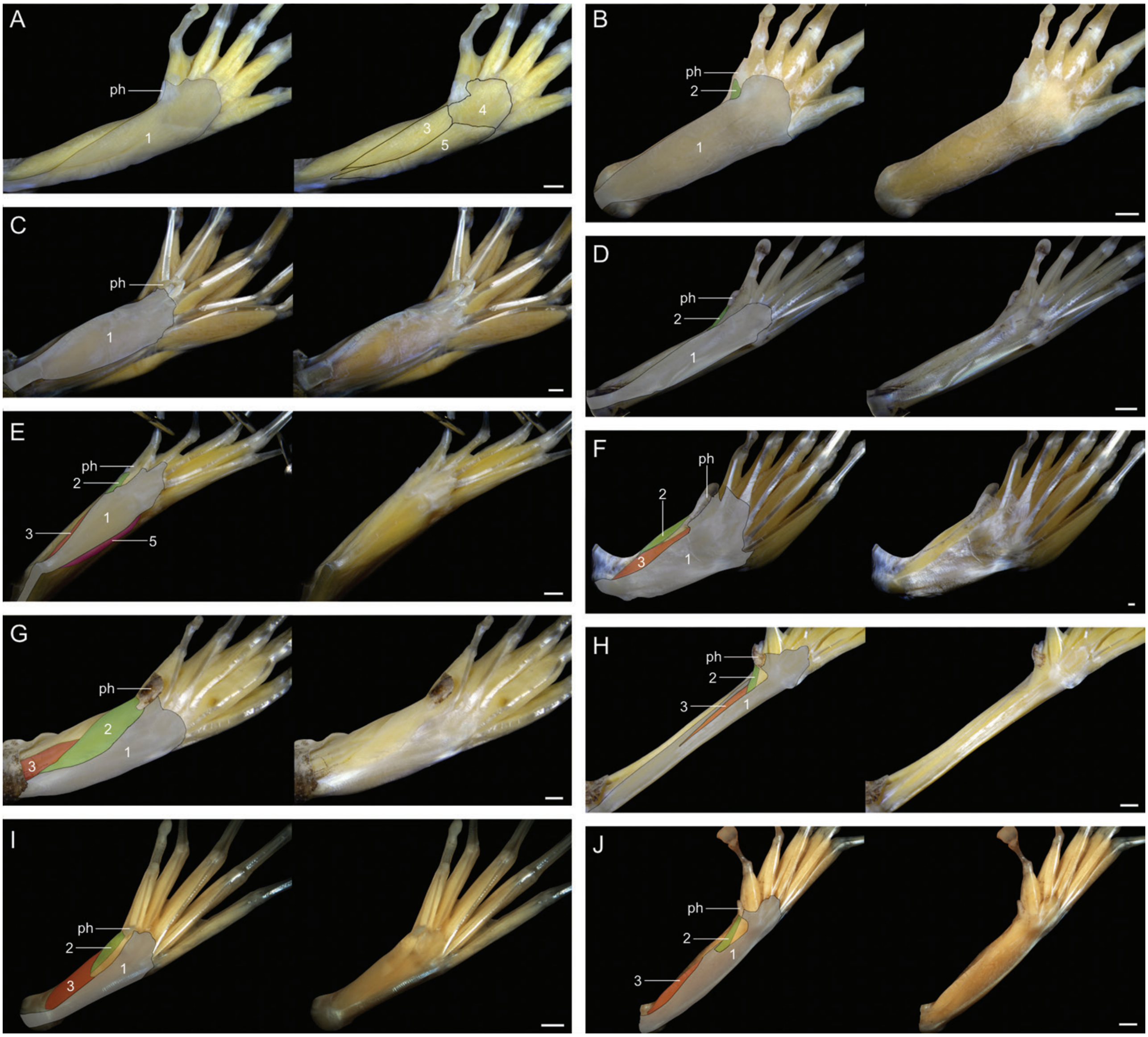

Figure 15. Plantar surface of the tarsal region of the foot of species that do not use or are unknown to use the hind limbs for digging. Note the development and relationships among the aponeurosis plantaris, m. abductor praehallucis, m. tibialis posterior, m. flexor accessorius and mm. flexores breves superficiales. On the left of each figure the thicker portion of the aponeurosis plantaris is coloured with the predefined grey shading, and with a white dashed line its approximate limits (which includes the medial and lateral thinner portions); compare the edited image with the same unedited picture on the right of the figure. A, *Ascaphus truei* (KU 153228); due to the very thin and partially translucent aponeurosis plantaris, we delimited with black lines the borders of the m. tibialis posterior, m. flexor accessorius and mm. flexores breves superficiales; note that the m. abductor praehallucis is absent in this specimen, but present in others (Dunlap, 1960: 34; this study). B, *Leiopelma hochstetteri* (UMMZ 177464); note that the presence of the m. abductor praehallucis in this specimen is possibly polymorphic for the species since it was reported as absent by Dunlap (1960: 34). C, *Xenopus epitropicalis* (KU 2085279). D, *Leptobrachella* cf. *ventripunctata* (KU 331621). E, *Sooglossus thomasseti* (UMMZ 144473). F, *Hoplobatrachus rugulosus* (KU 305458). G, *Fejervarya vittigera* (KU 326281). H, *Hemiphractus proboscideus* (KU 123141). I, *Pseudis minuta* (MACN 52409). J, *Scinax granulatus* (MACN 38218). Labelled elements: 1, aponeurosis plantaris; 2, m. abductor praehallucis; 3, m. tibialis posterior; 4, m. flexor accessorius; 5, mm. flexores breves superficiales. Scale bars = 1 mm.

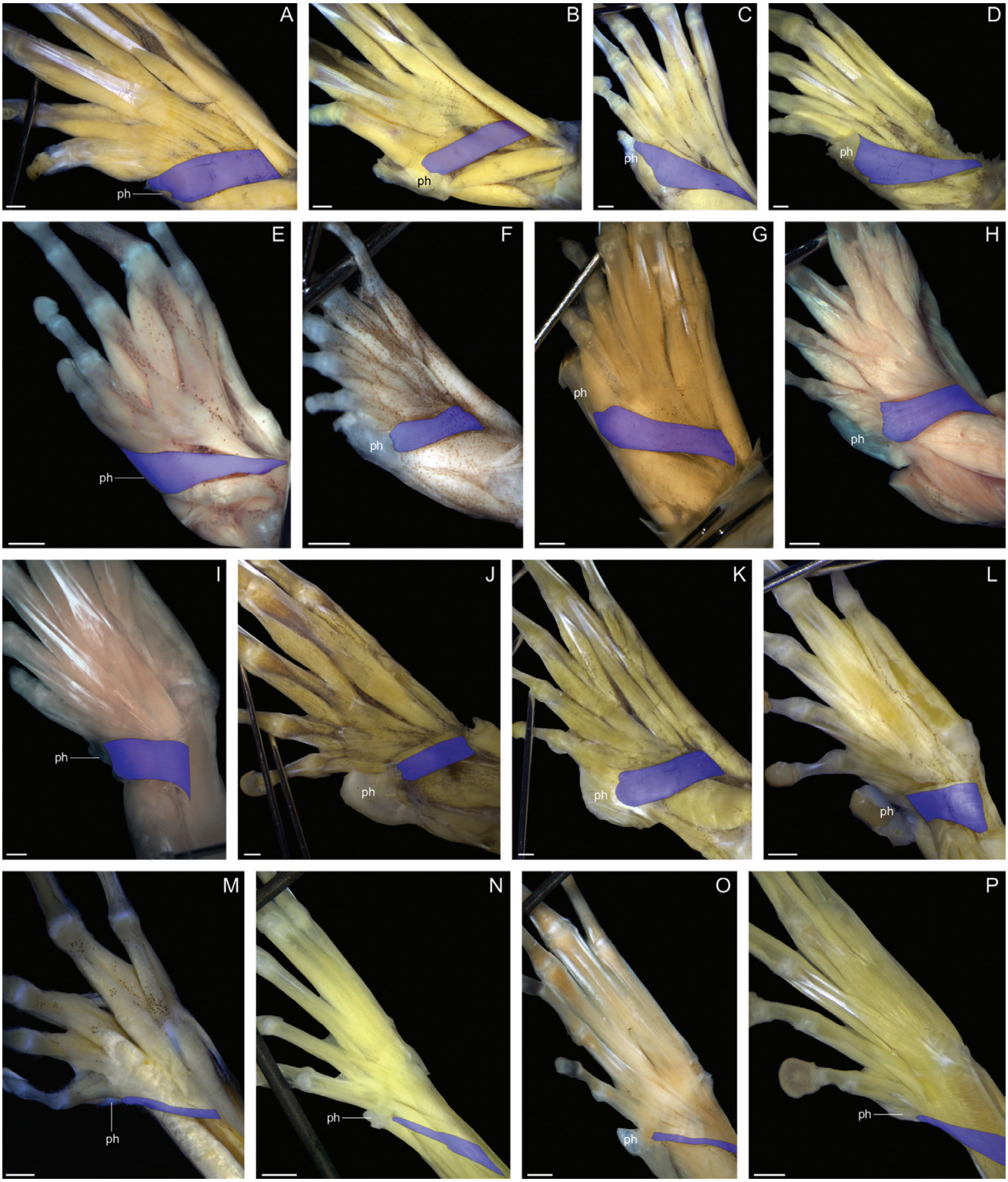

Figure 16. Dorsal surface of the foot of the first (A–C) or second (D–P) layer of musculature, showing the fleshy portion of the m. extensor brevis superficialis hallucis inserting on the prehallux (shaded with blue). The m. abductor digiti minimi was removed in I and L–P, partially removed in D–E, H and J, and the m. extensor brevis superficialis digiti V was removed in E, H–M and O. A, *Scaphiopus couchii* (KU 47023). B, *Spea hammondii* (CM 73782). C, *Pelobates cultripes* (CM 53273). D, *Nasikabatrachus sahyadrensis* (SDBDU 2009.06.01). E, *Hemisus marmoratus* (MACN 39130). F, *Notaden bennettii* (KU 175516). G, *Neobatrachus aquilonius* (KU 93576). H, *Platyplectrum ornatum* (CENAI 8544). I, *Ceratophrys cranwelli* (MACN

