EVOLUTION OF VOCAL SACS IN ANURA

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ABSTRACT

Of the many features that make frogs and toads unique, vocal sacs are among the most remarkable. Vocal sacs are inflatable, elastic chambers present in adult males of most anurans and are key elements in their social interactions. Traditionally vocal sacs have been associated primarily with acoustic communication, but their functions are currently being reinterpreted, and there is increasing evidence that they play a wider role in anuran biology. We surveyed the anatomical and histological structure of vocal sacs in all major clades of frogs by examining 777 specimens representing 605 species. Herein we characterize the morphological diversity of the three elements that compose the vocal sac: the gular skin, the superficial submandibular musculature, and the internal mucosa. We describe major anatomical patterns and define characters that we optimize on a comprehensive phylogenetic hypothesis of Anura. Integrating this anatomical information with images and videos of vocalizing frogs, we produce an updated morphological classification that includes 20 patterns of vocal sac morphology, each of which can be diagnosed by internal and external structures. Applying this classification to 4358 species, we discuss major evolutionary trends, taking ontogeny, homology, and multimodal communication into consideration. A single, spherical vocal sac is the most widely distributed vocal sac shape (present in 63% of known species), but some degree of lateralization (bilobate or paired sacs) has evolved in almost all anuran families. Some groups, such as Hylidae and Ranidae, are particularly diverse and contain more than 10 different vocal sac morphologies. Vocal sacs are absent in 18% of anurans and have been lost between 146 and 196 times, an astounding number considering their biological importance. Lastly, we review the morphological diversity and taxonomic relevance of vocal sac structures for each of the 58 families of recent anurans.

INTRODUCTION

The monophyly of Anura (with around 7700 described species) is well supported by many morphological, molecular, and behavioral synapomorphies (Duellman and Trueb, 1986; Haas, 2003; Frost et al., 2006, Frost, 2024). However, despite being the subject of extensive observation and experimentation in all biological disciplines, many character systems of anurans still remain scarcely explored. Of all the characters that make frogs and toads unique, vocal sacs are among the most remarkable. They are sexually dimorphic structures present in males of most species and play a key role in their social interactions.

Structure of Anuran Vocal Sacs

The term "vocal sac" refers to the association of three elements: the gular skin, a thin layer of superficial muscles, and an internal mucosa, derived from the buccal floor (fig. 1; Noble, 1931; Tyler, 1971a). During postmetamorphic ontogeny, the buccal floor projects ventrally into submandibular muscles to form a pair of diverticula that open into the buccal cavity via an orifice on each side of the tongue. The shapes of these orifices, the vocal slits, vary greatly among species (Liu, 1935; Tyler, 1971a). In most species, the paired mucosae fuse in the midline to form a single cavity in adults, but in others, they remain separate (Inger, 1956, 1958; McAlister, 1959; Tyler, 1975; Elias-Costa and Faivovich, 2019). The muscle layer, composed of the mm. intermandibularis and interhyoideus, is present in males and females of all species and lifts the buccal floor during ventilation, prey capture, and ingestion (De Jongh and Gans, 1969; Gans, 1973; Nishikawa, 2000). However, in adult males with vocal sacs, this layer performs an additional function; it supports and deflates the vocal sac by active contraction of the muscle fibers and by a passive, elastic recoil (Tyler, 1971a; Jaramillo et al., 1997; Targino et al., 2019). Of the three elements composing the vocal sac, the muscle layer has been studied the most, both in anatomical

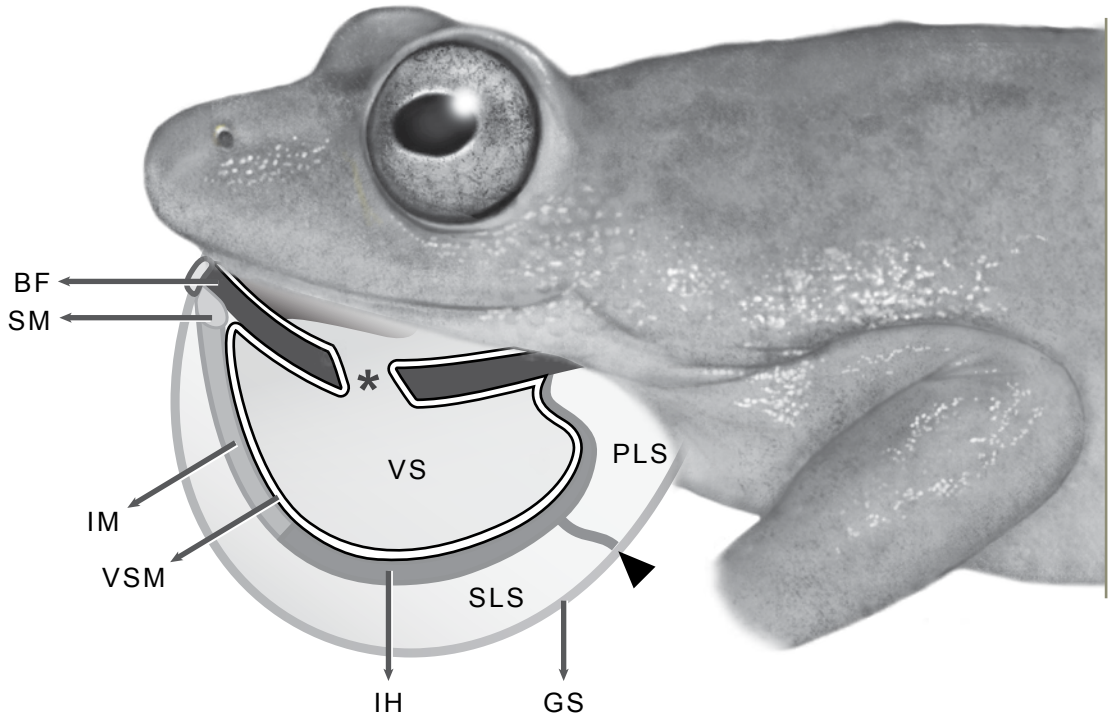


Fig. 1. Schematic representation of the vocal sac general structure in a parasagittal section, modified from Targino et al. (2019). The internal vocal sac mucosa (VSM) is an extension of the buccal floor (BF) that projects ventrally during post-metamorphosis. The buccal and vocal sac cavities connect with one another via paired slits at the side of the tongue (*). The mucosa is externally enveloped by a thin layer of muscle fibers, the m. submentalis (SM), the m. intermandibularis (IM), and the m. interhyoideus (IH). Externally, these muscles are separated from the gular skin (GS) by the submandibular and pectoral lymphatic sacs (SLS and PLS, respectively), which are in turn separated by the post-mandibular lymphatic septum (black triangle), which connects the gular skin and the m. interhyoideus.

descriptions and as characters in phylogenetic studies (see review by Elias-Costa et al., 2021). In contrast, the diversity of gular skin and internal mucosa has been explored much less (Liu, 1935, 1936; Inger, 1956; Liem, 1970; Tyler, 1971a, 1971b; Drewes, 1984; Elias-Costa et al., 2017; Moura et al., 2021). Some studies have addressed sexually dimorphic structures, mainly the dermal glands in the gular skin of several groups, but in most cases, the effect of these modifications on vocal sac shape and function is unknown (Noble, 1931; Le Quang Trong, 1976; Schiøtz, 1963, 1999; Stewart, 1967; Amiet, 2007; Brunetti et al., 2015a; Starnberger et al., 2013, 2014).

Functional Considerations

In most anurans, sound is produced when air is forced through the larynx, the phonation organ located between the lungs and the oral cavity (Martin and Gans, 1972; Gans, 1973; Dudley and Rand, 1991). Most anuran species vocalize by expiration, but a few do so by inspiration, and others, by a combination of both mechanisms (Schneider, 1988; Wells, 2007). Alternatively, some pipids call without airflow by clicking their highly modified larynges (Rabb, 1960; Rabb and Rabb, 1963; Yager, 1992a, 1992b). Airflow is generated by the alternate action of the m. transversus and submandibular muscles, with the

mouth and nares closed (Inger, 1956). Vocal sacs are "secondary" vocalization organs because they do not produce the sound but rather affect its emission. Moreover, a vocal sac is not necessary for sound production, as demonstrated by males and females of several species that call despite lacking them. Several hypotheses have been proposed to understand vocal sac function:

Vocal sacs were originally thought to act as resonance chambers that amplify the call (Gaupp, 1899); however, this hypothesis was rejected by experiments in a helium-oxygen atmosphere (Rand and Dudley, 1993). These authors showed that, by replacing the medium in which the sound is transmitted, the frequency of the vocalization does not vary, which would be expected if resonance occurred in the vocal tract of the anurans and as it does in other groups such as primates (Fitch and Hauser, 2002). However, in *Engystomops pustulosus* (Leptodactylidae), the dominant frequency was reported to drop when the vocal sac reaches its maximum inflated volume. The reason is that the internal pressure of the buccal and vocal sac cavities hinders the airflow through the larynx, producing a slight frequency modulation (Dudley and Rand, 1991). Moreover, in certain conditions, this effect might be advantageous for competing males, because a lower dominant frequency could be interpreted as a proxy for larger body size. Thus, frogs that vocalize while floating can reach larger vocal sac volumes, thereby convey a dishonest signal by "sounding larger" than their conspecifics vocalizing from the ground (Goutte et al., 2020).

Alternatively, it was proposed that vocal sacs could facilitate sound transmission between the animal's internal medium and the environment by reducing what is known as "impedance mismatch." Impedance is the measure of acoustic conductivity and it differs in air and in the phonation organ. During vocalization in air, the efficiency of sound transmission is low and much of that sound is reflected back to the source (Watkins et al., 1970). Analogous to a loudspeaker, the presence of a large vibrating, elastic structure could couple the two media and increase the efficiency of the transmittance of low frequencies to the environment (Fitch and Hauser, 2002). Consistent with this hypothesis, it was observed that the vocal sac radiates a large proportion of the acoustic output that becomes detuned and weakened when the mouth is open (Gridi-Papp, 2008). On the other hand, the presence of a vocal sac also shapes the output of the frequencies produced by the larynx because the soft tissues of the vocal tract (including the vocal sac) filter part of the frequencies produced by the larynx (Gridi-Papp, 2014).

A third scenario involves the conservation of strain energy. Male frogs of many species vocalize for several hours a day during the reproductive season, and they do so at much higher volumes than other animals (Wells, 2007). The production of these signals represents the most energetically expensive metabolic activity in anurans (Prestwich, 1994), which means that there are energetic limitations to vocalization that can act as selective pressures and shape morphological variation. The trunk and laryngeal muscles of male anurans are better developed than are those of females, and males have more aerobic muscle fibers, more mitochondria, vascularization, and energy reserve substrates (Eichelberg and Schneider, 1974; Ressel, 2001). Also, in many species, the extraordinary elasticity of the vocal sacs is evident to the naked eye, as the sacs receive enormous volumes of air and recover their original shape at high speed. However, the functional importance of this elasticity was introduced by Ryan (1985), who suggested that the vocal sac could store the strain energy of the air column during vocalization and recycle it for inflation of the lungs. In the absence of a diaphragm or rib cage, the lungs of anurans are filled by the "buccal pump," a mechanism by which air is actively pumped from the oral cavity by depression and compression of the floor of the mouth (Gans, 1973). In this context, if males vocalized with an open mouth, air would easily dissipate into the atmosphere, forcing repeat

lung filling, which is costly both in time and energy (Bucher et al., 1982; Prestwich, 1994). Storing the air in the elastic vocal sac chamber greatly reduces the energy costs of vocalization, because the fluid column and mechanical energy are readily recycled (Dudley and Rand, 1991). Thus, males with vocal sacs would be able to produce vocal sounds at higher repetition rates and to sustain calling for longer periods than species without vocal sacs. A higher call rate has a positive impact on male reproductive success because, as shown in *Engystomops pustulosus* (Leptodactylidae), females tend to prefer males that call more often (Welch et al., 1998; Bosch et al., 2000; Pauly et al., 2006). Subsequently, the hypothesis that vocal sac stores strain energy was supported by the documentation of a substantial layer of elastic fibers in each of the structures associated with vocalization (lungs, trunk muscles, and vocal sac; Jaramillo et al., 1997; Targino et al., 2019).

Recently, new evidence has broadened our perspective on the function of vocal sacs beyond their role in acoustic communication. The visual cues provided by the pulsatile inflation of the sacs, as well as the sexually dimorphic pigmentation and reflectance of the gular skin, play an important role in intra- and intersexual interactions (Narins et al., 2003; Cummings et al., 2008; Gómez et al., 2009; Sztatecsny et al., 2010; Preininger et al., 2013; Starnberger et al., 2013, 2014). In some cases, acoustic stimuli alone are insufficient to evoke a positive response from females, which occurs only when acoustic signals are coupled with the inflation of the vocal sac (Lüddecke, 1999; Rosenthal et al., 2004; Taylor et al., 2008). Moreover, unilateral inflation of paired vocal sacs seems to play a role in communication in some species (de Sá, 2016, 2018; Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019). Additionally, Starnberger et al. (2013, 2014) suggested that vocal sacs might contribute to the volatilization of pheromones produced in the gular glands of some hyperoliids, thereby highlighting the importance of vocal sacs in multimodal communication.

Previous Attempts to Study Vocal Sac Diversity

Vocal sacs in frogs and toads are morphologically diverse, varying in size, color, and degree of lateralization, and ranging from small subgular spheres to paired, posterodorsally projecting lobes. Moreover, vocal sacs are absent in many species, including a series of early-diverging clades (where they are plesiomorphically absent), but also secondarily absent in several species deeply nested in all major anuran clades (Boulenger, 1882; Liu, 1935).

There have been attempts to understand vocal sac diversity since the beginning of modern herpetology (Rösel von Rosenhof, 1758; Günther, 1859; Boulenger, 1882). Traditionally, four categories have been defined: single subgular, bilobate, paired subgular, and paired lateral (fig. 2; Noble, 1931; Liu, 1935; Duellman, 1970; Tyler, 1971a). Moreover, all of them can be "internal" or "external," depending on the absence or presence of conspicuous skin modifications that are evident in noncalling males (a terminology criticized by some authors because all vocal sacs are internal chambers; Liu, 1935). In general, this classification is appropriate for most of the 7700 known species of anurans. However, it does not account for a great deal of known variation in vocal sacs and has neither been reformulated nor expanded since its creation. Working with Günther's (1859) four-model vocal sac classification, Liu (1935) explored the diversity of anuran vocal sacs in many species across all major anuran clades. Although he described several forms of skin modification and the ways in which these could affect vocal sac shape, Liu did not include this information in his classification (e.g., different types of lateral lobes and projections were condensed under the term "external vocal sac"). Our knowledge of vocal sac structure and diversity was greatly expanded by the work of Michael J. Tyler (1937–2020), who dedicated several papers to the matter, mainly focusing on the submandibular musculature, a component rarely considered by his predecessors (Tyler, 1971a,

1972, 1974a, 1974b, 1975, 1980, 1985; Trueb and Tyler, 1974; Tyler and Duellman, 1995). Tyler (1971a) noted that the distinction between "internal" and "external" was insufficient to capture the diversity of skin modifications in the vocal sac, and described some cases, but without providing detailed structural descriptions, photographs, or histological sections. Thus, the classification of Günther (1859) was never updated, even though the vocal sacs in anurans greatly exceed the four aforementioned categories (fig. 3).

Aims of the Present Study

Our survey of vocal sac morphology in Anura will include the following: (1) The fine structure of the vocal sacs (including external and internal components) is described in all major groups. (2) The terminology describing vocal sac shape is updated and standarized for all anuran clades. (In the taxonomic literature of distantly related taxa, different authors use similar terms to refer to different structures, and vice versa, which complicates the recognition of general patterns.) (3) Hypotheses of homology are defined. (4) Phylogenetic characters are optimized in a comprehensive phylogenetic hypothesis of Anura to infer major evolutionary patterns, identifying the origin of the vocal sac in anurans and all its major transformations. (5) Major synapomorphies are identified and the relevance of vocal sac structure in the taxonomy of all anuran families is discussed.

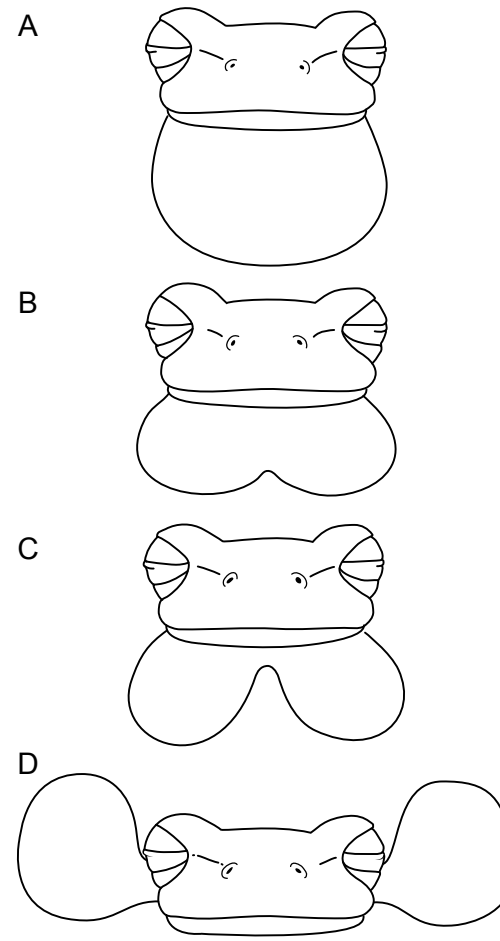


Fig. 2. The traditional classification of vocal sacs: **A,** single, median, subgular. **B,** bilobate, subgular. **C,** Paired subgular. **D,** Paired lateral. These four vocal sac patterns were introduced in the 19th century and have changed little since, despite the extensive variation that they bracket. Taken from Duellman (1970).

MATERIALS AND METHODS

Taxonomic Sampling

To study the diversity and evolution of vocal sacs in Anura, we sampled all major clades as densely as possible. We studied the internal anatomy of 777 specimens of 605 species, belonging to all anuran families except Nasikabatrachidae, for which no available material was examined. (See appendix 1 for a list of specimens studied.) We reviewed the literature and scored vocal sac internal (when available) and external morphology for another 3753 species across all anuran families (all 4358 species are listed in the online supplement file S1, available online: https://doi.org/10.5531/sd.sp.73). For as many species as possible, we supplemented published information with photographs and videos of vocalizing males available online, to assess the shape of the fully inflated vocal sac. Our sampling focused on taxa in which extensive diversity in vocal sacs had been reported (e.g., Dicroglossidae, Hylidae, Leptodactylidae, Mantellidae,


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and Ranidae; Liu, 1935; Dubois, 1992; Glaw and Vences, 2007; Elias-Costa and Faivovich, 2019; Moura et al., 2021). For anuran taxonomy we followed Frost (2024). Institutional collection abbreviations follow Sabaj (2022).

Anatomical and Histological Procedures

Internal anatomy was studied by dissections under a binocular stereomicroscope. Muscle fibers were stained by topical application of lugol, an iodine/potassium iodide solution to enhance contrast (Bock and Shear, 1972). The most ventral layer of submandibular muscles, composed of the mm. intermandibularis and interhyoideus, was deflected to expose ventrally the vocal sac internal cavity. The terminology of submandibular muscles and lymphatic septa is that of Kesteven (1944) and Tyler (1971a, 1971b).

Samples of gular skin of selected species were studied histologically. Specimens were fixed in 10% formalin and stored in 70% ethanol. Samples were dehydrated in ascending concentrations of ethanol, cleared in toluene, and embedded in Paraplast. All samples were sectioned at 5 μm and stained with Masson's Trichrome (Humason, 1972; Bancroft and Gamble, 2008).

Data Analysis

We described the observed diversity in each of the three elements that make up the vocal sac: the gular skin, the submandibular musculature, and the internal mucosa. Skin modifications were characterized from dissections and, when material was available, histological sections. Sexually dimorphic modifications, such as keratinizations, epidermal projections, or spines, found in the gular region of several species are excluded because they are not directly related to the vocal sacs. (For a review of these structures, see Luna et al., 2018.) For the submandibular musculature, we described only the variation not discussed by Elias-Costa et al. (2021). Characters related to the vocal sac mucosae were scored as inapplicable in species lacking a vocal sac. The treatment of inapplicable characters in phylogenetic analyses is still an unsolved issue and many authors have suggested that treating inapplicable data as missing ("?") is the least problematic approach (Maddison, 1993; Strong and Lipscomb, 1999; de Laet, 2005; Brazeau et al., 2019). Therefore, this coding strategy was preferred, and character optimization was performed as implemented in the TNT v.1.6 software (Goloboff et al., 2008).

Integrating the anatomical information with videos and images of fully inflated vocal sacs from academic and non-academic sources, we defined 20 patterns of external morphology of vocal sacs. Each one corresponds to a specific shape of the fully inflated vocal sac and is derived from a specific combination of character states. Subsequently, we scored these 20 vocal sac patterns in 4364 species across all anuran families, including all species for which the vocal sac anatomy was directly studied

Fig. 3. Diversity of vocal sacs in Anura. The traditional patterns encompass an extensive diversity in size, shape, and position: single subgular (A–D), bilobate (E–H), paired subgular (I–L) and paired lateral (M–P). Additionally, some shapes do not strictly correspond to any of these patterns (Q–T). **A,** *Boana pulchella* (Hylidae); **B,** *Atelopus flavescens* (Bufonidae, Q. Martinez); **C,** *Pseudis bolbodactyla* (Hylidae, R. Gaiga); **D,** *Anaxyrus speciosus* (Bufonidae, C. Harrison); **E,** *Hylarana nicobariensis* (Ranidae, W. Djatmiko); **F,** *Nidirana adenopleura* (Ranidae, Y. Chongwei); **G,** *Leptodactylus fuscus* (Leptodactylidae, D. Baldo); **H,** *Crossodactylus schmidti* (Hylodidae, V. Caldart); **I,** *Pseudis minuta* (Hylidae, W. Prado); **J,** *Ptychadena longirostris* (Ptychadenidae, D. Bree); **K,** *Hoplobatrachus tigerinus* (Dicroglossidae, Danielnasika1); **L,** *Itapotihyla langsdorffii* (Hylidae, W. Pertel); **M,** *Boreorana sylvatica* (Ranidae, D. Huth); **N,** *Pelophylax* sp. (Ranidae, R. Schmidt); **O,** *Trachycephalus typhonius* (Hylidae, M. Dewynter); **P,** *Hyperolius pusillus* (Hyperoliidae, M. and P. Fogden); **Q,** *Physalaemus biligonigerus* (Leptodactylidae); **R,** *Ceratophrys cornuta* (Ceratophryidae, Q. Martinez); **S,** *Nyctibatrachus grandis* (Nyctibatrachidae, A. Mandrekar); **T,** *Glyphoglossus molossus* (Microhylidae, W.K. Fletcher and D. Baylis).

(listed in appendix 1), as well as species scored from the literature and/or the above-mentioned videos or images. Species for which the shape of the fully inflated vocal sac was not specified in the literature or could not be inferred with a high degree of confidence, were excluded.

Homology hypotheses were scored in a matrix using Mesquite v3.03 (Maddison and Maddison, 2015, https://www.mesquiteproject.org/) as binary or multistate characters. Ancestral character states were reconstructed with parsimony as the optimality criterion using TNT v1.6 (Goloboff et al., 2008; Goloboff and Morales, 2023) on the topology of Anura obtained by Portik et al. (2023) using Fitch's (1971) and Farris' (1970, for additive characters) optimizations. .

To assess morphological disparity among major clades of Anura, we calculated mean pairwise distances (MPD) with the package *Claddis* in R v4.0.2 (Lloyd, 2016; R Core Team, 2020. https://www.r-project.org/). This value indicates the probability of two given terminals having different character states (i.e., it ranges between 0, all terminals equal, and 1, all terminals different).

RESULTS

Homology Hypotheses

We defined 17 characters that describe the vocal sac internal cavity (chars. 0–4), submandibular musculature (chars. 5–9), and skin associated with the vocal sac (chars. 10–17). Characters are nonadditive unless indicated otherwise. Even though ancestral character state reconstruction is a subsequent step in the analysis, we mention some relevant results (e.g., the recognition of major synapomorphies) in the context of each character to make the article easier to follow.

Character 0. Number of vocal slits in adult males: (0) none (vocal sac absent); (1) one (asymmetrical cavity); (2) two. Additive. State 0 renders several of the characters that follow inapplicable.

Vocal sacs are absent in several basal anuran families, as well as in many species nested in all major clades of the group (state 0). Asymmetrical vocal sac cavities, derived from the unilateral protrusion of the buccal floor (state 1; fig. 4A), were first described by Inger and Greenberg (1956) in *Sclerophrys regularis* (Bufonidae) and are present in many species, most of them bufonids. The side that develops to form the vocal sac varies intraspecifically and among males in the same population, as noted by several authors (Liu, 1935; Inger, 1966; Mendelson et al., 2005, Pramuk, 2006; Pereyra et al., 2021). Variation in the number of slits is widespread in Bufonidae; in some species, vocal slits are double, single, or absent (Cannatella, 1981; Osorno-Muñoz et al., 2001). We recovered the presence of a single vocal slit as a synapomorphy of an unnamed clade comprising most species of the family. Outside Bufonidae, asymmetrical vocal sac cavities had been reported in only a few scattered species. They are present in some (but not all) specimens of the dendrobatids *Andinobates bombetes*, *Phyllobates terribilis* (Myers, 1982), *Ameerega trivitta*, and *Ranitomeya fantastica* (this study). In a second specimen of *A. trivittata* examined, there are two vocal slits, suggesting that polymorphism in this character is more widespread in the family than currently recognized. Additionally, unilateral vocal slits are present in the holotype of *Arenophryne rotunda* (Myobatrachidae; Tyler, 1976) and *Craugastor arciano* (Craugastoridae, McCranie and Wilson, 2002). In contrast, in most anurans that have a vocal sac a pair of vocal slits flank either side of the tongue (state 2).

Character 1. Vocal sac internal mucosae: (0) disconnected in adult males; (1) fused in adult males. Only applicable if character 0 = 1 or 2.

Although contralateral mucosae are fused in adults of most anuran species with vocal sacs, they remain disconnected in many species. This condition was first described in *Ptychadena porosissima* (Ptychadenidae; Inger, 1956), *Spea* (Scaphiopodidae; McAlister, 1959), and some

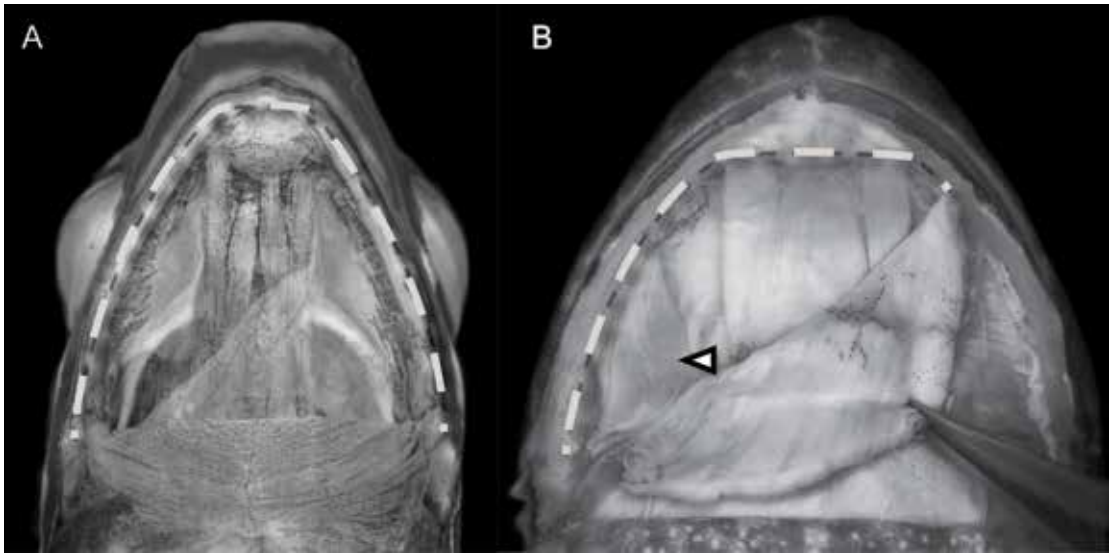


Fig. 4. Atypical conditions of the vocal sac mucosae. Ventral views of heads with gular skin and submandibular muscles deflected (dashed lines). **A,** Asymmetrical vocal sac in *Ameerega trivittata* (Dendrobatidae, ZMH 02796), in which only the left mucosa developed and occupied the entire gular region. This pattern is common in Bufonidae and is also found in a few species outside this family. **B,** Poorly developed, paired mucosae in *Pelodytes caucasicus* (Pelodytidae, ZFMK 72202). This pattern, likely represents the simplest vocal sac structure, with the buccal floor only slightly projecting toward submandibular muscles (white triangle).

hylids (Tyler, 1971a), and has been studied in a phylogenetic context for some groups (Hylodidae, Elias-Costa et al., 2017; Victoranura, Elias-Costa and Faivovich, 2019; Microhylidae, Targino et al., 2019; Lophyohylini, Hylidae, Moura et al., 2021).

We recovered ambiguous reconstructions for this character in some large clades of Anura. The first is Pelobatoidea, in which the mucosae are fused in *Scaphiopus* (Scaphiopodidae) and Megophryidae but disconnected in *Spea* (Scaphiopodidae) and Pelodytidae (and absent in Pelobatidae). This generates an ambiguity in all suprafamiliar nodes of the clade as well as in the base of Acosmanura (i.e., Pelobatoidea + its sister taxon, Neobatrachia, in which the mucosae are fused plesiomorphically). Another large ambiguity occurs in Natatanura. Disconnection of mucosae is plesiomorphic in Ptychadenidae, Odontobatrachidae, Ceratobatrachidae + Nyctibatrachidae, two clades of Dicroglossidae (*Nannophrys* + *Hoplobatrachus* + *Euphlyctis*, and all *Limnonectes* with vocal sacs), Ranidae, and some species of Rhacophoridae. In contrast, the mucosae are plesiomorphically fused in Allodapanura, Mantellidae, Pyxicephalidae, as well as several Dicroglossidae, Phrynobatrachidae, and Rhacophoridae. Several reconstructions are equally parsimonious, including disconnection of mucosae as a synapomorphy of Natatanura. Although the sampling of some families could be increased (e.g., Micrixalidae, Ranixalidae, Mantellidae, Rhacophoridae, and Pyxicephalidae) such that one might find one optimal reconstruction for Natatanura, it is evident that this character is highly homoplastic in this clade. A third large ambiguity occurs in Neoaustrarana, derived from the plesiomorphic disconnection of mucosae in Alsodidae, Hylodidae and Cycloramphidae, together with the fusion in Batrachylidae. Futhermore, disconnection of mucosae was recovered as a synapomorphy of *Mantidactylus* + *Gephyromantis*, *Ranoidea*

(Hylidae, although poorly sampled), an internal clade of *Pseudis* (Hylidae), and Lophyohylini under some reconstructions (Hylidae, but see Moura et al., 2021).

Character 2. Medial extension of paired mucosae: (0) large; (1) moderate; (2) reduced. Additive. Applicable only if character 1 = 0.

This character was defined and illustrated by Moura et al. (2021) and scored for Lophyohylini hylids. Aside from the disconnection of mucosae, the shape and degree of development of each lateral projection influence the morphology of the inflated vocal sac (see Moura et al., 2021: fig. 2). In some species disconnected mucosae are greatly developed medially and exhaled air can access a large portion of the gular region during vocalization. In extreme cases, contralateral mucosae might contact each other thereby resembling, functionally, a single-cavity vocal sac. On the other hand, in many species, mucosae are restricted to the lateral portion. These cases are typically associated with well-defined paired vocal sacs, where the gular region is not affected by the inflation of the sacs (which occurs only laterally). In most species that we observed, the condition is intermediate between these two patterns. Thus, disconnection of paired mucosae can occur in species with single subgular, bilobate, or lateral paired vocal sacs, all of which differ in the medial development of the contralateral elements.

Character 3. Relationship between the vocal sac internal mucosa and the m. interhyoideus: (0) mucosa completely enveloped; (1) mucosae covered only by scattered fibers of the m. interhyoideus; (2) mucosa projecting freely to the lymph sacs. Additive. Applicable only if character 0 = 1 or 2.

This character was defined by Elias-Costa et al. (2017) and modified by Elias-Costa and Faivovich (2019). In most species, the internal mucosae of the vocal sac are covered externally by mm. intermandibularis and interhyoideus, which form a single continuous layer (state 0; fig. 5A–K). However, in other species, the muscle layer is either extremely thin (reduced to scattered muscle fibers, state 1) or discontinuous (state 2; fig. 5L), exposing the vocal sac mucosae to the submandibular lymphatic sac. These patterns occur in species with both disconnected or fused vocal sac mucosae. When fused, the ventral protrusion of the mucosae can occur at different locations, as follow: posterior to the m. interhyoideus (recovered as a synapomorphy of Megophryidae; also present in *Sechellophryne gardineri*, Sooglossidae); between two muscle bellies of the m. interhyoideus (*Cophixalus tridactylus*, Microhylidae; Targino et al., 2019: fig. 3B); or between the mm. intermandibularis and interhyoideus (*Scaphiophryne calcarata*, Microhylidae).

Character 4. Vocal slits, shape: (0) small orifice; (1) elongate slit; (2) gaping hole. Additive. Applicable only if character 0 = 1 or 2.

States were described by Tyler (1971a), expanding the results of Liu (1935). Drewes (1984) assessed the nature of vocal slits in several Ranoides (although not using these character states) and described sphincteric apertures in some species; a survey subsequently expanded by some authors (Channing, 1989; Scott, 2005; Moura et al., 2021). Notably, when present, small, circular vocal slits always are located in a posterolateral position inside the mouth. In contrast, the other states involve an extension of the slit toward the mandibular symphysis.

Character 5. Shape of the subgular portion of the m. interhyoideus in adult males: (0) thin, transverse band of parallel fibers; (1) homogeneous anteroposterior expansion of the complete subgular portion; (2) ovoid expansion; (3) bilobate expansion; (4) discrete paired lobes. Additive.

This character is modified from Elias-Costa et al. (2021). This U-shaped muscle originates on each side of the head near the otic capsules and inserts on a median raphe or aponeurosis in the center of the gular region. The subgular and lateral portions of the muscle evolve independently, and thus are treated as different characters (Elias-Costa et al., 2021).

In species in which the vocal sac is absent or poorly developed, the m. interhyoideus forms a band of parallel fibers (state 0; fig. 5A). This state is plesiomorphic for Anura and is also present in juveniles, adult females of all species, and adult males of species that lack vocal sacs.

In many species, the submandibular muscles (particularly the m. interhyoideus) are remarkably hypertrophied, and this is always associated with a large development of the vocal sac (state 1; fig. 5B; Tyler, 1971a; Drewes, 1984; Faivovich, 2002). This pattern is very common and can be found in species from most families.

In a few species, the expansion of the m. interhyoideus is not uniform; the muscle is more developed laterally than medially and forms an ovoid body when the vocal sac is inflated (state 2; fig. 5C). This character state is associated with single subgular vocal sacs that are not spherical. The ratio between lateral and medial development is highly variable among species, resulting in a wide array of morphologies that range from a slighly ovoid subgular sac (e.g., *Dendropsophus marmoratus*, *Scinax crospedospilus*) to a large, kidney-shaped sac (e.g., *Physalaemus biligonigerus*, *Pleurodema thaul*). The character state is present in species of Allophrynidae, Ceratophryidae, Hylidae, Leptodactylidae, Limnodynastidae, Microhylidae, and Pyxicephalidae.

In an alternate arrangement, the lateral development of the m. interhyoideus greatly exceeds that of the median portion, resulting in a median notch, or less expanded area (state 3; fig. 5D). This state, which usually produces a bilobate vocal sac when inflated, was observed (although with variable degree of lobe independence) in species of Alsodidae, Aromobatidae, Arthroleptidae, Bombinatoridae, Ceratobatrachidae, Ceratophryidae, Cycloramphidae, Dicroglossidae, Hylidae, Leptodactylidae, Mantellidae, Pelodytidae, Petropedetidae, Ranidae, and Scaphiopodidae.

Hypertrophy of the subgular portion of the m. interhyoideus can be more localized, such that two discrete ventrolateral lobes are formed; the lobes are relatively independent of each other and separated by an unexpanded median portion (state 4; fig. 5E–I). In all cases, fibers originate near the otic capsule and radiate ventrally forming a single slip of parallel fibers, and then expand at the sides of the throat. The external correlate of this character state is paired vocal sacs, which greatly vary in shape depending on the orientation of these lobes (see next character).

Character 6. Orientation of paired subgular lobes of the m. interhyoideus: (0) ventrolateral; (1) posterior; (2) laterodorsal; (3) posterodorsal. Additive. Applicable only if character 6 = 4.

Lobes derived from the subgular portion of the m. interhyoideus can vary in orientation and in some cases, be tubular and relatively long, resulting in diverse vocal sac patterns. These arrangements are enabled by specific combinations of connective tissue, lymphatic septa, and the gular skin that affect the orientation of the muscle lobes and support their position during inflation.

In most species, the lobes are short and oriented ventrolaterally (state 0; fig. 5E), a condition present in Odontobatrachidae, Ptychadenidae, *Nannophrys* + *Hoplobatrachus* + *Euphlyctis* (Dicroglossidae), *Gephyromantis* (Mantellidae), some *Pseudis* (Hylidae), and *Hydrophylax* and some *Amerana*, *Amolops*, *Hylarana*, and *Odorrana* (Ranidae).

In other taxa, the lobes project posteriorly and vary in length (state 1; fig. 5F). They are short, lying next to the mandibular joints, as in some *Limnonectes* (Dicroglossidae), *Aquarana*, *Lithobates*, and *Rana* (especially common in *Aquarana*; Ranidae) or project farther posteriorly above the arms (fig. 5G), as in *Glyphoglossus molossus* (Microhylidae), *Boreorana*, and some *Lithobates* (e.g., *L. pipiens* group; Ranidae). Based on the shape of the inflated vocal sac, long posterior lobes are probably present in *Nyctibatrachus kempholeyensis* (Gururaja et al., 2014: fig. 10a; Nyctibatrachidae) and the species of the *Physalaemus olfersii* group (Cassini et al., 2010: fig. 19b; Leptodactylidae), neither of which were examined.

In *Leptodactylodon* (Arthroleptidae), *Pelophylax*, and a few *Lithobates* (*L. areolatus*, *L. berland-*

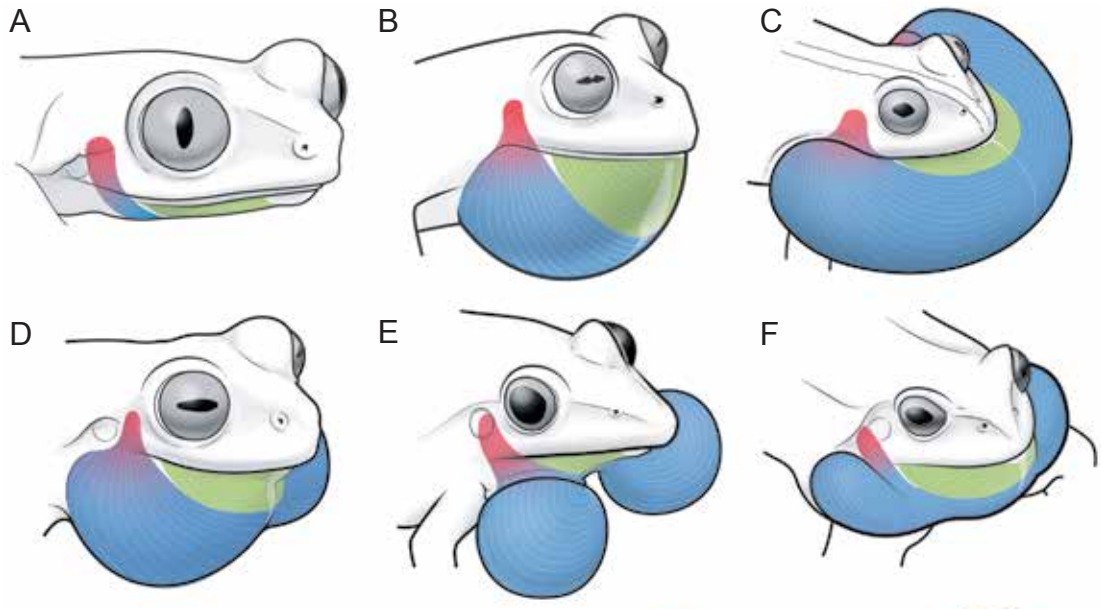


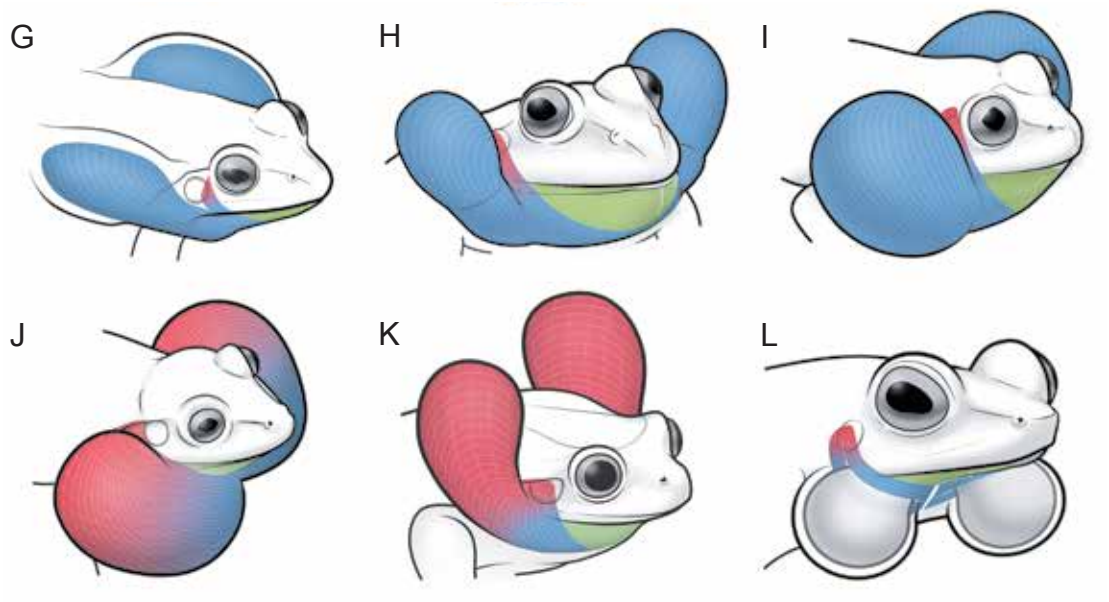
Fig. 5. (*above and opposite page*) Diversity of sexually dimorphic modifications of the mm. interhyoideus (IH; blue, subgular portion; and red, dorsolateral portion) and intermandibularis (IM, green), and their relationship to vocal sac shape. **A,** In species that lack a vocal sac (as well as in juveniles and females of all anurans), the IH is a thin band of parallel fibers that originate laterally, in the distal portions of the hyoid cornua near the otic capsules. Fibers then radiate ventromedially to meet with a median connective tissue (raphe or aponeurosis) in the center of the gular region; thus, this bilateral muscle is U-shaped (*Phasmahyla guttata*, Hylidae). **B,** In species with a single subgular vocal sac, both the IH and the IM are hypertrophied and uniformly expanded (*Vitreorana parvula*, Centrolenidae). **C,** In some species, the median and lateral portions of the single vocal sac are well developed forming a kidney shape around the head (semicircular vocal sac, *Pleurodema thaul*, Leptodactylidae). **D,** If a median notch is present in the midline, two lateral lobes are defined and the vocal sac is bilobate (*Hyloscirtus palmeri*, Hylidae). **E,** The IH forms two highly localized, independent lobes, so that the center of gular region hardly distends during vocalization and the vocal sac is paired subgular (*Ptychadena nilotica*, Ptychadenidae). **F,** These paired subgular lobes can be short and project posterodorsaly

ieri, *L. kauffeldi*, and *L. sphenocephalus*; Ranidae), the subgular lobes curve dorsolaterally at the sides of the mandibular joint (state 2). In *Leptodactylodon*, the muscular lobes are flat and tightly packed with connective tissue, and the surrounding skin is unmodified. In contrast, in the ranids, complex skin pouches surround the well-developed, tubular lobes of the m. interhyoideus that inflate dorsally at the sides of the head during vocalization (fig. 5H).

In *Nyctibatrachus* (Nyctibatrachidae), the ventrolateral lobes of the m. interhyoideus extend posterodorsally across the temporal region. These projections insert in the dorsal fascia, lateral to the m. depressor mandibulae, behind the tympanum (state 3; fig. 5I).

Character 7. Shape of the portion of the m. interhyoideus near the origin of fibers in the posttympanic region: (0) not expanded, i.e., thin band of medially oriented fibers; (1) expansion present, but restricted to the posttympanic region; (2) expanded and projected posteriorly. Additive. Applicable only to adult males.

This character was defined by Elias-Costa et al. (2021: char. 18). In most anurans, the m. interhyoideus originates from the hyoid near the otic capsule and radiates ventrally forming a



lateral to the mandibular joints (*Rana temporaria*, Ranidae). **G,** In other species, they can be extremely well developed and project posteriorly, extending the vocal sac above the arms producing paried posterolateral vocal sacs (*Lithobates pipiens*, Ranidae). Similar lobes of the IH can be found in some species with extremely developed single subgular vocal sacs (e.g., *Glyphoglossus molossus*, Microhylidae, not shown). **H,** The subgular lobes can be directed dorsally at the sides of the head by a specific configuration of the gular skin, resulting in paired dorsal vocal sacs (e.g., *Pelophylax ridibundus*, Ranidae). **I,** In a few species, the subgular lobes of the IH project dorsally and attach to the dorsal fascia (*Nyctibatrachus humayuni*, Nyctibatrachidae). **J,** The IH can also expend in its lateral portion, near the origin of fibers, producing a different pattern of paired lateral vocal sacs (e.g., *Nyctimantis siemersi*, Hylidae). **K,** In a few species, this lateral portion is hypertrophied and projects dorsally above the head (e.g., *Trachycephalus typhonius*, Hylidae). **L,** In some species, the internal mucosa is not completely covered by the IH, but rather projects through a gap in its fibers, resulting in structurally unique vocal sac morphology (*Hylodes phyllodes*, Hylodidae).

single slip of parallel fibers, with little or no posterior development (state 0; fig. 5A–I).

However, in some taxa, paired vocal sacs derive from the expansion of the dorsal portion of the m. interhyoideus (state 1; fig. 5J). Regardless of the configuration of the subgular portion of the muscle (see char. 6), this expansion increases the area available for the vocal sac in the postmandibular region. The anterior fibers of the muscle radiate ventrally, but the most posterior ones are directed posteriorly. This character state evolved in Rhinophrynidae, *Boophis albilabris* (Mantellidae; most likely representing a synapomorphy of its species group), and several times in Lophyohylini (Hylidae), being present in *Itapotihyla*, many species of *Osteocephalus* and *Osteopilus*, *Nyctimantis siemersi*, *Tepuihyla*, and some *Trachycephalus* (but see Moura et al., 2021).

Moreover, in some species of *Trachycephalus* (Lophyohylini, Hylidae), the dorsal portion of the m. interhyoideus is remarkably hypertrophied and projects posteriorly, often inserting on the dorsal fascia (state 2; fig. 5K). This pattern allows for the dorsalization of the vocal sac above the head, producing a unique pattern that is recognized as a synapomorphy of the genus.

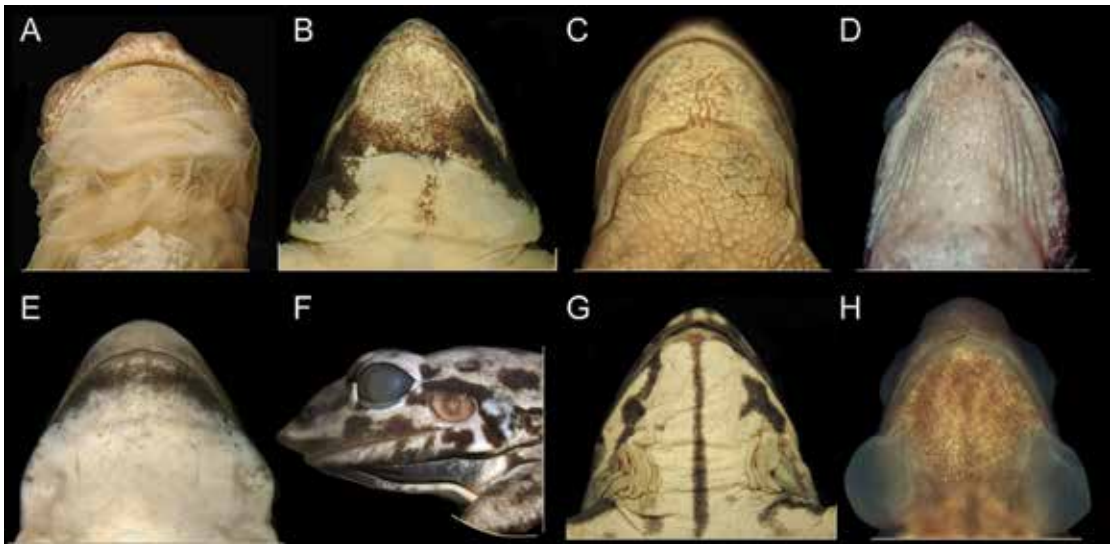


Fig. 6. (*above and opposite page*) Diversity of sexually dimorphic modifications in the gular skin of anurans. **A,** *Dendropsophus leali* (Hylidae, USNM 201989) showing uniform expansion of the vocal sac, in which the entire gular skin is thin and distensible. **B,** *Fejervarya vittigera* (Dicroglossidae, USNM 513084) with a bilobate vocal sac, in which the skin gradually differentiates forming two large distensible areas. **C,** *Boana pulchella* (Hylidae, MACN 40485) showing extensive myo-integumentary contact with the m. interhyoideus. **D,** *Phrynobatrachus calcaratus* (Phrynobatrachidae, ZFMK 77151) showing a series of small longitudinal folds. **E–F,** *Leptodactylus bufonius* (Leptodactylidae, MACN 52862) showing a deep, longitudinal fold of elastic and pigmented skin that runs parallel to the mandible. **G,** *Hoplobatrachus rugulosus* (Dicroglossidae, USNM 520480) showing well-defined, paired patches of elastic skin. **H,** *Hylodes phyllodes* (Hylodidae, MACN 17252) showing the same pattern but with distended lobes. **I,** *Lithobates virgatipes* (Ranidae, USNM 541251) showing lateral elastic areas posterior to the head. **J,** *Lithobates kauffeldi* (Ranidae) showing a lateral view of the same pattern.

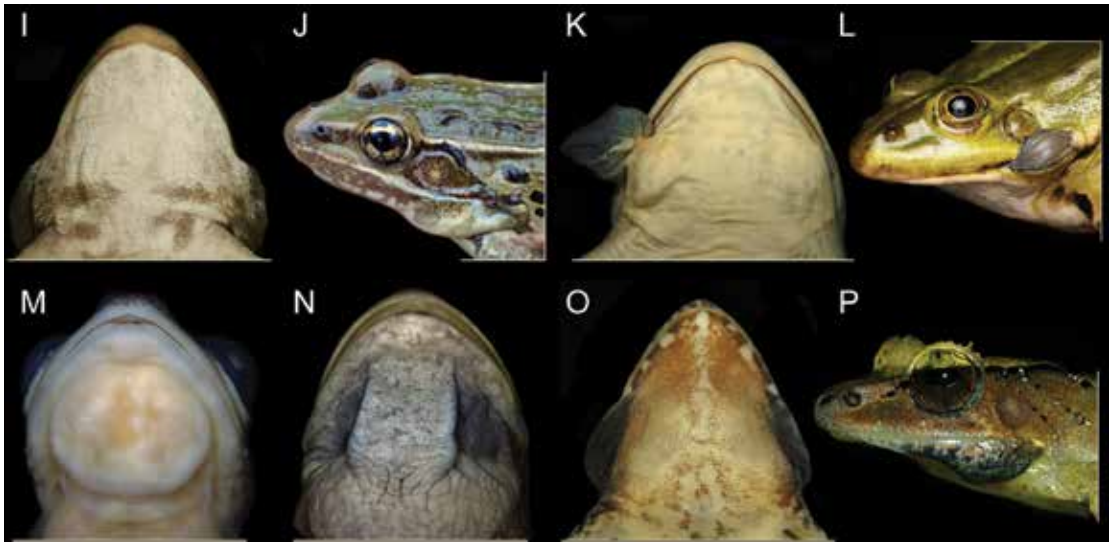
Character 8. Hypertrophy of the elastic component of the m. interhyoideus in adult males: (0) absent (1) present.

We follow the definition of Elias-Costa et al. (2021: char. 23; discussion provided therein). State 1 was observed in several species of Bufonidae, Ceratophryidae, Dicroglossidae, Eleutherodactylidae, Hylidae, Hyperoliidae, Leptodactylidae, Limnodynastidae, Microhylidae, Myobatrachidae, Odontophryinidae, Pyxicephalidae, and Ranidae.

Character 9. Distribution of highly elastic areas in the IH: (0) uniform, (1) only in the posterior portion of the muscle, (2) only in a transverse band, (3) only in paired lateral lobes. Only applicable if character 8 = 1.

We follow the definition of Elias-Costa et al. (2021: char. 24; see discussion provided therein). Homogenously distributed elastic fibers (state 0) were observed in species of Dicroglossidae, Eleutherodactylidae, Hylidae, Hyperoliidae, Leptodactylidae, Limnodynastidae, Microhylidae, Myobatrachidae, Odontophryinidae, Pyxicephalidae, and Ranidae.

In some species, however, only the posterior portion of the m. interhyoideus is elastic (state 1). This character state is found in several Bufonidae, often with the muscle deeply pigmented (present at least in members of *Adenomus*, *Anaxyrus*, *Ansonia*, *Bufotes*, *Duttaphrynus*, *Epidalea*, *Incilius*, *Ingerophrynus*, *Peltophryne*, *Phrynoidis*, *Rentapia*, *Rhaebo*, *Rhinella*, *Schismaderma*, *Sclerophrys*, *Strauchbufo*, *Vandijkophrynus)*, in which it evolved between one and four times, and in a few Microhylidae (see Targino et al., 2019).



K, *Euphlyctis ehrenbergii* (Dicroglossidae, USNM 249112) showing gular pouches (right pouch, extended; left pouch, folded), a complex pattern involving an eversible lobe folded inside a pocket of more rigid skin. **L,** *Pelophylax* sp. (Ranidae) showing a lateral view of the same pattern, although in *Pelophylax*, the openings of the gular pouches are oriented vertically, producing dorsal projection of the vocal sacs. **M,** *Heterixalus madagascariensis* (Hyperoliidae, ZFMK 62890) with a disclike macrogland that defines a posterior flap of thin, pleated skin. **N,** *Kassina senegalensis* (Hyperoliidae, ZFMK 70815) showing a central band of poorly differentiated skin flanked by two highly elastic, pigmented patches, and a large elastic portion posteriorly. **O,** *Gephyromantis boulengeri* (Mantellidae, FMNH 261388) showing pigmented patches on the paired vocal sacs. **P,** *Gephyromantis luteus* showing a lateral view of the same pattern. Photo credits: **J,** B.R. Curry, taken from Feinberg et al. (2014); **L,** R. Schmidt; **P,** G.M. Rosa.

In *Ceratophrys cornuta* (and likely its sister species, *C. calcarata*) the m. interhyoideus has three parts. The anterior and posterior portions are thick and muscular, approximately as thick as the m. intermandibularis. However, the central portion is extremely thin and elastic, forming a band across the gular region (state 2).

In species with paired vocal sacs, elastic fibers are concentrated around paired areas of the m. interhyoideus, whereas the portion between them remains muscular (state 3). This character state occurs in *Euphlyctis* + *Hoplobatrachus* (Dicroglossidae); *Trachycephalus* (Hylidae); *Leptodactylus bufonius* and *L. fuscus* (Leptodactylidae); *Glyphoglossus molossus* (Microhylidae), *Boreorana*, *Pelophylax*, and several members of *Amerana*, *Aquarana*, *Lithobates*, and *Rana* (Ranidae).

Character 10. Vocal sac skin modification: (0) absent (i.e., "internal" vocal sac); (1) present (i.e., "external" vocal sac). In many species, the skin of the vocal sac is not visibly expanded, leading to what is referred to as "internal" vocal sacs (state 0). However, several species in most anuran families show some degree of skin modification (state 1; Liu, 1935; Duellman, 1970; Liem, 1970; Tyler, 1974a; Drewes, 1984; Elias-Costa et al., 2017; Moura et al., 2021). Usually, this character state, typically related to large vocal sacs, is evident externally as loose, highly pleated skin in both living and fixed specimens (fig. 6A). Histologically, this modification includes an important reduction in thickness and glandular content, and an increased abundance of elastic fibers in the stratum compactum of the dermis, in contrast to the pectoral skin (fig. 7).

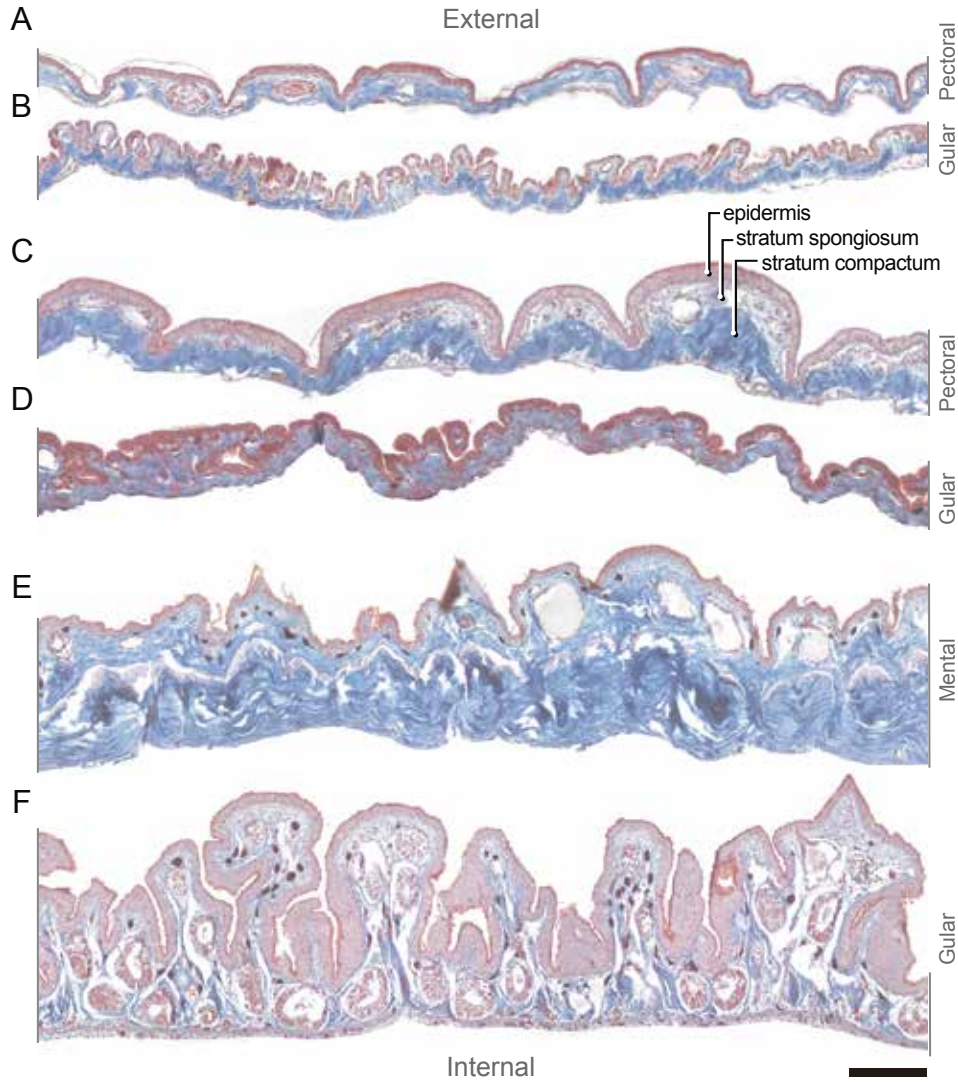


Fig. 7. Generalized gular skin modification (external vocal sac). Cross sections of gular skin (vocal sac) stained with Masson´s trichrome, compared with samples of pectoral/mental regions for reference (i.e., unmodified skin). **A, B,** *Dendropsophus nanus* (Hylidae, MACN 43436). The pectoral skin contains large dermal papillae (*verrucae hydrophilicae*) giving a granulate aspect. The stratum compactum of the dermis (dark blue) is abundant and continuous, while the stratum spongiosum (light blue), rich in capillaries and mucous and serous glands, is more fragmented. In contrast, the skin overlying the vocal sac is considerably more elastic, as indicated by the folded outline of the epidermis and collagen fibers in the dermis. In this region, the density of dermal glands is strongly reduced. **C, D,** *Scinax granulatus* (Hylidae, MACN 41197). In this case, the thickness of the gular skin is relatively thinner, a common feature in anurans with vocal sacs. **E, F,** *Rhinella dorbignyi* (Bufonidae, MACN 52494). The mental skin (E) presents a very thick dermis with little irrigation and glandular content. The epidermis contains a large number of cell layers and has a significant keratinized layer. In contrast, the gular skin (F) is much more pleated, suggesting greater elasticity. The dense layer of the dermis is almost completely reduced, while the glandular content and pigmentation are notably increased. The most internal layer of the dermis is rich in elastic fibers. Scale bar: 100 μm.

Some species have modifications of the skin such as folds or pouches (described in chars. 12–15). The presence of any of them therefore implies that character 10 = 1. If a species has skin modification but lacks any of those structures, then the skin modification corresponds to thecharacter state described above.

Character 11. Distribution of skin modification: (0) uniformly present and widespread in the gular region; (1) present in the whole gular region and concentrated around two lateral areas; (2) present in two independent, lateral patches; (3) lateral patches in the body extending from the gular region. Additive. Inapplicable if character 10 = 0.

In most species with single, external vocal sacs, the skin modification is uniformly distributed in the center of the gular region (state 0), although the anteroposterior extent varies highly among species (e.g., restricted to the throat or extending anteriorly to the mental region). This character state is present in many species of several families.

In other species, skin modification is concentrated in two ventrolateral patches, separated by a less-modified portion (state 1; fig. 6B, D, F). This character state is found in some members of Aromobatidae, Arthroleptidae, Brachycephalidae, Calyptocephalellidae, Ceratophryidae, Dendrobatidae, Dicroglossidae, Eleutherodactylidae, Hylidae, Hyperoliidae, Leptodactylidae, Mantellidae, Myobatrachidae, Pyxicephalidae, and Ranidae. In most of these species, the patches of modified skin are gradually differentiated, lacking a discrete boundary. That is, its edges blend into the surrounding skin. In a few species, however, the skin forms specific folds, treated in characters 12 and 13.

If the skin between the differentiated patches is unmodified, the distensible portions of the skin are independent of one another (state 2; fig. 6G, H, K). Paired modifications that increase the size and definition of each lobe usually are present in species with paired subgular vocal sacs. They are present in all *Euphlyctis* + *Hoplobatrachus* (Dicroglossidae), *Hylodes*, *Phantasmarana* (Hylodidae), Odontobatrachidae, Ptychadenidae, *Huia*, *Meristogenys*, *Pelophylax* (Ranidae), as well as some species of *Cornufer* (Ceratobatrachidae), *Eleutherodactylus* (Eleutherodactylidae), *Gephyromantis* (Mantellidae), *Amnirana*, *Amolops*, *Hylarana* (species assigned to the subgenera *Humerana* and *Hydrophylax*), *Odorrana*, *Staurois* (Ranidae), *Kurixalus*, and *Rhacophorus vampirus* (Rhacophoridae).

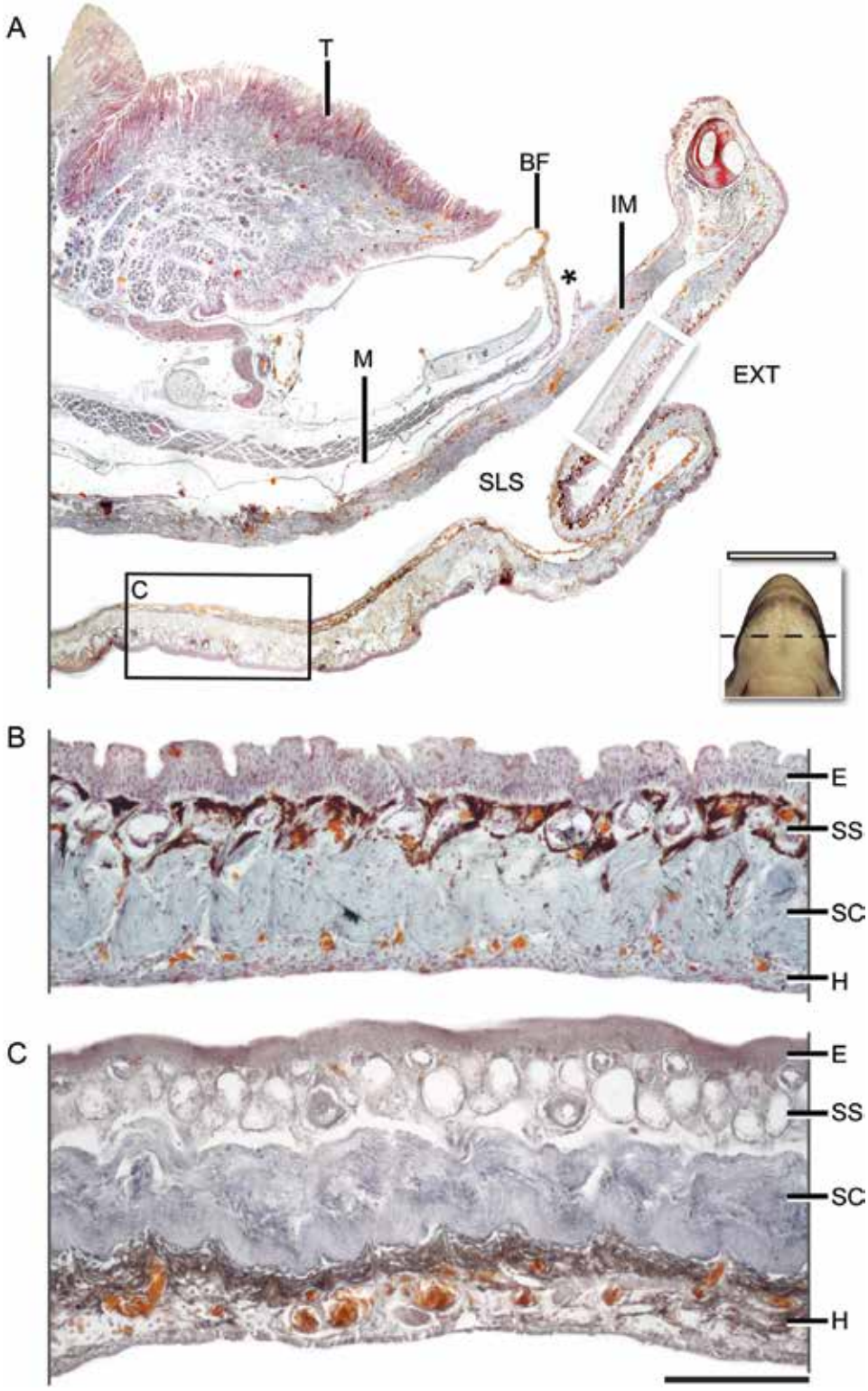
Typically, in species with lateral and dorsolateral vocal sacs (state 3; fig. 6I, J), the elastic skin patches are located in the posttympanic region. Externally, these portions are evidenced by a high degree of folding and, in some cases, dark pigmentation. This character state was observed in some species of *Dryaderces*, *Itapotihyla*, *Nyctimantis*, *Osteocephalus*, *Osteopilus*, *Trachycephalus* (Hylidae, see Moura et al., 2021: fig. 5), *Boophis* (Mantellidae), *Nyctibatrachus* (Nyctibatrachidae), *Aquarana*, *Boreorana*, and *Lithobates* (Ranidae).

Chracter 12. Two groups of small longitudinal folds: (0) absent; (1) present.

This character state consists of two lateral groups of small, shallow folds that parallel the mandible (fig. 6D). These pleated portions are separated by a median area of unfolded skin. It occurs in some species of *Phrynobatrachus* (Phrynobatrachidae; Schiøtz, 1967; Stewart, 1967; see the account for this family below for a discussion on the taxonomic distribution) and some *Limnonectes* (Dicroglossidae, e.g., Köhler et al., 2021). Presence of state 1 implies that character 10 = 1 and character 11 = 1 or 2.

Chracter 13. Two large, lateral longitudinal folds: (0) absent; (1) present.

Character state 1 is characterized by two large folds that parallel the mandible, across the entire gular region, and often extending posteriorly to the base of the arms (figs. 6E, F). This character state occurs both in species with single or bilobate vocal sacs. In the former, the inflated vocal sac is spherical, indicating that these folds (which are clearly evident in the relaxed skin) do not affect vocal sac shape (but possibly, its size). Character state 1 was recovered as a synapomorphy of *Anstisia* (Myobatrachidae), and it is present in some


A
T
BF
IM
*
M
EXT
SLS
C
B
E
SS
SC
H
C
E
SS
SC
H

species of *Ischnocnema* (Brachycephalidae), *Colostethus inguinalis* (Dendrobatidae), some *Noblella* (Strabomantidae), and possibly *Nothophryne ribauensis* (Pyxicephalidae). Additionally, it evolved between between 9 and 15 times in Eleutherodactylidae. (The folds are present in several members of *Adelophryne*, *Diasporus*, and *Eleutherodactylus*; see distribution in the account for the family below). Alternately, the folds can be larger and the skin thinner than the median gular skin, producing bilobate vocal sacs when inflated. This was obtained as synapormorphies of the *Hyloscirtus bogotensis* group (Hylidae) and the genus *Adenomera* (Leptodactylidae). It was observed in several *Leptodactylus* (Leptodactylidae; although the elasticity of the folded skin is variable among species, affecting the shape of the inflated vocal sac, e.g., minimum in *L. luctator*, intermediate in *L. latinasus*, and greater in *L. bufonius* and *L. fuscus*), and some *Amietia* (Pyxicephalidae). Figure 8 shows a transverse section of the gular region of *L. bufonius*, comparing the two portions of the skin. Presence of state 1 implies that character 10 = 1 and character 11 = 1 or 2.

Character 14. Gular flap: (0) absent, (1) present.

In the hyperoliid genera *Alexteroon*, *Afrixalus*, *Arlequinus*, *Callixalus*, *Chrysobatrachus*, *Congolius*, *Cryptothylax*, *Heterixalus*, *Hyperolius Morerella*, *Opisthothylax*, and *Tachycnemis*, adult males have a disc-shaped gular macrogland (Drewes, 1984; Schiøtz, 1999, Rödel et al., 2009; Starnberger et al., 2013, 2014; Nečas et al., 2021). In most species, this dermal gland generates a transverse flap posteriorly in which the skin is much thinner and highly folded (state 1; fig. 6M; recovered as a synapomorphy of Hyperoliidae). This large extension of loose skin allows for the inflation of voluminous, spherical vocal sacs. The macrogland also forms a gular flap in the species that lack a vocal sac (*Arlequinus krebsi*, *Callixalus pictus*, and *Hyperolius koehleri*). In members of *Hylambates* and *Kassina* (fig. 6N), a macrogland is absent, but the gular skin is full of scattered dermal acini (the straplike band observed externally corresponds to muscle fibers; Elias-Costa et al., 2021). A slightly similar pattern, with a transverse or U-shaped fold in the gular region, can be observed externally in several Eleutherodactylidae and Phrynobatrachidae (Stewart, 1967; Diaz and Hedges, 2015; Pickersgill et al., 2017); see the Discussion for a more detailed comment on the taxonomic distribution in both families. However, unlike hyperoliids, the gular flap in these two clades does not derive from the presence of a large, rigid macrogland. Information on gular skin histology is not available for species with this morphology, so the specific arrangement of skin tissue that generates this pattern is unknown. Presence of state 1 implies that character 10 = 1 and character 11 = 0.

Character 15. Paired gular pouches: (0) absent; (1) present.

Some species have a more complex type of skin modification, the gular pouch, which combines the histological modifications described above with a complex and highly specific tridimensional folding (fig. 9). The skin forms a thin, elastic, usually pigmented lobe that folds over itself and is

Fig. 8. Two large, lateral longitudinal folds. Gular skin modification in male *Leptodactylus bufonius* (Leptodactylidae, MACN 38169). **A,** Cross section of the mandible at the level of the vocal slits (*, asterisk) stained with Masson's trichrome. **B, C,** Details of the lateral skin fold, and ventral (undifferentiated) skin for reference. The skin in B has a high concentration of melanophores in the stratum spongiosum of the dermis. The epidermis and the stratum compactum of the dermis are highly folded, evident from the irregular outline of their surface and the undulating course of the collagen fibers (light blue). The glandular content is low. The hypodermis, rich in elastic fibers, is well developed. The gular skin in C resembles the skin of the rest of the body, with abundant mucous and serous glands in the dermis and an epidermis without abundant folding. Abbreviations: **BF,** buccal floor; **E,** epidermis; **H,** hypodermis; **IM,** m. intermandibularis; **M,** vocal sac mucosa; **SC,** stratum compactum of the dermis; **SLS,** submandibular lymphatic sac; **SS,** stratum spongiosum of the dermis; **T,** tongue. White scale bar: 500 μm; black scale bar: 200 μm.