accessorius), adduction (m. adductor praehallucis) and extension (supplementary slip from the tibiale of the m. extensor brevis superficialis hallucis, portion inserting on the prehallux of the m. extensor brevis superficialis hallucis, the m. extensor brevis medius hallucis observed in *Rhinophrynus*).

Predictive value?

There are species in which digging behaviour is unknown but that share one character state with other HLD species, including *Crossodactylus schmidti*, *Leptobrachium lumadorum*, *Limnodynastes peronii*, *Microhyla heymonsi* and *Physalaemus biligonigerus*. While digging behaviour is unreported in *Leptobrachium* (e.g. see Brown *et al*., 2010; Keeffe & Blackburn, 2020), there are reports of HLD behaviour in other species (not sampled by us) of *Crossodactylus*, *Glyphoglossus* (Microhylidae), *Limnodynastes* and *Physalaemus* (e.g. Emerson, 1976; Sanders & Davies, 1984; Weygoldt & Carvalho e Silva, 1992; Giaretta & Facure, 2006), and it is suspected to occur in some *Microhyla* (Poyarkov *et al*., 2019).

Limnodynastes peronii possesses the m. adductor praehallucis (Char. 40.1), which is restricted to HLD specialist species. The character state that *Crossodactylus schmidti*, *Glyphoglossus guttulatus*, *Microhyla heymonsi* and *Physalaemus biligonigerus* share with known HLD species is 43.1 (broad insertion of the m. abductor digiti minimi, reaching at least the proximal 1/2 of metatarsal V), which should be considered with caution due to its preliminary and arbitrary delimitation in two character states despite its continuous variation (see comments in Appendix 1). Thus, the occurrence of HLD behaviour is expected in these species, particularly in *Limnodynastes peronii* because it possesses a muscle so far observed in HLD species. The case of *C. schmidti* is peculiar because, contrary to most species, the hind limbs are possibly used for the construction of underwater nesting sites beneath stones, as it was reported for *C. gaudichaudii* (Weygoldt & Carvalho e Silva, 1992) and other hylodids (*Hylodes dactylocinus* and *H. japi*; Narvaes & Rodrigues, 2005; de Sá *et al*., 2015).

Keeffe & Blackburn (2020) suggested that their studies on the variation of the pectoral girdle and humerus would be helpful for identifying putative forward-burrowing species (which mainly use the forelimbs) when their natural history is poorly known. Similarly, the detailed knowledge provided here on the phenotypic transformations in the foot musculature might be useful as two complementary heuristic tools: for predicting species that use hind limbs for digging and for guiding further behavioural and morpho-functional research.

FINAL REMARKS

This study represents a substantial advance in terms of the knowledge of the hand and foot musculature of Sooglossoidea within a phylogenetic context that considers all major relevant clades for comparison. Although the character sampling was restricted to morphological variation observed in Sooglossoidea and muscles with putative relation to HLD behaviour, their occurrence and variation in other groups allowed the inference of synapomorphies for diverse anuran clades of different taxonomic levels. Furthermore, the diversity of the taxon sampling in this study allowed us to clarify the identity of several anuran palmar and plantar muscles.

The deviations from the pattern of convergences of character states that are possibly related to hind limb digging behaviour reveal a complex scenario, suggesting the occurrence of a many-to-one form to function phenomenon. These deviations leave a series of open questions regarding the modifications of the foot musculature in relation to digging behaviour. Resolution of these questions would require: (1) an extended taxon sampling; (2) the consideration and formal elaboration of refined categories for a more precise understanding of the different purposes, intensities, gender involved, habitat uses and locomotion mode in species that use the hind limb for digging; (3) detailed studies considering different ways of using the hind limbs for digging, with particular emphasis on the role of the inner metatarsal tubercle; and (4) experimental and theoretical morpho-functional studies for establishing and testing more precisely the function and performance of the muscles addressed here in relation to digging activity.

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49007). J, *Macrogenioglottus alipioi* (MZUSP 126264). K, *Odontophrynus carvalhoi* (MZUSP 98179). L, *Proceratophrys concavitympanum* (CFBH 5135). M, *Ascaphus truei* (KU 153228). N, *Hyperolius semidiscus* (KU 195874). O, *Limnomedusa macroglossa* (MACN 49261). P, *Triprion petasatus* (KU 296231). Scale bars = 1 mm.

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DATA AVAILABILITY

The data underlying this article are available in the article and in its online Supporting Information.

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SUPPORTING INFORMATION

Appendix S1. Taxonomic comments on some specimens included in this study.

Appendix S2. Character matrix.
Appendix S3. Ancestral character state reconstructions.
Appendix S4. References for data employed in Figure 13 for the use of hind limbs for digging.

APPENDIX 1

CHARACTER DEFINITION

Following the definition of the characters, we briefly describe the taxonomic distribution of the character states and the anuran clades for which they are synapomorphies according to the ACSRs, with more detailed references for Sooglossoidea (see Supporting Information, Appendices S2 and S3 for complete taxonomic distribution and ACSRs). We also indicate the previous phylogenetic use of the characters from the literature, including those characters that were defined considering homology but not included in quantitative phylogenetic analyses (i.e. Burton, 1986, 1998a, 1998b; Blotto *et al.*, 2017, 2020). Characters modified from previous phylogenetic studies are indicated with asterisks (*). The characters are arranged in the following order: ventral hand (Chars. 1–17), dorsal hand (Chars. 18–21), ventral foot (Chars. 22–42) and dorsal foot (Chars. 43–52). Within each group, the characters are arranged following the position of the muscles: from superficial to deep layers, and, within each layer, from proximal to distal and from radial/tibial to ulnar/fibular side.

Character 1

M. flexor indicis superficialis proprius: (0) absent (Blotto *et al.*, 2020: pl. 6A); (1) present (Blotto *et al.*, 2020: pls 2A, 6B–D; Figs 1A, 8A).

Definition: See Blotto *et al.* (2020: char. 1).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This muscle is present in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 1).

Character 2

M. caput profundum digiti III: (0) absent (Blotto *et al.*, 2020: pl. 6A; Fig. 8A); (1) present (Blotto *et al.*, 2020: pls 2A, 6B–D; Fig. 1A).

Definition: This muscle originates from the distal carpals and inserts on the dorsal surface of the tendo superficialis digiti III, and attaches to the palmar surface of the distal phalanx of digit III via a common tendon with the tendo superficialis digiti III (Burton, 1996, 1998a, 1998b; Blotto *et al.*, 2020).

Burton (1998a) described this muscle as present in his sample of *Xenopus* (*X. laevis*, *X. muelleri* and *X. tropicalis*); however, it is absent in the species of the genus examined by us (*X. borealis*, *X.* cf. *borealis*, *X. epitropicalis* and *X.* cf. *victorianus*). We propose three partially complementary explanations for this disagreement. First, the morphology of the m. lumbricalis brevis digiti III of *Xenopus* resembles that of the m. caput profundum digiti III: a triangular muscle with the apex located distally and the base proximally. However, the m. lumbricalis brevis digiti III of *Xenopus* differs from the m. caput profundum digiti III in that the former originates from the flexor plate and inserts on the metacarpophalangeal joint and/or proximal end of basal phalanx of digit III, while the m. caput profundum digiti III originates from the distal carpals and inserts widely on the tendo superficialis digiti III (and both attach to the distal phalanx via a common tendon). Second, the m. flexor accessorius may insert on the flexor plate, reaching the proximodorsal surface of the tendo superficialis digiti III, in which case it may be confused with, or interpreted as, a short m. caput profundum digiti III (see below). Third, and to be considered together with the previous point, some species possess a thin raphe separating the origin of the m. lumbricalis brevis digiti III from the insertion of the m. flexor accessorius (the portion originating on the distal carpals and/or ulnare); this particular morphology also could lead to confusing it with the m. caput profundum digiti III.

Burton (1998a) described the m. caput profundum digiti III as absent in *Hemisus marmoratus*; however, it is present and well developed in the single specimen examined by us. The m. caput profundum digiti III is extremely reduced in *Philoria frosti* (Limnodynastidae), *Rheobatrachus silus* and *Taudactylus diurnus* (Myobatrachidae), and in one of the two specimens of *Spea bombifrons* (Scaphiopodidae) studied by us. The problems regarding the identity of this muscle in relation to the portion of the m. flexor accessorius originating on the distal carpals, discussed by Blotto *et al.* (2020: 39), applies to these four species as well.

ACSR and taxonomic distribution: The absence of this muscle optimizes as synapomorphies of Sooglossidae and Dendrobatoidea [although our taxon sampling of Dendrobatoidea is deficient, Burton (1998a) corroborated its absence in several additional species]. It is also absent in *Ascaphus truei* (Ascaphidae), *Leiopelma hochstetteri* (Leiopelmatidae), Costata, Xenoanura, *Hadromophryne natalensis*, *Heleophryne orientalis* (both Heleophrynidae), *Kaloula pulchra* (Microhylidae), *Hylodes phyllodes* (Hylodidae) and *Pseudopaludicola falcipes* (Leptodactylidae). See Burton (1998a, 1998b) for its occurrence in other taxa.

Previous phylogenetic studies: Burton (1998a: char. 1; 1998b: char. 8*).

Character 3

M. lumbricalis longus digiti III: (0) absent (Blotto *et al.*, 2020: pls 2A, 6A–B, D; Figs 1A, 8A); (1) present (Blotto *et al.*, 2020: pl. 6C).

Definition: See Blotto *et al.* (2020: char. 2).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This muscle is absent in Sooglossoidea.

Previous phylogenetic studies: Burton (1998a: char. 2; 1998b: char. 7); Blotto *et al.* (2020: char. 2).

Character 4

M. lumbricalis brevis indicis, origin from flexor plate: (0) absent; (1) present.

Definition: See Blotto *et al.* (2020: char. 3).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). The origin from the flexor plate is absent in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 3).

Character 5

M. lumbricalis brevis indicis, origin from distal carpals: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 6D; Figs 1C, 12A, B).

Definition: See Blotto *et al.* (2020: char. 4).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). The origin from the distal carpals is present Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 4).

Character 6

M. lumbricalis brevis digiti III, slip originating from flexor plate and/or tendo superficialis digiti III: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 6A, C).

Definition: See Blotto *et al.* (2020: char. 5).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). The slip originating from flexor plate/tendo superficialis digiti III is absent in Sooglossoidea. Within Odontophrynidae, the presence of this slip optimizes as a synapomorphy of *Odontophrynus*, and it is also present in *Proceratophrys concavitympanum* and one of the two specimens of *P. boiei*.

Previous phylogenetic studies: Burton (1998a: char. 3*); Blotto *et al.* (2020: char. 5).

Character 7

M. lumbricalis brevis digiti III, slip originating from the distal carpals: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 2B, C; Fig. 12A, B).

Definition: See Blotto *et al.* (2020: char. 6).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). The slip originating from the distal carpals is present in Sooglossoidea.

Previous phylogenetic studies: Burton (1998a: char. 3*); Blotto *et al.* (2020: char. 6).

Character 8

Medial m. lumbricalis brevis digiti IV, supplementary medial slip originating from the distal carpals: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 7).

Definition: See Blotto *et al.* (2020: char. 7).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This supplementary slip is absent in Sooglossoidea (the condition in *Sechellophryne* is unknown). Besides Megophryidae, this supplementary slip is also present in the odontophrynid *Proceratophrys avelinoi*.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 7).

Character 9

M. contrahentis digiti V, insertion on the distal end of metacarpal V, medially to the m. flexor minimus digiti V: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 8A–B).

Definition: As discussed by Blotto *et al.* (2020: 46–47), the m. contrahentis digiti V has up to three distinct and sometimes co-occurring points of insertion: (1) a medial one, which is a fleshy insertion on the mediodistal end of the palmar surface of metacarpal V, medial to the m. flexor minimus digiti V (Blotto *et al.*, 2020: pl. 8A–B); (2) an intermediate one, which is a tendinous insertion on the metacarpophalangeal joint (Fig. 8B) or basal phalanx of digit V (Blotto *et al.* 2020: pl. 8C), next to or shared with the insertion of the m. flexor minimus digiti V in some species; and (3) a lateral one, which is a fleshy insertion on the lateropalmar surface of metacarpal V, lateral to the m. flexor minimus digiti V (Blotto *et al.*, 2020: pls 2C, 8A–B, 9B; Figs 1C, 2). The pattern of co-occurrence of these three distinct insertions (compare ACSRs in Supporting Information, Appendix S3) provides evidence of their historical independence via the conjunction test (Patterson, 1982), and we code each as a separate transformation series based on this ground.

ACSR and taxonomic distribution: The presence of the medial insertion optimizes as a synapomorphy of Costata (within this clade it is secondarily lost in the alytid *Discoglossus pictus*); it is also present in *Pseudis minuta* (Hylidae) and *Rhacophorus pardalis* (Rhacophoridae). The medial insertion is absent in Sooglossoidea (the condition in *Sechellophryne* is unknown). Characters 9–11 are inapplicable in Pipidae (except *Xenopus*) and *Chaperina fusca* (Microhylidae) because they lack the m. contrahentis digiti V.

Character 10

M. contrahentis digiti V, insertion on the metacarpophalangeal joint or basal phalanx of digit V: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 8C; Fig. 8B).

Definition: We consider the insertions on the metacarpophalangeal joint (e.g. Fig. 8B) and on the basal phalanx (e.g. Blotto *et al.*, 2020: pl. 8C) as primary homologous based on their topological and morphological similarity; an expanded taxon sampling and additional comparative studies are required to test this hypothesis. See Character 9 for further comments.

ACSR and taxonomic distribution: The presence of the insertion on the metacarpophalangeal joint or basal phalanx of digit V optimizes as a synapomorphy of Sooglossidae or *Sooglossus* (depending on the condition in *Sechellophryne*, which is unknown). This insertion is also present in *Bombina bombina* and *B. variegata* (Bombinatoridae), *Heleophryne orientalis* (Heleophrynidae), *Hemiphractus proboscideus* (Hemiphractidae), and in one of the two specimens of *Rhinophrynus dorsalis* (Rhinophrynidae).

Character 11

M. contrahentis digiti V, insertion on the distal end of metacarpal V, laterally to the m. flexor minimus digiti V: (0) absent; (1) present (Blotto *et al.*, 2020: pls 2C, 8A–B, 9B; Figs 1C, 2, 12A, B).

Definition: see Character 9.

ACSR and taxonomic distribution: The absence of this insertion is a putative synapomorphy of Sooglossidae or *Sooglossus* (depending on the condition in *Sechellophryne*, which is unknown), and an internal clade of *Xenopus*. It is also absent in *Heleophryne orientalis*.

Character 12

Medial m. flexor indicis brevis profundus: (0) absent (Fig. 8B); (1) present (Blotto *et al.*, 2020: pls 2D, 9–10; Figs 1D, 2B; 12A, C).

Definition: The medial m. flexor indicis brevis profundus originates from the distal carpals and has a broad fleshy insertion on the mediopalmar surface of metacarpal II; see Blotto *et al.* (2020: 48) for further comments on its identity and nature. *Sooglossus thomasseti* has two unidentified muscles in digit II (labelled as 30 and 31 in Fig. 8B); these muscles originate from distal carpal 3-4-5 and insert on the mediopalmar surface of the metacarpophalangeal joint of digit II. Although it is possible that one or both of these two unidentified muscles represent a modified medial m. flexor indicis brevis profundus, we tentatively coded it as absent based on their notably different points of insertion and presumed different function.

ACSR and taxonomic distribution: The absence of the medial m. flexor indicis brevis profundus is a synapomorphy of Sooglossidae or *Sooglossus* (depending on the condition in *Sechellophryne*, which is unknown). Its absence optimizes also as a synapomorphy of *Hymenochirus* (Pipidae), and it is absent in the pipid *Pipa parva*.

Character 13

M. flexor minimus indicis: (0) absent; (1) present (Blotto *et al.*, 2020: pls 8C, 9A; Fig. 8B).

Definition: See Blotto *et al.* (2020: char. 8).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). Its presence is a synapomorphy of Sooglossidae or *Sooglossus* (depending on the condition in *Sechellophryne*, which is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 8).

Character 14

M. flexor minimus digiti IV, position of the origin with respect to the m. intermetacarpalis II: (0) m. flexor minimus digiti IV ventral to the m. intermetacarpalis II (Blotto *et al.*, 2020: pls 8C, 9A, 9C–D, 10A; Fig. 8B); (1) m. flexor minimus digiti IV dorsal to the m. intermetacarpalis II (Blotto *et al.*, 2020: pls 2D, 10B; Figs 1D, 12A); (2) m. flexor minimus digiti IV ventral and dorsal to the m. intermetacarpalis II (Blotto *et al.*, 2020: pl. 8B).