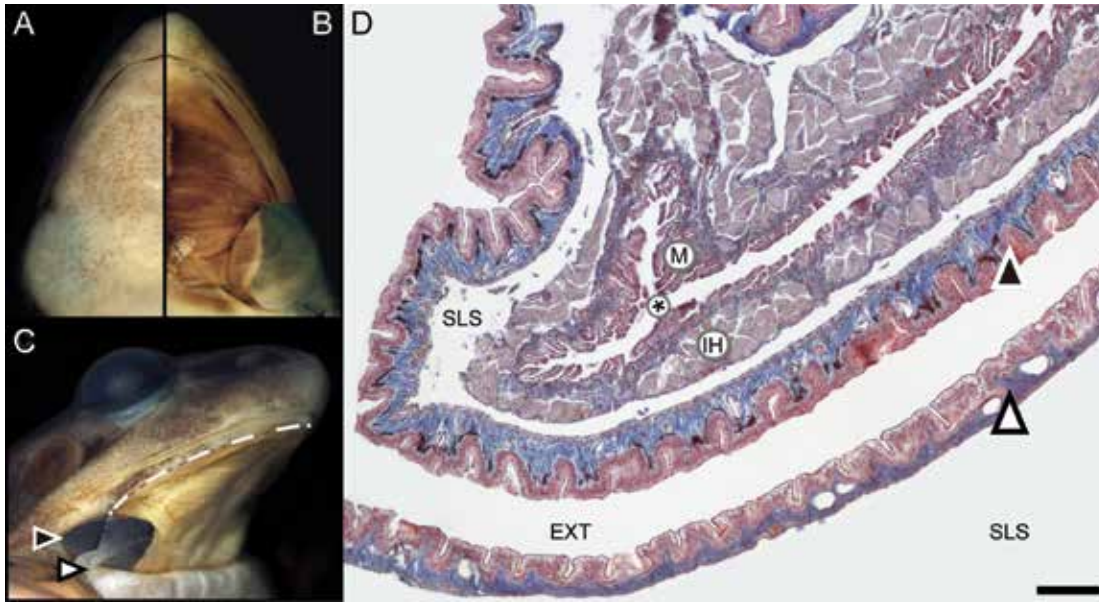


Fig. 9. Gular pouches. *Ptychadena* cf. *nilotica* (Ptychadenidae, MACN 39150). **A,** ventral view of the gular region. **B,** same view with gular skin removed and muscles stained with lugol for contrast. The m. interhyoideus forms paired ventrolateral lobes that are in close contact with the elastic portions of the skin. **C,** Lateral view showing how the ventrolateral skin folds on itself and forms an elastic eversible lobe that is contained within a pouch below the jaw articulation. The skin that covers the pocket (black triangle) is thick and rigid, with very low glandular content. The eversible lobe of skin (white triangle) is markedly more elastic, as indicated by the undulated outline of the epidermis and dermal papillae. With a few exceptions, the eversible lobe is darkly pigmented. **D,** Transverse section of the vocal sac stained with Masson's trichrome. The internal mucosa is hypertrophied and markedly folded, and the muscle fiber bundles are embedded in an extracellular matrix rich in elastic fibers. Abbrevations: * (asterisk), cavity of the vocal sac; **EXT,** exterior; **IH,** m. interhyoideus; **M,** vocal sac mucosa; **SLS,** submandibular lymphatic space. Scale bar: 100 μm.

covered by a portion of rigid, unmodified, and unpigmented skin (Inger, 1956). The histological differentiation is highly localized and restricted to the eversible lobe. In most species, the lobes of the m. interhyoideus and the gular pouch are adjacent layers connected only by the lymphatic septa (i.e., separated by the submandibular lymphatic sac). However, in Ptychadenidae, these two layers are in close myo-integumentary contact, with the epimysium tightly associated with the hypodermis via trabeculae of connective tissue. Gular pouches are present in all the examined species of *Euphlyctis* (Dicroglossidae), Ptychadenidae, and *Pelophylax* and some *Hylarana* (i.e., *H. galamensis*, *H. guentheri*, and all species formerly assigned to *Humerana* and *Hydrophylax*; Ranidae). The direction of inflation of the vocal sacs is a result of the position and fine-scale architecture of the skin pouch. In some taxa (*Euphlyctis* [subgenus *Phrynoderma*], Ptychadenidae, and the *Hylarana* with this pattern), vocal sacs inflate ventrolaterally (fig. 3K), whereas in *Euphlyctis* (subgenus *Euphlyctis*), the projection is somewhat more frontal, at 45° of the midline; and in *Pelophylax* and a few *Lithobates* (*L. areolatus*, *L. berlandieri*, *L. kauffeldi*, and *L. sphenocephalus*), the gular pouches are more lateral and dorsally oriented, so that vocal sacs project dorsally at the sides of the head (fig. 3O). In most species, the eversible lobe is black or gray, but in some *Ptychadena*, they are yellow or bicolored black and yellow (see account for the family below).

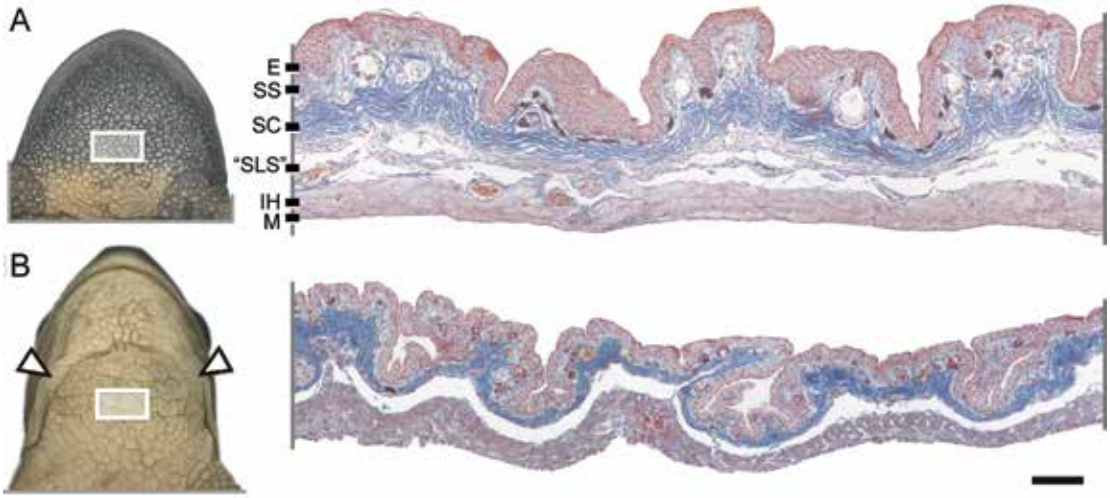


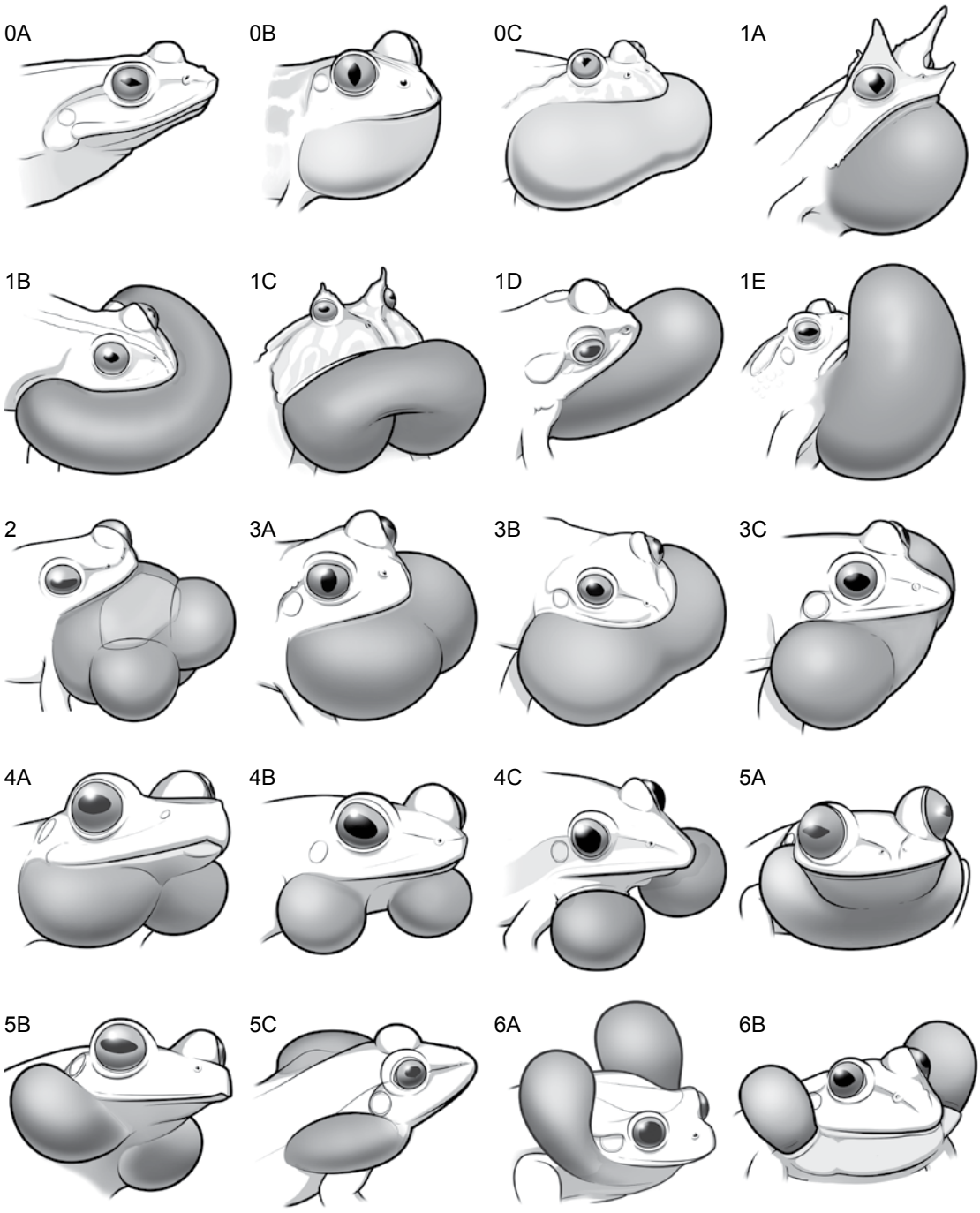
FIG. 10. Extensive myo-integumentary contact. Histological sections of the gular region of males of two species stained with Masson's trichrome. In most anurans the m. interhyoideus and the gular skin only contact via the postmandibular lymphatic septum. On the contrary, in adult males of some groups, the contact occurs in a more extensive area, where fine trabeculae of connective tissue connect the hypodermis with the epimysium (black triangles). **A,** *Odontophrynus americanus* (Odontophrynidae, MACN 49002), showing a large fold of the skin, which stretches markedly during inflation of the vocal sac. **B,** In *Boana pulchella* (Hylidae, MACN 42655), the contact is externally evident, since the rigid area of contact forms an anterior fold characteristic of this species group (white triangles). Abbreviations: **E,** epidermis; **IH,** m. interhyoideus; **M,** vocal sac internal mucosa; **SC,** stratum compactum of the dermis; **SS,** stratum spongiosum of the dermis; **"SLS,"** remains of the submandiblar lymphatic sac, partially obliterated by myo-tegumentary contact. Scale bar: 100 μm.

In the taxonomic literature of some groups (particularly from the early 20th century), the term "gular pouch" is used as synonym of "vocal sac" or to refer to the modified portion of the skin in species in which a conspicuous differentiation is present. Herein, we redefine this term and restrict it to the highly organized pleating of the lateral portion of the gular skin present in the abovementioned taxa. Presence of state 1 implies that character 10 = 1 and character 11 = 2.

CHARACTER 16. Myo-integumentary contact between the gular skin and the m. interhyoideus: (0) absent; (1) through the postmandibular lymphatic septum; (2) through lymphatic septa and a few median muscle fibers; (3) through lymphatic septa and an extensive median portion of the m. interhyoideus; (4) through lymphatic septa and paired portions of the m. interhyoideus.

This character was used by Elias-Costa et al. (2021) and is expanded here. In anurans, large lymphatic sacs separate the skin from the underlying musculature over most of the body; there are a few septa providing anchorage in conserved positions. In most species, the gular skin and the m. interhyoideus are connected by the postmandibular lymphatic septum (state 1), a thin band of elastic connective tissue. In *Discoglossus* (Alytidae), Bombinatoridae, and Pipidae, however, this septum is absent (state 0; Tyler, 1971b). The m. interhyoideus of some Hyperoliidae has longitudinally oriented supplementary fibers that insert on the gular skin (Elias-Costa et al., 2021: char. 22). This generates several scattered anchor points in the gular region (state 2). This was recovered as a synapomorphy of Hyperoliinae, but the character is absent in the specimen of *Morerella* examined.

In some species, the m. interhyoideus is in close contact with the skin over a wide median portion (state 3; Tyler, 1971b; Elias-Costa et


0A
0B
0C
1A
1B
1C
1D
1E
2
3A
3B
3C
4A
4B
4C
5A
5B
5C
6A
6B

al., 2021). There are numerous trabeculae of connective tissue between the hypodermis and the epimysium of m. interhyoideus (fig. 10). This pattern occurs in many species of *Boana* (variable among species, weakly developed in *B. faber* and *B. raniceps* and more developed in species of the *B. pulchella* group), all *Pseudis* with single vocal sacs (Hylidae), *Odontophrynus* (Odontophrynidae, in which the contact between the m. interhyoideus and a median patch of gular skin is not evident externally), and some *Ceratophrys* (Ceratophryidae). Tyler (1971b) reported that this state is present in some neartic hylids (e.g., *Pseudacris regilla*). However, he did not provide a detailed taxonomic distribution; thus, the occurrence of character state 3 is likely underestimated here.

In a few taxa this type of contact was observed in two independent, ventrolateral areas, between paired lobes of the m. interhyoideus and the elastic pouches of the skin (state 4). This happens in some with paired external vocal sacs (some *Pseudis* [Hylidae], *Euphlyctis* [Dicroglossidae], and all Ptychadenidae), but also some with a specific type of single subgular vocal sac (i.e., "triple vocal sac" as defined below; *Hyperolius pusillus*, and all members of *Hylambates*, and *Kassina* [Hyperoliidae]).

An Updated Classification of Vocal Sacs

We integrated our observations of the diversity of each of the elements that make up the vocal sac (internal mucosa, submandibular muscles and gular skin) and described 20 vocal sac patterns (fig. 11). Each is characterized by a unique combination of external and internal character states, including the shape of the inflated vocal sac at its maximum volume during vocalization (the diagnostic combination of character states is specified in each case and summarized in table 1). In some cases (e.g., bilobate vocal sacs), specific skin modifications produce different vocal sac morphologies and diagnose specific clades; thus, a distinction between internal and external vocal sacs was employed. In other species (e.g., with single subgular vocal sacs), skin modification does not alter the shape of the vocal sac enough to justify the recognition of a different pattern. Thus, the distinction between internal and external vocal sacs was employed only when informative.

0. Vocal Sac Absent

Among the many species of anurans without a vocal sac, three main patterns were observed, depending on the degree and nature of the expansion of the buccal floor.

Fig. 11. Vocal sac diversity in Anura. **0A–0C,** Vocal sac and apertures absent (i.e., the buccal floor does not project ventrally during post-metamorphosis). **1A–6B,** A true vocal sac is present. **0A,** Buccal floor not expanded (*Conraua goliath*, Conrauidae). **0B,** Buccal floor with isometric expansion (*Neobatrachus wilsmorei*, Limnodynastidae). **0C,** Buccal floor with bilobate expansion (*Bombina bombina*, Bombinatoridae). **1A,** Spherical single subgular vocal sac (*Pelobatrachus nasutus*, Megophryidae). **1B,** Semicircular single subgular vocal sac (*Pleurodema thaul*, Leptodactylidae). **1C,** C-shaped single subgular vocal sac (*Ceratophrys cornuta*, Ceratophryidae). **1D,** Anteriorly projected single subgular vocal sac (*Poyntonophrynus fenhouletti*, Bufonidae). **1E,** Anterodorsally projected single subgular vocal sac (*Anaxyrus cognatus*, Bufonidae). **2,** Triple vocal sac (*Hyperolius pusillus*, Hyperoliidae). **3A,** Internal bilobate vocal sac (*Spea multiplicata*, Scaphiopodidae). **3B,** External bilobate vocal sac, with diffuse skin modification (*Smilisca fodiens*, Hylidae). **3C,** External bilobate vocal sac, with longitudinal skin folds (*Leptodactylus fuscus*, Leptodactylidae). **4A,** Internal paired subgular vocal sacs (*Amolops wuyiensis*, Ranidae). **4B,** External paired subgular vocal sacs, with diffuse skin modification (*Hylodes asper*, Hylodidae). **4C,** External paired subgular vocal sacs, with discrete gular pouches (*Ptychadena mascareniensis*, Ptychadenidae). **5A,** Paired lateral vocal sacs with subgular inflation (*Osteocephalus verruciger*, Hylidae). **5B,** Paired lateral vocal sacs without subgular inflation (*Itapotihyla langsdorffii*, Hylidae). **5C,** Posterolateral vocal sacs (*Boreorana sylvatica*, Ranidae). **6A,** Dorsally projecting, lateral ocal sacs (*Trachycephalus coriaceus*, Hylidae). **6B,** Dorsally projecting, subgular vocal sacs (*Pelophylax lessonae*, Ranidae).

TABLE 1
Summary of Character-State Combinations That Define Each Vocal-Sac Pattern
Character and respective state numbers are indicated in parentheses.

Vocal-Sac Pattern	Internal Mucosae	Submandibular Musculature	Associated Skin
0A. Vocal sac absent, buccal floor not expanded	Not developed (0.0).	No sexually dimorphic modifications (5.0, 7.0)	No sexually dimorphic modifications (10.0)
0B. Vocal sac absent, buccal floor with isometric expansion.	Not developed (0.0).	Uniform expansion of mm. *intermandibularis* and *interhyoideus* (5.1)	No sexually dimorphic modifications (10.0)
0C. Vocal sac absent, buccal floor with bilobate expansion.	Not developed (0.0).	Mm. *geniohyoidei* projecting through gaps of the m. *interhyoideus* (not scored as a character).	No sexually dimorphic modifications (10.0).
1A. Spherical single vocal sac.	Vocal sac present, with one or two vocal slits (0.1/2), vocal sac mucosae fused or, if disconnected, largely extended medially (1.1; or 1.0, 2.0).	Subgular portion of the m. *interhyoideus* either poorly developed or uniformly expanded in variable degree (5.0/1), lateral portion of the m. *interhyoideus* not expanded (7.0). Ventral supplementary fibers can occurr in the m. *interhyoideus,* but never forming a large belly or paired rings around a central point (not scored).	Modification absent or uniformly present in the entire gular region (10.0; or 10.1, 11.0). In a few species, paired groups of folds can appear without affecting the spherical shape of the sac (12.1; or 13.1).
1B. Semicircular single vocal sac	Vocal sac mucosae fused (0.2; 1.1).	Subgular portion of the m. *interhyoideus* with ovoid expansion (5.2), usually highly elastic (8.1, 9.1), lateral portion of the m. *interhyoideus* not expanded (7.0). In extreme cases (e.g. *Glyphoglossus molossus*), the m. *interhyoideus* forms two lateral lobes that extend posteriorly (5.4 and 6.3).	Modification uniformly present in the entire gular region (11.0).
1C. C-shaped single vocal sac	Vocal sac mucosae fused (0.2; 1.1).	Subgular portion of the m. *interhyoideus* uniformly expanded (5.1) and with a highly elastic central band (9.2); lateral portion of the m. *interhyoideus* not expanded (7.0), extensive myo-integumentary contact in a median patch (16.3), and a specific arrangement of the postmandibular septum (see text).	Modification uniformly present in the entire gular region (11.0).
1D. Anteriorly projected single subgular vocal sac	One or two vocal slits present (0.1/2); if two, vocal sac mucosae are fused (1.1).	Subgular portion of the m. *interhyoideus* uniformly expanded (5.1), with a highly elastic posterior portion (8.1, 9.1), lateral portion of the m. *interhyoideus* not expanded (7.0).	Modification present in the entire gular region (11.0), but concentrated anteriorly.
1E. Anterodorsally projected subgular single vocal sac	One or two vocal slits present (0.1/2); if two, vocal sac mucosae fused (1.1).	Subgular portion of the m. *interhyoideus* uniformly expanded (5.1), with a highly elastic posterior portion (8.1, 9.1), lateral portion of the m. *interhyoideus* not expanded (7.0).	Modification present in the entire gular region (11.0), but concentrated anteriorly.
2. Triple vocal sac	Vocal sac mucosae fused (0.2; 1.1).	Subgular portion of the m. *interhyoideus* with bilobate expansion (5.1), lateral portion of the m. *interhyoideus* not expanded (7.0). Ventral supplementary fibers in the m. *interhyoideus,* forming either a large anteroposterior belly or paired rings around a central point (not scored as a character).	Highly modified gular skin, with two particularly elastic patches and a posterior transverse fold (11.1)
3A. Internal bilobate vocal sac	Two vocal slits present (0.2), vocal sac mucosae disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* with bilobate expansion (5.1), lateral portion of the m. *interhyoideus* not expanded (7.0)	No sexually dimorphic modifications (10.0)

Vocal-Sac Pattern	Internal Mucosae	Submandibular Musculature	Associated Skin
3B. External bilobate vocal sac with diffuse skin modification	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* with bilobate expansion (5.1), lateral portion of the m. *interhyoideus* not expanded (7.0)	Modification present in two ventrolateral patches separated by a less-modified portion (11.1)
3C. External bilobate vocal sac with longitudinal skin folds	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* with bilobate expansion (5.1), lateral portion of the m. *interhyoideus* not expanded (7.0)	Modification present in the form of paired, often pigmented longitudinal folds that parallel the mandible (13.1)
4A. Internal paired subgular vocal sacs	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* forming two ventrolateral lobes (5.4 and 6.0), lateral portion of the m. *interhyoideus* not expanded (7.0). In a few species, paired mucosae projecting through gaps of the m. *interhyoideus* (3.1/2).	No sexually dimorphic modifications (10.0)
4B. Paired subgular vocal sacs with diffuse skin modification	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* forming two ventrolateral lobes (5.4 and 6.0), lateral portion of the m. *interhyoideus* not expanded (7.0). In a few species, paired mucosae projecting through gaps of the m. *interhyoideus* (3.1/2).	Modification present in two independent ventrolateral patches (11.2)
4C. Paired subgular vocal sacs with gular pouches	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Subgular portion of the m. *interhyoideus* forming two ventrolateral lobes (5.4 and 6.0), lateral portion of the m. *interhyoideus* not expanded (7.0)	Gular pouches (15.1).
5A. Paired lateral vocal sacs with subgular inflation	Two vocal slits present (0.2), disconnected or fused (1.0/1).	Either (a) subgular portion of the m. *interhyoideus* not expanded (5.0) but lateral portion of the m. *interhyoideus* expanded, not exceeding the supratympanic fold (7.1); or (b) subgular portion of the m. *interhyoideus* expanded, forming paired lobes (5.4).	Absent or present as paired elastic portions next to mandibular joints (10.0; or 10.1, 11.3).
5B. Paired lateral vocal sacs without subgular inflation	Two disconnected vocal slits present (0.2, 1.0)	Subgular portion of the m. *interhyoideus* not expanded (5.0), lateral portion of the m. *interhyoideus* expanded, not exceeding the supratympanic fold (7.1)	Absent or present as paired elastic portions next to mandibular joints (10.0; or 10.1, 11.3).
5C. Posterolateral vocal sacs	Two disconnected vocal slits present (0.2, 1.0)	Subgular portion of the m. *interhyoideus* forming two tubular lobes that extend posteriorly (5.4, 6.3), lateral portion of the m. *interhyoideus* not expanded (7.0).	Absent or present as paired elastic portions next to mandibular joints, often extending posteriorly (10.0; or 10.1, 11.3).
6A. Dorsally projecting lateral vocal sacs	Two disconnected vocal slits present (0.2, 1.0)	Subgular portion of the m. *interhyoideus* not expanded (5.0), lateral portion of the m. *interhyoideus* greatly expanded, projecting beyond the supratympanic fold (7.3).	In most cases present as paired elastic portions at the sides of the head (11.3).
6B. Dorsally projecting submandibular vocal sacs	Two disconnected vocal slits present (0.2, 1.0)	Subgular portion of the m. *interhyoideus* forming two tubular lobes that project dorsally (5.4, 6.2), lateral portion of the m. *interhyoideus* not expanded (7.0).	Gular pouches (15.1).

0A. Vocal sac absent, buccal floor not expanded

The vocal sac mucosa does not protrude ventrally between deep and superficial submandibular muscles (i.e., mm. geniohyoidei and mm. intermandibularis and interhyoideus, respectively). These two muscle layers are in mutual contact in adult males, as they are in juveniles and adult females of all species. Vocal slits are absent (char. 0.0). This is the most widespread condition among species lacking a vocal sac and is present in 17.5% of species included in the present survey.

0B. Vocal sac absent, buccal floor with isometric expansion

In males of a few species, vocal sacs are absent, but the buccal floor and the mm. geniohyoidei are highly distended and pleated, which allows for greater expansion of the oral cavity during vocalization (Tyler, 1972). This pattern does not correspond to the strict definition of vocal sacs, because there is no evagination of the oral mucosa toward the submandibular musculature. However, it is possible that this condition is functionally analogous to a true, single subgular vocal sac, because the oral cavity receives the exhaled air and recycles it back into the lungs. Hypertrophied buccal floors are present in all *Heleioporus*, and some *Neobatrachus* (Limnodynastidae; Tyler, 1972, 1980), optimizing as a synapomorphy for this clade (0.3% of sampled species) and are absent in other groups of anurans.

0C. Vocal sac absent, buccal floor with bilobate expansion

A different condition is observed in *Bombina bombina* (Bombinatoridae, but not in other species of *Bombina*), in which the m. geniohyoideus lateralis (a paired muscle) is hypertrophied and protrudes through spaces between the mm. intermandibularis and interhyoideus (Boulenger, 1897; Liu, 1935; Tyler, 1980; Elias-Costa et al., 2021). Although there are no vocal slits or true vocal sac, the bilateral protrusion of this muscle allows the buccal floor to inflate with a bilobate shape during vocalization (Köhler et al. 2017: fig. 1A). In *Neobatrachus sutor* (Limnodynastidae), the buccal floor also inflates resembling a bilobate vocal sac (Anstis et al., 2007); however, the anatomical basis of this shape is unknown.

1. Single Subgular Vocal Sac

Most (63% of sample) anurans have a single subgular vocal sac, the morphology of which varies taxonomically. The shape of the fully inflated vocal sac is rarely described in detail in the taxonomic literature; it has been generally assumed that all subgular vocal sacs are spherical. While this is true for many species, some species have single, nonspherical vocal sacs. Five main patterns were described depending on the predominant axes of deformation from a sphere. Skin modifications can be present or absent in all of them. Reports on gular skin modifications and how they affect vocal sac morphology are scarce for most taxa, but if present, these modifications are uniformly distributed in the entire gular region.

1A. Spherical single vocal sac

This pattern is diagnosed by the following combination of character states: vocal sac present, with one or two vocal slits (char. 0.1/2), vocal sac mucosae fused or, if disconnected, largely extended medially (char. 1.1; or char. 1.0 and char. 2.0), subgular portion of the m. interhyoideus either poorly developed or uniformly expanded (char. 5.0/1, depending on the degree of the development of the vocal sac), lateral portion of the m. interhyoideus not expanded (char. 7.0).

In most species, the single subgular vocal sac is approximately spherical and occupies the center of the gular region. The anterior and posterior limits of the inflatable portion, as well as the relative contribution of the mm. intermandibularis and interhyoideus, are highly variable among species (fig. 12A–E). For example, in some, the vocal sac scarcely expands during vocalization, whereas

in others, the stored volume of air is considerably larger. The posterior limit of the vocal sac (partly determined by the position and extension of the lymphatic septa) ranges from the gular to the pectoral region. In contrast, the anterior limit (determined by the extension of internal mucosae and the distensibility of the m. intermandibularis) ranges from the inferior lip to the center of the gular region. Although differences among these conditions are evident, the morphological variation occurs as a continuum with several intermediate morphologies. Unfortunately, the size and boundaries of the vocal sac can be reliably assessed only with direct observation of vocalizing males, which in turn can be accessed only in a few species. Accordingly, only a single category was recognized for all spherical vocal sacs, owing to the practical difficulty of differentiating states in all species.

1B. Semicircular single vocal sac

This pattern is diagnosed by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), vocal sac mucosae fused (char. 1.1), subgular portion of the m. interhyoideus with ovoid expansion (char. 5.2), lateral portion of the m. interhyoideus not expanded (char. 7.0). In extreme cases (see below), the m. interhyoideus forms two lateral lobes that extend posteriorly (chars. 5.4, 6.3).

In some groups with a single vocal sac, the transverse axis is clearly predominant. The shape of the inflated vocal sac ranges from kidney shaped to crescentic (depending on the degree of lateral expansion), but always maintains median inflation in the gular region. This pattern differs from a bilobate vocal sac by the absence of a median notch. The skin is usually uniformly modified and thinner than the abdominal skin. The m. interhyoideus often is expanded both medially and laterally to variable degrees among species. Moderate lateral expansion is present in *Allophryne* (Allophrynidae), and some *Hyla*, *Litoria*, and *Scinax* (Hylidae, fig. 12F).

In species of *Engystomops*, *Physalaemus*, *Pleurodema* (Leptodactylidae), *Notaden* (Limnodynastidae), *Kaloula*, *Uperodon*, and in *Scaphiophryne madagascariensis* (Microhylidae), the semicircular pattern is conspicuous, and the vocal sac expands greatly at the sides of the head while retaining median inflation (fig. 12G). Extreme cases of this condition are seen in *Glyphoglossus molossus* (Microhylidae; fig. 3T), members of the *Physalaemus olfersii* group (Leptodactylidae), and *Proceratophrys cristiceps* (Odontophrynidae). In *G. molossus* the only one of these species with available information on internal anatomy, the m. interhyoideus forms two tubular projections that extend posteriorly above the arms (Targino et al., 2019). Except for *P. cristiceps*, all these species vocalize floating or partially submerged in small bodies of water, storing massive volumes of air in the lungs and the vocal sac.

1C. C-shaped single vocal sac

This pattern is diagnosed by the following combination of character states: vocal sac mucosae fused (char. 1.1), subgular portion of the m. interhyoideus uniformly expanded (char. 5.1) and with a highly elastic central band (char. 9.2); lateral portion of the m. interhyoideus not expanded (char. 7.0), extensive myo-integumentary contact in a median patch (char. 16.3), and a specific arrangement of the postmandibular septum (see below). This pattern occurs only in two species of the genus *Ceratophrys* (Ceratophryidae), *C. cornuta* and *C. calcarata*. The vocal sac inflates as a large subgular structure, which is continuous anteriorly but curves medially in its posterior portion (fig. 12H). The pattern derives from a specific configuration of the m. interhyoideus and the postmandibular lymphatic septum (fig. 13). The muscle is not uniform in all its extension, but forms two large slips (one anterior and one posterior) separated by an extremely thin, elastic portion that houses the vocal sac. This central portion of the m. interhyoideus is greatly distensible in its median region, but it also expands laterally forming two lobes. The postmandibular lymphatic septum, which in other anurans connects the posterior portion of

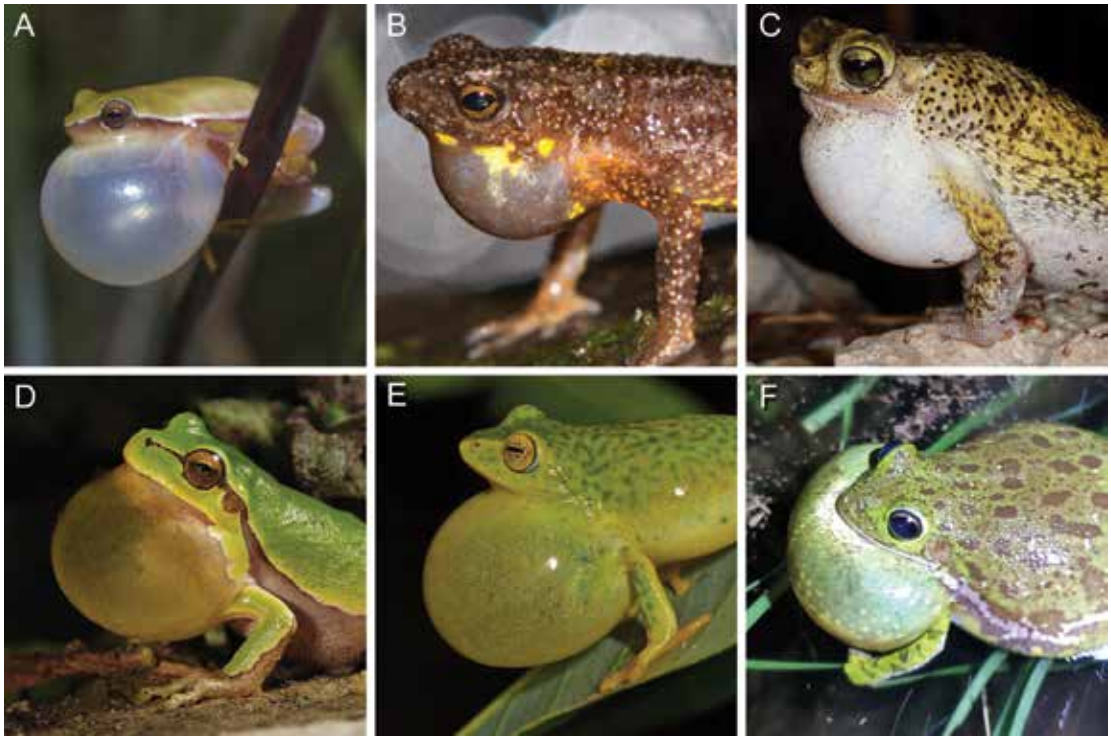
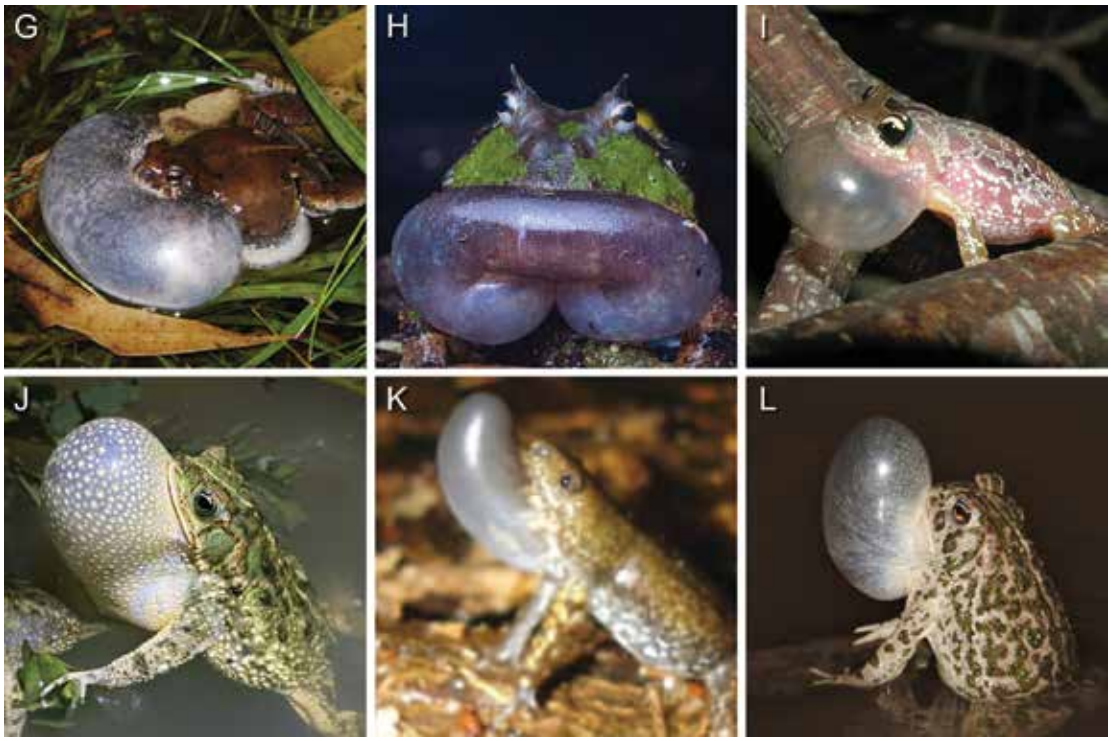


FIG. 12. (*above and opposite page*) Diversity of single subgular vocal sacs. **A–E,** The spherical vocal sac (vocal sac pattern 1A) is approximately isometric, but its relative size (compare A and B), its posterior limit (extending to the pectoral region or not, compare B and C) or anterior limit (reaching the lower lip or not, by expansion of the m. intermandibularis, compare D and E) are highly variable among species. **F–G,** The semicircular vocal sac (vocal sac pattern 1B) is a single, laterally expanded structure that inflates around the head, ranging from a slightly ellipsoid to horseshoe-shaped. **H,** The C-shaped vocal sac is continuous anteriorly but curved medially in its posterior end (vocal sac pattern 1C). **I–J,** The anteriorly projecting vocal sac (vocal sac pattern 1D) is an ellipsoid structure with a longitudinal predominant axis that extends beyond the limit of the snout

the m. interhyoideus with the skin, passes anterior to the lobes in these species, likely providing necessary support during the development of this pattern. In addition, abundant connective tissue connecting the ventral skin to the pectoral musculature; this provides additional anchorage to the posterior portion of the vocal sac and contributes to the posterior constriction that characterizes this pattern. The vocal slits are elongate and located relatively posterior in the mouth.