Definition: See Blotto *et al.* (2020: char. 9).

ACSR and taxonomic distribution: As obtained by Blotto *et al.* (2020), a dorsal origin (state 1) optimizes as a synapomorphy of the pipid tribe Hymenochirini (i.e. *Hymenochirus* + *Pseudhymenochirus*), while a ventral and dorsal origin (state 2) is a synapomorphy of Bombinatoridae. However, and different from Blotto *et al.* (2020), a dorsal origin (state 1) does not optimize as an unambiguous synapomorphy of Nobleobatrachia, due to the impact of the dorsal origin in *Nasikabatrachus* on the optimization for the deep nodes of Neobatrachia (compare Supporting Information, Appendix S3 with Blotto *et al.*, 2020: 124); see Appendices S2 and S3 for complete taxonomic distribution.

Previous phylogenetic studies: Burton (1998a: no character number assigned; 1998b: char. 11*); Blotto *et al.* (2020: char. 9).

Character 15

M. flexor minimus digiti IV, origin from metacarpal III: (0) absent; (1) present.

Definition: The m. flexor minimus digiti IV originates from metacarpal III and/or metacarpal IV, and inserts on the palmar surface of the basal phalanx of digit IV (Gaupp, 1896; Burton, 1996, 1998b; Blotto *et al.*, 2020; this study).

ACSR and taxonomic distribution: Although the presence of the origin from metacarpal III has several instances of homoplasy, it is a putative synapomorphy of: (1) *Sooglossus* or Sooglossidae (depending on the condition in *Sechellophryne*, which is unknown); and (2) Microhylinae or a more inclusive clade (the taxon sampling is incomplete at this point). See complete taxonomic distribution in Supporting Information, Appendices S2 and S3.

Character 16

M. interphalangeus digiti V, intermediate slip: (0) absent (Figs 1D, 2B); (1) present (Blotto *et al.*, 2020: pls 9C, 10A; Figs 8B, 12A, C).

Definition: Up to three slips of the m. interphalangeus digiti V may be present: medial, intermediate and lateral. The medial and lateral slips have fleshy origins from the medio- and lateropalmar surface of the basal phalanx of digit V, respectively. The intermediate slip originates via a short tendon from the metacarpophalangeal joint of digit V or distal end of metacarpal V, and it is located approximately between the medial and lateral slips. They insert on the second phalanx of digit V, via a common or independent tendons (Burton, 1996, 1998b; Blotto *et al.*, 2020; this study).

Burton (1998b: char. 15) considered the presence of the mm. interphalangei digitorum IV and V to be subject to much variation between and within species, and he did not indicate their taxonomic distribution. However, the intraspecific variation and high levels of homoplasy are restricted to specific clades (this study). Consequently, we consider these data for the following reasons: (1) it is informative from a phylogenetic perspective; and (2) the knowledge of which specific clades are intraspecifically or highly variable (homoplasy) is relevant for other studies that are not exclusively focused on taxonomy or phylogenetics (e.g. evolutionary processes, biomechanics). We present here the data referring to the presence of the intermediate slip of digit V.

ACSR and taxonomic distribution: Although with several instances of homoplasy (see Supporting Information, Appendices S2 and S3 for complete taxonomic distribution and polymorphisms), the presence optimizes as synapomorphies of Xenoanura, Pelodytidae + Pelobatidae + Megophryidae, *Sooglossus* or Sooglossidae (depending on the condition in *Sechellophryne*, which is unknown), and *Macrogenioglottus* + *Odontophrynus* (Odontophrynidae).

Character 17

M. contrahentis caput longus distalis: (0) absent (Blotto *et al.*, 2020: pls 9D, 10A; Fig. 1D); (1) present (Blotto *et al.*, 2020: pls 2D, 9A–C, 10B; Figs 2B, 8B, 12A, C).

Definition: See Blotto *et al.* (2020: char. 10).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). Besides Anomocoela, it is also absent in the male specimen of *Nasikabatrachus*, representing the single instance of homoplasy so far reported for the character; the condition in *Sechellophryne* is unknown.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 10).

Character 18

M. extensor brevis medius digiti III, slip from the mediodistal end of radioulna: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 13).

Definition: See Blotto *et al.* (2020: char. 11).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This slip is absent in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 11).

Character 19

M. extensor brevis medius digiti III, slip from element Y: (0) absent (Fig. 3C); (1) present (Blotto *et al.*, 2020: pl. 3C).

Definition: See Blotto *et al.* (2020: char. 11).

ACSR and taxonomic distribution: The absence of this slip is restricted to a few species scattered across the phylogeny (see Supporting Information, Appendices S2 and S3 for complete taxonomic distribution). Within Sooglossoidea, the absence is an autapomorphy of *Nasikabatrachus* (the condition in *Sechellophryne* is unknown).

Character 20

M. extensor brevis medius digiti IV, origin from the radiale: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 13; Fig. 3C).

Definition: See Blotto *et al.* (2020: char. 12).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This origin is present in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 12).

Character 21

Medial m. dorsometacarpalis proximalis digiti IV, slip from metacarpal III: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 3D; Fig. 3D).

Definition: See Blotto *et al.* (2020: char. 13).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This slip is present in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 13).

Character 22

Tendo superficialis praehallucis, origin from the tendon of insertion of the mm. flexores breves superficiales: (0) absent; (1) present (Figs 4C, 5A).

Definition: The tendo superficialis praehallucis, tendo superficialis hallucis and tendo superficialis digiti II originate from the aponeurosis plantaris in most species, while in a few species (e.g. some Costata and Pipidae) they originate from the combined aponeurosis plantaris and tendon of insertion of the m. tibialis posterior (Gaupp, 1896; Dunlap, 1960; Burton, 2004; Blotto *et al.*, 2020; this study). *Nasikabatrachus* exhibits a condition previously unreported in Anura: the tendo superficialis praehallucis, tendo superficialis hallucis and tendo superficialis digiti II arise, in addition to the origin from the aponeurosis plantaris, from the tendon of insertion of mm. flexores breves superficiales (see the description in Results and Figs 4C, 5A).

ACSR and taxonomic distribution: The presence of this origin is an autapomorphy of *Nasikabatrachus sahyadrensis*.

Character 23

Tendo superficialis hallucis, origin from the tendon of insertion of the mm. flexores breves superficiales: (0) absent; (1) present (Figs 4C, 5A).

Definition: See previous character.

ACSR and taxonomic distribution: The presence of this origin is an autapomorphy of *Nasikabatrachus sahyadrensis*.

Character 24

Tendo superficialis digiti II, origin from the tendon of insertion of the mm. flexores breves superficiales: (0) absent; (1) present (Figs 4C, 5A).

Definition: See Character 22.

ACSR and taxonomic distribution: The presence of this origin is an autapomorphy of *Nasikabatrachus sahyadrensis*.

Character 25

M. lumbricalis brevis hallucis: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 4B; Figs 4B, 9A).

Definition: Philoria frosti (Limnodynastidae) has a massive and almost undifferentiated muscle with a broad origin from the aponeurosis plantaris. This muscle might correspond to a partial fusion of some or all the following muscles: m. abductor brevis plantaris hallucis, m. lumbricalis brevis hallucis, m. contrahentis pedis hallucis and m. flexor hallucis accessorius. This muscle (or group of muscles) inserts on the prehallux, ventromedial surface of metatarsal I (mostly fleshy) and the complete plantar surface of the metatarsophalangeal joint of digit I. The portion of this muscle that connects the aponeurosis plantaris with the metatarsophalangeal joint supports its recognition as m. lumbricalis brevis hallucis. However, the portion inserting on the prehallux is unclear, while the portion inserting on metatarsal I could be attributed to a portion of the m. lumbricalis brevis hallucis inserting on metatarsal I, to the m. flexor hallucis accessorius or to part or the totality of the m. abductor brevis plantaris hallucis. Burton (2001: 550–551) reported that the presence of the m. flexor hallucis accessorius is variable in *P. frosti*, without additional details or describing the other relevant muscles of digit I. This information is required for inferring whether this absence means that the muscle is missing or that the muscle is not a discrete and differentiated from other(s) muscle(s). In the meanwhile, and pending a more detailed comparative study (e.g. more specimens of *Philoria* and other closely related species), we consider the m. lumbricalis brevis hallucis to be present (as done by Blotto *et al.*, 2020), while we scored the characters referring to the m. flexor hallucis accessorius and m. contrahentis pedis hallucis (addressed below) as missing data. See also Blotto *et al.* (2020: char. 14) for further comments.

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). The m. lumbricalis brevis hallucis is present in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 14).

Character 26

M. lumbricalis brevis digiti II, supplementary dorsal slip with insertion on metatarsal II: (0) absent; (1) present (Blotto *et al.*, 2017: fig. 2B).

Definition: See Blotto *et al.* (2017: char. 5). Note, however, that Blotto *et al.* (2017: 428) described this supplementary slip as inserting on 'Metatarsus III', which is a lapsus for 'Metatarsus II' (or metatarsal II, as referred here).

ACSR and taxonomic distribution: The presence of this supplementary slip was suggested by

Blotto *et al.* (2017) as a synapomorphy of *Odontophrynus americanus* + *O. cultripes* based on its optimization on the topology of Pyron (2014). The analysis of Jetz & Pyron (2018), employed here, recovered *O. cultripes* as the sister taxon of *O. americanus* + *O. occidentalis*, turning the optimization ambiguous in this region of the tree (see Supporting Information, Appendix S3). This supplementary slip is also present in some specimens of the odontophrynid *Macrogenioglottus alipioi* (Blotto *et al.*, 2017) and in *Hymenochirus boettgeri* (this study), while it is absent in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2017: char. 5).

Character 27

M. lumbricalis brevis digiti III, supplementary dorsal slip with insertion on metatarsal III: (0) absent; (1) present (Blotto *et al.*, 2017: fig. 2B).

Definition: See Blotto *et al.* (2017: char. 6). As evidenced from the extended taxon sampling of the present study, there is an extraordinary phenotypic variation in the nature of the insertion on metatarsal III. While the insertion in *Macrogenioglottus* + *Odontophrynus* is fleshy with a differentiated dorsal supplementary slip, the condition within Pipidae differs in the following aspects: (1) the insertion on metatarsal III can be fleshy, partially tendinous or tendinous; (2) the insertion may be via a differentiated slip attaching to metatarsal III, or via a single muscle (i.e. without differentiated slips) inserting from metatarsal III to the metatarsophalangeal joint; and (3) it may attach to metatarsal III via a single and medial insertion, a single and lateral insertion, or a medial and lateral insertion (being the medial and lateral insertions relative to the m. flexor minimus digiti III). As a preliminary step, we consider the pipid condition as a primary homologue with respect to the odontophrynid condition. However, further comparative and detailed studies are required to state whether the insertions on metatarsal III in those taxa represent different transformation series. In any case, additional character(s) will be required to accommodate the great variation in the insertions reported here.

ACSR and taxonomic distribution: This supplementary slip is present in all the species of *Odontophrynus* examined, but the polymorphic condition of *Macrogenioglottus alipioi* turns the optimization ambiguous for *Macrogenioglottus* + *Odontophrynus* (see further comments in Blotto *et al.*, 2017). The supplementary slip inserting on metatarsal III is also present in *Pipa* (Dunlap, 1960: 36; this study) and Hymenochirini, while it is absent in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2017: char. 6).

Character 28

Medial m. lumbricalis brevis digiti IV, supplementary dorsal slip with insertion on metatarsal IV: (0) absent; (1) present (Blotto *et al.*, 2017: fig. 2B).

Definition: See Blotto *et al.* (2017: char. 7).

ACSR and taxonomic distribution: Its presence is a synapomorphy of *Macrogenioglottus* + *Odontophrynus* (as also obtained by Blotto *et al.*, 2017); the supplementary slip inserting on metatarsal IV is also present in *Pseudhymenochirus merlini* (Pipidae), and it is absent in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2017: char. 7).

Character 29

Medial m. lumbricalis brevis digiti IV, point of origin: (0) aponeurosis plantaris (Blotto *et al.*, 2020: pl. 4B; Fig. 4B); (1) tendon of insertion of the mm. flexores breves superficiales (Fig. 9B).

Definition: In non-acosmanurans (i.e. Ascaphidae + Leiopelmatidae, Costata and Xenoanura), the distal portion of the aponeurosis plantaris is fused to the distal portion and tendon of insertion of the mm. flexores breves superficiales (Dunlap, 1960: 27, 29; this study). Consequently, it is not possible to individualize the exact point of origin for several muscles in those clades (i.e. origin from the aponeurosis plantaris or from the tendon of insertion of the mm. flexores breves superficiales). Based on this, we consider inapplicable this character in those clades (except Pipidae, which is scored as missing data pending more detailed studies regarding the nature and relationship between the aponeurosis plantaris and the tendon of insertion of the mm. flexores breves superficiales). Distinctly, the mm. flexores breves superficiales are mostly or completely free from the distal end of the aponeurosis plantaris in Acosmanura (i.e. Anomocoela + Neobatrachia), and it is possible to score each point of origin in separate character states.

ACSR and taxonomic distribution: The origin from the mm. flexores breves superficiales optimizes as a synapomorphy of Sooglossidae with no instances of homoplasy.

Character 30

Lateral m. lumbricalis brevis digiti IV, presence of a supplementary origin from the proximal end of metatarsal IV: (0) absent; (1) present.

Definition: See Blotto *et al.* (2020: char. 15).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This supplementary origin is absent in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 15).

Character 31

M. contrahentis pedis hallucis, origin: (0) element Y; (1) distal tarsals (Blotto *et al.*, 2020: pl. 11A; Fig. 9C); (2) mediodistal and dorsal region of the aponeurosis plantaris; (3) fused distal portions of the tibiale and fibulare (Fig. 4D).

Definition: The coding scheme differs from Blotto *et al.* (2017) in the incorporation of two additional character states to accommodate the observed variation: origin from element Y (state 0) and from the fused distal portions of the tibiale and fibulare (state 3). Distinctly to the origin of the m. flexor hallucis accessorius, we code the different points of origin of the m. contrahentis pedis hallucis within a single multistate character because, with the single possible exception of *Nasikabatrachus* (see below), there is no co-occurrence of more than one point of origin.

The condition observed in *Nasikabatrachus* is peculiar. Both specimens have an origin from the fused distal portions of the tibiale and fibulare, and have proximal (female) or almost complete (male) fusion with the m. flexor hallucis accessorius. This fact implies that both muscles share a common and single tendon of origin. The tendon of origin of the male also has a tendinous perpendicular connection with element Y (see Figs 4D, 5C), tentatively considered as an additional point of origin. Considering this morphology, three problems preclude a consistent scoring for the condition observed in *Nasikabatrachus*.

First, due to the common tendon of origin of the m. contrahentis pedis hallucis and m. flexor hallucis accessorius, there is a problem of redundancy due to the lack of independence in the scoring for the origin of both muscles. Second, we tentatively code the origin of the m. contrahentis pedis hallucis as being only from fused distal portions of the tibiale and fibulare (state 3), despite its additional origin from element Y in the male. Considering the coding scheme suggested here for the origin of the m. contrahentis pedis hallucis (a single multistate character), two alternative treatments would be to score it as inapplicable or missing data in the multistate character as defined here, or to define an additional character for the presence of the origin from element Y (so far observed only in *Atelopus*; Dunlap, 1960: 39; this study). Considering the taxonomic distribution of the character states, the ACSR is not modified in these alternative treatments beyond the branch of *Nasikabatrachus* (results not shown).

Third, and to be considered along with the last point, we are introducing an additional inconsistency in our scoring. This is because, differently to the scoring for the origin of the m. contrahentis pedis hallucis, the origin of the m. flexor hallucis accessorius from element Y (Char. 34) is scored as polymorphic (present in the male and absent in the female). Note that scorings for *Nasikabatrachus* (e.g. as missing data or inapplicable) other than those tentatively implemented here for the origins of the m. flexor hallucis accessorius do not modify the ACSRs beyond the branch of *Nasikabatrachus*, due to the combination of the inapplicability of these characters in Sooglossidae (m. flexor hallucis accessorius absent) and the taxonomic distribution of the character states outside Sooglossoidea. Thus, the scoring and resulting ACSRs for the origin of the m. contrahentis pedis hallucis and m. flexor hallucis accessorius in *Nasikabatrachus* should be critically interpreted taking into account these considerations.

ACSR and taxonomic distribution: An origin from the aponeurosis plantaris is a synapomorphy of *Odontophrynus* (state 2), which evolved from an origin from the distal tarsals (state 1), as also obtained by Blotto *et al.* (2017). The origin from the fused distal portions of the tibiale and fibulare (state 3) optimizes as a synapomorphy of *Discoglossus* (Alytidae), which evolved from an origin from the distal tarsals (state 1). Additionally, the origin from the fused distal portions of the tibiale and fibulare (state 3) is an autapomorphy of *Nasikabatrachus* (but see comments for the origin from element Y above, and for its fusion with the m. flexor hallucis accessorius in the Results and Discussion), which evolved from an origin from the distal tarsals (state 1). The ambiguity observed for the terminals in the ACSR is due to inapplicability (m. contrahentis pedis hallucis absent), except for *Lepidobatrachus laevis* (Ceratophryidae), *Melanophryniscus klappenbachi* (Bufonidae), *Philoria frosti* (Limnodynastidae) and *Pipa*, which are missing data. See Character 25 for further comments for the condition in *Philoria frosti*.

Previous phylogenetic studies: Blotto *et al.* (2017: char. 3*).

Character 32

M. contrahentis pedis digiti V: (0) absent; (1) present (Blotto *et al.*, 2017: fig. 3B; Blotto *et al.*, 2020: pl. 11A).

Definition: See Blotto *et al.* (2020: char. 16).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This muscle is absent in Sooglossoidea.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 16).