1D. Anteriorly projected single subgular vocal sac

This pattern is diagnosed by the following combination of character states: vocal sac present, with one or two vocal slits (char. 0.1/2), vocal sac mucosae fused (char. 1.1), subgular portion of the m. interhyoideus uniformly expanded (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0). The single subgular vocal sac projects anteriorly, forming a nonspherical structure that greatly extends beyond the anterior limit of the snout (fig. 12I, J). Inflation begins at the posterior end of the gular region and expands anteriorly. This form of vocal sac probably reflects the differences in the elasticity of the submandibular muscles; the anterior portion (i.e., the m. intermandibularis, and, in many cases, the anterior portion of the m. interhyoideus) is thick and hardly distensible, whereas the posterior portion of the m. interhy-



at variable degree. **K–L,** The anterodorsally projecting vocal sac (vocal sac pattern 1E) curves dorsally in front of the head. **A,** *Dendropsophus jimi* (Hylidae, T. Pezzuti); **B,** *Ansonia inthanon* (Bufonidae, taken from Quah et al., 2019); **C,** *Peltophryne armata* (Bufonidae, taken from Landestoy et al., 2018); **D,** *Hyla intermedia* (Hylidae, B. Trapp); **E,** *Raorchestes jayarami* (Rhacophoridae, Froggydame); **F,** *Hyla gratiosa* (Hylidae, Turkboy); **G,** *Physalaemus biligonigerus* (Leptodactylidae); **H,** *Ceratophrys cornuta* (Ceratophryidae, Q. Martinez); **I,** *Julianus uruguayus* (Hylidae, D. Baldo); **J,** *Rhinella dorbignyi* (Bufonidae); **K,** *Chiasmocleis royi* (Microhylidae, taken from Peloso et al., 2014); **L,** *Anaxyrus cognatus* (Bufonidae, V. Mata-Silva).

oideus is extremely thin and highly elastic. The anterior portion of the skin usually is modified (thinner, more elastic) in its anterior portion; this may contribute to directing the sac anteriorly. Vocal sacs that project anteriorly occur in the following taxa: several members of *Anaxyrus*, *Duttaphrynus*, *Poyntonophrynus*, *Scleophrys*, the *Rhinella granulosa* group (Bufonidae); some *Litoria*, *Pseudacris*, and *Pseudis* (Hylidae); *Pseudopaludicola* (a synapomorphy of the genus, Leptodactylidae); and some *Chiasmocleis*, *Elachistocleis*, *Gastrophryne*, and *Uperodon* (Microhylidae). In many of these species (e.g., *Rhinella dorbignyi*, *Elachistocleis bicolor*, and *Pseudopaludicola falcipes*), males commonly vocalize in an upright posture such that the vocal sac is thrust upward. This behavior may be associated with pushing the vocal sac out of the water in the flooded fields where they usually call while semisubmerged.

1E. Anterodorsally projected subgular single vocal sac

This pattern is defined by the following combination of character states: vocal sac present, with one or two vocal slits (char. 0.1/2), vocal sac mucosae fused (char. 1.1), subgular portion of the m. interhyoideus uniformly expanded (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0). In fixed specimens, this pattern is hardly distinguishable from the previous one, but it is readily recognized in vocalizing males. In extreme

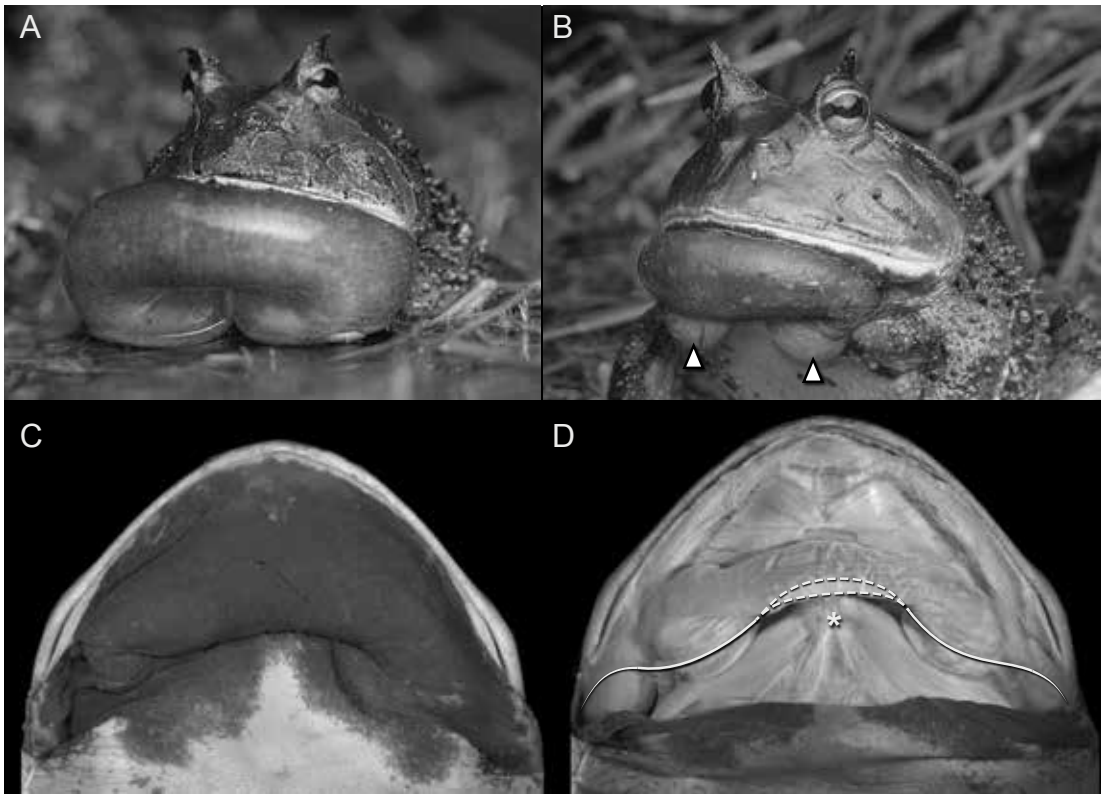


Fig. 13. The C-shaped, single subgular vocal sac of *Ceratophrys cornuta* (Ceratophryidae). **A,** The vocal sac inflates as a large subgular structure, which is continuous anteriorly but curves medially in its posterior portion. **B,** When only partially inflated, the two posterior lobes of thinner, less-pigmented gular skin are distinguishable (white arrowheads). **C,** In a fixed specimen (MZUSP 151492), a median constriction in the gular skin is visible. **D,** the postmandibular lympatic septum expands in the median portion (dotted lines, shaded area), tightly connecting the gular skin and the posterior portion of the m. interhyoideus. This connective tissue extends to the pectoral musculature (*), providing an additional anchorage. Credit A, B: Q. Martinez.

cases of anterior projection, the distal portion of the sac curves dorsally and forms a large structure in front of the head (fig. 12K, L). It was observed in species in clades in which anterior projection occurs, including four species of *Anaxyrus* (*A. cognatus*, *A. compactilis*, *A. quercicus* and *A. speciosus*, Bufonidae; Dickerson, 1907; Wright and Wright, 1949; McAlister, 1961), as well as in *Chiasmocleis royi* and *Uperodon systoma* (Microhylidae; Peloso et al., 2014; Prasad et al., 2022), and *Hemisus marmoratus* (the only species of Hemisotidae in which the shape of the fully inflated vocal sac was reported; M. Schäfer, personal commun.). In the bufonids, the vocal sac remains inflated during the period of latency between calls; it is associated with an upright posture of the males and likely serves as a visual signal. Information on the dynamics of the inflation of the vocal sac is lacking for the other three species mentioned. Likewise, reports on the shape of the fully inflated vocal sac are scarce for the diverse genera *Chiasmocleis* and *Uperodon* as well as Hemisotidae. Thus, it is possible that this pattern occurs in other related species.

2. Triple Vocal Sac

This pattern is defined by the following combination of character states: vocal sac present,

with two vocal slits (char. 0.2), vocal sac mucosae fused (char. 1.1), subgular portion of the m. interhyoideus with bilobate expansion (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0), ventral supplementary fibers of the m. interhyoideus (not scored here as a character owing to their highly restricted taxonomic distribution discussed below).

The triple vocal sac is extremely rare in Anura, but its characteristic shape justifies differentiating it from single subgular vocal sacs. A triple vocal sac consists of a large subgular sphere from which two smaller spheres sprout anteriorly (fig. 14). The inflated structure combines elements of single and bilobate vocal sacs, because there is significant inflation of the subgular in addition to the two secondary lobes. The vocal sac is a single cavity with fused internal mucosae. This pattern was observed only in Hyperoliidae, having had two independent origins, each forming a distinct pattern.

Hyperolius pusillus is the only species of the genus with a triple vocal sac. In all species of the diverse genus *Hyperolius* (and in other genera of the family), males have large, disclike gular macroglands that form a very conspicuous transverse posterior fold (Liem, 1970). In almost all species, the fold is single and continuous; however, in *H. pusillus*, the pleated skin behind the gland is concentrated around two points (fig. 14C). The m. interhyoideus in male *H. pusillus* is greatly hypertrophied and in extensive myo-integumentary contact with the gular skin. Around the two areas of highly folded skin, the muscle forms two thinner, more distensible ventral lobes. In addition, the accessory fibers of the m. interhyoideus (synapomorphic to Hyperoliidae and present in most species; see Elias-Costa et al., 2021) form a unique pattern in *H. pusillus*. Instead of being longitudinal as in all other hyperoliids, they form two circles around a central point of anchorage (fig. 14D). When the vocal sac begins to inflate, it is spherical until, exceeding a certain pressure threshold, the secondary lobes inflate.

In adult male *Kassina* + *Hylambates*, accessory fibers of m. interhyoideus are longitudinal but form a large mass of fibers that is evident externally (Elias-Costa et al., 2021). What externally appears to be the gular gland is the supplementary belly of m. interhyoideus in these species. Glands are present but in the form of small, scattered acini (Le Quang Trong, 1976). On both sides of this rigid central mass of fibers, the m. interhyoideus forms two distensible lobes that are in intimate contact with patches of highly elastic and pigmented gular skin. The distribution and shape of these pigmented areas varies among species and has been widely studied (Noble et al., 1924; Power, 1925; Rose, 1962; Wager, 1965, Liem, 1970; Drewes, 1984; Schiøtz, 1999, Amiet, 2007), but with almost no reference to the internal anatomy or the shape of the inflated vocal sac. During the initial steps of inflation, the sac is spherical, but after a certain threshold of internal pressure, the two secondary lobes inflate (Power, 1925; Rose, 1962; Wager, 1965; Drewes, 1984). Unlike *H. pusillus*, in which circular muscle fibers circumscribe the secondary lobes precisely, in *Hylambates* + *Kassina*, the secondary lobes are more continuous with the main subgular lobe (fig. 14F).

3. Bilobate Vocal Sacs

Bilobate vocal sacs are a single subgular structure in which the ventrolateral lobes expand more than the median portion. The term "lobe" is accurate inasmuch as it describes a protrusion that is part of a larger structure, and not an independent element. No correlation was observed between the degree of bilaterality (i.e., the relationship between median and lateral inflation) and the disconnection of internal mucosae of the vocal sac. Clearly defined, paired lobes can be seen in species with a single vocal cavity (e.g., *Leptodactylus fuscus*, Leptodactylidae) or species with disconnected mucosae (e.g., *Calyptocephalella gayi*; Calyptocephalellidae). Three major categories were distinguished in relation to the modification of the gular skin. Bilobate vocal sacs are either internal or external, and these can be categorized as to their skin modifications.

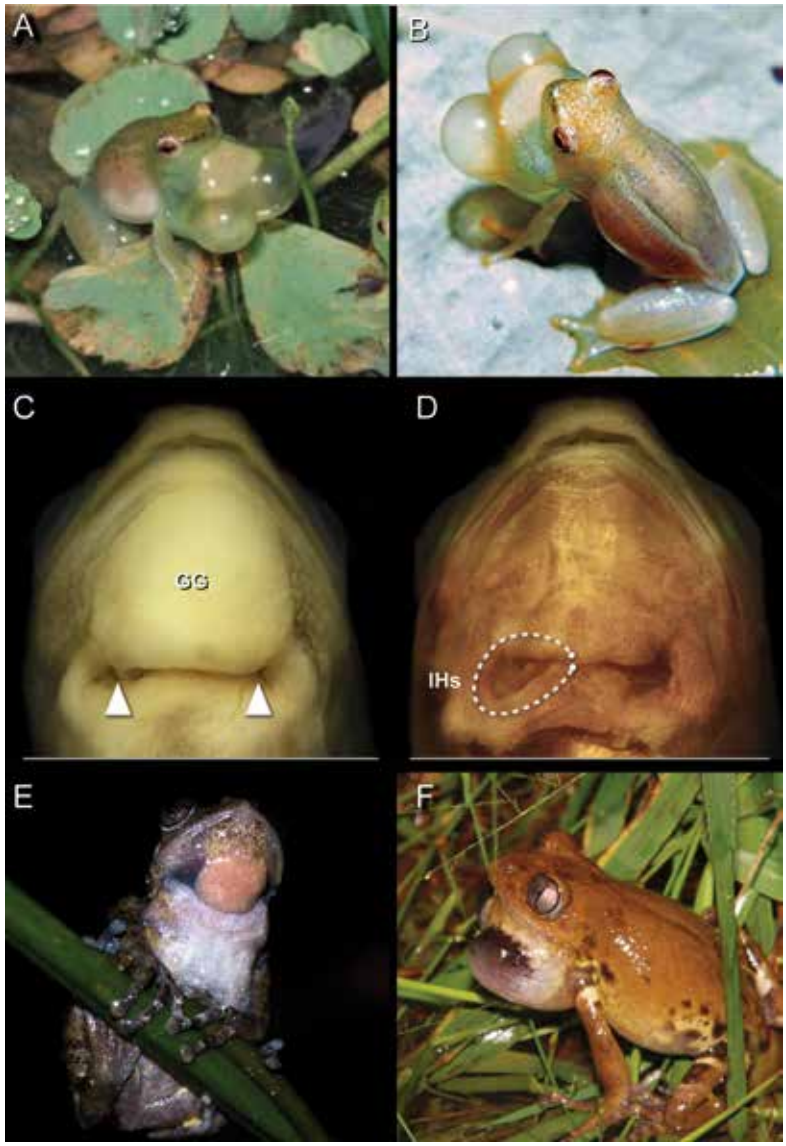


Fig. 14. Triple vocal sacs. **A–D,** *Hyperolius pusillus* (Hyperoliidae). In this unique species, the vocal sac has two secondary lobes on a subgular sphere. **C–D,** USNM 153348 showing that the gular skin presents transverse gular flap (caused by the presence of the gular gland, GG, something typical of *Hyperolius*), but the folding is concentrated in two ventrolateral areas (white triangles). Internally, the ventral supplementary fibers of the m. interhyoideus (IHs, dotted line), form two rings around a central point, a feature present only in this species. These rings likely delimit the secondary lobes with respect to the rest of the vocal sac. **E,** *Hylambates verrucos*us and **F,** *Hylambates leonardi* (Hyperoliidae) showing a similar pattern. In *Hylambates* and *Kassina*, the triple sac is generated by a central mass of less distensible anteroposterior fibers. On both margins of this mass, the gular skin and the m. interhyoideus are hypertrophied, thus projecting further, although not as defined as in *H. pusillus*. Credits: A, M. and P. Fogden; B, taken from Phaka et al. (2017); E, I. Starnberger; F, V. Gvoždik.

3A. Internal bilobate vocal sac

This pattern is diagnosed by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), subgular portion of the m. interhyoideus with bilobate expansion (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0), skin modification absent (char. 10.0).

The pattern is characterized by a subtle lateral expansion of m. interhyoideus, combined with unmodified gular skin (fig. 3F). The vocal sac in these species usually is small and has a small degree of bilaterality. Mucosae can be fused or disconnected. Vocal sacs of this type are present in many species of different families, including members of Alsodidae, Arthroleptidae, Centrolenidae, Ceratobatrachidae, Cycloramphidae, Dicroglossidae, Hylidae, Hyperoliidae, Leptodactylidae, Mantellidae, Megophryidae, Nasikabatrachidae, Petropedetidae, Pyxicephalidae, Ranidae, and Rhacophoridae.

3B. External bilobate vocal sac with diffuse skin modification

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), subgular portion of the m. interhyoideus with bilobate expansion (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0), skin modification by the presence of two ventrolateral patches separated by a less-modified portion (chars. 10.1, 11.1).

Two patterns of skin modification occur in species with external bilobate vocal sacs. In the first, the sexually dimorphic modification is uniform and widespread in the entire gular region or, in some cases, is represented by two large ventrolateral patches. The transition between the modified and unmodified portions of the skin is gradual and diffuse. This pattern is the most common type of external bilobate vocal sac and consists generally of a large structure that inflates radially from the gular region. It was observed in species of the following genera: *Allobates* (Aromobatidae); *Astylosternus* and *Leptodactylodon* (Arthroleptidae); *Cornufer* (Ceratobatrachidae); *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus* (Ceratophryidae); *Fejervarya*, *Minervarya*, *Sphaerotheca* (Dicroglossidae); *Dendropsophus*, *Hyla*, *Scinax*, *Smilisca*, *Triprion* (Hylidae); *Babina*, some *Hylarana* (species formerly assigned to *Chalcorana*, *Papurana*, *Pulchrana*, and *Sylvirana*; Ranidae); and *Spea* (Scaphiopodidae).

3C. External bilobate vocal sac with longitudinal skin folds

The second pattern is diagnosed by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), subgular portion of the m. interhyoideus with bilobate expansion (char. 5.1), lateral portion of the m. interhyoideus not expanded (char. 7.0), gular skin modified by presence of paired, often pigmented longitudinal folds that parallel the mandible (char. 13.1; fig. 8). Unlike the previous pattern (3A), skin modification in these species is spatially restricted to the lateral portion of the gular region.

The pattern is apparently related to a specific inflation dynamic. During vocalization, the vocal sac first inflates ventrally from the center of the gular region and expands laterally soon after in the area of the skin folds. Thus, vocal sacs do not inflate homogeneously and radially as do the vocal sacs in 3B. The modified skin is more elastic and compliant than the medial unmodified skin; thus, it expands more in response to the internal air pressure. In the vocal sacs with longitudinal skin folds (as with triple vocal sacs), the skin modification is so localized that it produces a specific shape and dynamic of inflation.

External bilobate vocal sacs with longitudinal folds are present in numerous species of *Adenomera* and *Leptodactylus* (Leptodactylidae) and are common in species of the *Leptodactylus fuscus* group. This pattern also may be present in a few *Amietia* and *Nothophryne* (Pyxicephalidae), and two species of *Ischnocnema* (Brachycephalidae), *I. bocaina* (Taucce et al., 2019: fig. 2) and *I. crassa* (Silva-Soares et al., 2021: fig. 1).

4. Paired Subgular Vocal Sacs

In paired subgular vocal sacs, the independent ventrolateral structures are separated by a medial, nonexpanding region, which distinguishes this state from that of a single, bilobate vocal sac (fig. 3). Three patterns can be recognized on the basis of the gular skin differentiation: paired subgular internal vocal sacs; external with diffuse skin modification; and external with skin pouch. The more modified the skin, the greater the delimitation of the inflatable portions.

4A. Internal paired subgular vocal sacs

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus forming two ventrolateral lobes (chars. 5.4, 6.0), lateral portion of the m. interhyoideus not expanded (char. 7.0), skin modification absent (char. 10.0).

In all specimens examined with this pattern, paired mucosae are disconnected and with little medial development, which probably supports the independence of the two ventrolateral lobes. This pattern occurs in species of the following genera: *Limnonectes* and *Nannophrys* (Dicroglosside); *Crossodactylus* (Hylodidae); *Amerana*, *Amolops*, *Hylarana*, *Odorrana*, *Staurois*, and *Sumaterana* (Ranidae). In a few species (e.g., some members of *Crossodactylus*, *Amolops*, *Hylarana*), paired mucosae are moderately developed medially, which expands the ventrolateral lobes and generates a pattern that could be difficult to differentiate from bilobate sacs in dissections of fixed specimens (Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019).

4B. Paired subgular vocal sacs with diffuse skin modification

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), lateral portion of the m. interhyoideus not expanded (char. 7.0), skin modification present in two independent ventrolateral patches (chars. 10.1, 11.2).

Depending on the species, this vocal sac shape derives from two different anatomical configurations that are indistinguishable externally and produce the same overall shape. The m. interhyoideus forms two ventrolateral lobes in the following taxa: *Callyptocephalella* (Callyptocephalellidae); *Hoplobatrachus* (Dicroglossidae), *Pseudis minuta* + *P. cardosoi* (Hylidae), *Gephyromantis* (Mantellidae), some *Odorrana*, *Hylarana*, and *Staurois* (Ranidae), (chars. 5.4, 6.0). In an alternate arrangement, the mucosae project through the fibers of the muscle forming two paired lobes in *Hylodes* and *Phantasmarana* (Hylodidae), Odontobatrachidae, *Amolops*, *Huia*, *Meristogenys*, some *Odorrana*, and some *Staurois* (Ranidae), (char. 3.1/2). This same pattern is also present in *Cornufer guppyi* (Ceratobrachidae), although the condition of the internal anatomy is unknown. In all cases, the gular skin is configured in two ventrolateral, thin elastic patches that are more distensible than the median portion. When relaxed, these elastic areas are loose and wrinkled (fig. 6G, H). Internal mucosae are disconnected in all species examined with this pattern.

4C. Paired subgular vocal sacs with gular pouches

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus forming two ventrolateral lobes (chars. 5.4, 6.0), lateral portion of the m. interhyoideus not expanded (char. 7.0), skin modification in the form of paired gular pouches (char. 15.1).

In some species with paired subgular vocal sacs, there are discrete pouches of highly elastic skin covered by a region of unmodified skin (fig. 6K, L). The eversible portion is highly elastic and, in most species, darkly pigmented. Internal mucosae are disconnected and the m. interhyoideus forms two discrete ventrolateral lobes that inflate inside these pockets during vocalization.

This pattern was observed in *Euphlyctis* (Dicroglossidae), Ptychadenidae, and some *Hylarana* (*H. galamensis*, *H. guentheri*, and all former *Humerana* and *Hydrophylax*; Ranidae).

5. Paired Lateral Vocal Sacs

In some species, the m. interhyoideus has a pair of dorsolateral projections that extend the internal cavity of the vocal sac toward each side of the head. The projection originates from the expansion of one of two different parts of the m. interhyoideus—either the dorsolateral part of the muscle near the origin of fibers adjacent to the otic capsule, or the subgular portion, next to the insertion point of muscle fibers (Elias-Costa et al., 2021: fig. 7). In addition to the presence of well-developed lateral lobes, paired lateral vocal sacs may include subgular inflation, depending on the medial extension of the internal mucosae. Based on this observation, we include a type of vocal sac (pattern 5A) that previously could not be assigned to any category in traditional classifications (Liu, 1935; Duellman, 1970; Moura et al., 2021).

5A. Paired lateral vocal sacs with subgular inflation

This pattern is diagnosed by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected but greatly developed medially or fused (chars. 1.0 and 2.0 or char. 1.1), either (a) subgular portion of the m. interhyoideus not expanded (char. 5.0), but lateral portion of the m. interhyoideus expanded, not exceeding the supratympanic fold (char. 7.1); or (b) subgular portion of the m. interhyoideus expanded, forming paired lobes (char. 5.4).

Some species have a unique vocal sac morphology resulting from combined lateral and median inflation (fig. 15A–C). The m. interhyoideus in males forms paired lobes and occasionally, the muscle may insert on the fascia dorsalis; the mucosae may be fused or disconnected, but well developed medially (Moura et al., 2021). The pattern occurs in the following taxa: Rhinophrynidae; a clade of *Limnonectes* (Dicroglossidae); some *Dryaderces*, *Osteocephalus*, *Osteopilus*, and *Tepuihyla* (Hylidae); *Nyctibatrachus* (Nyctibatrachidae), *Aquarana*, and some species of *Rana* (Ranidae). Depending on the internal anatomy, anurans having this vocal sac pattern are in one of two groups. In the hylids and rhinophrynid, the vocal sac is contained by the expanded dorsal portion of the m. interhyoideus near the origin of fibers, whereas in the nyctibatrachids and ranids, paired lobes derived from the subgular portions of the muscle are pushed dorsolaterally. Subgular inflation is evident in both groups and the lateral lobes merge ventrally. Although these patterns are anatomically distinct, they produce a similar inflated vocal sac (see fig. 5I, J).

5B. Paired lateral vocal sacs without subgular inflation

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus not expanded (char. 5.0), lateral portion of the m. interhyoideus expanded, not extending beyond the supratympanic fold (char. 7.1).

In some species there is lateral development of m. interhyoideus, and the mucosae (which are always disconnected) are poorly developed medially and restricted to the lateral region. Thus, the two vocal sacs are independent of one another (fig. 15D, E). In most species with the pattern, the skin behind the angles of the jaw is elastic and pleated. This pattern was observed in *Itapotihyla*, *Nyctimantis siemersi*, some *Tepuihyla* (Lophyohylini, Hylidae), and the *Boophis albilabris* group (Mantellidae).

5C. Posterolateral vocal sacs

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus forming two tubular lobes that extend poste-



FIG. 15. Paired lateral and dorsal vocal sacs. **A–C,** Lateral vocal sacs with subgular inflation (pattern 5A); **D–E,** Lateral vocal sacs without subgular inflation (pattern 5B); **F–G,** Posterolateral vocal sacs (pattern 5C); **H–I,** dorsal vocal sacs (patterns 6A and 6B, respectively). **A,** *Osteocephalus vilarsi* (Hylidae, taken from Ferrão et al., 2019); **B,** *Aquarana catesbeiana* (Ranidae, Vargas-Salinas et al., 2014); **C,** *Rhinophrynus dorsalis* (Rhinophrynidae, taken from Sandoval-Vargas et al., 2015); **D,** *Nyctimantis siemersi* (Hylidae, N. Fariña, taken from Moura et al., 2021); **E,** *Boophis occidentalis* (Mantellidae, taken from Vences et al., 2010); **F,** *Nyctibatrachus kempholeyensis* (Nyctibatrachidae, Gururaja et al., 2014); **G,** *Boreorana sylvatica* (Ranidae, D. Huth); **H,** *Trachycephalus mesophaeus* (Hylidae, L. Drummond, taken from Moura et al., 2021); **I,** *Pelophyax* sp. (Ranidae, R. Schmidt).

riorly (chars. 5.4, 6.3), lateral portion of the m. interhyoideus not expanded (char. 7.0).

In taxa in which the m. interhyoideus is configured into two long, tubular projections that extend posteriorly along the body (fig. 15F, G), the lymphatic septa are modified, so that they extend the submandibular lymphatic sac over the arms. This pattern occurs mainly in the ranids *Boreorana sylvatica* and the diverse genus *Lithobates* (Ranidae), particularly in the *L. pipiens* group. It also is present in *Nyctibatrachus kempholeyensis* (Nyctibatrachidae), in which the lateral lobes extend posteriorly along the body; in the other species of the genus, the lobes inflate at the sides of the head.

6. Paired Dorsal Vocal Sacs

Paired vocal sacs evolved several times in Anura and include a wide range of forms with varying degrees of bilaterality. In most of these species, vocal sacs either remain subgular to form two small spheres below the angles of the mandible (pattern 4 of vocal sacs) or develop posteriorly occupying the posttympanic region (pattern 5 of vocal sacs; Boulenger, 1882; Liu, 1935; Inger, 1954; Glaw and Vences, 2007; Biju et al., 2011; Barej et al., 2015; Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019; Targino et al., 2019, Moura et al., 2021). Dorsal projection of the vocal sacs above the supratympanic fold evolved in three anuran clades: *Trachycephalus* (Hylidae), *Pelophylax*, and some *Lithobates* (Ranidae), each with a distinctive pattern.

6A. Dorsally projecting lateral vocal sacs

This pattern is defined by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus not expanded (char. 5.0), lateral portion of the m. interhyoideus greatly expanded, projecting beyond the supratympanic fold (char. 7.3).

In some species of *Trachycephalus* (Hylidae), vocal sacs are inflated dorsally above the head. In these frogs, the dorsolateral lobes of the m. interhyoideus curve dorsally and attach above the head via a unique association between the epimysium of the m. interhyoideus and the fascia dorsalis (Moura et al., 2021); futher, that part of the muscle close to the origin of the fibers is expanded (figs. 3O, 15H; Duellman, 1956; Tyler, 1971a; Elias-Costa et al., 2021). Internal mucosae are disconnected in all species and the degree of medial expansion varies. In most species, the lateral skin is markedly modified and pigmented, forming an elastic, highly pleated lobe that hangs loosely behind the tympanum (fig. 3O). Notably, in *T. mesophaeus*, skin differentiation is more diffuse and does not form a defined lobe (fig. 15H), but the lobes of the m. interhyoideus have the configuration described above, indicating some degree of independence between these two structures (Moura et al., 2021).

6B. Dorsally projecting submandibular vocal sacs

This pattern is diagnosed by the following combination of character states: vocal sac present, with two vocal slits (char. 0.2), mucosae disconnected (char. 1.0), subgular portion of the m. interhyoideus forming two tubular lobes that project dorsally (chars. 5.4, 6.3), lateral portion of the m. interhyoideus not expanded (char. 7.0).

In some ranids, paired vocal sacs project dorsally lateral to the mandibular joints (fig. 15I). Unlike the previous pattern, the lobes of the m. interhyoideus are protrusions of the subgular region (fig. 5H). These tubular projections curve laterally at the level of the mandibular joints and enter folds of densely pigmented skin. The median portion of the m. interhyoideus is poorly developed and the lateral lobes represent most of muscle mass; most of the gular region is occupied by the m. intermandibularis. The vocal slits are small and extremely posterolateral in position. In all species examined with this pattern, the internal mucosae are separate and strongly restricted to the lateral portion of the gular region; thus, the medial gular region is only slightly expanded during vocalization. The postmandibular lymphatic septum is inserted directly posterior to the mandibular

joint, thereby restricting posterior expansion of the paired lobes (distinguishing these vocal sacs from pattern 5C).

Vocal sacs of pattern 6B occur in two genera of Ranidae. First, they are a synapomorphy of *Pelophylax* and are practically identical in all species of the genus. In this genus, the gular skin is configured into paired pouches that resemble those described above for *Ptychadena* (fig. 9), although their position is different. In Ptychadenidae, the pouches are located ventrolaterally in the gular region and have a lateral opening, whereas in *Pelophylax*, they lie next to the mandibular joints and are dorsally oriented. The pouch inflates dorsally because the skin ventral to the eversible lobe is less distensible than that dorsal to it.

Additionally, in a few species of the ranid genus *Lithobates* (*L. areolatus*, *L. berlandieri*, *L. kauffeldi*, and *L. sphenocephalus*), the vocal sacs inflate dorsally in the form of two spheres on either side of the head. However, unlike in *Pelophylax*, the elastic portions of the skin are diffuse and do not form discrete pouches with such complex folding. Moreover, although the inflatable lobes are more densely pigmented than the surrounding skin in some species, pigmentation is not highly localized and restricted to the most elastic portion as in *Pelophylax*. Many other species of *Aquarana*, *Amerana*, *Boreorana*, *Rana*, and *Lithobates* have similar lobes of the m. interhyoideus; however, because they lack a distensible portion, the vocal sacs do not project dorsally. These observations highlight the significance of this type of skin modification for the dorsal projection of vocal sacs in *Pelophylax*, unlike the previous vocal sac pattern.

Evolutionary Patterns

We scored the 17 characters described earlier in 4358 species of Anura to reconstruct evolutionary patterns and infer synapomorphies. Our sampling encompasses ~57% of currently recognized anuran species. The full data matrix and references can be found in the online supplement files S1 and S2 (https://doi.org/10.5531/sd.sp.73). We performed ancestral character state reconstructions in the phylogeny of Portik et al. (2023), the most densely sampled hypothesis to date regarding taxa and character sampling.

Additionally, we scored the 20 vocal sac shapes for most species based on scientific and nonscientific sources (e.g., online image databases with reliable taxonomic information). We also optimized these 20 shapes treating them as a nonadditive, multistate character. Despite not being strictly a homology hypothesis (but rather a combination of several independent character states), this reconstruction synthesizes the information contained in the 17 characters we described and enables us to discuss major patterns of vocal sac evolution with greater clarity. Ancestral character state reconstruction of vocal sac shape is shown in figure 16 (summarized to the family level) and fully developed in the online supplement file S3 (https://doi.org/10.5531/sd.sp.73). Note that even though the phylogenetic hypothesis of Portik et al. (2023) includes 5242 species of anurans, several species from our matrix are not present in the tree. Thus, the number of transformations and the patterns present in some families are underestimated. For information on specific groups of interest, see the data matrix and the Discussion below, which include the data for all the species.

In addition to the 20-state codification scheme of vocal sac shape, we include two alternate arrangements—one based on seven scores (vocal sac absent, single subgular, bilobate, triple, paired subgular, paired lateral, and paired dorsal) and the other on only two scores (vocal sac present or absent). These were used to calculate disparity measures and maximize the utility of this dataset for a variety of future studies.

The vocal sac is absent in the early diverging clades of Anura (Ascaphidae, Leiopelmatidae, Alytidae, and Bombinatoridae), but it evolved relatively early in the order. However, the origin of the vocal sac in Anura is ambiguous, because it is present in Rhinophrynidae and Acosma-

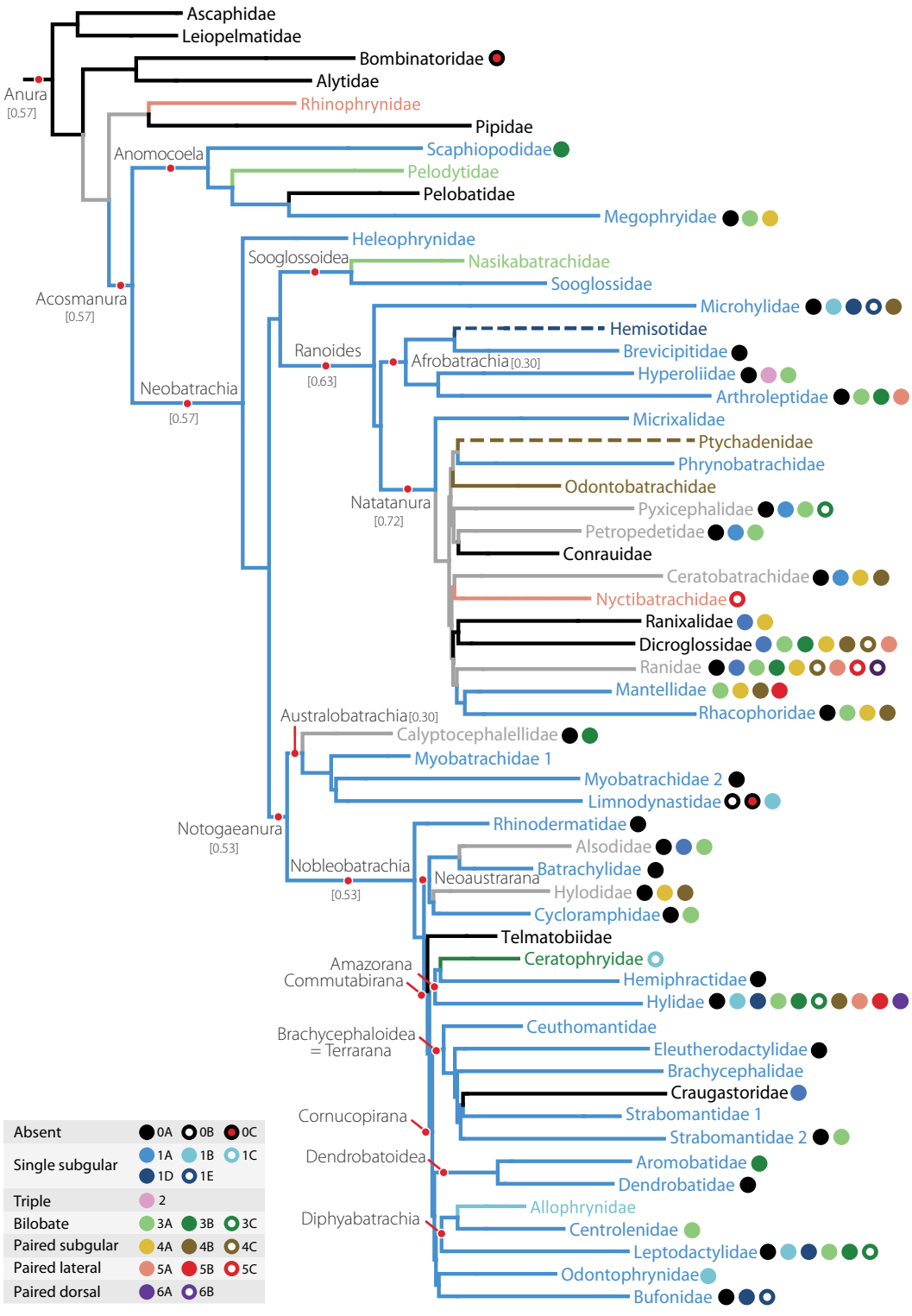
nura, but absent in Pipidae (fig. 16). This implies that it is equally parsimonious to infer a single origin in the sister group of Bombinatoridae + Alytidae with a subsequent reduction in pipids, or two independent origins (one in Rhinophrynidae and another in Acosmanura). Considering that pipids are a highly modified clade, the first scenario seems more likely, even though our evidence does not allow us to prefer one hypothesis over the other. On the other hand, the morphology of the vocal sac in Rhinophrynidae and early acosmanurans is considerably different. In *Rhinophrynus*, vocal sacs are paired lateral with subgular inflation and involve unique features of the mm. intermandibularis and interhyoideus. In Acosmanura, vocal sacs inflate as spherical, single subgular vocal sacs in most early diverging clades. This condition was retained in many species, mainly in Notogaeanura, Microhylidae, and Afrobatrachia, with subsequent transformation to all other vocal sac patterns. Although *Bombina bombina* lacks a proper vocal sac (i.e., vocal slits and protruding mucosae absent), the buccal floor in males greatly expands during vocalization. This species could arguably represent a third independent origin of cooptation of the buccal cavity by the vocal apparatus in the history of anurans.