Character 33

M. flexor hallucis accessorius: (0) absent; (1) present (Blotto *et al.*, 2020: pls 4D, 11; Fig. 4D).

Definition: This muscle has different and sometimes co-occurring points of origin (element Y, distal tarsals, aponeurosis plantaris, and fused distal portions of the tibiale and fibulare) and usually has a fleshy insertion on metatarsal I (Dunlap, 1960; Burton, 1986, 2001, 2004; Blotto *et al.*, 2017, 2020; this study). Differently to the m. contrahentis pedis hallucis and to the coding scheme presented by Blotto *et al.* (2017: char. 2), there are several taxa with multiple points of origin observed in our expanded taxon sampling; on this basis, we code each origin in a different character. However, it must be noted that, when more than one point of origin occurs, it is the product of a single tendon of origin that is proximally expanded to include more than one of the above-mentioned points of origins, and not a product of independent tendons (with the possible exception of the male of *Nasikabatrachus*; see description in the Results and for Char. 31).

The dorsal fibres of the m. lumbricalis brevis hallucis of *Crinia signifera* (Myobatrachidae) have a fleshy insertion on metatarsal I, topologically compatible with the insertion of the m. flexor hallucis accessorius; pending a more detailed comparative study, and in light of its similarity with the condition found in *Philoria frosti* described above (see Char. 25), we scored the presence of the m. flexor hallucis accessorius as missing data in *C. signifera*.

ACSR and taxonomic distribution: The absence of the m. flexor hallucis accessorius optimizes as synapomorphies of Scaphiopodidae and Sooglossidae. It is also absent in Pipidae (except *Pipa carvalhoi*) and in *Micryletta* aff. *inornata* (Microhylidae).

Character 34

M. flexor hallucis accessorius, origin from element Y: (0) absent; (1) present (Figs 4D, 5C).

Definition: See previous character.

ACSR and taxonomic distribution: Its presence optimizes as a synapomorphy of Bufonidae, and it is also present in *Breviceps adspersus* (Brevicipitidae). *Nasikabatrachus* is scored as polymorphic due to the presence of the origin from element Y in the male (Figs 4D, 5C) and the absence in the female; see comments for Character 31 regarding the coding and scoring criteria in this case. The optimization is ambiguous for Ascaphidae + Leiopelmatidae (present) and Lalagobatrachia (absent), and it is contingent on the condition in Caudata (see Discussion).

Character 35

M. flexor hallucis accessorius, origin from distal tarsals: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 4D).

Definition: See Character 33.

ACSR and taxonomic distribution: The absence of the origin from the distal tarsals optimizes as synapomorphies of Brevicipitidae, Limnodynastidae, an internal clade of Myobatrachidae, Bufonidae and *Odontophrynus*. This origin is also absent in *Nasikabatrachus*, but due to the absence of the m. flexor hallucis accessorius in Sooglossidae (implying the inapplicability of this character in this family), the optimization is ambiguous for Sooglossoidea.

Previous phylogenetic studies: Burton (1986 char. 23*); Blotto *et al.* (2017: char. 2*).

Character 36

M. flexor hallucis accessorius, origin from the aponeurosis plantaris: (0) absent; (1) present.

Definition: The aponeurosis plantaris inserts via a short and discrete tendon on distal tarsal 2-3 (or on the lateral-most distal tarsals) and/or on the connective tissue joining distal tarsal 2-3 (or the lateral-most distal tarsals) to the fused distal portions of the tibiale and fibulare (this study). Some species have a complete origin from the dorsal and mediodistal region of the aponeurosis plantaris (e.g. *Odontophrynus*), next to the above-described tendon connecting to the distal tarsals, while others have an origin totally or partially from this tendon; we consider both conditions homologous and code them within the same character state.

ACSR and taxonomic distribution: The origin from the aponeurosis plantaris optimizes as a synapomorphy of *Odontophrynus*. This origin is also present in some megophryids, *Hemisus marmoratus* (Hemisotidae), some Microhylidae, and the ceratophryids *Ceratophrys cranwelli* and *Lepidobatrachus laevis*. The origin from the aponeurosis plantaris is also present in *L. llanensis* (Blotto *et al.*, 2017). It must be stated that Blotto *et al.* (2017) omitted the reference of Burton (1986: char. 23), who first described an origin of this muscle from the aponeurosis plantaris in his sample of microhylids.

Previous phylogenetic studies: Burton (1986: char. 23*); Blotto *et al.* (2017: char. 2*).

Character 37

M. flexor hallucis accessorius, origin from the fused distal portions of the tibiale and fibulare: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 11A; Fig. 4D).

Definition: See Character 33.

ACSR and taxonomic distribution: The origin from the fused distal portions of the tibiale and fibulare optimizes as a synapomorphy of Myobatrachoidea. This origin is also present in *Leiopelma hochstetteri*, Costata, Rhinophrynidae and *Nasikabatrachus*. The absence of the m. flexor hallucis accessorius in Sooglossidae turns the optimization for the origin from the fused distal portions of the tibiale and fibulare ambiguous for Sooglossoidea.

Character 38

M. abductor brevis plantaris digiti V, extension of the insertion: (0) proximal 2/3 or less of metatarsal V (Blotto *et al.*, 2020: pl. 11B; Fig. 9C); (1) proximal 3/4 or more of metatarsal V (Blotto *et al.*, 2020: pl. 4D; Fig. 4D).

Definition: The m. abductor brevis plantaris digiti V has a fleshy or tendinous origin from the laterodistal end of the fibulare and/or from a heavy connective tissue at the level of the laterodistal portion of the fibulare plus the proximal end of metatarsal V, product of the attachment of the aponeurosis plantaris to this region. The m. abductor brevis plantaris digiti V has a fleshy insertion on the lateroplantar surface of metatarsal V, and the extension of this insertion varies (Dunlap, 1960; Burton, 2001; this study).

The identity of this muscle in relation to the lateral m. lumbricalis brevis digiti V is unclear in Bombinatoridae and Hymenochirini (this study; see also Dunlap, 1960: 45), and we scored it as missing data pending additional comparative studies. Although this character is continuous, we preliminarily delimited it into two character states following Dunlap (1960: 45), Burton (2001: 553) and our observations, because most species clearly fit into one of these two character states. Further studies are required to complete the extensive missing data (30 out of the 167 species of this study).

ACSR and taxonomic distribution: The insertion onto the proximal 2/3 or less of metatarsal V (state 0) optimizes as synapomorphies of Microhylidae, Sooglossidae or *Sooglossus* (depending on the unknown condition in *Sechellophryne*), and Leiuperinae or a more inclusive clade of Leptodactylidae (unknown in Leptodactylinae and Paratelmatobiinae). The insertion on the proximal 2/3 or less of metatarsal V also occurs in several Myobatrachidae (see also Burton, 2001: 553) and a few additional species across Anura. The optimization of this character is ambiguous for Ascaphidae + Leiopelmatidae (state 0) and Lalagobatrachia (state 1), which is contingent on the condition in Caudata (see Discussion).

Character 39

M. flexor minimus hallucis: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 11B; Fig. 9C).

Definition: This muscle was distinguished from the m. contrahentis pedis hallucis by Burton (2004: 201). The m. flexor minimus hallucis has a fleshy origin on the plantar surface of metatarsal I, laterally to the insertion of the m. flexor hallucis accessorius; it tapers to a tendon that passes through an internal channel of the metatarsophalangeal joint, and inserts on the plantar surface of the basal phalanx of digit I (Burton, 2004; Blotto *et al.*, 2020; this study). The m. flexor minimus hallucis also originates from a ligament joining element Y to metatarsal I in *Sooglossus* (see Fig. 9C); this supplementary origin is absent in *Sechellophryne*.

ACSR and taxonomic distribution: Its presence optimizes as synapomorphies of *Heleophryne*, Sooglossidae, an internal clade of Microhylidae, and the hylid tribes Dendropsophini and Lophyohylini (but note that our taxon sampling is not adequate for these tribes). It is present in one of the two specimens of *Ascaphus truei*, while *Discoglossus galganoi* exhibits bilateral asymmetry (only present in the left foot). See also Burton (2004), and Supporting Information, Appendices S2 and S3 for complete taxonomic distribution.

Previous phylogenetic studies: Burton (2004: char. 29); Araujo-Vieira *et al* (2019: char. 176).

Character 40

M. adductor praehallucis: (0) absent; (1) present (Fig. 4D).

Definition: This muscle was first defined by Burton (2001) as an m. intermetatarsalis-like joining the prehallux to metatarsal I. It consists of a sheet of parallel fibres with fleshy origin from the prehallux (and also from the adjoining aponeurosis plantaris attaching to the prehallux) and a fleshy insertion on metatarsal I, which may reach distally the metatarsophalangeal joint (Burton, 2001; Blotto *et al.*, 2017, 2020).

ACSR and taxonomic distribution: Its presence optimizes as synapomorphies of Scaphiopodidae and Pelobatidae. The presence of this muscle is an autapomorphy of *Nasikabatrachus*. It is also present in some limnodynastids (see also Burton, 2001), although we could not corroborate its presence in our sample of *Adelotus brevis* (*contra* Burton, 2001).

Character 41

M. flexor accessorius proximalis, extension of origin: (0) distal, occupying at most the distal 1/3 of the fibulare (Figs 9B, C); (1) broad, occupying more than the distal 1/3 of the fibulare (Fig. 5B).

Definition: The m. flexor accessorius proximalis (or the proximal portion of the m. flexor accessorius if not differentiated into a proximal and distal muscle) usually has a fleshy origin from the fibulare, passes dorsad to the mm. flexores breves superficiales and inserts on the dorsal surface of the aponeurosis plantaris opposite to the prehallux; it may additionally insert on the distal end of the tibiale or connective tissue associated with the prehallux (Dunlap, 1960; Burton, 2001, 2004; this study).

ACSR and taxonomic distribution: The broad origin (state 1) optimizes as synapomorphies of Rhinophrynidae, Scaphiopodidae, Pelobatidae, Nasikabatrachidae and Brevicipitidae + Hemisotidae (note that our taxon sampling of Brevicipitidae is far from covering its diversity). It is also broad in the limnodynastids *Neobatrachus aquilonius* and *Notaden bennettii* (see also Burton, 2001, for the taxonomic distribution within Myobatrachoidea). The origin is distal in *Sooglossus*, while the condition in *Sechellophryne* is unknown; it is inapplicable in *Hymenochirus* (m. flexor accessorius absent).

Character 42

M. flexor accessorius distalis (or distal portion of m. flexor accessorius if undifferentiated), origin from the tendon of origin of one or more mm. lumbricales of digits IV and V: (0) absent (Fig. 9B); (1) present (Blotto *et al.*, 2017: fig. 3; Fig. 5B).

Definition: In some species, the m. flexor accessorius distalis (or the distal portion of the m. flexor accessorius if it is undifferentiated) originates from the medial surface of the plantar cartilage (also from the distal tarsals in some species) and inserts on the dorsal surface of the aponeurosis plantaris, laterally and distally to the m. flexor accessorius proximalis (Dunlap, 1960; Burton, 2004; Blotto *et al.*, 2020). In other species, the distal portion originates from a heavy tendinous portion of the aponeurosis plantaris at the base of metatarsal V and/or the distal end of the fibulare instead (Dunlap, 1960: 29; this study).

ACSR and taxonomic distribution: The origin from the tendon of origin of one or more mm. lumbricales of digits IV and/or V optimizes as synapomorphies of Scaphiopodidae, Pelobatidae and *Odontophrynus*. It also occurs in *Nasikabatrachus* and *Neobatrachus*. It is inapplicable in the xenoanurans *Rhinophrynus*, *Pipa* and *Xenopus*, because the distal portion is missing (i.e. no fibres of the m. flexor accessorius originate from the distal end of fibulare), and in *Hymenochirus*, due to the absence of the m. flexor accessorius.

Previous phylogenetic studies: Blotto *et al.* (2017: char. 8*).

Character 43

M. abductor digiti minimi, extension of insertion: (0) proximal, less than the proximal 1/2 of metatarsal V (Blotto *et al.*, 2020: pl. 5A; Fig. 10B); (1) broad, reaching at least the proximal 1/2 of metatarsal V (Figs 6D, 7).

Definition: The m. abductor digiti minimi has a fleshy origin from the dorsal surface of the fibulare, and inserts fleshy and/or via a short tendon on the dorsolateral surface of metatarsal V (Dunlap, 1960; Burton, 2001, 2004; Blotto *et al.*, 2020); the extension of the insertion on metatarsal V varies. Although this character could be better addressed as a continuous one, we define two discrete character states as a preliminary approach. Most species coded as state 0 have an insertion that does not exceed the proximal 40% of metatarsal V. The insertion is exceptionally broad in *Nasikabatrachus sahyadrensis* (reaching the 87% of the metatarsal), *Hemisus marmoratus* (78%) and some *Odontophrynus* (78–83%).

There are a few species with an insertion extended around the limit between both character states. The species with the insertions reaching between 48 and 52% of metatarsal V are: (1) *Spea hammondii* (Scaphiopodidae), *Phrynomantis bifasciatus* (Microhylidae) and *Proceratophrys avelinoi* (Odontophrynidae), with the insertion reaching 48% of metatarsal V (state 0); (2) *Spea bombifrons*, *Leptobrachium lumadorum* (Megophryidae), *Kaloula pulchra* (Microhylidae) and *Proceratophrys laticeps*, with the insertion reaching 50% of metatarsal V (state 1); and (3) *Microhyla heymonsi* (Microhylidae), *Crossodactylus schmidti* (Hylodidae) and *Leptodactylus latinasus* (Leptodactylidae), with the insertion reaching 52% of metatarsal V (state 1).

ACSR and taxonomic distribution: The broad insertion (state 1) optimizes as synapomorphies or autapomorphies of Rhinophrynidae, *Scaphiopus* (Scaphiopodidae), *Spea bombifrons* + *Spea intermontana* (but see above for the condition in *Spea hammondii*), *Leptobrachium lumadorum*, Nasikabatrachidae, Hemisotidae, the microhylid clades *Kaloula* + *Uperodon* and *Glyphoglossus* + *Microhyla*, *Tomopterna delalandii* (Pyxicephalidae), *Notaden bennettii* (Limnodynastidae), Ceratophryidae, *Crossodactylus schmidti*, *Leptodactylus latinasus* and *Physalaemus biligonigerus* (Leptodactylidae), *Odontophrynus*, and an internal clade of *Proceratophrys* (but see above for the condition in *P. avelinoi*).

Character 44

M. extensor brevis superficialis hallucis, supplementary slip from the tibiale: (0) absent; (1) present (Blotto *et al.*, 2017: fig. 4A).

Definition: Blotto *et al.* (2017: 435–436) described this supplementary slip from the tibiale in *Breviceps* (Brevicipitidae) and *Odontophrynus* (Odontophrynidae), and compared it with a similar supplementary extensor muscle originating from the tibiale in *Uperodon systoma* (Microhylidae; Blotto *et al.*, 2017: fig. 4D, labelled as 'X'). They described similarities and differences between *Uperodon systoma* and the condition observed in *Breviceps* and *Odontophrynus*, preventing them from identifying this muscle as part of the m. extensor brevis medius hallucis, m. extensor brevis superficialis hallucis, or as a novel muscle at that time. However, we tentatively consider the muscle observed in *Uperodon systoma* to be a primary homologue of the slip observed in *Breviceps* and *Odontophrynus*, based on the similarities noted by Blotto *et al.* (2017), and by its co-occurrence with a typical m. extensor brevis medius hallucis; consequently, the differences in development pointed out by Blotto *et al.* (2017) between these species should be transferred to a different transformation series.

ACSR and taxonomic distribution: Its presence is an autapomorphy of *Breviceps adspersus*, and optimizes as a synapomorphy of *Odontophrynus americanus* + *O. occidentalis* (note that, in comparison with Blotto *et al.*, 2017, *O. achalensis* and *O barrioi* are treated as junior synonyms of *O. occidentalis*). Differently, Blotto *et al.* (2017) obtained an ambiguous optimization within *Odontophrynus* because they employed the topology of Pyron (2014), which has topological differences within *Odontophrynus* in comparison with that of Jetz & Pyron (2018).

Previous phylogenetic studies: Blotto *et al.* (2017: char. 9).

Character 45

M. extensor brevis superficialis digiti II: (0) absent (Fig. 10A); (1) present (Blotto *et al.*, 2020: pls 5B, 12A; Fig. 6B).

Definition: The m. extensor brevis superficialis digiti II has a fleshy or tendinous origin from the fibulare. It inserts at one or more of the following points: fleshy or tendinous insertion on the dorsal surface of metatarsal II, tendinous insertion on the metatarsophalangeal joint, and/or tendinous insertion on the interphalangeal joint of digit II; the insertion on the metatarsophalangeal and interphalangeal joint may be via a common tendon with the m. extensor brevis medius or the mm. dorsometatarsales proximales of digit II (Dunlap, 1960; Burton, 2004; Blotto *et al.*, 2020; this study).

ACSR and taxonomic distribution: The absence is an autapomorphy of *Sooglossus thomasseti*; it is also absent in the rhacophorids *Polypedates leucomystax* and *Rhacophorus pardalis*.

Character 46

M. extensor brevis superficialis digiti III: (0) absent (Fig. 10A); (1) present (Blotto *et al.*, 2020: pls 5B, 12A; Fig. 6B).

Definition: See Blotto *et al.* (2020: char. 17).

ACSR and taxonomic distribution: Due to the plesiomorphic presence outside Sooglossoidea, the polymorphic presence in *Nasikabatrachus*, the unknown condition in *Sechellophryne* and the absence in *Sooglossus*, the optimization is ambiguous in that part of the tree. See also Blotto *et al.* (2020) for further details of its taxonomic distribution.

Previous phylogenetic studies: Blotto *et al.* (2020: char. 17).

Character 47

M. extensor brevis medius digiti IV: (0) absent (Blotto *et al.*, 2020: pl. 5C; Figs 6C, 10B); (1) present (Blotto *et al.*, 2020: pl. 12B).