Vocal sacs were lost between 146 and 196 times in Acosmanura, the most inclusive clade in which vocal sacs are plesiomorphically present. Examples of species that have lost vocal sacs can be found in almost all anuran families. Interestingly, although there are several relatively large clades in which the loss of the vocal sac is homologous (e.g., Ranixalidae + Dicroglossidae, Telmatobiidae, Craugastoridae, *Rana*, *Scutiger* + *Oreolalax*), usually vocal sacs are secondarily absent in clades with fewer than five species. Further, in some diverse genera, vocal sacs were lost and regained several times resulting in complex patterns. For example, regardless of the resolution of nodes with low support, in *Craugastor* (Craugastoridae), *Gastrotheca* (Hemiphractidae), *Amolops*, *Lithobates*, *Odorrana*, and *Rana* (Ranidae), and *Pristimantis* (Strabomantidae), several internal transformations occurred; each taxon is discussed below.

We recovered an ambiguous reconstruction regarding the fusion of mucosae in the early evolution of vocal sacs. They are absent in Pipidae and Pelobatidae; disconnected in adult Rhinophrynidae, *Spea* (Scaphiopodidae), and Pelodytidae, but they are fused in *Scaphiopus* (Scaphiopodidae), Megophryidae, and Phthanobatrachia. Thus, we could not determine whether the ancestral vocal sac of Acosmanura evolved as a single or a paired structure. Unfortunately, this ambiguity cannot be resolved by the addition of new information (e.g., the condition for Heleophrynidae, unavailable for the present study).

Plesiomorphically, vocal slits are elongate in Acosmanura. Subsequently, small, circular orifices located in the posterolateral ends of the buccal floor evolved independently in Megophryidae and several times in Indianura (e.g., in Arthroleptidae, Brevicipitidae, Ceratobatrachidae, Ranidae + Mantellidae + Rhacophoridae, Sooglossidae). However, a large ambiguity was recovered in the optimization of suprafamiliar nodes. This includes species with both disconnected and fused mucosae. In contrast, in many species of Hyperoliidae, Microhylidae, Phrynobatrachidae, Pyxicephalidae, and Notogaeanura (all cases in which vocal sacs are most commonly single, subgular), vocal slits are large, elongate slits located in the anterior half of the buccal floor.

The shape of the fully inflated vocal sac is highly variable. We recovered 314 transformations of vocal sac shape using the 20-state scheme. Most families have more than one pattern and in some, there is an astounding diversity of patterns (e.g., Ranidae, 11 patterns; Hylidae, 9 patterns; Dicroglossidae, 7 patterns). The single, spherical vocal sac is the most common, being present in 66.7% of sampled species. Plesiomorphically present in Acosmanura, it has persisted in many families across anuran evolution. A detailed discussion of the results in the context of the taxonomy of each family, including the recognition of synapomorphies for several taxa, is provided below (Systematic and Taxonomic Accounts).


Ascaphidae
Leiopelmatidae
Bombinatoridae
Alytidae
Anura
[0.57]
Rhinophrynidae
Pipidae
Anomocoela
Scaphiopodidae
Pelodytidae
Pelobatidae
Megophryidae
Heleophrynidae
Sooglossoidea
Nasikabatrachidae
Sooglossidae
Acosmanura
[0.57]
Microhylidae
Hemisotidae
Ranoides
[0.63]
Afrobatrachia [0.30]
Brevicipitidae
Hyperoliidae
Neobatrachia
[0.57]
Arthroleptidae
Micrixalidae
Ptychadenidae
Phrynobatrachidae
Odontobatrachidae
Natatanura
[0.72]
Pyxicephalidae
Petropedetidae
Conrauidae
Ceratobatrachidae
Nyctibatrachidae
Ranixalidae
Dicroglossidae
Ranidae
Mantellidae
Rhacophoridae
Australobatrachia [0.30]
Calyptocephalellidae
Myobatrachidae 1
Myobatrachidae 2
Limnodynastidae
Notogaeanura
[0.53]
Rhinodermatidae
Alsodidae
Batrachylidae
Nobleobatrachia
[0.53]
Neoaustrarana
Hylodidae
Cycloramphidae
Telmatobiidae
Ceratophryidae
Amazorana
Commutabirana
Hemiphractidae
Hylidae
Ceuthomantidae
Brachycephaloidea
= Terrarana
Eleutherodactylidae
Brachycephalidae
Craugastoridae
Cornucopirana
Strabomantidae 1
Strabomantidae 2
Dendrobatoidea
Aromobatidae
Dendrobatidae
Allophrynidae
Diphyabatrachia
Centrolenidae
Leptodactylidae
Odontophrynidae
Bufonidae
Absent
0A 0B 0C
Single subgular
1A 1B 1C
1D 1E
Triple
2
Bilobate
3A 3B 3C
Paired subgular
4A 4B 4C
Paired lateral
5A 5B 5C
Paired dorsal
6A 6B

Disparity Measures

The vocal sac is a highly variable structure, but this diversity is not equally distributed in all groups. Using the 20-state vocal sac classification, we calculated mean pairwise distances (MPD; indicative of the internal diversity of a group) for all anuran families and major suprafamiliar clades (appendix 2). Values vary among families from zero (all species equal; e.g., Telmatobiidae, Ptychadenidae, etc.) to one (all species different; e.g., Calyptocephalellidae). The MPD is independent of clade size (e.g., both Hylidae and Hylodidae have a value of 0.47, with 1037 and 48 species, respectively). Among major Neobatrachian clades, Natatanura has the highest MPD value, 0.72 (fig. 16). In contrast, vocal sac morphology is much less variable in Afrobatrachia, Australobatrachia, and Nobleobatrachia, (MPD values 0.29, 0.30, and 0.53, respectively).

Independent Origins and Transformations between States

We calculated the number of independent origins of each vocal sac shape and the inferred transformations among them (fig. 17) based on the phylogenetic hypothesis of Portik et al. (2023; thus, only considering the species included therein). To simplify and clarify our results, we show transformations calculated with the seven-state classification (instead of the 20-state classification).

Most vocal sac shapes evolved several times in Anura, but the number of independent origins was highly variable. Whereas paired dorsal vocal sacs (i.e., pattern 6) originated only six times in the group, the loss of a vocal sac (i.e., pattern 0) evolved between 125 and 160 times, depending on the optimization. This number was calculated using the seven-state scheme, which differs, for methodological reasons, from the number presented above (146–196 times) calculated with the two-state scheme. At the same time, some transformations were much more frequent than others (e.g., 1→0 occurred 108–138 times), and not all transformations were observed. The single subgular vocal sac is the plesiomorphic state when the vocal sac is most frequently lost and the most common vocal sac shape present in groups that regained a vocal sac. In some groups (e.g., Bufonidae, Craugastoridae, Strabomantidae), the single subgular vocal sac is lost and regained several times independently, whereas in others (e.g., Centrolenidae, Dendrobatoidea, Mantellidae, Microhylidae), it is present in most of the species. Likewise, in *Lithobates* and *Rana* (Ranidae), there are several transformations between the paired vocal sacs and the absence of a vocal sac (both ways) unlike in other taxa (e.g., Nyctibatrachidae; *Pelophylax*), in which they are never lost.

DISCUSSION

A Highly Diverse System

Anuran vocal communication has long fascinated both science and culture. Historically, bioacoustics and especially the study of advertisement calls as premating isolation mechanisms useful for species identification have played an important role in anuran taxonomic and reproductive studies (Köhler et al., 2017). In the past 15 years, new evidence has broadened our understanding of the

Fig. 16. Evolution of vocal sacs in Anura. Optimization of the 20 vocal sac patterns defined here in the phylogenetic hypothesis of Portik et al. (2023) condensed to family level clades (See online supplement S3 for the full optimization). Colors of terminal branches indicate the plesiomorphic/ancestral condition for the family, often present in most species of each clade. Additionally, other vocal sac patterns evolved secondarily inside each family, which is indicated by colored circles next to the family names. The presence of a novel pattern is indicated only once, regardless of the number of independent origins inside the family. Branches and circles follow the same color key (below left). Note that the ancestral state for Ptychadenidae is pattern 4C and 1E for Hemisotidae. Gray branches represent missing data or ambiguous optimizations. No circle next to a family name implies that all studied species of the clade retain the plesiomorphic state. Numbers in brackets indicate the value of Mean Pairwise Distance (MPD) for each clade.

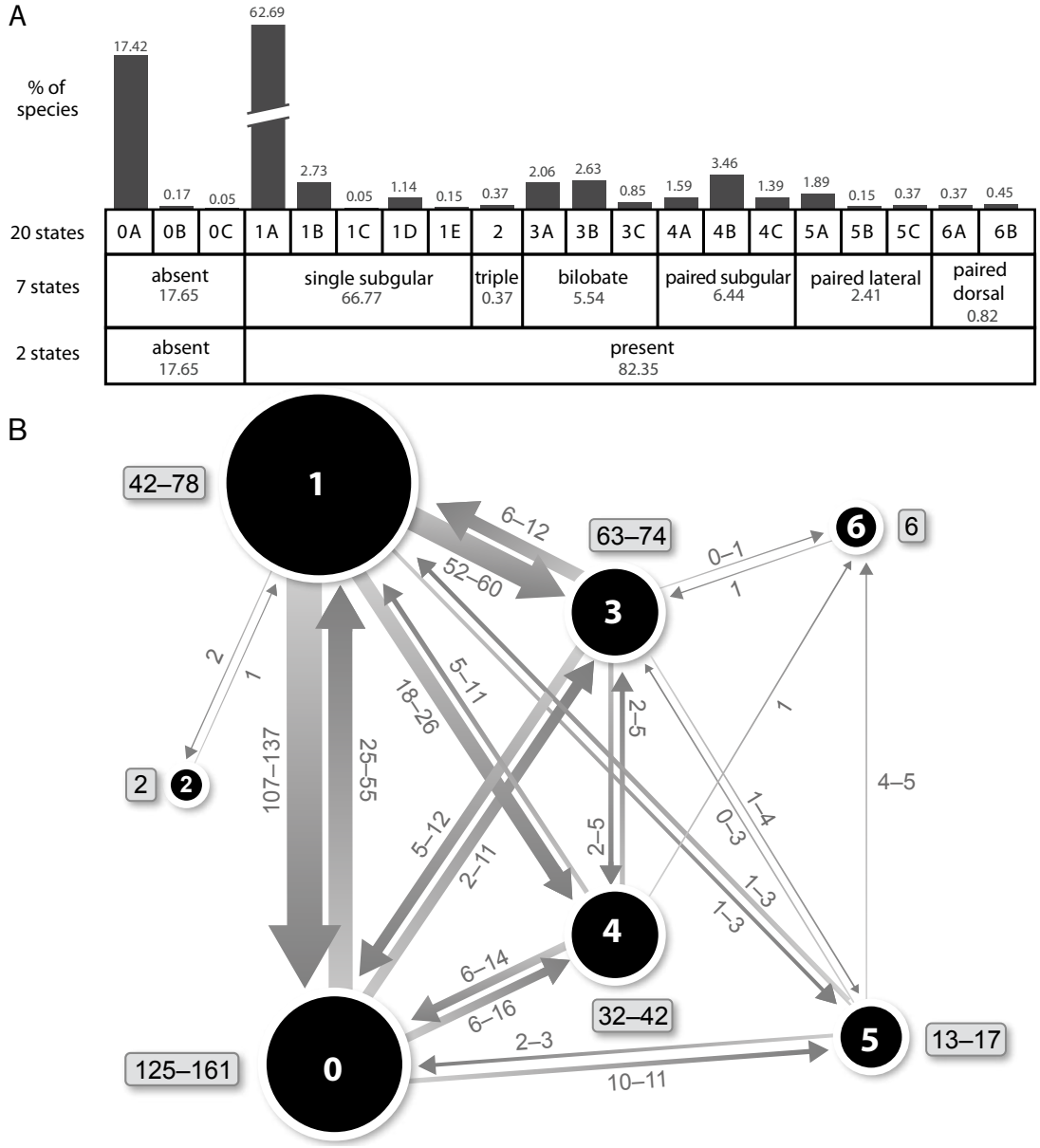


FIG. 17. **A.** Proportion of each vocal sac pattern in the studied species, based on a sample size of 4023 species. Values are shown for the three alternate codifications, 20 states, 7 states, and 2 states. **B.** Transformations among character states using the seven-state classification to facilitate the communication of our results, based on optimization of our matrix in the phylogenetic hypothesis of Portik et al. (2023). The maximum and minimum number of independent origins (considering alternate, equally parsimonious reconstructions) is shown in gray squares next to each character state. Numbers next to arrows indicate the number of independent transitions from one state to the other. Circle size represents proportion of species with that pattern and arrow thickness reflects the frequency of each transformation.

function of the vocal sacs, indicating that they are not restricted to acoustic communication (Narins et al., 2003; Cummings et al., 2008; Gómez et al., 2009; Sztatecsny et al., 2010; Preininger et al., 2013; Starnberger et al., 2013, 2014).

The anatomical diversity of anuran vocal sacs (fig. 3) is generated by combinations of states of the same three elements (a thin internal mucosa, a flat layer of muscle fibers and the gular skin). Evidently, the gular region of anurans was a site of evolutionary innovations. This is particularly true for the m. interhyoideus, the homology of which can be traced back to early gnathostomes or even cyclostomes (Diogo et al., 2018). In most vertebrates, this muscle consists only of a band of parallel fibers supporting the gular region; however, in anurans the muscle architecture is diverse. The number of bellies, fiber orientation (often forming orthogonal layers), attachments, and relative thickness of the muscle varies greatly (Elias-Costa et al., 2021).

Among the several features of the anuran musculoskeletal system that might have favored this diversification are the relative expansion of the head and the mandibular arch (relative to body size), the composition of bony elements of the jaw, and/or the structure of the hyoid. In addition, the large lymphatic sacs that separate the gular skin from the underlying musculature may have fostered the independent evolution of the gular skin and the muscles; as an example, the m. interhyoideus can expand and protrude in different directions irrespective of the gular skin. Also, a key element that contributed to the diversification of vocal sacs in frogs and toads is the enrichment of elastic fibers in the m. interhyoideus. Although atypical of skeletal muscles, the m. interhyoideus in many anuran species accumulates large amounts of elastic fibers in its extracellular matrix (Jaramillo et al., 1997; Targino et al., 2019) and elastin can form specific arrangements that determine vocal sac shape and function (Savitzky, 2000, 2002; Elias-Costa et al., 2021).

Traditionally, four categories were employed to describe vocal sac shapes in anurans (fig. 2; Liu, 1935; Duellman, 1970). The variation in the internal mucosae, submandibular muscles, and sexually dimorphic skin modifications revealed a great deal of internal diversity in each of them. Moreover, by integrating this anatomical information with images and videos of vocalizing males we produced a new classification, which we applied to more than 4300 species. This updated classification, in which each pattern is diagnosed by a set of internal anatomical structures, has several implications. First, it provides a standard terminology that differentiates structures that were traditionally merged under the same terms. For instance, the term "dorsal vocal sacs" was applicable to both *Pelophylax* (Ranidae) and *Trachycephalus* (Hylidae), even though they are anatomically and evolutionary distinct. Thus, we are able to identify new synapomorphies and diagnostic characters for several taxa (treated below in the Systematic and Taxonomic Accounts). In addition, our focus on internal anatomy allows us to understand the transformations that led to the evolution of each pattern. For example, several features of the m. interhyoideus that define the dorsal vocal sacs in *Pelophylax* and *Trachycephalus* are plesiomorphic for these genera and can be found in other closely related species. Similarly, it is useful to understand the differences among vocal sacs that may resemble one another externally but that are internally distinct (e.g. *Nyctimantis siemersi*, Hylidae and *Nyctibatrachus major*, Nyctibatrachidae; see fig. 5I, J). Additionally, a considerable portion of the diversity of vocal sac shapes is related to modifications of the gular skin. Although Boulenger (1896) and Liu (1935) considered this diversity when describing the vocal sacs of many species, the information was not incorporated into their classification. These authors differentiated between "internal" and "external" vocal sac—a distinction still broadly used—but without specifying the nature of that modification. Thus, a detailed characterization of skin modifications has taxonomic value, providing

insights into the dynamic of vocal sac inflation, such as directing air in specific directions. For instance, two types of external bilobate vocal sacs were identified here (patterns 3B and 3C), where specific arrangements of rigid and elastic areas produce specific patterns of inflation.

The Ambiguous Origin of the Vocal Sac

The origin of the vocal sac in Anura is ambiguous, because two scenarios are equally parsimonious (fig. 16). They either evolved (1) in the sister group of Bombinatoridae + Alytidae with a subsequent reduction in Pipidae or (2) in Rhinophrynidae and Acosmanura independently. This ambiguity cannot be resolved given the evidence currently available. One key question is whether the absence of a vocal sac in pipids is homologous to that of basal anurans. Pipimorpha, the total group that includes extant pipids, has an abundant fossil record (Báez, 1996; Gómez, 2016), but the lack of preserved soft tissues hinders the reconstruction of the evolutionary history of this character system. Extant pipids lack a tongue, have an extremely modified hyoid and larynx, and vocalize underwater producing clicks that are not based on airflow (although airflow was regained in *Hymenochirus*; Irisarri et al., 2011). It is plausible that this major rearrangement of the gular region caused the loss of the vocal sacs at some point in the history of this group.

It is difficult to establish whether the vocal sac in *Rhinophrynus* is homologous to that of acosmanurans. The structure of the vocal sac in this species is essentially the same as those found in all other anurans (paired mucosae derived from the buccal floor, externally covered by submandibular muscles), which is consistent with a common origin. However, *Rhinophrynus* has a highly derived overall morphology, including features of the mm. intermandibularis and interhyoideus not found in any other species (Walker, 1938; Trueb and Gans, 1983; Tyler, 1974b; Trueb and Cannatella, 1982; Elias-Costa et al., 2021). Moreover, males have a complex, paired lateral vocal sac that inserts in the sternum and develops dorsally around the head. Even though hypothesis "(1)" appears more likely, this question remains unresolved.

Transformations of Vocal Sac Shape

The vocal sac is a highly plastic structure, both in terms of morphological diversity and its evolution. Nonetheless, we identified some general patterns of diversity and some factors that are likely to constrain the evolution of the vocal sac and the origin of novel vocal sac shapes. Moura et al. (2021) showed that the shape of the internal mucosae has a great impact on the overall shape of the inflated vocal sac. Our results suggest that the fusion or disconnection of mucosae also may have had an important, yet more indirect, effect on vocal sac evolution, by establishing constraints for the origin of novel shapes.

In several clades in which the mucosae are plesiomorphically fused forming a single cavity, the most frequent source of new vocal sac morphologies was the deformation of the spherical shape. For example, in Microhylidae, Bufonidae, Leiuperinae (Leptodactylidae), *Hyla* or *Pseudacris* (Hylidae), lateral, anterior, and/or anterodorsal projection evolved several times independently, always from a spherical ancestor. However, among these taxa that include about 1500 species, bilobate or paired vocal sacs occur only in two species (*Hyla hallowellii* and *Otophryne pyburni*, respectively).

In contrast, in some clades in which two separate vocal sac cavities are retained in adults (e.g., Natatanura or Lophyohylini [Hylidae]), the structure of the paired vocal sacs diversified. For instance, several groups in Natatanura evolved paired vocal sacs with pouchlike projections of the subgular portion of the m. interhyoideus. In these taxa, the orientation of these pouches is interspecifically variable, which produces a considerable diversity of vocal sac shapes (summarized in fig. 5). The best example of this is Ranidae, in which the ventral portion of this muscle projects ventrally, posteriorly, or dorsally depending on the species.

Vocal Slits

Liu (1935) reported that paired vocal sacs were associated with small, posterior vocal slits—an observation that is largely corroborated here. Species with paired vocal sacs usually have smaller vocal slits located further posteriorly than do species with single subgular sacs. While 14% of species with a single subgular sac have small orifices, 74% have elongate slits, and 12% have gaping holes, in species with paired vocal sacs (subgular, lateral and dorsal), the same proportions are 60%, 25%, and 15%. Moreover, in some clades, transformation from paired to single vocal sacs is coupled with the evolution of larger, more elongate slits (e.g., *Nidirana*, Ranidae). This trend is not surprising given that large, anterior vocal slits would allow air into the center of the gular region, whereas small posterolateral slits conduct air directly to the posterolateral portions of the vocal sac. Nevertheless, several exceptions to this general trend were observed. Vocal slits are elongate or gaping holes in some species with paired vocal sacs, such as *Euphlyctis* and *Hoplobatrachus* (Dicroglossidae), *Itapotihyla*, and some *Osteocephalus*, *Osteopilus*, *Pseudis*, and *Trachycephalus* (Hylidae), most Hylodidae, and Rhinophrynidae. In some of these taxa, phylogenetic inertia probably is responsible for the conservation of the shape of vocal slits. (For example, vocal apertures in hylids are usually elongate or large holes, even in species with paired vocal sacs; Tyler, 1971a.) In addition, several species with single, spherical vocal sacs have small, posteriorly located vocal slits; for example, the following taxa: *Arthroleptis*, *Cardioglossa*, some *Leptopelis* and *Leptodactylodon* (Arthroleptidae); *Cruziohyla*, *Phyllodytes* (Hylidae); *Blommersia*, *Boophis*, *Mantella* (Mantellidae); all megophryids with vocal sacs; *Kurixalus* (Rhacophoridae), and *Sechellophryne* (Sooglossidae). In many of these species, the vocal sac is relatively small in relation to body size and is located in the posterior part of the gular region (fig. 3B). Moreover, small circular slits always are located in the posterior third of the buccal floor; thus, the anterior limit of the inflated vocal sac is usually posterior to that of species with long, elongate slits or gaping holes. Although it could be argued that small vocal apertures may restrict the flow of air that enters the vocal sac during vocalization and potentially constrain the evolution of voluminous vocal sacs, the fact that some species have both relatively large vocal sacs and small circular slits tends to question that hypothesis or at least its level of generality (i.e., perhaps it is the small vocal apertures in combination with other particular, as yet unknown character state that produce an evolutionary constraint).

Drewes (1984; although first reported by Perret, 1966) described muscle fibers derived from the m. petrohyoideus anterior that form a sphincter around the vocal slits of some species of Arthroleptidae, Phrynobatrachidae, and Ranidae. Macroscopically, these apertures have thickened, rigid margins compared with the surrounding buccal mucosa. These structures were observed here in some species of Ceratobatrachidae, Hyperoliidae, Mantellidae, Nyctibatrachidae, *Ptychadena*, Rhacophoridae, and in additional ranid and arthroleptid species that were not reported by Drewes (1984). Outside Ranoides, sphincteric vocal slits also occur in *Phyllodytes* (Hylidae), but the muscle fibers are derived from the m. geniohyoideus lateralis in these species (Moura et al., 2021). Vocal slit sphincters may permit the frog to open its mouth and/or the nares without loosing (or reducing the loss of) air pressure inside the vocal sac, as would happen in species with larger vocal slits, in which the pressure of the buccal and vocal sac cavities are equaled (Gans, 1973; Drewes, 1984). To our knowledge, no direct observations of this phenomenon have been reported.

In several species, the vocal slits are small and posterior; superficially, they resemble those described above but they lack muscle fibers (e.g., *Corythomantis*, *Itapotihyla*, *Osteocephalus*; Hylidae; Moura et al., 2021). The presence or absence of muscle fibers could not be determined without histological examination

of species in the following taxa: Megophryidae, Sooglossidae, Ptychadenidae, Nyctibatrachidae, Odontobatrachidae, several Arthroleptidae, Ceratobatrachidae, Dicroglossidae, Hyperoliidae, Rhacophoridae, Ranidae, *Litoria longirostris*, and *Gastrotheca trachyceps*.

Multiple Losses of Vocal Sacs

Given the key role that vocal sacs play in anuran communication, the number of independent losses we inferred, between 146 and 196, is remarkable, especially because the losses occur in species having extremely diverse habits and life histories. We expect this to be the result of several factors and clade-specific processes. Most clades in which vocal sacs are lost are relatively small (1–5 species); only a few groups contain more taxa, suggesting that small scale, local processes are more influential than any macroevolutionary tendency. Moreover, there are many examples of ecologically similar sister taxa, in which one has a vocal sac and the other does not.

The selective pressures responsible for the high rate of vocal sac loss in anurans are unclear, particularly because many of the groups in which they are lost still retain a vocalization (Wells, 2007). Although the subject has not been addressed from a global perspective, preliminary hypotheses have been proposed for some specific groups. These include the influence of ambient noise that would hinder the correct interpretation of the signals (Menzies, 1976; Trueb, 1979; Penna and Veloso, 1987, 1990); low population density, oxygen pressure, and temperature at high altitudes, affecting the energetically expensive process of vocalization (Hu et al., 1985; Liao and Liu, 2008; Che et al., 2009); or recurrence to stable breeding sites across seasons that do not require the attraction of females through long-distance signals (Wells, 1977, 2007). However, all these hypotheses attempt to explain the loss of vocalization, but not necessarily explain the loss of vocal sacs. Many species have lost the vocal sac but still vocalize, and even call similarly to their closely related, vocal sac-bearing species (e.g., Faivovich et al., 2010; Pombal et al., 2010; Bezerra et al., 2021; Santos et al. 2022). To fully understand this interesting phenomenon, a specific, quantitative analysis is required, such as a correlation analysis between the presence of vocal sac and ecological and acoustic variables.

In a few species, the processes driving the loss of a vocal sac seem more obvious. One of the proposed functions of the vocal sac is to reduce the impedance mismatch between the internal medium of the animal and the environment. This mismatch is greatest in the air, where most species vocalize, but some species call underwater, where the mismatch is diminished. Accordingly, it has been suggested that species that vocalize underwater tend to lack vocal sacs (Wells, 2007; Zheng and Xie, 2022). It seems unlikely that an anuran with vocal sacs would vocalize underwater because of the difficulty of storing large volumes of air in the lungs while submerged. Reports of underwater vocalization include members of Alsodidae, Megophryidae, Pelodytidae, Pipidae, Ranidae, and Telmatobiidae (Yager, 1992a; Northen, 1993; Platz, 1993; Christensen-Dalsgaard and Elepfandt, 1995; Given, 2005; Wells, 2007; Zheng et al., 2011; Brunetti et al., 2017; Zheng, 2019; Zheng and Xie, 2022). Doubtless this list is incomplete because underwater calls usually are weak and can be masked by the noise of flowing streams and, thus, are easily overlooked. Vocal sacs are absent in all these species, with the exception of pelodytids (in which they are poorly developed) and some ranids, all of which also vocalize above water (*Lithobates palustris*, although many specimens lack them, *L. pipiens* and *Amerana boylii*; Hillis and de Sá, 1988; MacTague and Northen, 1993; Given, 2005; Wheeler and Welsh, 2008: Díaz-Rodríguez et al., 2017).

Multiple Origins of Paired Vocal Sacs

Paired vocal sacs (subgular, lateral, or dorsal) originated between 45 and 60 times in Anura. These evolved in clades or species of Dicro-

glossidae, Hylidae, Hylodidae, Mantellidae, Nyctibatrachidae, Odontobatrachidae, Ptychadenidae, Ranidae, Ranixalidae (but see comment below), and Rhinophrynidae. In all these taxa, apart from some *Osteocephalus* and *Osteopilus* (Lophyohylini, Hylidae), the internal mucosae of the vocal sacs are always disconnected. Thus, there is a nearly perfect cooccurrence of external lateralization and internal disconnection of the mucosae. Moreover, most species with paired vocal sacs are found in Natatanura, the largest clade in which the disconnection of mucosae is homologous. Possibly, the early origin of disconnected mucosae allowed subsequent, independent evolution of vocal sac lateralization.

Paired vocal sacs evolved by means of one of three transformational patterns of the unmodified m. interhyoideus, each with its own range of variation. In one pattern, there is a pair of expansions of the subgular portion of the muscle; in some taxa, these expansions may come to project either posteriorly or dorsally. This pattern characterizes all species with paired vocal sacs in Natatanura (except in the *Boophis occidentalis* group, Mantellidae), as well as a few taxa outside this clade (some *Pseudis*, *Smilisca*, Hylidae, and possibly a clade of *Eleutherodactylus*, Eleutherodactylidae). In the second pattern, the lateral part of the m. interhyoideus is expanded to produce vocal sacs that inflate at the sides of the head, behind the jaw articulations. This pattern was found only in *Rhinophrynus*, some Lophyohylini hylids, and the *Boophis occidentalis* group. In the third pattern, each internal mucosa protrudes through a gap in the m. interhyoideus; this arrangement is found only in some Hylodidae and Ranidae. Notably, the pattern occurs in diurnal species that perform visual displays during courtship and agonistic encounters, and (at least in some species) is likely related to the production of visual signals through the selective inflation of only one of the paired subgular vocal sacs (Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019).

Tyler (1971a, 1971b, 1971c, 1972) suggested that the presence of the m. cutaneus pectoris could affect the evolution of vocal sacs. This paired muscle, which originates in the abdominal fascia and inserts in the ventral skin, adjacent to the posterior surface of the pectoral lymphatic septum, is a putative synapomorphy of Natatanura (with reversions in a few rhacophorids and phrynobatrachids; Liem, 1970; Tyler, 1971b; Drewes, 1984; Scott, 2005). Tyler (1971a) suggested that the tension produced by this muscle (both active and passive) would restrict the distensibility of the pectoral skin, hampering the inflation of a large, subgular vocal sac. Thus, the presence of this muscle could favor the origin of paired vocal sacs because the mass of air is directed laterally. However, the muscle is well developed in many species with large, single vocal sacs (e.g., *Occidozyga*, *Phrynobatrachus*, *Cacosternum*, *Pyxicephalus*, *Philautus*), suggesting that a causal link between paired vocal sacs and the presence of the m. cutaneous pectoris is incidental. In addition, the muscle is thought to play a role in moving the lymph of the abdominal and pectoral lymphatic sacs (Gaupp, 1899; Drewes et al., 2007). The m. cutaneus pectoris probably affects (or even controls) the distensibility of the pectoral lymphatic septum and defines the posterior limit of the vocal sac. In species lacking this muscle, the abdominal skin could be freer to expand, allowing the inflated vocal sac to extend toward the abdomen (e.g., *Microhyla*, *Megophrys*, several Bufonidae, *Rhinoderma*). However, the evolution of paired vocal sacs does not require the presence of the m. cutaneous pectoris, as evidenced by the Notogaeanura with paired vocal sacs that lack the muscle.

Another key element in the evolution of paired vocal sacs is skin modification. The topological variation in skin properties (namely thickness, elasticity, gland composition) in the gular skin is highly localized, particularly in species with paired vocal sacs. Restricted patches of elastic skin, separated by nondistensible skin, are necessary for the differentiation of two individual vocal sacs. Moreover, they are fundamental for the projection of the vocal sacs in different

directions. This is particularly evident in gular pouches, which have a specific arrangement of elastic and rigid portions that direct the air ventrolaterally (e.g., *Ptychadena*), anterolaterally (*Euphlyctis cyanophlyctis*), or dorsally (*Pelophylax*) (see char. 15).

Systematic and Taxonomic Accounts

The available knowledge on vocal sac diversity in each anuran family is reviewed below. Specific patterns of vocal sac evolution are discussed in a taxonomic context, and fine-scale structural variation is described. The most relevant synapomorphies are identified, along with unique features of specific groups that might be relevant in the evolution of vocal sacs and acoustic behavior. Synapomorphies are inferred based on the ancestral character state reconstruction on the phylogenetic hypothesis of Portik et al. (2023), available in the online supplementary file S3, which includes figures S1–S19.

Allophrynidae

Vocal sacs in this small family are single, subgular, and semicircular, with uniformly distributed skin modification, and relatively large inflation volumes (Lynch and Freeman, 1966; Hoogmoed, 1969: pl. 2; Castroviejo-Fisher et al., 2012: fig. 2E; Caramaschi et al., 2013: fig. 5). This semicircular shape is synapomorphic for the family (online supplement S3: fig. S17). Vocal slits are gaping holes in the only species for which there is information, *A. ruthveni*. In *Allophryne resplendens* and *A. ruthveni*, adult males have white markings on the lower lip, but these do not extend posteriorly to the vocal sac, which have a dark, grayish coloration and are semitransparent (Hoogmoed, 1969; Castroviejo-Fisher et al., 2012). In *A. relicta*, the vocal sac is somewhat more spherical than semicircular, and is bright yellow (Caramaschi et al., 2013). Tyler (1971) reported on the submandibular musculature of female *A. ruthveni.*

Alsodidae

Each of the three genera of the family has a different pattern of vocal sac (online supplementary file S3: fig. S9). First, they are absent in *Alsodes*, a condition that was recovered here as a synapomorphy of the genus. Curiously, the taxonomic literature of *Alsodes* lacks specific mentions of the absence of vocal sacs (Cei and Roig, 1965; Cei, 1976, 1980; Formas et al., 1997; Cuevas and Formas, 2001, 2005; Cuevas, 2008; Charrier et al., 2015). Likewise, little is known about the genus *Eupsophus*, in which the single, subgular, internal sacs are poorly developed but are undoubtedly present (Cei, 1962; Nuñez et al., 2012; Correa and Durán, 2019). Third, vocal sacs are bilobate and internal in the remainig genus of the family, *Limnomedusa* (Cei. 1980, Elias-Costa and Faivovich, 2019).

In the species of *Eupsophus* and *Limnomedusa* examined, vocal slits are elongated; the internal mucosae are disconnected and highly developed medially to occupy most of the gular region (Elias-Costa and Faivovich, 2019: fig. 1). The phylogenetic position of *Limnomedusa* is poorly supported and the genus is only provisionally included in this family (Blotto et al., 2013; Sabbag et al., 2018; Portik et al., 2023); thus, it is possible that disconnection of mucosae evolved independently in this monotypic genus and in *Eupsophus*. The submandibular musculature of representatives of the three alsodid genera was studied by Burton (1998). Cei and Roig (1965) mentioned that male *Alsodes pehuenche* (as *Telmatobius montanus:* Cei, 1976) call underwater during the day. Some species of *Eupsophus* vocalize from underground burrows, which amplify and affect the spectral parameters of the calls (Formas, 1985; Penna and Veloso, 1990; Penna and Solís, 1999; Penna, 2004; Muñoz and Penna, 2016).

Alytidae

Vocal sacs are absent in *Alytes* and *Discoglossus* (Boulenger, 1882; Liu, 1935). Tyler (1980)

revised the submandibular muscles in representatives of these genera and close relatives. A unique type of vocalization mode was reported for *Discoglossus galganoi*, *D. pictus*, and *D. sardus* (but not *D. montalentii*); it consists of an alternating sequence of both expiratory and inspiratory notes (Weber, 1974, Glaw and Vences, 1991). Presumably, the same mechanism is also present in *Latonia*, in which males produce calls with low frequency and very low intensity (Perl et al., 2017). Females of *Alytes cisternasii* and *A. muletensis* also emit courtship and advertisement calls, an atypical feature in anurans (Márquez and Verrel, 1991; Bush, 1997; Wells, 2007). Vocal sacs in *Latonia* are not evident externally (Perl et al., 2017) and probably are absent, although internal anatomical information is lacking for this monotypic genus.

Aromobatidae

Single, spherical vocal sacs of moderate size are present in all species of the family, except for *Allobates femoralis*, in which the sac is bilobate (Grant et al., 2006, 2017). Mucosae are fused in all the species examined and vocal slits are elongate and relatively large. The vocal repertoire and aggressive behavior of *A. femoralis* have been studied extensively, because this was the first anuran species documented to use the vocal sac in bimodal communication (Narins et al., 2003; Amézquita et al., 2006; Gasser, 2009; Montanarin et al., 2011). Visual displays are likely also present in *Allobates kingsburyi* (Castillo-Trenn and Coloma, 2008). The throat coloration in frogs of the genus *Mannophryne* is atypical. Both sexes have a characteristic dark collar that is synapomorphic of the genus, and female *Mannophryne* have a bright yellow gular coloration (La Marca, 1994; Grant et al., 2006; Barrio-Amorós, et al., 2010; Rojas-Runjaic et al., 2018; Greener et al., 2020). Yellow throat coloration in males is common for many species (e.g., *Boana pulchella* group, *Aquarana*, *Phrynobatrachus*, *Rhinella granulosa* group; see accounts in respective families), but its presence in females is exceptional. Females are highly territorial and pulsate their throat without emiting audible sound (to humans) when their territories are invaded (Wells, 2007).