Definition: See Blotto *et al.* (2020: char. 18).

ACSR and taxonomic distribution: No changes with respect to Blotto *et al.* (2020). This muscle is absent in Sooglossoidea (the condition in *Sechellophryne* is unknown).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 18).

Character 48

Medial m. dorsometatarsalis proximalis digiti II, slip from metatarsal II: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 14, labelled as 6).

Definition: This slip has a fleshy origin on the dorsomedial surface of metatarsal II, and converges into a common tendon of insertion with the slip from metatarsal I of the medial m. dorsometatarsalis proximalis digiti II (Blotto *et al.*, 2020: pl. 14; this study; see also Dunlap, 1960: 55–56).

ACSR and taxonomic distribution: Its presence optimizes as synapomorphies or autapomorphies of the megophryid Leptobrachiinae (with a reversion in *Scutiger*), *Arthroleptis variabilis* (Arthroleptidae), *Neobatrachus aquilonius* (Limnodynastidae), *Crinia signifera* (Myobatrachidae) and *Stefania evansi* (Hemiphractidae); it is also a putative synapomorphy of Sooglossidae or *Sooglossus* (depending on the unknown condition in *Sechellophryne*). This slip is also present in *Ascaphus truei* (Ascaphidae), *Leiopelma hochstetteri* (Leiopelmatidae), *Barbourula busuangensis* and *Bombina orientalis* (Bombinatoridae), *Hymenochirus boettgeri* and *Xenopus* cf. *victorianus* (Pipidae). Its presence is polymorphic in *Alytes obstetricans* (Alytidae) and *Alsodes neuquensis* (Alsodidae).

Character 49

Medial m. dorsometatarsalis proximalis digiti III, slip from metatarsal III: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 14, labelled as 9).

Definition: This slip is similar to the one described in the previous character. It has a fleshy origin on the dorsomedial surface of metatarsal III, and converges into a common tendon of insertion with the slip from metatarsal II of the medial m. dorsometatarsalis proximalis digiti III (Dunlap, 1960: 56; Blotto *et al.*, 2020: pl. 14; this study).

ACSR and taxonomic distribution: The taxonomic distribution of the character states has some similarities with Character 48. Its presence optimizes as synapomorphies or autapomorphies of *Xenophrys aceras*, the megophryid Leptobrachiinae (with a reversion in *Scutiger*), Arthroleptidae (although our taxon sampling is inappropriate for this family), *Neobatrachus aquilonius* (Limnodynastidae), *Crinia signifera* (Myobatrachidae) and *Ceratophrys cranwelli* (Ceratophryidae); it is also a putative synapomorphy of Sooglossidae or *Sooglossus* (depending on the unknown condition in *Sechellophryne*). This slip is also present in *Ascaphus truei* (Ascaphidae), *Leiopelma hochstetteri* (Leiopelmatidae) and Bombinatoridae. Its presence is polymorphic in *Alytes obstetricans* (Alytidae). The basal ambiguity is due to the combination of the polymorphic condition of *Alytes*, the presence in Ascaphidae + Leiopelmatidae and Bombinatoridae, and the unknown condition in Caudata.

Character 50

M. abductor brevis dorsalis hallucis, type of origin: (0) fleshy (Blotto *et al.*, 2020: pls 5D, 12C); (1) tendinous (Blotto *et al.*, 2020: pl. 14; Fig. 6D).

Definition: The m. abductor brevis dorsalis hallucis has a fleshy or tendinous origin from the prehallux and/or element Y and a fleshy insertion on the dorsomedial surface of metatarsal I (Dunlap, 1960; Burton, 2004; Blotto *et al.*, 2020). Within our sample, the m. abductor brevis dorsalis hallucis is absent in *Leiopelma hochstetteri* (Leiopelmatidae), *Rhinophrynus dorsalis* (Rhinophrynidae), *Pseudophryne coriacea* (Myobatrachidae) and *Pseudopaludicola falcipes* (Leptodactylidae).

ACSR and taxonomic distribution: The tendinous origin optimizes as synapomorphies or autapomorphies of Scaphiopodidae, Ceratophryidae, Nasikabatrachidae, *Uperodon systoma* (Microhylidae) and *Neobatrachus aquilonius* (Limnodynastidae).

The condition within Pelobatidae requires further studies. While *Pelobates varaldii* has a conspicuous tendon of origin, *Pelobates cultripes* has an origin that is partly fleshy and partly via a short tendon (it was tentatively coded as tendinous); data for *Pelobates fuscus* are missing.

Character 51

M. abductor brevis dorsalis digiti II: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 14; Figs 6D, 7).

Definition: See Blotto *et al.* (2020: char. 19).

ACSR and taxonomic distribution: There are no changes with respect to Blotto *et al.* (2020), except for Sooglossoidea. With the addition of *Nasikabatrachus* to the sampling, the presence of the m. abductor brevis dorsalis digiti II optimizes as a synapomorphy of Sooglossoidea, and not Sooglossidae. However, considering the unknown condition in *Sechellophryne*, if it is found to be absent in this genus, the optimization will result in ambiguity in this portion of the tree (it would be equally parsimonious as a gain in Sooglossoidea and a loss in *Sechellophryne*, or two independent gains in *Nasikabatrachus* and *Sooglossus*).

Previous phylogenetic studies: Blotto *et al.* (2020: char. 19).

Character 52

M. abductor brevis dorsalis digiti III: (0) absent; (1) present (Blotto *et al.*, 2020: pl. 14; Figs 6D, 7).

Definition: See Blotto *et al.* (2020: char. 20).

ACSR and taxonomic distribution: There are no changes with respect to Blotto *et al.* (2020), except for Sooglossoidea. With the addition of *Nasikabatrachus* to the sampling, the presence of the m. abductor brevis dorsalis digiti III optimizes as a synapomorphy of Sooglossoidea, and not Sooglossidae. However, considering the unknown condition in *Sechellophryne*, if it is found to be absent in this genus, the optimization will result in ambiguity in this portion of the tree (it would be equally parsimonious as a gain in Sooglossoidea and a loss in *Sechellophryne*, or two independent gains in *Nasikabatrachus* and *Sooglossus*).

Previous phylogenetic studies: Blotto *et al.* (2020: character 20).

APPENDIX 2

RE-IDENTIFICATION OF SOME PALMAR MUSCLES OF DIGIT V FROM BLOTTO *ET AL.* (2020)

Muscle equivalences between Blotto et al. (2020) and this study

The m. abductor secundus digiti V of Blotto *et al.* (2020) corresponds entirely to our m. abductor digiti minimi. The m. abductor digiti minimi of Blotto *et al.* (2020) is a combination of our lateral m. lumbricalis brevis digiti V (the portion with origin from the flexor plate and fleshy insertion on metacarpal V) and our m. flexor brevis profundus digiti V (the portion from the distal carpals). The m. flexor brevis profundus digiti V of Blotto *et al.* (2020) is a combination of our homonym muscle and our m. opponens digiti V. Below we re-identify some of the muscles from the plates of Blotto *et al.* (2020) following the new criteria.

Blotto et al. (2020: pl. 2D)

The fused m. abductor digiti minimi and m. abductor secundus digiti V corresponds to our m. flexor brevis profundus digiti V (portion originating from distal carpal 3-4-5, labelled as 9–10) and our m. abductor digiti minimi (portion from the ulnare, labelled as 8), respectively. Our m. opponens digiti V is absent in *Triprion petasatus*.

Blotto et al. (2020: pl. 6B, D)

Although it is not shaded, the lateral m. lumbricalis brevis digiti V is present in *Spea intermontana* (pl. 6B) and *Tomopterna delalandii* (pl. 6D), laterally to the tendo superficialis digit V and m. lumbricalis longus digiti V. The origin is from the laterodistal portion of the flexor plate, and its morphology is similar to the lateral m. lumbricalis brevis digiti V depicted in Figure 12.

Blotto et al. (2020: pl. 9A–B, D)

The unidentified muscles labelled as 22 in *Ascaphus truei* (pl. 9A) and 20 in *Bombina orientalis* (pl. 9B) correspond to our lateral m. lumbricalis brevis digiti V. The muscles labelled as 7 and 8 in *Scaphiopus hurterii* (pl. 9D), considered the m. flexor brevis profundus digiti V, and a fused muscle composed of the m. abductor digiti minimi plus the m. abductor secundus digiti V, respectively, require further comparative studies (their identities remain unclear).

Blotto et al. (2020: pl. 10)

The muscle labelled as 2* in *Scutiger mammatus* (pl. 10A) corresponds to our lateral m. lumbricalis brevis digiti V, while the muscles labelled as 12–14 require further comparative studies (their identities remain unclear). The muscle labelled as 7 in *Eleutherodactylus coqui* (pl. 10B) as a fused m. abductor digiti minimi and m. abductor secundus digiti V corresponds to our m. flexor brevis profundus digiti V (portion originating from distal carpal 3-4-5) and m. abductor digiti minimi (portion from ulnare).