Arthroleptidae

Vocal sacs are plesiomorphically single, subgular, and spherical (fig S3). Vocal slits usually are small and posterior, and in many cases (particularly in *Leptopelis*), they have associated muscle fibers consistent with a sphincter (see comment on char. 4).

In Arthroleptinae, vocal sacs usually are small and lack skin differentiation, and internal mucosae are fused in most species (Liu, 1935; Schiøtz, 1963; Perret, 1966; Stewart, 1967; Channing and Rödel, 2019). Exceptionally, disconnected mucosae were observed in *Arthroleptis stenodactylus* (this study), where skin modification is present and seems to be slightly concentrated in two lateral areas, rather than homogenously distributed in the whole gular region (see Zimkus and Blackburn, 2008: fig. 3), suggesting some degree of bilobation in the vocal sac of this species.

In most species of Leptopelinae, the vocal sacs are single, subgular, and internal, and vary considerably in size interespecifically (Liu, 1935; Perret, 1966; Liem, 1970; Drewes, 1984). Based on the specimens that we examined, we corroborated Drewes' (1984) observation that all *Leptopelis* possess sphincteric vocal slits. Videos or photographs of fully inflated vocal sacs are available only for a few species, and they suggest that vocal sacs in *Leptopelis* rarely protrude beyond the snout anteriorly (as is common, for instance, in hyperoliids). Vocal sacs tend to inflate directly below the jaws and extend slightly posteriorly toward the pectoral region (e.g., Starnberger et al., 2014: fig. 1); inflation is coupled with the emission of one or two short notes and followed by complete deflation in each cycle. Many species vocalize concealed in burrows or dense vegetation (Du Preez and Carruthers, 2009).

Astylosterninae is the most diverse arthroleptid subfamily in terms of vocal sac morphology. However, the results of Portik and Blackburn (2016) and Portik et al. (2019, 2023) challenge the monophyly of the subfamily because these authors found that *Lepodactylodon* forms a separate clade with respect to the remaining genera. As currently defined, the subfamily contains species with no vocal sacs (*Astylosternus robustus*, the only arthroleptid with this condition), species with single, subgular sacs (*Astylosternus fallax*, *Nyctibates*, and *Scotobleps*; Boulenger, 1900; Schiøtz, 1963; Perret, 1966; Channing and Rödel, 2019), and several species with bilobate sacs that have varying degrees of gular skin differentiation (Perret, 1966; Rödel et al., 2012). The bilobate sacs are internal in some species (e.g., *Astylosternus diadematus*, *A. perreti*, *Leptodactylodon boulengeri*, *L. ovatus*), but in others, the gular skin forms two dark elastic portions (e.g., *Leptodactylodon stevarti*; Rödel and Pauwels, 2003). The gular skin is highly modified in some species to include two subgular areas of distended, elastic skin and conical spicules present in the ventral region (e.g *Astylosternus laticephalus* and *A. occidentalis*; Parker, 1936a; Rödel et al., 2012).

Ascaphidae

Vocal sacs are absent in *Ascaphus* (Tyler, 1974a; Wever, 1985; Johnston, 2011). Males apparently do not vocalize, and mate location occurs by active search alongside rocky streams where the species breeds (Noble and Putnam, 1931, Stephenson and Verrell, 2003).

Batrachylidae

Single, subgular, spherical vocal sacs with elongate vocal slits are plesiomorphic for the family (online supplementary file S3: fig. S9), and this condition is found in *Batrachyla*, *Hylorina*, and *Atelognathus nitoi* (although information was lacking for most species of this genus). If present, paired mucosae are fused in all species. In *Batrachyla*, vocal sacs are small to medium size, and males vocalize from the ground, partially concealed by leaf litter (Penna and Veloso, 1990; Penna, 1997). Inflated vocal sacs are largest in *Hylorina*, in which males call exposed, usually perched on vegetation, showing a bright yellow gular coloration (Penna and Veloso, 1990). In contrast, vocal sacs are absent in *Chaltenobatrachus* and *Atelognathus patagonicus*. Based on our current sampling, we cannot determine whether this condition is synapomorphic for *Atelognathus* + *Chaltenobatrachus*, or alternately, the vocal sacs were lost independently in these two species (according to the phylogenetic hypothesis of Basso et al., 2011).

Bombinatoridae

Vocal sacs are absent in all members of the family. The configuration of the submandibular musculature in male *Bombina bombina* is unique; the buccal floor is enveloped by the m. geniohyoideus lateralis, which projects ventrally through paired gaps in the m. interhyoideus (Liu, 1935; Tyler, 1980; Fei and Ye, 2016; Elias-Costa et al., 2021). This herniation allows the buccal cavity to expand beyond the restriction imposed by superficial submandibular muscles. Although a vocal sac is absent because there are no vocal slits, the buccal cavity expands considerably during vocalization and, externally, might be confused with a bilobate vocal sac. This submandibular muscle condition is absent in the closely related *Bombina orientalis* and *B. variegata*, and unknown in all the remaining species of the genus. Vocalization in all *Bombina* occurs by inspiration and active compression of the buccal floor and consists of simple whistlelike sounds (Bosch and Boyero, 2003, Walkowiak, 2007). Males vocalize while floating, and water waves influence intraspecific communication (Seidel et al., 2001). Male *Barbourula busuangensis* lack vocal sacs but vocalize from the ground and from the water, partially or totally submerged, and produce extremely low-pitched calls for a frog that calls in fast-flowing streams (250 Hz). In *Barbourula kalimantanensis*, lungs are extremely reduced, so

vocalizing capacity is likely scarce (Blackburn et al., 2024).

Brachycephalidae

Vocal sacs are single, subgular, and internal in all *Brachycephalus*. The m. interhyoideus is relatively large and most of it expands posteriorly to the postmandibular lymphatic septum. Thus, the vocal sac inflates toward the pectoral region, with little expansion on the gular region (Pombal et al., 1994: fig. 2A). Vocal slits are short and elongate. Observation of vocal slits is particularly relevant for the taxonomy of the group, since they are the only phenotypical sexually dimorphic structure in the genus (Condez et al., 2017). Some male *Brachycephalus* combine vocal and visual signals to guard their territories during the breeding season, emphasizing the importance of multimodal communication in the group (Pombal et al., 1994; Condez et al., 2014).

In *Ischnocnema*, vocal sacs are single and subgular; vocal slits are elongate and the gular skin is variably modified (greater in *I. randorum*; Heyer, 1985; Hedges et al., 2008) and often is darkly pigmented. The gular skin texture has been used in a taxonomic context (e.g., Heyer et al., 1990; Taucce et al., 2018, 2019). In at least two species, *I. bocaina* (Taucce et al., 2019: fig. 2) and *I. crassa* (Silva-Soares et al., 2021: fig. 1), males have a pair of longitudinal folds that parallel the jaw from the middle of the gular region to the base of the arm. We did not examine specimens of these species, but these folds do not seem deep enough to produce a bilobate vocal sac when inflated (as in several *Adenomera* and *Leptodactylus*; see account for Leptodactylidae), but this must be evaluated by direct observation of vocalizing males.

Brevicipitidae

Vocal sacs in Brevicipitidae are single, subgular, and spherical in most species, and are absent only in *Balebreviceps hillmani* (Liu, 1935; Largen and Drewes, 1989; Channing and Rödel, 2019). Males have a large m. interhyoideus that extends posteroventrally beyond the mandibular joints, thereby allowing for the inflation of a massive vocal sac (Tyler, 1974a: fig. 21). Vocal slits are relatively small and round and have no indication of a sphincter. Adult males have darkly pigmented throats, and several species vocalize from shallow burrows or depressions, partially concealed by vegetation (Du Preez and Carruthers, 2009).

Bufonidae

As it occurs with many character systems in this diverse family, the evolutionary history of vocal sacs in Bufonidae is complex (online supplementary file S3: figs. S18, S19). Most species have single, subgular sacs of variable size and elongate vocal slits, but vocal sacs are absent in many species. The diversity of vocal sacs in Bufonidae has been assessed in multiple studies (Günther, 1859; Boulenger, 1892, 1897; Dickerson, 1907; Liu, 1935; Inger, 1958; McAlister, 1961; Cannatella, 1986; Mendelson et al., 2000, 2011; Pramuk, 2006; Pereyra et al., 2021, Elias-Costa et al., 2021).

One of the most remarkable features of the vocal sacs in bufonids is the presence of asymmetrical vocal sac cavities, whereby only one vocal sac mucosa develops and occupies the entire gular region. Many species have either one (left or right) or two vocal slits, with the trait varying intraspecifically. Even though the presence of unilateral vocal slits occurs in few species outside Bufonidae, it is notably common in this group, and has been found in most genera of the family (*Adenomus*, *Amazophrynella*, *Anaxyrus*, *Ansonia*, *Atelopus*, *Bufotes*, *Duttaphrynus*, *Epidalea*, *Incilius*, *Ingerophrynus*, *Leptophryne*, *Oreophrynella*, *Osornophryne*, *Pelophryne*, *Peltophryne*, *Phrynoidis*, *Poyntonophrynus*, *Pseudobufo*, *Rentapia*, *Rhaebo*, *Rhinella*, *Sclerophrys*, *Strauchbufo*, and *Vandijkophrynus*). Moreover, it was recovered here as a synapomorphy of the sister group of *Frostius*, although with several subsequent transformations.

In most bufonids that have vocal sacs, the sacs usually are single, subgular, and subspherical, and often large in numerous species (e.g., *Incilius coniferus*, *Schismaderma carens*, or *Sclerophrys gutturalis*). In many, the pectoral lymphatic septum is broad, which allows for the pectoral skin to stretch during vocalization, giving the appearance that the vocal sac extends toward the abdomen (fig. 12C). In many species belonging to the sister clade of *Nannophryne*, the m. interhyoideus is composed of two well-differentiated portions—a thick anterior one, formed almost exclusively by muscle fibers, and a thin, elastic, and often pigmented posterior one (Mendelson et al., 2005; Elias-Costa et al., 2021). The m. intermandibularis and the anterior portion of the m. interhyoideus in these species are scarcely distensible; thus, the air column is conducted posteriorly during vocalization.

In a few species, the posterior elastic portion of the m. interhyoideus curves ventrally to configure vocal sacs that when inflated protrude anteriorly or anterodorsally (figs. 12J, 12L). In our optimization, this pattern evolved once in *Anaxyrus*, although with two subsequent reductions. The most striking example of this anterodorsal projection occurs in male *Anaxyrus cognatus*, in which vocal sacs reach extraordinary volumes in front of the head (McAlister, 1961). Males of this species emit very long thrills in an upright posture, keeping the dark vocal sac fully inflated, which suggests a role in visual communication.

The gular skin in many adult male bufonids is darkly pigmented during the reproductive season, as it is in many other anurans (fig. 3A). However, many bufonids share a unique feature in which the posterior portion of the m. interhyoideus is densely pigmented; this pigmentation is visible by transparency through the relaxed skin and contributes to the overall coloration of the vocal sac (Elias-Costa et al., 2021). In addition, yellow pigmentation in the anterior portion of the gular skin evolved several times in the family (e.g., *Duttaphrynus scaber*, *Incilius coccifer*, *Rhinella granulosa* group, *Sclerophrys maculatus*).

William F. Martin and colleagues assessed the mechanics of sound production, and the evolution of advertisement calls in bufonids, providing a link between laryngeal anatomy and acoustic variables, which served as a general model for anurans (Martin, 1971, 1972; Martin and Gans, 1972). Mating calls in many bufonids are characterized by long trills with a nonmodulated dominant frequency of a narrow bandwidth and prominent amplitude modulation (Martin, 1972). Amplitude modulation derives from a combination of active (i.e., contraction of laryngeal muscles) and passive (i.e., anatomy of arytenoid cartilages and additional fibrous masses) components (Martin, 1972). Emission of long trills without frequency modulation occurs in many species of the the family (e.g., *Anaxyrus* and *Incilius*, in which they are particularly lengthy; Martin, 1972, Crocroft and Ryan, 1995; *Ansonia*, Amram et al., 2018; *Bufotes*, Giacoma et al., 1997; *Frostius*, Juncá et al., 2012; *Peltophryne*, Hernández et al., 2010; *Ingerophrynus*, Amram et al., 2018; *Rhinella*, Caldwell and Shepard, 2007; Lima et al., 2007; Guerra et al., 2011; *Sigalegalephrynus*, Sarker et al., 2019). The duration of the trills seems to be positively influenced by the presence of other competing males (Wells, 2007). In some species, the trill is preceded by a sequence of short, unpulsed notes (e.g., several *Melanophryniscus*; Baldo and Basso, 2004; Kwet et al., 2005, Caldart et al., 2013). In contrast, many species emit only a single or a short series of pulsed notes (e.g., some *Atelopus*, Crocroft et al., 1990; *Barbarophryne*, Doglio et al., 2009; *Rhinella hoogmoedi*, Roberto et al., 2011; and several African species, reviewed by Tandy and Tandy, 1976). With few exceptions, species of almost all bufonid genera have mating systems that include explosive reproductive aggregations, with scramble competition and pervasive interspecific mating (Wells, 1977, 2007; Pereyra et al., 2016a; but see Pereyra et al., 2016b: S5 for taxonomic distribution of mating systems in Bufonidae).

Vocal sacs have been lost at least 22 times in Bufonidae, including all species of *Altiphrynoides*, *Bufo*, *Capensibufo, Didynamipus*, *Mertensophryne*,

Metaphryniscus, *Nectophryne*, *Nectophrynoides*, *Nimbaphrynoides*, *Sabahphrynus, Truebella*, and *Werneria*, and some species of *Amazophrynella*, *Anaxyrus*, *Ansonia*, *Atelopus*, *Dendrophryniscus*, *Duttaphrynus*, *Incilius*, *Nannophryne, Osornophryne*, *Oreophrynella*, *Rhaebo*, *Rhinella* (the *R. arunco*, *R. veraguensis*, and *R. spinulosa* groups), and *Sclerophrys* (references in the online supplementary file S1). Because these include a wide array of species with highly diverse life histories, it is impossible to associate vocal sac reduction with a single variable or factor.

The tympanic middle ear is absent in the most recent common ancestor of Bufonidae, but it was regained and lost again several times in the family in a pattern that is unparalleled among tetrapods (Pereyra et al., 2016b). The tympanum, annulus, and columella are absent in almost 200 species, which most likely influenced the evolution of mating calls and vocal sacs in the clade. However, many of these species not only vocalize but also maintain acoustic diversity, emphasizing the importance of extratympanic hearing pathways (McDiarmid and Gorzula, 1989; Boistel et al., 2011, 2013; Pereyra et al., 2016b).

Caligophrynidae

Vocal sacs in the single species of the family, *Caligophryne doylei*, are single, subgular, and internal (Fouquet et al., 2023; the plesiomorphic condition for Brachycephaloidea). This montypic family is endemic of the Neblina Massif in the Pantepui region on the border of Brazil and Venezuela. It was described on the basis of a few specimens; thus, little is known about the biology and variation of these anurans.

Calyptocephalellidae

Vocal sacs are paired and subgular in *Calyptocephalella*; the well-developed vocal slits are elongate, and the mucosae are disconnected. The gular skin in adult males is distended and darkly pigmented in two ventrolateral areas. Males call partially submerged at the edge of shallow bodies of water; only the top half of the head is exposed, and vocal sacs are inflated above the water. These anurans often produce aggressive calls when disturbed (Veloso, 1977; Penna and Veloso, 1990).

Vocal sacs are absent in the specimen of *Telmatobufo australis* examined. Given the absence of reports of vocal sacs and vocal slits in the genus, these structures may be absent in all other species (Schmidt, 1952; Formas and Pugin, 1979; Penna and Veloso, 1990; Formas et al., 2001). Species of *Telmatobufo* breed in mountain streams, lack a tympanic middle ear, and produce a weak call (Donoso-Barros, 1972; Formas, 1988; Penna and Veloso, 1990).

Centrolenidae

In most glassfrogs, vocal sacs are single, subgular, and subspherical. The sacs usually are small to moderate in size, extending to the pectoral region and not exceeding the snout anteriorly when inflated; the vocal slits are elongate. The vocal sac wall is thin and transparent. In some species, the m. interhyoideus is extremely thin and has crisscrossed fibers, which likely increase its resistance during vocalization (Elias-Costa et al., 2021).

Four of the five species of *Sachatamia* differ in having a bilobate vocal sac, with variable degrees of lateralization and skin modification among species. The vocal sac is small in *S. ilex* and *S. punctulata*, intermediate in *S. albomaculata*, and large in *S. orejuela*. Brunner and Guayasamin (2020) described the vocal sacs of *S. orejuela* as "paired" (although we consider it bilobate according to the criteria provided here). This torrential species performs complex visual signaling, as did several nonrelated species that call in these environments and have paired vocal sacs (Elias-Costa and Faivovich, 2019). It is not known whether the vocal sac has a median constriction in the fifth species, *Sachatamia electrops*, or not (Rada et al., 2017: fig. 10A).

Male glassfrogs vocalize near fast-flowing streams. They call from: (1) the upper side of

leaves, usually with the snout directed toward the tip of the leaf; (2) the underside of leaves, usually with the snout toward the base of the leaf; or (3) from rocks on the walls of waterfalls, or within or near spray zones (Cisneros-Heredia and McDiarmid, 2007). The calls are highly variable in the family (Señaris and Ayarzagüena, 2005). Some species are highly territorial, and males guard the arboreal nests until tadpoles hatch and fall into the water (McDiarmid and Adler, 1974; Savage, 2002; Pérez-Gonzalez et al., 2018).

Ceratobatrachidae

Information on vocal sac morphology is extremely scarce for the family; reports usually are limited to the presence of vocal slits (online supplementary file S1). Plesiomorphically, the mucosae are disconnected.

Vocal sacs are absent in all Liuraninae (Jiang et al., 2019; Saikia and Sinha, 2019). Although little is known about the reproductive biology of these species except that males of one species call from the leaf litter (Jiang et al., 2019; Roy et al., 2019).

Vocal sacs are also absent in three species of Alcalinae, *Alcalus mariae*, *A. rajae*, and *A. tasanae*, whereas they are present and internal in the other two, *A. baluensis* and *A. sariba* (Inger, 1966; Brown et al., 2015). In *A. baluensis*, the paired mucosae are poorly developed.

Most Ceratobatrachinae have vocal sacs. In many of the species, they are internal, single, and subspherical, relatively small, and restricted to the posterior portion of the gular region, and the vocal slits are small and round (online supplementary file S3: fig. S5). However, *Cornufer bufoniformis*, *C. citrinospilus*, *C. guentheri*, *C. guppyi*, *C. opisthodon*, *C. papuensis*, *C. vertebralis*, and *Platymantis corrugatus* have paired, subgular vocal sacs. Most have internal vocal sacs, but *C. guppyi* has two white, distensible skin patches ventrally adjacent to the mandibular joints. Optimization in the phylogenetic hypothesis of Brown et al. (2015, data not shown) revealed that paired vocal sacs evolved between two and five times in *Cornufer*, making the genus an interesting model to study vocal sac evolution. Vocal sacs are absent in a few *Cornufer* (at least *C. batantae* and *C. bufonulus*; Zweifel, 1969; Kraus and Allison, 2007), and Günther (2006) reported that vocal slits were present or absent in adult male *Cornufer wuenschorum*. Female courtship calls, a rare feature in anurans, have been reported in captive *Cornufer guentheri* and *Platymantis vittiensis* (Yoshimi et al., 1996; Boistel and Sueur, 1997).

Ceratophryidae

Vocal sac morphology has received surprisingly little attention in Ceratophryidae, despite the major taxonomic revisions and descriptions of this family (Rivero, 1961; Reig and Cei, 1963; Reig and Limeses, 1963; Barrio, 1968a, 1968b, 1980; Cei, 1980; Lynch, 1982; Fabrezi, 2006; Faivovich et al., 2014). The hyoid, lingual and submandibular musculature of ceratophryids was revised by Fabrezi and Lobo (2009); see comments by Elias-Costa et al. (2021) regarding apical supplementary elements of the m. intermandibularis. Vocal sacs are bilobate and external in *Chacophrys*, *Lepidobatrachus*, and some species of *Ceratophrys*, and this condition was recovered as a synapomorphy of the family (online supplement S3: fig. S10). In these species, the m. interhyoideus is well developed as two large, muscular lobes. In all its extension, the thickness of the muscle is constant. Vocal slits are elongate, and mucosae are fused in all species examined.

Owing to the darkly pigmented gular skin of adult male *Ceratophrys* and *Chacophrys*, the inflated vocal sac is blackish purple. In contrast, in all *Lepidobatrachus*, pigmentation is highly concentrated in the entire extension of the internal mucosa (starting in the vocal slit), rather than in the gular skin. Consequently, the area around each vocal slit looks black (because of soft tissue transparency) in contrast to the pink/white buccal floor. Pigmentation also is concentrated in the anterior portion of the palate, the

eustachian tubes, and the internal surface of the odontoid processes. Pigmentation of the vocal sac mucosae occurs in only few anurans (e.g., some bufonids, *Hoplobatrachus*) and was identified here as a synapomorphy of *Lepidobatrachus*.

The clade composed of *Ceratophrys calcarata* and *C. cornuta* evolved a unique type of vocal sac. This C-shaped vocal sac (as defined herein, pattern 1C) has an extremely thin and elastic posterior portion of the m. interhyoideus, combined with a peculiar configuration of the postmandibular lymphatic septum (fig. 13). In *Ceratophrys cornuta*, the dark gular pigmentation is not sexually dimorphic (i.e., it is also present in females and juveniles) and contrasts with the creamy white pectoral and abdominal regions. A concentration of dark pigmentation in the throat in the absence of a vocal sac is uncommon and occurs in only few other frogs (e.g., *Mannophryne*, Aromobatidae).

Ceratophryids vocalize from shallow temporary ponds or flooded grasslands, usually after heavy rains. The calls of different species are similar and consist of a series of long, multipulsated notes (Barrio, 1968a, 1968b, 1980; Márquez et al., 1995; Lescano, 2011). Tadpoles of *Ceratophrys cranwelli* and *C. ornata* have been reported to vocalize underwater. Sounds are emitted as a part of an antipredatory mechanism, including from conspecific tadpoles, but more research is needed to understand the mechanistic origin of this vocalization (Natale et al., 2011; Salgado Costa et al., 2014).

Ceuthomantidae

Vocal sacs are single, subgular, and internal, and poorly developed in three of the four species of *Ceuthomantis* currently recognized. The fourth species, *C. aracamuni* is known only from subadult specimens, so the condition of the vocal sac is unknown (Barrio-Amoros and Molina, 2006.) Males call during daytime (an unusual trait for brachycephaloids), concealed in rock crevices, or hidden in the ground vegetation (Myers and Donnelly, 1997; Heinicke et al., 2009; Barrio-Amorós, 2010).

Conrauidae

Absence of vocal sacs was recovered as a synapomorphy of the family (online supplementary file S3: fig. S4). Several species have whistlelike advertisement calls (Rödel, 2003; Amiet and Goutte, 2017), which are apparently emitted with an open mouth. This is common for distress calls, but highly unusual for advertisement calls, even in species without vocal sacs (Amiet, 1989).

Craugastoridae

The absence of vocal sacs optimized as a synapomorphy of the family (online supplementary file S3: fig. S13). They are absent in *Haddadus* and at least 57 species of *Craugastor.* (We surveyed information on 106 of the 122 currently recognized species; see file S1 in the online supplement. Vocal sacs were regained several times in *Craugastor* and are present in 45 species; in all species, they are single, subgular, spherical, and internal. Optimization in the phylogenetic hypothesis of Portik et al. (2023) revealed between four and nine independent origins in the group; however, because only 47 species of the genus were included in this tree, these numbers are tentative.

The presence or absence of vocal sacs has been a traditional, but complex, taxonomic character of *Craugastor* (Savage, 1975; Campbell and Savage, 2000; Lynch, 2000). For example, Hedges et al. (2008) identified the presence of a vocal sac as a diagnostic character (in combination with other features) of their *C. fitzingeri* series, whereas its absence was diagnostic for their *C. gulosus*, *C. laticeps*, *C. mexicanus*, *C. podiciferus*, and *C. rhodopis* series (yet present in some species).

Zweifel (1956) speculated that vocal slits in *Craugastor augusti* probably develop relatively late in adult ontogeny, based on his examination of a

broad sample of adult males in which only one had a vocal sac. Campbell and Savage (2000) reviewed the impact of vocal slits in the taxonomy of the genus and reported that in some species (e.g., *C. pozo*, *C. rupinius*, *C. vocalis*), only a few adult males (usually the largest ones) have vocal slits. Possibly, this phenomenon characterizes other *Craugastor*; therefore, reports of absence of vocal sacs that are based on examination of few specimens should be taken as tentative. The holotype of *C. anciano* has a single, dextral vocal slit (Savage et al., 1988), a rare condition in Anura (char. 0). Several *Craugastor*, such as *C. bransfordii*, *C. gollmeri*, *C. noblei*, *C. stejnegerianus*, and *C. underwoodi*, vocalize without a vocal sac (Savage, 2002; Ibáñez et al., 2012; Salazar-Zúñiga and García-Rodríguez, 2014). These authors suggested that in some of these species, the loss of vocal sacs might be coupled with the behavior of calling inside hidden cavities such as tree holes, which may amplify the sounds. Although this effect has been described in a microhylid with a vocal sac (Lardner and bin Hakim, 2002), it has not been specifically tested in *Craugastor* (Cossel et al., 2019). Females of a few species of the *Craugastor fitzingeri* group produce distress calls (e.g., *C. crassidigitus* and *C. fitzingeri*; Lynch and Myers, 1983; Ibáñez et al., 2012).

Cycloramphidae

Vocal sacs are plesiomorphically present in the family (online supplementary file S3: fig. S9). However, information on vocal sac morphology is unavailable for most species, most likely because males vocalize at night from inside rock crevices near fast-flowing streams, usually behind waterfalls, or below the leaf litter (Haddad and Sazima, 1989; Weber et al., 2011; Silva and Ouvernay: 2012; Verdade et al., 2019). In *Cycloramphus boraceiensis*, mucosae are disconnected but medially expanded and almost touch each other; the vocal sacs are bilobate when inflated (Fábio de Sá, personal commun.). There are no descriptions of the vocal sac for the remaining species that possess one. In all cases, vocal sacs are internal and poorly developed, but the condition of the mucosae and the external shape are unknown; thus, their single, subgular score is conditional.

Vocal sacs are absent in several species of *Cycloramphus* and *Thoropa*. Optimization in the phylogenetic hypotheses of Sabbag et al. (2018) and de Sá et al. (2020) revealed that vocal sacs were plesiomorphically present in the family but were lost four times independently (data not shown). Some species lack vocal sacs but have folds in the buccal floor that could be mistaken as vocal slits and lead to erroneous reports of their presence (Heyer, 1983). In *Thoropa taophora* and *T. miliaris*, vocal slits have been reported variously as present (Feio et al., 2006, for both species; Lynch, 1971; Tyler, 1974a; Verdade, 2005; and Grant et al., 2006, for *T. miliaris*) and absent (Assis et al., 2021, for both species; Liu, 1935, Elias-Costa et al., 2017, for *T. taophora*). This discrepancy may reflect polymorphism or late development of vocal sacs in these species, although the complex taxonomic history of *Thoropa* calls for a careful interpretation of these observations (Sabbag et al., 2018). Small- and large-sized species of the genus have different vocalizations. In the small ones (*T. bryomantis*, *T. lutzi*, and *T. petropolitana*, all with vocal sacs), the temporal and harmonic structure of the calls resemble aggressive calls emitted with an open mouth, despite being emitted, at least in *T. bryomantis*, with the mouth closed (Nunes-de-Almeida et al., 2016; Assis et al., 2021). This poses interesting questions about the impact of the vocal sac in the vocalization in this group.

Dendrobatidae

Vocal sacs are single subgular in most species, except in species of the *Hyloxalus edwardsi* group (Lynch, 1982; Anganoy-Criollo et al., 2022) and in *Ranitomeya reticulata* (Myers, 1982), both of which lack vocal sacs. When present, vocal sacs are small, spherical, and usually indistinct externally (i.e., inter-

nal). They are restricted to the posterior half of the gular region and do not extend posteriorly to the pectoral region. Vocal slits are elongate and relatively large (as in Aromobatidae). In a few species, the number of vocal slits is polymorphic, a condition only found in this family, in Bufonidae (in which it is more widely distributed), in *Craugastor anciano* (Craugastoridae) and *Arenophryne rotunda* (Myobatrachidae). Adult male *Adelphobates quinquevittatus* may or may not have a vocal sac (Myers, 1982). In *Ameerega trivittata* (this study), *Phyllobates terribilis*, and *Andinobates bombetes* (Myers, 1982), some adult males have two vocal slits, whereas others have only one. We found a unilateral vocal sac in the single specimen of *Ranitomeya fantasastica* examined. It seems likely that polymorphism in the number of vocal slits occurs in other species of the family as well. All specimens examined with two vocal slits have fused mucosae forming a single cavity.

Dendrobatid advertisement calls are highly variable (Lötters et al., 2003; Grant et al., 2006; Erdtmann and Amézquita, 2009). Vocal diversification in this diurnal clade apparently is related to the evolution of aposematism, because aposematic species, which generally call exposed, vocalize at higher rates and lower pitches than non-aposematic species, which vocalize from concealed sites (Santos et al., 2014). Multimodal displays are commonplace in the family, and males of many species have sexually dimorphic gular pigmentation; this probably indicates that the vocal sac has a visual function, as reported for *Allobates femoralis* and likely *A. kingsburyi* (Aromobatidae; Hödl and Amézquita, 2001; Narins et al., 2005; Grant et al., 2006; Castillo-Trenn and Coloma, 2008). Sympatric poison frogs have complex mechanisms of call recognition that avert interspecific interference without spatial and temporal segregation of the calls (Amézquita et al., 2011). Male *Ranitomeya reticulata* have well-developed advertisement calls despite lacking vocal sacs (Myers, 1982).

Dicroglossidae

Dicroglossidae has at least eight different patterns of vocal sacs and thus is one of the most diverse families in terms of vocal sac morphology. Plesiomorphically, vocal sacs are absent in the family (a synapomorphy of Dicroglossidae + Ranixalidae), a condition retained by several species (online supplementary file S3: fig. S5).

Vocal sacs are highly variable in the subfamily Occidozyginae. They are absent in two species, *Ingerana tenasserimensis*, which retains the plesiomorphic condition of the family and *Occidozyga magnapustulosa*, in which the loss is secondary (Bourret, 1942; Taylor, 1962; Dubois, 1987). Vocal sacs are single and subgular (as in *Occidozyga laevis* and *O. lima*; Liu, 1935), or paired, subgular, and internal in *Ingerana borealis*, *Occidozyga baluensis*, *O. diminutiva*, and *O. tompotika* (Inger, 1954, Iskandar et al., 2011, Malkmus et al., 2002; Sailo et al., 2009). Little is known about the shape of the fully inflated vocal sac in these species.

Male *Hoplobatrachus*, *Euphlyctis*, and *Nannophrys* have paired, subgular vocal sacs with separate mucosae and ventrolateral expansions of the m. interhyoideus, but the pattern of gular skin differs in each genus. In *Nannophrys*, vocal sacs are poorly developed and lack sexually dimorphic skin modifications (Boulenger, 1882; Clarke, 1983). Species of this genus vocalize inside narrow rock crevices (Wickramasinghe et al., 2004; Senanayake et al., 2019); thus, the small vocal sac size may be related to constraints imposed by this cramped environment (as was proposed for *Corythomantis greeningi*, Hylidae; Moura et al., 2021). In *Hoplobatrachus*, the gular skin has two ventrolateral patches of distended, wrinkled skin (fig. 4G). The two large vocal sacs are darkly pigmented, but the melanocytes are located in the internal mucosae (as is found in some bufonids and *Lepidobatrachus*) instead of in the dermis (as occurs in almost all anurans with gular pigmentation). The throats of males look creamy white, but darken when they vocalize. The bright blue vocal sacs of *H. tigerinus*

during the breeding season clearly seem related to visual signaling (fig. 1L). In *Euphlyctis*, vocal sacs are folded inside a dermal pouch similar to that described for *Pelophylax* (Ranidae) or Ptychadenidae (fig. 4K). The presence of paired lobes in the m. interhyoideus inside gular skin pouches misled Nigam (1978) into recognizing two pairs of vocal sacs, one internal and one external. The eversible lobes are black in all species of the clade, except for *Euphlyctis hexadactylus*, in which they are dark yellow (Dinesh et al., 2021). The position of the vocal sacs differ in the two subgenera of *Euphlyctis*; the sac is posterior in *Phrynoderma* (i.e., right below the angles of the jaw, inflating at the sides of the head) and more anterior in *Euphlyctis* (i.e., below the middle of the jaws, inflating frontolaterally at 45°). Males vocalize in choruses, partly submerged or floating on the surface of ponds, and vocal sacs project above water level (Joshy et al., 2009; Howlader et al., 2015).

Detailed information on the morphology of the vocal sacs is lacking for most species of the tribe Paini (i.e., *Allopaa*, *Chrysopaa*, *Nanorana*, *Ombrana*, and *Quasipaa*), probably because the sacs are inconspicuous; if present, vocal sacs are always internal and poorly developed. Moreover, it is difficult to observe vocalizing males in the high-altitude habitats occupied by many of these species. We scored presence/absence of vocal slits in 37 of the 47 described species of the clade, obtaining contradictory reports for some of them. Vocal sacs are present in 24 species and absent in 13 (comprising several independent losses; Nanhoe and Outbouter, 1987; Inger et al., 1999; Ohler and Dubois, 2006). Internal mucosae are fused in the species of the tribe examined here (*Nanorana liebigii* and *Quasipaa boulengeri*); thus, reports of "paired internal vocal sacs" are tentatively scored as bilobate vocal sacs for the genus *Quasipaa*. Dubois (1976) stated that in *Nanorana liebigii*, the vocal sacs in some individuals are resorbed outside the reproductive season. This would be unique in anurans and could account for the contradictory literature reports; however, the feature requires corroboration and study of vocal sac variation. The absence of vocal sacs and advertisement calls in a high-altitude clade of *Nanorana* (*N. parkeri*, *N. pleskei*, and *N. ventripuctata*; Liu, 1950, Ohler and Dubois, 2006) was proposed as an adaptation to the low oxygen concentrations that hinder intense metabolic activities such as vocalization (Hu et al., 1985; Che et al., 2009). However, vocal sacs are also absent in lowland species of the genus (e.g., *N. quadranus*, *N. unculanu*s, *N. aenea*; Dubois, 1992) and present in *N. liebigii*, which calls and occurs as high as 3500 m (Dubois and Martens, 1984; Che et al., 2010). Furthermore, the only species of *Quasipaa* lacking vocal sacs (*Q. delacouri* and *Q. fasciculispina*; Bourret, 1942, Dubois, 1992) are restricted to mainland Southeast Asia at elevations of 1000 m or less (Yan et al., 2021). Obviously, hypotheses explaining vocal sac reduction or loss deserve further evaluation.

In the clade composed of *Fejervarya*, *Minervarya*, and *Sphaerotheca*, the vocal sac is plesiomorphically bilobate (with a bilobate m. interhyoideus as a synapomorphy of the clade); the sac is formed by a single cavity (fused mucosae) and has a diffuse skin modification. Males of these species have a pattern of gular pigmentation that distinguishes them from all other anurans. The ventral skin is creamy white and a pair of dark, subtriangular patches flank the gular region (fig. 6B; Dinesh et al., 2015; Howlader et al., 2016; Prassad et al., 2019; Yodthong et al., 2019). In some species, these dark patches converge anteromedially. When the vocal sac is inflated, the dorsal half is darkly marbled, whereas the ventral half is more lightly colored. A single, subgular vocal sac evolved at least twice in *Minervarya* from a plesiomorphic bilobate vocal sac, as indicated by the relationships obtained by Garg and Biju (2021); a single vocal sac is present in *M. chilapata*, *M. gomantaki*, *M. nicobariensis*, *M. sahyadris*, and *M. syhadrensis.*

Most species of *Limnonectes* lack a vocal sac, retaining the plesiomorphic condition of the genus. Many of these species appar-

ently do not vocalize, earning them the name of "voiceless frogs" (Boulenger, 1920; Inger, 1966; Emerson, 1992, 1996; Emerson and Inger, 1992; Emerson and Barrigan, 1993; Matsui, 1995). However, short, subtle advertisement calls have been reported for some of these species, both in males and females (Emerson, 1992; Matsui, 1995; Emerson and Ward, 1998). Given the low amplitude and short duration of these calls, as well as the background noise of the streams where they are emitted, it is likely that vocalization may have been overlooked for several other species (Rowley et al., 2014). Some authors reported that *Limnonectes palavanensis* lacks vocal sacs, having observed vocalizing males (Inger, 1966; Goyes Vallejos et al., 2017); however, Van Kampen (1923) reported vocal sacs as present. The video provided by Goyes Vallejos et al. (2017: suppl. material) shows considerable inflation of the gular region in *L. palavanensis*, coupled with sound emission. If vocal slits are in fact absent in this species, the buccal floor must be highly distensible, functionally compensating for their absence, as was described for some limnodynastids (vocal sac pattern 0C). Bourret (1942) noticed that male *L. hascheanus* and *L. limborgi* lack vocal slits but have a highly pleated gular skin with two groups of longitudinal folds (similar to those shown in fig. 6D)—an observation that was corroborated here for *L. hascheanus* and *L. doriae*. In addition, Yodthong et al. (2021) documented a great gular expansion in *L. doriae*. These observations suggest that the presence of a true vocal sac should not be inferred from external observations, and that a highly distensible buccal floor might be more widespread than currently recognized. This is particularly relevant for this clade, because the lack of vocal slits traditionally has been associated with the lack of vocalizations (e.g., using the term "voiceless frogs," Emerson and Berrigan, 1993).

Vocal sacs evolved at least three times in *Limnonectes*. Paired, internal, and subgular vocal sacs occur in *L. namiyei* (apparently the only member of the *L. kuhlii* complex to have a vocal sac; Inger, 1947, McLeod, 2008; Suwannapoom et al., 2016). In a clade from Thailand and adjacent regions, males have vocal slits and the gular skin configured into a pair of grouped shallow folds that parallel the jaws in some species; the shape of the vocal sac has not been described (e.g., *L. coffeatus*, *L. lauhachindai*, *L. kohchangae*, *L. macrognathus*, *L. pseudodoriae*, *L. savan*; Aowphol et al., 2015; Phimmachak et al., 2019; Yodthong et al., 2019). Lastly, in a Philippine and Sulawesian clade, males have small, paired vocal sacs that extend posterolaterally behind the angles of the jaw. In the species examined (*Limnonectes acanthi* and *L. magnus*), mucosae are disconnected and greatly expanded medially; the vocal sacs probably have a considerable degree of subgular inflation, forming a vocal sac pattern that was recovered as a synapomorphy of the clade. In all the *Limnonectes* having vocal sacs that we examined, the vocal slits are small and posterior, and lack a sphincter.

Eleutherodactylidae

Vocal sacs are plesiomorphically single, subgular, and spherical with elongate vocal slits in Eleutherodactylidae, and the condition is retained by most species (online supplementary file S3: fig. S13). Several members of the family have a pair of longitudinal folds in the gular skin. Curiously, this character, although well developed in many species, has not received much attention in the taxonomy of the group. For example, the vocal sac in the family is often described only as "external," without specifying the nature of skin modifications (i.e., with or without longitudinal folds). Many species descriptions include images of the dorsum only of the holotype; thus, the condition of the gular skin cannot be evaluated. This pattern is characterized by two long folds that parallel the jaws and extend toward the chest. In some species, a transverse fold is also present, forming

a U-shaped gular flap (Díaz et al., 2015: fig. 9). These longitudinal folds are best developed in the genus *Diasporus* and they are also present in several *Adelophryne* (*A. adiastola*, *A. baturitensis*, *A. gutturosa*, *A. pachydactyla*; apparently absent in *A. glandulata* and *A. maranguapensis*), both species of *Phyzelaphryne*, and several *Eleutherodactylus* (Dunn, 1926; Lynch, 2001; Hoogmoed and Lescure, 1984; Hoogmoed et al., 1994; Lynch and Duellman, 1997; Hedges et al., 2008; Batista et al., 2016; Rivera-Correa et al., 2017; Simões et al., 2018; Ospina-Sarria et al., 2022). Optimization of character 13 indicated that the skin folds evolved between five and 10 times independently in the family. The folds do not seem to affect the spherical shape of the fully inflated vocal sac—i.e., although obvious in relaxed/fixed specimens, the folds disappear during vocalization. Although these folds resemble those present in some *Leptodactylus* or *Hyloscirtus*, they do not produce a bilobate vocal sac when inflated.

Nonspherical vocal sacs, an extremely rare feature in Brachycephaloidea, are present in some *Eleutherodactylus*. They are bilobate and internal in *E. martinicensis*. However, because the bilobate configuration is evident only in the fully inflated vocal sac (e.g., Boistel et al., 2011: fig. 1B), the pattern also may be present in other species. Vocal sacs are paired and subgular in most species of the *E. bakeri* group (sensu Padial et al., 2014; although single in *E. dolomedes*), and they can be either internal (*E. amadeus*) or external (*E. caribe*, *E. corona*, *E. eunaster*, and *E. glaphycompus*). Moreover, "bilateral vocal sacs" are present in an undescribed brachycephaloid collected by Charles W. Myers (see Duellman, 2019).

On the other hand, the vocal sac is absent in several *Eleutherodactylus*, mostly those of the Jamaican radiation (Hedges, 1989) and in *Diasporus sapo*, apparently the only species of the genus with this condition. Hedges (1989) reported that the presence of the vocal sac is polymorphic in two species of *Eleutherodactylus*. However, many *Eleutherodactylus* without vocal sacs do vocalize, some of them quite loudly.

Heleophrynidae

Vocal sacs are single and subgular in *Hadromophryne natalensis* (Lynch, 1971; material not available for the present study), but published reports on vocal sac morphology are curiously absent for the family. Superficial submandibular muscles of some species were studied by Tyler (1974a; although he studied only females) and Burton (1998). Males emit weak calls from cracks and crevices in rocks close to waterfalls and cascades. They also vocalize underwater, producing short, high-pitched clicks that stand out against the loud background noise (Boycott, 1982, 2004).

Hemiphractidae

Vocal sacs are plesiomorphically present in Hemiphractidae, a condition that is retained in *Flectonotus*, *Fritziana*, and most *Gastrotheca* (online supplementary file S3: fig. S10). In these species, vocal sacs are subgular, spherical, and relatively large; they often extend to the pectoral region and are slightly dark in color (Duellman and Hillis, 1987; Duellman, 2015). The mucosae are fused in all species examined, and the presence of vocal slits as gaping holes is a synapomorphy of the family. Optimization in the phylogenetic hypothesis of Castroviejo-Fisher et al. (2015) indicates that vocal sacs were lost seven or eight times in the family, as follow: in *Cryptobatrachus*, *Hemiphractus*, and *Stefania* (recognized as synapomophies of each of these three genera), and four or five times in *Gastrotheca* (data not shown). In *Gastrotheca*, vocal sacs are absent in *G. albolineata*, *G. andaquiensis*, *G. atympana*, *G. cornuta*, *G. dendronastes*, *G. longipes*, *G. microdiscus*, and *G. testudinea* (Tyler and Duellman, 1995; Duellman, 2015). The submandibular musculature and vocal sac structure in the family were revised by Tyler (1971a, 1974a), and considerably augmented by Tyler and Duellman (1995) and Duellman (2015), who identified three main muscular patterns and reported on vocal slit distribution.

Hemisotidae

Vocal sacs in *Hemisus* are single, subgular, and darkly pigmented (Laurent, 1972; Channing and Rödel, 2019). In at least *H. marmoratus*, the anterior portion of the gular skin forms a loose, narrow, tubular pouch that extends anteriorly. When inflated, the vocal sac projects anterodorsally in front of the tip of the snout (resembling the condition found in some microhylids; M. Schäfer, personal commun.). Given the overall similarity among species, this type of vocal sac (here reported only for *H. marmoratus*) may be a synapomorphy of the family. Mucosae are fused and the vocal slits are elongate; the m. interhyoideus is well developed and greatly extends posteriorly toward the abdomen (Tyler, 1974a). Males call from concealed sites under vegetation at the edge of pools or from within burrows (Channing, 2003; Alexander, 2004).

Hylidae

Hylid frogs have the greatest vocal sac diversity among anurans; 11 of the patterns described here are included. Plesiomorphically, the vocal sac in hylids is single, subgular, and spherical, but vocal sacs were lost 13 times in the family and lateralized in variable degree in several clades (online supplementary file S3: figs. S10–S12). Although vocal slits are elongate in most species, some species have gaping holes and a few have small orifices. The structure and diversity of vocal sacs in hylids have been studied by several authors (e.g., Liu, 1935; Duellman, 1970, 2001; Trueb, 1970a, 1970b; Trueb and Duellman, 1971; Trueb and Tyler, 1974; Tyler, 1971a, 1972, 1974a; Faivovich, 2002; Faivovich et al., 2011; Elias-Costa et al., 2021; Moura et al., 2021; Araujo-Vieira et al., 2023), who studied vocal sac and submandibular musculature in representatives of all major clades. Moreover, Tyler (1971a) provided a terminology for vocal slits and supplementary elements of the m. intermandibularis that have been applied for all anurans. In this section, we follow the taxonomy of higher clades of Hylidae of Faivovich et al. (2018).

Vocal sacs are single, subgular, and spherical in most Pelodryadinae, although absent or bilobate in a few species. Vocal sac diversity in this group has been assessed by some authors (Tyler, 1971a, 1972; Tyler and Davies, 1978). Among the species with a single vocal sac, there is considerable diversity in size, coloration, and degree of skin modification. However, knowledge on the phylogenetic relationships of this subfamily is still insufficient, which hampers the recognition of vocal sac related synapomorphies and the inference of major evolutionary patterns. In some species, the spherical vocal sac is internal, poorly developed, and restricted to the posterior portion of the gular region (e.g., *Litoria havinia*, *L. mucro*, *L. pronimia*, *L. watjulumensis*; *Ranoidea citropa* group), whereas in others, it is exceptionally large, extending beyond the snout anteriorly (e.g., *Ranoidea chloris* and *R. gracilienta* groups; *Litoria microbelos*).

In four pelodryadine clades, the single, subgular vocal sac is large and somewhat flattened dorsoventrally; it expands laterally at the sides of the head when fully inflated. The degree of lateral development varies, ranging from a subtle ellipsoid shape to a semicircular vocal sac. An ellipsoid vocal sac is present in several members of the *Litoria rubella* group: *Litoria balatus*, *L. dentata*, *L. electrica*, *L. quiritatus*, and *L. rubella*. In these species, the vocal sac is almost exclusively located above the hypertrophied m. interhyoideus (Rowley et al., 2021). The shape of the fully inflated vocal sac could not be determined in the non-Australian members of the group (*L. capitula*, *L. congenita*, and *L. pygmaea*), thus hampering the recognition of this vocal sac pattern as a synapomorphy of the group. Secondly, a similar pattern is present in *Litoria verreauxii* and most likely *L. paraewingii*, but not in the remaining members of the *L. ewingi* group. A slightly ellipsoidal vocal sac is present in *Ranoidea aurea*, *R. moorei*, *R. raniformis*, and "*Litoria*" *castanea*, all members of the *R. aurea* group; possibly this is a synapomorphy of the clade, but the condition of *R. cyclorhynchus* and *R. dahlii* could not be assessed. An ellipsoidal vocal sac is a syn-

apomorphy of a clade of species formerly recognized as *Cyclorana* (now *Ranoidea*). In some species (e.g., *R. alboguttata*), lateral expansion is minimal, whereas in others (e.g., *R. cryptotis* and *R. platycephala*), there is a large, semicircular vocal sac that resembles vocal sacs of distantly related clades that vocalize while floating (e.g., *Engystomops*, *Pleurodema*, *Kaloula*, *Notaden*, etc.). Internal bilobate vocal sacs evolved at least in *Ranoidea dayi* and *Ranoidea rheocola*. Tyler (1971a: 337) suggested that in *Nyctymystes infrafrenatus*, the spherical vocal sac may appear as bilobate if the m. interhyoideus is ventrally constricted by a hypertrophied omosternum.

Most pelodryadines have some form of gular skin modification, including either yellowish or dark/grayish pigmentation. In particular, *Nyctimystes infrafrenatus* has two clearly defined regions in the gular skin; one is elastic and in contact with the m. interhyoideus, and the other is less distensible and lies ventral to the m. *intermandibularis.* A progressive differentiation of the skin can be observed in many species of frogs with a single subgular vocal sac, but in none it is as evident as in this species.

Vocal sacs have been lost several times in Pelodryadinae; however, lacking knowledge of the internal relationships of the group, we could not determine the exact number. The sacs are absent in the *Nyctimystes papua* group, *Nyctimystes avocalis*, the *Ranoidea eucnemis* and *R. lesueuri* groups, *R. andiirrmalin*, *R. exophthalmia*, *R. lorica*, *R. nannotis*, and *R. serrata* (Tyler, 1971a; Tyler and Davies, 1978; Barker et al., 1995; McDonald, 1997; Richards et al., 2010; Donnellan and Mahony, 2004; Menzies, 2014).

The vocal sac is internal, single, and subgular in most Phyllomedusinae and varies considerably in size (Tyler, 1971a; Faivovich et al., 2010, 2011; Baêta et al., 2016). Vocal sacs were lost twice in the subfamily—once in *Phasmahyla* and once in the *Phyllomedusa tarsius* group (recovered as synapomorphies for these clades). *Phyllomedusa venusta* lacks a vocal sac (Duellman, 1970); this species has been associated with the *P. tarsius* group (De la Riva, 1999; Barrio-Amorós, 2006; Faivovich et al., 2010) but it has not been included in molecular phylogenetic analyses. In both *Phasmahyla* and *P. venusta*, males vocalize inflating the buccal cavity; the acoustic parameters of the call of *P. venusta* resemble those of species of the *P. tarsius* group (Faivovich et al., 2010; Bezerra et al., 2021). The evolution of different aspects of the advertisement calls in the group has been recently assessed (Röhr et al., 2020; Bezerra et al., 2021).

With few exceptions, vocal sacs of Cophomantini (Hylinae) are single, subgular, and spherical; in many species, the sacs are large. In several *Boana* (particularly members of the *B. pulchella* group), there is extensive myo-integumentary contact between the gular skin and the median portion of the m. interhyoideus (Elias-Costa et al., 2021). This contact is evidenced externally by a marked pleating in the center of the gular region and, in some species, two lateral folds of loose skin (fig. 10). Vocal sac color varies extensively in the genus. It can be semitransparent (e.g., *B. beckeri*, *B. jaguariaivensis*), creamy white (e.g., *B. crepitans*, *B. geographica*), uniform yellow (e.g., *B. albopunctata*), yellow with white speckles (e.g., *B. pulchella*), green (e.g., *B. marginata*), or light blue in chlorotic species (e.g., *B. cinerascens*, *B. rufitela*). Moreover, several *Boana* perform multimodal displays (Giasson and Haddad, 2006; Toledo et al., 2007; Brunetti et al., 2014, 2015b). Tyler (1975) reported that *Limnodynastes tasmaniensis* could alter the shape of the vocal sac by independently contracting the mm. intermandibularis and interhyoideus. The same behavior was observed once in a male *Boana pulchella* (A.J.E.C., personal obs.). Bilobate vocal sacs were obtained here as a synapomorphy of the *Hyloscirtus bogotensis* group. They are ovoid, relatively small, and restricted to the posterior part of the gular region. (A large mental gland occupies the anterior gular region, which is scarcely distensible.) The vocal sac in these species is evident externally by a pair of longitudinal folds ventral to the mandibular joints, folds that extend to the base of the arms (e.g., Duellman, 1970: fig. 154). Because these folds also occur

in the holotype of *Hyloscirtus conscientia*, the vocal sac of this species, which originally was described as single subgular, may resemble the vocal sac shape of the remaining members of the species group (Yánez-Muñoz et al., 2021). Mucosae are fused. Vocal sacs are absent in *Bokermannohyla caramaschii* and *B. izecksohni*, both members of the *B. circumdata* group, and the only Cophomantini species with this condition (Jim and Caramaschi, 1979; Napoli, 2005). However, *B. caramaschii* vocalizes (Bang et al., 2023). The presence of a single subgular vocal sac is either polymorphic or developed late in the ontogeny (SVL >62 mm, according to our sample) in *Bokermannohyla saxicola* (i.e., vocal slits absent in some examined specimens with well-developed nuptial pads).

Almost all Dendropsophini have single, subgular, and spherical vocal sacs. They are small and internal in *Xenohyla*, and large, external, and yellow in most *Dendropsophus* (fig. 12A; Duellman, 1970, 2005; Tyler, 1971a; Izecksohn, 1998). The vocal sac wall is extremely thin and remains loosely pleated in fixed specimens of most species of the genus (fig. 6A). An interesting exception makes the phytotelm-specialist *Dendropsophus bromeliaceus*, in which the vocal sac seems to be considerably reduced (Ferreira et al., 2015: figs. 1–2), mirroring the correlation between small vocal sacs and breeding in bromeliads recovered in Lophyohylini hylids (Moura et al., 2021; see below). In a single species, *Dendropsophus bilobatus*, the vocal sac is bilobate, green, and relatively small, and restricted to the m. interhyoideus (Ferrão et al., 2020). Vocal sacs in several species of Dendropsophini slightly deviate from the spherical shape; however, this distinction is too subtle to be considered here as a different shape. For example, the vocal sacs of some members of the *Dendropsophus marmoratus* group have been termed bilobate (Ferrão et al., 2020). However, we consider the ellipsoidal vocal sacs of these species to be within the range of the diversity of single, subgular vocal sacs (a similar shape characterizes the vocal sacs of some *Hyla*, *Litoria*, *Ranoidea*, and *Scinax*). Furthermore, the *Dendropsophus marmoratus* group has been diagnosed by the presence of a large vocal sac (Bokermann, 1964; Orrico et al., 2009; Hepp et al., 2012; but see Faivovich et al., 2005), but all currently recognized species groups of *Dendropsophus* contain species with massive vocal sacs (e.g., *Dendropsophus bogerti*, *D. counani*, *D. ebraccatus*, *D. elegans*, *D. elianeae*, *D. jimi*, *D. luteoocellatus*, *D. mathiassoni*, *D. minutus*, *D. molitor*, *D. nanus*, and *D. sanborni*). In males of a clade of five chlorotic species (*D. mathiassoni*, *D. juliani*, *D. minusculus*, *D. cruzi*, *D. branneri*), the vocal sac looks green (Orrico et al., 2021).

In most species of Hylini, vocal sacs are single and subgular (Duellman, 1970; Tyler, 1971a). Often, the sacs are external and well developed, with yellow and/or black pigmentation (e.g., *Acris*, *Pseudacris*, *Hyla*). Most species have relatively large vocal sacs that can store large volumes of air (e.g., *Pseudacris triseriata*); thus, the inflated sacs extend beyond the tip of the snout anteriorly, even in species with spherical vocal sacs. Vocal slits are usually well developed and elongate (Tyler, 1971a). The vocal sac morphology in some genera, such as *Pseudacris*, *Smilisca*, and *Triprion*, is surprisingly diverse, making them good models for studying vocal sac evolution. For example, in all species of *Smilisca*, vocal sacs were described as bilobate and external (Duellman and Trueb, 1966; Duellman, 1970). However, images of fully inflated vocal sacs (available here for 3 of the 9 species) show a semicircular sac in *S. phaeota*, a bilobate sac in *S. fodiens*, and paired, subgular sacs in *S. baudinii*. Vocal sacs are absent in *Triprion spinosus*, spherical in *T. spatulatus*, and bilobate in *T. petasatus*.

Deformation of the spherical shape evolved several times in Hylini. A single, subgular vocal sac projects anteriorly in some *Pseudacris* (most developed in *P. fouquettei*, *P. illinoensis*, and *P. ornata*) while the frogs vocalize from a vertical position with the body half-submerged in ponds. Semicircular vocal sacs are present in some species of *Hyla* (e.g., *Hyla meridionalis*, *H. sanchian-*

gensis), a clade of *Pseudacris* (most evident in *P. hypochondriaca* and *P. regilla*, less developed in *P. sierra*, and only slightly expanded laterally in *P. cadaverina*), and *Smilisca phaeota*; typically, all these anurans vocalize while floating on the surface of ponds. Bilobate vocal sacs also evolved several times in Hylini. They are present in *Hyla arenicolor*, *H. hallowelli*, and *H. tsilingensis*, the *Isthmohyla pseudopuma* group, and *Triprion petasatus*, and most *Smilisca*. Vocal sacs are paired and subgular in *Smilisca baudinii*; the combination of paired vocal sacs and fused mucosae noticed by Duellman and Trueb (1966) is rare in anurans. Vocal sacs were lost several times independently in Hylini. The absence of a vocal sac is a synapomorphy of *Megastomatohyla*; however, the condition of *M. mixe* is unknown. Vocal sacs are also absent in some *Charadrahyla*, *Plectrohyla*, and *Sarcohyla*, although they are variably present in adult male *S. bistincta* and *S. hapsa* (Campbell et al., 2018). Despite lacking vocal sacs, *Triprion spinosus* produces loud calls that can be easily heard more than 100 m from the bromeliads or hole in bamboo from which the frogs call (Rodríguez-Brenes et al., 2013).

Traditionally, vocal sac diversity has had an important role in the taxonomy of the tribe Lophyohylini (Duellman, 1956, 1970, 1971; Trueb, 1970a, 1970b; Trueb and Duellman, 1971; Trueb and Tyler, 1974; Faivovich et al., 2005; Jungfer et al., 2013; Duellman, 2019). Moura et al. (2021) assessed this system and showed how variation in the shape of the internal mucosae and the skin modifications produce the different vocal sac patterns. Lophyohylini contains a wide variety of morphological patterns; vocal sacs can be absent, single, or paired with a variable degree of lateral and subgular inflation. The phylogenetic relationships among the main clades of this tribe are poorly supported (Blotto et al., 2021), and therefore our inferences should be taken cautiously.

The separation of the vocal sac mucosae is a synapomorphy of Lophyohylini, with subsequent fusions occurring in *Osteopilus* + *Phyllodytes*, and the *Osteocephalus taurinus* group. In *Phyllodytes*, *Phytotriades*, several *Nyctimantis*, and a clade of small-sized *Osteopilus*, vocal sacs are single, spherical, and internal. Most of these species are phytotelmic and vocalize from inside bromeliads (reviewed by Blotto et al., 2021). The possession of small, posterior vocal slits with sphincters is a synapomorphy of *Phyllotydes* and it is the only known case of this structure outside Ranoides. In *Corythomantis*, the vocal sac is bilobate internal, with disconnected mucosae (Moura et al., 2021). In *Osteocephalus*, *Tepuihyla*, and a clade of *Osteopilus*, the m. interhyoideus is enlarged around the origin of fibers, near the otic capsules, expanding the vocal sac to the sides of the head. Vocal sac mucosae are well developed medially; consequently, the median part of the gular region is considerably distended during vocalization. Subgular inflation is absent in *Itapotihyla*, *Nyctimantis siemersi*, and likely *Dryaderces pearsoni.* Vocal sacs of *Trachycephalus* are morphologically diverse and mostly differentiated by the relative development of the laterodorsal lobes of the m. *interhyiodeus.* Although some species have extraordinary dorsal projections of the vocal sac (e.g., *T. coriaceus*, *T. typhonius*; a feature described by Duellman, 1956, and Tyler, 1971a, and recognized as a synapomorphy of the genus by Faivovich et al., 2005), others have smaller lobes that do not exceed the supratympanic fold (e.g., *T. resinifictrix*). Moreover, a clade of two bromeligenous species deeply nested in the genus have bilobate vocal sacs (*T. hadroceps* and *T. helioi*).

A correlation between breeding in phytotelmata and the relative reduction of the lateral lobes of the vocal sac was proposed for species of *Osteocephalus* (Jungfer and Weygoldt, 1999; Jungfer et al., 2013; Duellman, 2019). Moura et al. (2021) reported a similar correlation for all Lophyohylini genera, demonstrating that in the 10 independent origins of phytotelm breeding (the highest per species in Anura; Blotto et al., 2021), vocal sacs show some degree of reduction. In contrast, evolution of laterodorsally projecting lobes of the vocal sac may be associated with vocalization in anurans floating in the surface of temporary ponds. Current knowledge on the

advertisement calls of species of the tribe was revised by Forti et al. (2018).

Members of Pseudini have a surprising diversity of vocal sac morphology, given the small number of morphologically and ecologically uniform species in the tribe, 13 (Frost, 2024; Gallardo, 1961; Klappenbach, 1985; Duellman and de Sá, 1988; Barrio-Amorós et al., 2006; Aguiar et al., 2007; Garda et al., 2010). Plesiomorphically, vocal sacs are single and subgular; the mucosae are fused and vocal slits are elongate, a condition retained by *Scarthyla* and *Lysapsus*. The clade composed of *Pseudis bolbodactyla*, *P. paradoxa*, and *P. platensis* evolved an anterior projection of the single subgular vocal sac (less developed in *P. bolbodactyla* and more elongate in the other two species; fig. 3C). The projection can be seen only when the frogs vocalize, and there is no external indication of this projection in preserved specimens. Because we have no images of either *Pseudis fusca* or *P. tocantins* with fully inflated vocal sacs, we cannot determine whether the vocal sac projects anteriorly. The gular skin is unmodified in adult male *Scarthyla*, uniformly distended in *Lysapsus*, and distended and dark yellow in *Pseudis*. The clade composed by *Pseudis cardosoi* and *P. minuta* evolved paired subgular vocal sacs (Gallardo, 1961; Kwet, 2000) in which the mucosae are disconnected (a synapomorphy of the clade), the m. interhyoideus is bilobate (with a unique insertion of the ventral surface of the omosternum; Elias-Costa et al., 2021), and the thin, elastic gular skin has two longitudinal folds. The dorsal half of the inflatable lobes are dark yellowish green, whereas the ventral portion is white, continuous with the abdominal coloration (see Goldberg et al., 2016: fig. 1). Vocal sacs in *P. minuta* develop and young males start vocalizing shortly after metamorphosis, showing a strikingly accelerated development for the structure (Goldberg et al., 2016). Male *Pseudis* and *Lysapsus* vocalize floating from the surface of ponds or from floating plants; although they call by day, vocalization is more intensive at night (Zank et al., 2008; Vaz-Silva et al., 2020).

Several authors have described vocal sac structure in members of the tribe Scinaxini (Liu, 1935; Duellman, 1970, 2001, 2005; Tyler, 1971a; Faivovich, 2002). The most recent review is that of Araujo-Vieira et al. (2023), who studied the evolution of the internal mucosa, submandibular muscles, and modification of the skin. They recovered single, spherical, and external vocal sac as plesiomorphic for the tribe, and the absence of skin modification as a synapomorphy of *Ololygon*. The size and position of the vocal sac, expressed mainly in the degree of anteroposterior expansion, are highly variable among species. For example, in the sister group of *Julianus camposseabrai* (i.e., the former *Scinax uruguayus* group), the vocal sac is spherical but anterior in position, such that it expands beyond the tip of the snout anteriorly (see Baldo et al., 2019). Araujo-Vieira et al. (2023) distinguished between weakly and strongly bilobate posterior portions of the m. interhyoideus, and reported the former state in many species of the tribe. Lacking photos of fully inflated vocal sacs for most species of the tribe, we do not know whether a weakly bilobate m. interhyoideus can produce a bilobate vocal sac (as defined here). In some (e.g., *Scinax acuminatus*) it is, whereas in others (e.g., S. *fuscovarius*), it is not. Based on the available anatomical observations, we tentatively score the following species as having bilobate vocal sacs: *Ololygon brieni*, *O. flavoguttata*, *O. garibaldiae*, *O. heyeri*, *O. rizibilis*, *O. trapicheiroi*, *Scinax albertinae*, *S. castroviejoi*, *S. chiquitanus*, *S. dolloi*, *S. funereus*, *S. hayii*, *S. ictericus*, *S. iquitorum*, *S. montivagus*, *S. onca*, *S. oreites*, *S. pachycrus*, *S. perereca*, *S. ruberoculatus*, *S. sateremawe*, *S. tropicalia*, *S. tsachila*, and *S. x-signatus*. Some species, in which the m. interhyoideus is weakly bilobate, were originally described as having "lateralized, subgular vocal sacs" (e.g., *Ololygon luizotavioi*, *O. ranki*; Andrade and Cardoso, 1987; Caramaschi and Kisteumacher, 1989); tentatively, these are considered here as bilobate. A strongly bilobate vocal sac was observed only in *Julianus camposseabrai*, which has the more lateralized vocal sac in the tribe. Vocal sacs were lost twice in Scinaxini, in *Ololygon ariadne* and *O. skaios* (Lourenço et al., 2016); the latter vocalizes in a similar way to

its closely related, vocal-sac bearing species (Pombal et al., 2010; Araujo-Vieira et al., 2023).

Single, subgular vocal sacs are external in all Sphaenorhynchini, and the gular skin is markedly pleated in adult males (Araujo-Vieira et al., 2019, 2020). The presence of vocal slits that are gaping holes is a synapomorphy of the clade. In *Sphaenorhynchus*, the m. interhyoideus is extremely hypertrophied; it extends toward the abdomen and is in broad contact with the gular skin. The volumes of the vocal sacs in the genus are immense and among the largest relative to body size in Anura (Tyler, 1971a); most of the air is retained in the vocal sac during vocalization with the shape of the sac remaining unchanged. Accelerated sexual maturity (including vocal sacs and calls) in metamorphic individuals was reported in some species (Bokermann, 1974; Araujo-Vieira et al., 2019).

Hylodidae

Vocal sacs are paired and internal in *Crossodactylus*, whereas they are paired and external, with extensive skin modifications in *Hylodes* and *Phantasmarana*, and absent in *Megaelosia*, *Hylodes glaber*, and *H. vanzolinii* (Elias-Costa et al., 2017; Vittorazzi et al., 2021; de Sá et al., 2022). Vocal slits are elongate and large. The structure and diversity of vocal sacs in Hylodidae were assessed by Elias-Costa et al. (2017). These diurnal, torrent-dwelling frogs have paired, subgular vocal sacs that have an unusual internal structure, whereby the disconnected internal mucosae project through a gap in the m. interhyoideus. This configuration may permit unilateral inflation of paired vocal sacs, a behavior described in the context of multimodal displays in *H. asper* (Hödl et al., 1997), *H. heyeri* (Struett et al., 2021), *H. japi* (de Sá et al., 2016), *H. meridionalis* (de Sá et al., 2018; Furtado et al., 2019), and *Crossodactylus timbuhy* (Lacerda et al., 2022). De Sá et al. (2022) argued that male *Phantasmarana*, which have well-developed paired subgular vocal sacs do not call. However, unlike the mute *Hylodes glaber*, *H. vanzolinii*, and *Megaelosia goeldii* (vocal sacs absent), they retain their vocal sacs; possibly this reflects the key role of vocal sacs in visual signaling during courtship and agonistic encounters (Augusto-Alves et al., 2018).

Hyperoliidae

Vocal sacs in most Hyperoliidae are single, subgular, and spherical, and often reach large volumes when inflated (online supplementary file S3: fig. S3). Although the size and shape of the vocal slits are highly variable in the family, there are two noteworthy synapomorphies: the presence of small orificies in *Tachycnemis* + *Heterixalus*, and large, gaping holes in *Hyperolius*. Perhaps the most striking feature is the presence of large platelike gular macroglands and bright-coloured patches, the morphological diversity and distribution of which have been studied extensively (Liem, 1970; Largen, 1974, 1975; Drewes, 1984, Schiøtz, 1999). Surprisingly, little is yet known about their histology and the nature of the macrogland's secretions, which include several volatile compounds (Le Quang Trong, 1976; Starnberger et al., 2013). Apparently, the pulsatile movement of the vocal sac during vocalization may contribute to the volatilization of these compounds, thereby playing a role in chemical communication (Starnberger et al., 2014). In several Hyperoliidae, longitudinal fibers of the m. interhyoideus insert in the dermis arround the gular gland (Elias-Costa et al., 2021). In *Arlequinus*, *Acanthixalus*, *Callixalus*, *Cryptothylax*, and *Morerella*, vocal sacs are relatively smaller than in other members of the family; however, in some species, particularly in *Hyperolius*, the vocal sacs are extraordinarily large (Schiøtz, 1999; Nečas et al., 2021). Drewes (1984) reported a slightly bilobate configuration of the m. interhyoideus in *Chrysobatrachus*. Vocalization apparently is absent in the clade of spiny-throated *Hyperolius*, all of which have well-developed vocal sacs (Schiøtz and Westergaard, 2000; Lawson et al., 2023). A unique type of vocal sac is present in *Hyperolius pusillus*, which is the only known species of frog with ringlike accessory fibers of the m. interhyoideus (Elias-Costa et al., 2021). These

fibers define two ventral secondary lobes that project from the subgular vocal sac when inflated (i.e., triple vocal sac, figs. 14A–D). In this species, the gular skin posterior to the macrogland does not form a continuous groove; instead, the folds are concentrated around two ventrolateral points, the secondary lobes.

Some species of Kassininae also have triple vocal sacs, but these are generated by a different arrangement of m. interhyoideus (fig. 14E–F). This type of vocal sac is present in all species of *Kassina* (with variable degree of development, most prominent in *Kassina senegalensis* and *K. cochranae* and least marked in *Kassina cassinoides* and *Hylambates*; Schiøtz, 1967; Largen, 1975; Amiet, 2007), *Kassinula*, and *Paracassina.* Male *Kassina* examined have a rigid central mass of longitudinal muscle fibers that separate two highly distensible portions of the muscle (Elias-Costa et al., 2021: fig. 2L). The mass of muscle fibers is evident externally by a strap or disclike patch in the gular skin, which resembles the gular macrogland of other hyperoliids. In *K. senegalensis*, dermal glands are present in this part of the skin, but only as small, isolated acini (Le Quang Trong, 1976; Elias-Costa et al., 2021). However, other species lack the straplike portion of the skin but have a transverse fold that defines a disclike patch (e.g., *Kassina schioetzi*, Rödel et al., 2002; *Hylambates boulengeri*, Amiet, 2007). Additionally, specimens of *Hylambates* studied lack this central mass of fibers but have a similar vocal sac as *K. senegalensis*. On the other hand, vocal sacs in *Semnodactylus* are single subgular spherical, and absent in *Acanthixalus* (the only genus of the family lacking vocal sacs). All these observations highlight the need of a thorough revision of gular skin diversity in Kassininae.

Drewes (1984: fig. 20G) described and illustrated a unique condition in the m. interhyoideus of *Paracassina kounhiensis* and *P. obscura*; the muscle "originates in the ventral fascia behind the frontoparietals and radiates ventromedially passing through a connective tissue trochlea." Specimens of this rare genus were not available for study, but this condition is doubtless a synapomorphy of the clade. The vocal sac internal mucosa apparently does not invade these dorsal slips, and the vocal sac resembles those of other kassinines (i.e., triple; Drewes, 1984; Largen, 2001).

Leiopelmatidae

Vocal sacs are absent in the family. Males apparently do not emit advertisement calls, although release calls have been described (Stephenson and Stephenson, 1957; Bell, 1978). Species of this family rely strongly on chemical communication (Wever, 1985; Lee and Waldman, 2002, Waldman and Bishop, 2004).

Leptodactylidae

Leptodactylidae is one of the most diverse families of Neotropical anurans in terms of vocal sac morphology. There are eight vocal sac patterns, with several independent origins, and considerable generic variation (online supplementary file S3: fig. S17). Vocal slits are elongate in almost all species.

Most members of *Engystomops*, *Physalaemus*, and *Pleurodema* have single, semicircular vocal sacs that can be inflated around the head (fig. 12G; Cei, 1980; Duellman and Veloso, 1977). In these genera, there is a large m. interhyoideus (often with criss-crossed muscle fibers) and elastic gular skin. Males vocalize either floating on the water or partly submerged in temporary ponds. Some species of these genera have a slightly different pattern. In species of the *Physalaemus olfersii* group, the vocal sac is much larger than in closely related species, and extends posteriorly inside the body wall. Instead of inflating anteriorly (in the reniform shape described in other groups), the vocal sac gradually extends above the arms and around the head as it inflates. Among other anurans, this pattern is only known in *Notaden* (Limnodynastidae; Tyler, 1972) and *Glyphoglossus molossus* (Microhylidae; Targino et al., 2019). Most species of the *Physalaemus olfersii* group have well-developed fibrous masses in

their larynges, which distinguishes them from other species of the genus (de la Vega et al., 2021). Interestingly, at least two species of this group (*P. lateristriga* and *P. olfersii*) produce tonal calls that likely derive from extensive filtering of harmonics by soft tissues (Carvalho et al., 2019a). In contrast, in species of the *Physalaemus deimaticus* group, the vocal sac is poorly developed (Nascimiento et al., 2005). In *Pleurodema* (except in *P. bufoninum* and *P. somuncurense*, which lack a vocal sac), lateral vocal sac development varies from slightly ovoid, subgular structures (e.g., *P. tucumanum*; Ferraro et al., 2016: fig. 1) to horseshoe-shaped structures that project posteriorly beyond the tympana (e.g., *P. thaul*). The evolution of male advertisement calls in *Physalaemus* was discussed by Hepp and Pombal (2020), who characterized the vocalization of most species in a broad comparative framework.

Engystomops pustulosus (i.e., the Túngara frog) is the best-studied model system of acoustic communication in anurans and includes descriptive and experimental approaches. Contributions on this species cover sexual selection and multimodal communication (Rand and Ryan, 1981; Ryan, 1985; Wilczynski et al., 2001; Rosenthal et al., 2004; Taylor et al., 2008, Goutte et al., 2020), functional morphology (Dudley and Rand, 1991; Pauly et al., 2006), larynx and vocal sac structure (Jaramillo et al., 1997; Guerra et al., 2014), metabolic, endocrine and nervous control (Bucher et al., 1982; Chakraborty and Burmeister, 2010; Kime et al., 2010), visual ecology (Cummings et al., 2008), and evolutionary ecology (Halfwerk et al., 2014; Ryan and Guerra, 2014), among other topics.

Vocal sacs are single and subgular, and often project anteriorly in *Pseudopaludicola*. Many species vocalize by day and night (Carvalho, 2012; Cardozo et al., 2018, Andrade et al., 2019). The gular skin can be black, bright white or yellow (Toledo et al., 2010; Pansonato et al., 2016; Andrade et al., 2020), which may suggest that the sac has a role in visual/multimodal communication.

Plesiomorphically, males of Paratelmatobiinae have internal, poorly developed, spherical vocal sacs and small, posterior vocal slits (i.e., *Rupirana*, some *Paratelmatobius* and *Crossodactylodes bokermanni*; Heyer, 1999; Pombal and Haddad, 1999; Santos et al., 2019, 2020). Vocal sacs have been lost two or three times in the subfamily, once in the *Paratelmatobius lutzii* group (*P. gaigae*, *P. lutzi*, *P. poecilogaster*; Santos et al., 2019) and once or twice in *Crossodactylodes*. Although vocal slits are present in *C. bokermanni* and *C. serranegra*, they are absent in all other species, showing a complex pattern of taxonomic distribution (*C. itambae*, *C. izecksohni*, *C. pintoi*, *C. septentrionalis* and *C. teixeirai*; Santos et al., 2020, 2023; Ferreira et al., 2023). Vocal sacs seem to develop relatively late in male ontogeny (i.e., later than nuptial pad spinelike projections or enlarged forearms) and this may account for some reports of their absence (Santos et al., 2023). Moreover, despite the lack of vocal sacs in some species, all species of *Crossodactylodes* produce low intensity calls inside bromeliads (see discussion on the evolution of acoustic signals in the group by Santos et al., 2022). Notably, a young male *C. serranegra* without vocal sacs produced a similar call to that of an older male with a vocal sac (Santos et al., 2023).

Four different vocal sac patterns occur in the genus *Leptodactylus:* The sacs are absent, single and subgular, or one of two forms of external bilobate vocal sacs; some of these patterns have several independent origins (online supplementary file S3: fig. S17). Bilobate vocal sacs evolved from a single subgular vocal sac between six and seven times in the genus (according to the total-evidence phylogenetic analysis of de Sá et al., 2014) or seven times in the phylogenetic hypothesis of Schneider et al. (2019, data not shown). This occurred in the following species of the *L. pentadactylus* group: *L. rhodonotus*, *L. lithonaetes*, *L. rugosus*, and *L. rhodomystax* (lateral lobes least developed in the first and most in the latter, Heyer and Barrio-Amorós, 2009; Barrientos et al., 2018). These species were recovered as a separate clade, unrelated to the remaining species of the *L. pentadactylus* group—although with low support—by Fouquet et al. (2013) and Schneider et al.

(2019). In these species, the gular region is highly modified to form two ventrolateral areas of thin, pleated, pigmented skin (i.e., diffuse external bilobate vocal sac; Heyer and Barrio-Amorós, 2009: fig. 8; Barrientos et al., 2018: fig. 1). Bilobate vocal sacs are also present in *L. macrosternum*, the only species of the *Leptodactylus latrans* group lacking a single spherical vocal sac (Gallardo, 1964a; Magalhaes et al., 2020). In this species, vocal sacs are external and have a diffuse skin modification. Bilobate sacs have evolved between four and five times in the *L. fuscus* group (see online supplementary file S3: fig. S17). In all these species (unlike *L. macrosternum* and the members of the *L. pentadactylus* group), there are two darkly pigmented longitudinal folds that parallel to the jaws in the gular skin (fig. 8). This pattern, present in several *Leptodactylus* and *Adenomera* (with a similar morphology occuring in a few species of *Amietia*, *Nothophryne*, and *Ischnocnema*) is rarely found outside the family and produces a unique shape when the vocal sac is inflated (fig. 3H). However, the presence of these longitudinal folds is not necessarily correlated with the presence of well-developed bilobate vocal sacs because some species of *Leptodactylus* with single, subgular vocal sacs also have superficial longitudinal folds and/or pigmented bands parallel to the jaws (e.g., *L. apepyta*, Schneider et al., 2021; *L. luctator*, *L. gracilis*; Gallardo, 1964a, 1964b).

The degree of bilobation of the vocal sac is highly variable in *Leptodactylus*, ranging from subtle lateral projections of a subgular vocal sac (e.g., *L. albilabris*) to well-developed ventrolateral lobes (most developed in *L. fuscus* and *L. rhodomystax*), including several intermediate stages (e.g., *L. bufonius*, *L. latinasus*, and *L. syphax*). Moreover, vocal sacs are absent in a single species—*L. riveroi*, in which males produce a low-amplitude advertisement call that differs from those of all other *Leptodactylus* (Heyer and Pyburn, 1983; de Sá et al., 2014). Most species of the *L. melanonotus* group have been described as having internal, single subgular vocal sacs. However, images of fully inflated vocal sacs were not available for several of this species, so we score them tentatively according to the literature. It is possible that, like in *L. podicipinus*, some degree of lateralization of the single subgular vocal occurs. Males of many species of *Leptodactylus* vocalize from inside subterranean chambers or rock crevices (Straughan and Heyer, 1976; Heyer, 1969, 1978, 1979, 1994; de Sá et al., 2014), a behavior that likely affected the evolution of vocal sacs in the group. Females of several species are known to vocalize (see de Sá et al., 2014: char. 131).

In all male *Adenomera* examined, there is a pair of folds in the gular skin that extend posteriorly from the angles of the jaw onto the forearms, recovered here as a synapomorphy of the genus (Heyer, 1974; Kok et al., 2007; Carvalho et al., 2019b, 2021). These resemble those described for the *Leptodactylus fuscus* group, but the folds are shorter in *Adenomera* (i.e., always restricted to the posterior third of the mandible) and extend posteriorly. The degree of development of these folds, and consequently, the bilobation of the vocal sac, shows a subtle variation among species and even individuals (T.R. de Carvalho, personal commun.). Thus, we score all species of *Adenomera* as having bilobate vocal sacs, but stressing that variation in vocal sac shape occurs in the genus.

In *Hydrolaetare*, vocal sacs are internal, and descriptions of their inflated shape are lacking (Cochran and Goin, 1959; Gallardo, 1963; Souza and Haddad, 2003; Jansen et al., 2007; Ferrão et al., 2014). In *H. caparu*, the only species of the genus examined here, the internal mucosae are disconnected and greatly expanded medially; this, in combination with a slightly bilobate m. interhyoideus, suggests that poorly developed bilobate vocal sacs are present.

Limnodynastidae

The vocal sac structure and submandibular musculature of the family was studied by Tyler (1972, 1974a). Most species have a large, spherical subgular vocal sac with elongate vocal slits. Species of *Heleioporus* + *Neobatrachus* lack

vocal sacs but have a unique configuration of the buccal cavity (pattern 0B of this paper; Tyler, 1972: fig. 3). The buccal floor and the mm. geniohyoidei are notably expanded and pleated at the sides of the tongue, allowing for considerable distension during vocalization; externally, this resembles a single, subgular vocal sac (pattern 0B). The vocal sac is also absent in *Platyplectrum platyceps*, but the buccal cavity apparently is not modified (Tyler, 1972). Single, semicircular vocal sacs are extremely well developed in *Notaden*, in which the m. interhyoideus is both medially and laterally expanded (Tyler, 1972). Males of these species vocalize while floating or partially submerged; the vocal sacs have a large air capacity. Male *Limnodynastes tasmaniensis* (which have bright yellow, single, subgular vocal sacs) were reported to alter the shape and position of the partially inflated vocal sac, indicating the presence of finely tuned, independent control of the mm. intermandibularis and interhyoideus (Tyler, 1971c). A similar situation was observed in *Boana pulchella* (Hylidae; A.J.E.C., personal obs.).

Mantellidae

Vocal sacs are plesiomorphically single, subgular, and spherical with fused mucosae in the family, a condition retained by most species (Glaw and Vences, 2007). In several taxa, however, the vocal sac is weakly distensible (e.g., *Blommersia*, several *Boophis*, *Mantella*; Glaw and Vences, 2007; Glaw et al., 2010). In the species examined in these groups, the vocal sac cavity has little anterior development; it is restricted to the posterior portion of the gular region and enveloped only by the m. interhyoideus.

The vocal slits in all species examined are small and posterior, and possibly compatible with the presence of a sphincter such as that described for several Ranoides (Drewes, 1984; Scott, 2005). They are particularly reduced in *Blommersia* and *Mantella*; this may be correlated with the small size of the vocal sac. The only exception was *Mantidactylus opiparis* (ZFMK 60097), in which the buccal floor projects only slightly toward the submandibular muscles to generate a similar condition to that illustrated in figure 4B. The combination of single subgular vocal sacs and small, posterior vocal slits (also plesiomorphic for Rhacophoridae) is rare in Anura but could respond to phylogenetic inertia in this case, as that type of vocal slit is widespread in Natatanura.

Other vocal sac shapes evolved in a few species in Mantellidae. Bilobate vocal sacs originated at least four times. In the monotypic *Laliostoma*, the vocal sac is relatively large, extends posteriorly to the bases of the arms, and includes considerable distension of the gular and pectoral skin. Additionally, internal bilobate vocal sacs probably are a synapomorphy of the *Boophis luteus* group (present in *Boophis andohahela*, *B. andreoni*, *B. anjanaharibeensis*, *B. elenae*, *B. englaenderi*, *B. jaegeri*, *B. luteus*, *B. sandrae*, *B. septentrionalis*, *B. tampoka*, and absent in all remaining *Boophis*; Blommers-Schlösser and Blanc, 1991; Cadle, 1995; Glaw and Vences, 2007). The monophyly of this group was recovered by several studies (Glaw et al., 2010, 2021; Hutter et al., 2018, Portik et al., 2023). Additionally, vocal sacs are "paired or at least slightly bilobed" in two sister species of *Spinomantis*, *S. bertini* and *S. guibei* (Glaw and Vences, 2007). Last, a bilobate vocal sac is present in at least *Gephyromantis tschenki* (Köhler et al., 2017: fig. 2), an atypical condition for the genus.

Gephyromantis is an interesting clade in which to study vocal sac evolution, owing to the morphological diversity in vocal sacs, along with their complex patterns of taxonomic distribution. Several species have a large, well-developed spherical vocal sac (e.g., *G. cornutus*, *G. redimitus*), but it is clear that this condition is apomorphic. Although evolution of a single, subgular, spherical vocal sac from a paired structure is infrequent in Anura, this transformation seems to have occurred several times independently in *Gephyromantis.* And in at least one species, *G.*

tschenki, the vocal sac is bilobate. However, most *Gephyromantis* have paired, subgular vocal sacs with separate mucosae, the condition that is synapomorphic for the genus. The gular skin always bears two diffuse ventrolateral patches of pleated skin, but the degree of skin differentiation varies. (We tentatively scored some species as lacking skin modification based on images of taxonomic literature; however, the condition of the gular skin should be verified by direct examination of specimens in the reproductive season.)

Moreover, several *Gephyromantis* have sexually dimorphic thickenings of the skin immediately below the jaws (fig. 6P; notably, a structure present only in species with paired subgular vocal sacs). Macroscopic examination of this relatively rigid structure could suggest a glandular nature. In most cases, this mass is darkly pigmented and develops over the vocal sacs (Vences et al., 2017: fig. 11D). It is surprising that this tissue and its histological structure have received very little attention in the literature, given that another sexually dimorphic structure present in the same species, the femoral gland, has been extensively studied in the family (Blommers-Schlösser, 1979; Blommers-Schlösser and Blanc, 1991; Glaw et al., 2000; Vences et al., 2017).

A unique vocal sac pattern is recovered as a synapomorphy of the *Boophis albilabris* group (Boulenger, 1888; Blommers-Schlösser and Blanc, 1991; Andreone et al., 2002). In these species, the dorsal part of the m. interhyoideus is greatly expanded, resulting in paired vocal sacs that inflate at the sides of the head. The pattern is extremely rare in Anura and found elsewhere only in few Lophyohylini hylids (fig. 5J; Moura et al., 2021). The skin at the sides of the body is expanded and loose, but does not seem to be modified or particularly elastic.

Megophryidae

Vocal sacs are absent or single and subgular in most members of the family; in a few species, they are paired and subgular (online supplementary file S3: fig. S1). If present, vocal slits are extremely small and posterior (recovered as a synapomorphy for the family). In most species, the vocal sac extends far posteriorly toward the abdomen, but it never extends beyond the lower lip anteriorly. We could not determine whether the vocal slits were surrounded by muscle fibers to produce sphincters. In all members of Megophryinae studied here (i.e., *Ophryophryne hansi*, *Pelobatrachus nasutus*, and *Xenophrys major*), the large, posterior portion of the vocal sac mucosa lacks ventral support by the m. interhyoideus and is directly exposed to the submandibular and pectoral lymph sacs. Vocal sacs were lost at least five times in the clade, but in all cases in single species or two-species clades: *Atympanophrys shapingensis*, *Boulenophrys caudoprocta*, *B. mirabilis* + *B. shuichengensis*, *Ophryophryne gerti*, and *Xenophrys aceras* (online supplementary file S1).

Vocal sacs in all *Leptobrachella* are internal (Das et al., 2010). In most species, they are single, subgular, and spherical and poorly developed, but in some others, the sacs show some degree of bilobation. In *L. aerea*, *L. bondangensis*, *L. fritinniens*, *L. fusca*, *L. hamidi*, *L. isos*, *L. itiokai*, *L. juliandringi*, *L. marmorata*, and *L. minima*, vocal sacs are paired and subgular. Among these species, images of fully inflated vocal sacs were available for only *L. fritinniens* and *L. hamidi* (Dehling and Matsui, 2013). Thus, it was not possible to determine whether vocal sacs are paired subgular or bilobate (as defined herein) in the remaining eight species; these taxa were scored as paired and subgular based on the literature. The lack of published data prevents us from assessing the diversity of vocal sac shapes and internal anatomy of vocal sacs in *Leptobrachella*.

A sister taxon relationship between *Oreolalax* and *Scutiger* has been recovered consistently in the past couple of decades (Frost et al., 2006; Delorme et al., 2006; Pyron and Wiens, 2011; Jetz and Pyron, 2018). Under this scenario, this clade composed by 48 species would be the second largest anuran radiation in which the vocal sac has been lost (the first one being Telmatobiidae with 61 species). However, the results of Portik et al. (2023) chal-

lenge the monophyly of this group and indicate that vocal sacs were lost independently in an internal clade of *Scutiger* (excluding the basal species *S. gongshanensis*, *S. wuganfui*, where vocal sacs are present; Jiang et al., 2012), and in *Oreolalax* (although regained in *Oreolalax omeimontis*; Hou et al., 2020). Vocal sacs are also present in *Scutiger adungensis* (Dubois, 1979), but its phylogenetic position is uncertain. Given that it shares many features with *Oreolalax*, it is likely that it is an early diverging species in *Scutiger*, making the presence of vocal sacs plesiomorphic. Some *Scutiger* (*S. glandulatus* and *Scutiger* sp., related to *S. mammatus*) vocalize underwater, producing long and relatively simple, multipulsated calls, a feature that also may be found in some *Oreolalax* (Zheng and Xie, 2022). These species have aquatic habits in high-altitude mountain streams and have reduced tympanic-middle ears. Underwater vocalization is known in four species of *Leptobrachium* (Zheng et al., 2011; Rao et al., 2006). In *L. ailaonicum*, *L. boringii*, and *L. leishanense*, males call completely submerged and lack a vocal sac (they are the only *Leptobrachium* without vocal sacs); *L. liui*, which calls partly submerged, has a single subgular, internal vocal sac, the condition found in all remaining species of the genus (Gu et al., 1986). Underwater vocalization in anurans is a rare feature that has begun to be explored only recently; thus far, it has been reported in some species of Alsodidae, Megophryidae, Pelobatidae, Pelodytidae, Pipidae, Ranidae, and Telmatobiidae (Brunetti et al., 2017; Zheng, 2019).

Micrixalidae

Vocal sacs in Micrixalidae are single, subgular, internal, and usually small (Inger, 1954, Biju et al., 2014). Information on vocal slits is lacking for most species. The gular skin in males usually is bright white and stands out in the rocky streams where they vocalize (Krishna and Krishna, 2006). Unlike other clades of diurnal, torrent-dwelling frogs that perform visual displays (e.g., *Hylodes*, *Staurois*), vocal sacs in *Micrixalus* are single and spherical.

Microhylidae

The diversity and evolution of vocal sacs in Microhylidae were studied by Targino et al., (2019), who described the nature and distribution of a dorsal fold in the m. interhyoideus—a feature unique to this family. Vocal sacs are present in most species, absent only in *Hoplophryne* and *Ctenophryne* (synapomorphic for these genera) and in a few species of *Austrochaperina*, *Chiasmocleis*, *Cophixalus*, and *Sphenophryne*. Most of the species of the family have single, subspherical vocal sacs, with the following exceptions. (1) External, semicircular vocal sacs are present in several *Kaloula*, some *Uperodon*, and *Scaphiophryne madagascariensis*. Males of these species vocalize while floating in small ponds and have large vocal sacs (Prasad et al., 2022). (2) Male *Glyphoglossus molossus* have paired tubular projections of the subgular portions of the m. interhyoideus that extend posteriorly over the arms to form a unique type of vocal sac (fig. 3T; Taylor, 1962; Targino et al., 2019: fig. 3D). Males of this species store massive volumes of air in their vocal sacs and vocalize in large choruses while floating in small forest ponds (Altig and Rowley, 2014). (3) In some species, single, subgular vocal sacs project anteriorly. For example, in some *Chiasmocleis* and *Elachistocleis*, males usually call in an upright posture from flooded fields, projecting the vocal sacs above the water surface. And in some *Uperodon*, males call floating in small ponds but curve their trunks dorsally and project their vocal sacs anteriorly. (4) In *Chiasmocleis royi* and *Uperodon systoma*, the vocal sac is greatly expanded and curved anterodorsally in front of the head (fig. 12K; Peloso et al., 2014; Prasad et al., 2022). (5) There are paired, subgular, and external vocal sacs in *Otophryne pyburni* (pattern 4B; J.-C. de Massary, personal commun.; not reported by Targino et al., 2019). Vocal slits

are plesiomorphically elongate in the family and this condition is retained by most species.

Myobatrachidae

The vocal sac structure and submandibular musculature of representatives of the family was studied by Tyler (1972, 1974a). Unlike all remaining Myobatrachoidea, a single vocal slit is present in the holoype of *Arenophryne rotunda* (Myobatrachidae; Tyler, 1972, 1976). This feature is only found in Bufonidae (in which it is relatively common), some dendrobatids and one species of *Craugastor*. Most myobatrachids have single, subgular vocal sacs. Adult males of *Anstisia* have a pair of longitudinal folds in *A. rosea* (the only species of the genus for which we have information), these folds do not affect the spherical shape of the vocal sac.

Vocal sacs are absent in two species of *Taudactylus* (*T. diurnus* and *T. eungellensis*). These species, as well as the members of the genus with vocal sacs, vocalize inside rock crevices near to mountain streams, both at night and during the day, although these two species call at much lower volumes than the rest of the genus (Liem and Hosmer, 1973; Ingram, 1980, Clarke, 2006). Most myobatrachids call from the ground, hidden under leaf litter, or from inside shallow burrows, whereas a few others (e.g., some *Crinia*, *Spicospina*, *Taudactylus rheophilus*) call partly submerged in water or afloat (Clarke, 2006).

Nasikabatrachidae

Bilobate internal vocal sacs are a synapomorphy of *Nasikabatrachus* (online supplementary file S3: fig. S1). Unfortunately, specimens of this family were not available for the present study. Similar to what occurs with other anurans with round bodies, proportionally small heads and large vocal sacs (e.g., *Rhinophrynus*, *Breviceps*, *Notaden*, *Myobatrachus*), it appears as if the entire anterior part of body inflates during vocalization. Since the gular skin is not modified with respect to the surrounding skin, the vocal sac is not clearly defined (see Thomas et al., 2014). Males vocalize hidden in shallow burrows near seasonal streams (Zachariah, et al., 2012; Janani et al., 2017).

Neblinaphrynidae

Male *Neblinaphryne mayeri*, the single species of the family, have a single, subgular vocal sac, which is dark and externally conspicuous in some individuals (Fouquet et al., 2023; the plesiomorphic condition for Brachycephaloidea). Vocal slits are located posterolaterally. Little is yet known about the biology of this frog.

Nyctibatrachidae

The plesiomorphic condition (presence and morphology) for the family could not be determined because of lack of information for two of the three genera, *Astrobatrachus* and *Lankanectes* (online supplementary file S3: fig. S5). *Lankanectes* has internal vocal sacs, but their inflated shape has not been described (Dubois and Ohler, 2001; Senevirathne et al., 2018). The condition of vocal sacs in the monotypic genus *Astrobatrachus* is unknown (Vijayakumar et al., 2019).

Male *Nyctibatrachus* have paired, internal, and lateral vocal sacs, with large lobes that inflate at the sides of the head (fig. 3S; Gururaja, 2012; Willaert et al., 2016). The lobes are derived from tubular projections of the subgular portion of the m. interhyoideus that curve dorsally behind the mandibular joint. In at least one species, *N. kempholeyensis*, the paired lobes project farther posteriorly to terminate along the flanks of the body (Gururaja et al., 2014: fig. 10A). The condition of two species closely related to *N. kempholeyensis* (*N. athirappillyensis* and *N. mewasinghi*) could not be evaluated here and could possibly show a similar vocal sac pattern. In the species examined, the mucosae are separate and extremely lateral in position; the vocal slits are small and posterior. It is possible the vocal slits have sphincters, but we could not determine whether muscle fibers are present. According to Biju et al. (2011),

paired lateral vocal sacs are present in all species of *Nyctibatrachus* included in his revision; accordingly, we recognize this as a synapomorphy for the genus (and potentially of the whole family). However, little is known about the natural history of several species (Kunte, 2004), and pictures of vocalizing males with fully inflated vocal sacs are available for only a few species. Most of these frogs are large, torrent-dwelling species from the northern clade of Van Bocxlaer et al. (2012; e.g., *Nyctibatrachus humayuni*, *N. jog*, *N. major*, and *N. petraeus*), but a similar condition also is present in *N. minor*, a small, terrestrial member of the southern clade (Biju et al., 2011: fig. 42B; Van Bocxlaer et al., 2012). Gururaja et al. (2014) did not observe any vocal sac expansion in calling *N. kumbara*; thus, vocal sacs may be absent but this is not confirmed. Given the morphological and ecological diversity of species of *Nyctibatrachus* and the scarcity of information on natural history of most species, it is likely that vocal sac diversity in the genus is underestimated. Moreover, sexually dimorphic skin modification is absent in the family, so vocal sac structure can only be properly assessed by means of internal dissections and behavioural observations.

In *Nyctibatrachus humayuni*, females were observed to call from high perches in trees and also from the rocks next to fast-flowing streams. However, they emit very different calls as their male conspecifics despite lacking vocal sacs (Willaert et al., 2016).

Odontobatrachidae

Vocal sacs are paired and subgular, with diffuse patches of elastic skin next to the angles of the jaws (Barej et al., 2014a, 2014b, 2015). The vocal sacs of *Odontobatrachus natator* have disconnected mucosae, and small and posterior vocal slits (Elias-Costa and Faivovich, 2019) as do other members of the family (M. Schäfer, personal commun.). Schäfer et al. (2024) referenced vocal sac anatomy in the family in his description of sexually dimorphic adipose tissue deposits in the submandibular lymphatic space. Little is known about the reproductive biology of this West African family, but all species are nocturnal and found on rocks along rapids and cascades (Doumbia et al., 2018; Channing and Rödel, 2019; Schäfer et al., 2021).

Notably, unilateral inflation of paired vocal sacs was observed in reproductively active, captive specimens of *Odontobatrachus smithi* (A.J.E.C. personal obs.). Initially, this behavior was described in other ecologically similar, but phylogenetically distant, genera: *Crossodactylus* and *Hylodes* (Hylodidae), and *Staurois* (Ranidae; de Sá et al., 2016; Elias-Costa and Faivovich, 2019; Lacerda et al., 2022). In these species, this behavior is enabled by a unique configuration of the m. interhyoideus, which only partly envelops the internal vocal sac mucosa (char. 3.1 or 3.2; Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019). A very similar configuration is present in all *Odontobatrachus* (Schäfer et al., 2024): thus, the mechanism responsible is likely the same as described for the previous species. This is the first report of unilateral inflation of paired vocal sacs in Odontobatrachidae, the third anuran family in which it is known. The behavior occurs in species that reproduce in noisy, torrential habitats, in which visual communication may be relevant; however, the behavior has not been observed in the wild.

Odontophrynidae

Vocal sacs in the family are single, subgular, and spherical, and in most species, they are relatively large (Liu, 1935; Lynch, 1971). Vocal slits are elongate. In at least one species of *Proceratophrys*, *P. cristiceps*, the inflated vocal sacs extend above the arms in a horseshoe shape. Males often have a black or dark yellow gular pigmentation and vocalize from the banks of small streams or ponds, or partially submerged in shallow water (Abravaya and Jackson, 1978; Kwet and Faivovich, 2001; Rosset et al., 2007; Rosset, 2008; Caramaschi and Napoli, 2012, Dias et al., 2013; Mângia et al., 2014; Rocha et al., 2017). In *Odontophrynus*, the gular skin is closely

associated with the submandibular muscles, with the inner layer of the hypodermis continuous with the epimysium in a broad median portion of the throat (fig. 10A).

Pelobatidae

Absence of vocal sacs optimized as a synapomorphy of the family (online supplementary file S3: fig. S1; Boulenger, 1897; Liu, 1935). However, males vocalize at night in large, shallow ponds in the spring (Nyström et al., 2002). Males and females are known to vocalize underwater, producing weak, low-frequency calls (Schneider, 1966; Lizana et al., 1994; Frommolt et al., 2008, Seglie et al., 2013). Also, young terrestrial metamorphs start emitting calls long before sexual maturity, as early as in Gosner's stages 42 or 43, but the biological function of these vocalizations is not yet clear (Ten Hagen et al., 2016).

Pelodytidae

Pelodytid vocal sacs are rudimentary. Paired, poorly developed mucosae are present: the buccal floor projects only slightly in two large areas beside the tongue (fig. 4B). The entrances to these rudimentary projections are large (i.e., vocal slits as gaping holes, inferred as a synapomorphy of the family). Vocal sacs are bilobate (with a bilobate m. interhyoideus that was recovered as a synapomorphy of the family) but relatively small and internal. Males vocalize partly submerged at the edge of temporary ponds or slow streams, producing a series of different notes, and at least one species, *Pelodytes punctatus*, calls partially or fully submerged underwater. Males produce a series of different notes, and the structure of the calls has geographic variation (Pargana et al., 2003; Diaz-Rodriguez et al., 2017).

Petropedetidae

Due to a large ambiguity in the base of Natatanura, the plesiomorphic condition of vocal sacs in Petropedetidae could not be determined. They are single and subgular in *Ericabatrachus* and absent in *Arthroleptides* + *Petropedetes* (online supplementary file S3: fig. S4). There is little information about vocal sac morphology in the family in the taxonomic literature (Amiet, 1973, 1983; Klemens, 1998; Barej et al., 2010, 2014a; Sánchez-Vialas et al., 2018; Channing and Rödel, 2019). Moreover, reports in the available information often are contradictory. For example, internal vocal sacs have been reported as present in some species: single in *Ericabatrachus* (Largen, 1991) and *Petropedetes johnstoni* (Liu, 1935) and paired in *P. palmipes* (Boulenger, 1905) and *Arthroleptides martiensseni*, *Petropedetes johnstoni*, *P. newtoni*, and *P. parkeri* (Perret, 1966; Scott, 2005). However, vocal sacs were reported as absent in *Arthroleptides martiensseni* (Liu, 1935), and *P. parkeri* (Parker, 1936b, as *P. johnstoni*; Narins et al., 2001). We examined male *Petropedetes juliawurstnerae*, *P. palmipes*, *P. parkeri*, *P. perreti*, and *P. vulpiae* and none had vocal slits or expansions of the buccal floor; sex was identified by the presence of tympanic papillae, hypertrophied arms, and well-developed femoral glands. In contrast, *Petropedetes cameronensis* (ZFMK 81154) has two poorly developed projections of the anterior portion of the buccal floor (underlain only by the m. intermandibularis), in a pattern resembling that shown in figure 4B, which is probably the pattern that Perret (1966: 374) described as a "double vocal sac without vocal apertures."

These incongruencies likely stem from the following factors: (1) The vocal sac structure observed in *P. cameronensis* is rare and may not have been interpreted by all authors as a true vocal sac owing to the slight projection of the buccal floor and large, undefined vocal slits; a similar vocal sac could be also present in other species. (2) Although resorption of vocal sacs after the breeding season has not been demonstrated for any species (although suggested by Dubois, 1976), this particular type of vocal sac could be subject to seasonal variation, as do other secondary sexual characters in the genus, such as tympanic papillae and dermal spicules (Amiet, 1983; Barej et al.,

2010). (3) Because most petropedetids breed in torrents and fast-flowing streams, and often vocalize close to waterfalls or from rock crevices (Barej et al., 2010; Channing and Rödel, 2019), inflated vocal sacs are difficult to observe.

During the breeding season, male *Petropedetes* develop a unique dermal papilla that projects from the center of the tympanum (Perret, 1966; Amiet, 1983). The papilla may affect the vibratory frequency of the tympanic membrane, consistent with the use of the eardrum as a call receiver and as call radiator, similar to that which was observed in some *Lithobates* (Purgue, 1997; Narins et al., 2001). However, the presence of dermal exocrine glands in the tip of the papilla, and the movement of the papillae during ventilation suggests a broader role in multimodal communication.

Phrynobatrachidae

All phrynobatrachids have single, spherical vocal sacs, and all species examined have fused mucosae except *Phrynobatrachus calcaratus* (online supplementary file S3: fig. S4). Vocal slits are elongate but narrow and short. The greatest source of variation in the family is the pigmentation and/or folding of the gular skin, forming several patterns.

A few species of *Phrynobatrachus* have internal vocal sacs in which the gular skin, pigmented or not, is smooth. These include *Phrynobatrachus annulatus*, *P. bibita*, *P. brongersmai*, *P. dispar*, *P. jimzimkusi*, *P. njiomock*, *P. steindachneri*, *P. taiensis*, *P. uzungwensis*, and *P. villiersi* (Zimkus and Blackburn, 2008; Pickersgill et al., 2017; Goutte et al., 2019; Channing and Rödel, 2019).

In other species, the lateral portions of the gular skin have shallow, longitudinal folds parallel to the jaw (fig. 6D). Several shallow folds are present in adult male *Phrynobatrachus acridoides*, *P. alleni*, *P. anotis*, *P. arcanus*, *P. auritus*, *P. chukuchuku*, *P. horsti*, *P. latifrons*, *P. plicatus*, and *P. sandersoni* (Stewart, 1967; Largen, 2001; Zimkus and Blackburn, 2008; Zimkus, 2009; Pickersgill et al., 2017; Channing and Rödel, 2019).

In a third configuration, there is greater degree of skin modification, which forms a rigid central patch, defined by a U-shaped transverse fold (Schiøtz, 1967; Pickersgill et al., 2017). Mentions of this character are commonplace in taxonomic descriptions, but the histological structure of this gular fold has not been studied, and it is unclear whether this arrangement is caused by the presence of sexually dimorphic gular glands (as in Hyperoliidae), a thickened dermis, or an overall expansion of the skin with a particular configuration of the postmandibular lymphatic septum. The presence of a gular flap was recovered as a synapomorphy of the *P. calcaratus* group (sensu Goutte et al., 2019; clade B of Zimkus et al., 2010; data not shown) and only occurs in this clade.

Regardless of the presence of folding or pleating, sexually dimorphic gular pigmentation is widespread in Phrynobatrachidae. Most adult male *Phrynobatrachus* have gray to black throats and minute spicules (Largen, 2001; Zimkus and Blackburn, 2008; Pickersgill et al., 2017, Channing and Rödel, 2019). Most species of the family have dark gular pigmentation, but a pale gular region evolved several times independently (Zimkus and Blackburn, 2008; Pickersgill et al., 2017; Channing and Rödel, 2019; Goutte et al., 2019). In some species, the vocal sacs are bright yellow and used as part of male reproductive displays. Moreover, in some male-male agonistic encounters, male *P. kreffti* inflate their vocal sacs without producing any audible sounds, demonstrating the importance of the sacs in visual communication (Hirschmann and Hödl, 2006). Yellow vocal sacs have been reported in *P. alleni*, *P. ambanguluensis*, *P. dendrobates*, *P. discogularis*, *P. kreffti*, *P. latifrons*, *P. minutus*, *P. scheffleri*, *P. sulfureogularis*, and *P. uzungwensis* (Largen, 2001; Hirschmann and Hödl, 2006; Köhler et al., 2017; Pickersgill et al., 2017; Channing and Rödel, 2019; Greenwood et al., 2020). Optimization of gular skin pigmentation in several available hypotheses indicates that bright yellow coloration evolved between four and six times in the family (data not shown, Zimkus et al., 2010; Jetz and Pyron, 2018; Goutte et al., 2019, Gvoždík et al., 2020).

Pipidae

Vocal sacs are absent in Pipidae (Liu, 1935). Most members of the family have a unique type of underwater vocalization that does not involve airflow or vocal cords. Calls in *Hymenochirus*, *Pipa*, and *Xenopus* consist of a series of clicks produced with the arytenoid cartilages in their highly modified larynges (Rabb, 1960; Rabb and Rabb, 1963; Yager, 1992a, 1992b). The larynx and its associated musculature (including fiber type composition) are sexually dimorphic in these species, being in males greatly enlarged and the cartilages ossified. The vocal system is completely different from that of all other anurans (Ridewood, 1897, 1900; Sassoon and Kelly, 1986; Sassoon et al., 1987). Based on behavioral observations, Irisarri et al. (2011) suggested that airflow-based vocalization may have reevolved in *Pseudhymenochirus*, in which the larynx resembles that of other pipids.

Owing to the absence of vocal sacs in Pipidae, we cannot determine whether vocal sacs evolved independently in Rhinophrynidae and Acosmanura, or instead arose in their common ancestor and were subsequently lost in pipids. Pipids lack a tongue and have a highly modified hyoid plate (Ridewood, 1897). The evolution of these unique characteristics likely involved a large number of transformations in the gular region, which might be associated with the loss of vocal sacs. Although Pipimorpha has a rich fossil record (Báez, 1996; Gómez, 2016), the soft-tissue structures of the vocal sac are not preserved. Thus, current evidence indicates that both hypotheses are equally parsimonious.

Ptychadenidae

The presence of a pair of subgular vocal sacs with gular pouches in all species of Ptychandenidae is a synapomorphy for the family (online supplementary file S3: fig. S4; Boulenger, 1882; Liu, 1935; Laurent, 1954; Poynton, 1970; Lanza, 1978). Plesiomorphically, the mucosae are separate and restricted to a lateral position; vocal slits are small and posterior. The presence of gular pouches distinguishes ptychadenids from all other African amphibians except *Hylarana galamensis* and *Pelophylax* (Ranidae). The morphology and development of this vocal sac pattern was studied in detail by Inger (1956) in a publication that was likely the first to explore the internal anatomy of anuran vocal sacs in detail. In all species, paired lobes are spherical and well defined due to the marked contrast between the differentiated and undifferentiated portions of the skin (fig. 9). Paired lobes are large in *Hildebrandtia* and touch each other ventrally at the point of maximum inflation, whereas male *Ptychadena* have relatively smaller and clearly separated lobes (Du Preez and Carruthers, 2009: 301; Channing and Rödel, 2019: 331). The diversity of vocal sac morphology is limited in *Ptychadena* with the greatest sources of variation being the position of the pouch relative to the arm and the color of the eversible pouches. The aperture of the fold that holds the eversible pouch often is referred to as a "gular slit" (e.g., Stewart, 1967); the term is not used here to avoid confusion with the vocal slits. The relative position of the skin fold varies slightly among species (above or below arm insertion), and has been employed taxonomically (Perret, 1979; Bwong et al., 2009; Dehling and Sinsch, 2013).

In all *Hildebrandtia* and *Lanzarana*, and most *Ptychadena* (as well as the ranids with similar vocal sacs, e.g., *Hydrophylax*, *Humerana*, *Pelophylax*), the pouches are darkly pigmented (Channing and Rödel, 2019). In some species of the *Ptychadena naumanni* complex, the elastic pouches are bright yellow (*Ptychadena amharensis*, *P. beka*, *P. erlangeri*, *P. goweri*, *P. levenorum*, *P. nana*, *and P. neumanni*; Goutte et al., 2021). Moreover, the entire gular region, which is creamy white in most ptychadenids, is yellow in some species (e.g., *Ptychadena nilotica*; Dehling and Sinsch, 2013). Unlike black pigment, the yellow color is completely lost in preserved specimens; thus, the character cannot be evaluated in fixed material.

Pyxicephalidae

Vocal sacs are single subgular with elongate slits and fused mucosae in most species of the family; however, there is some variation in its shape among species (Liu, 1935; Perret, 1966; Dubois, 1992; Du Preez and Carruthers, 2009; Conradie et al., 2018; Channing and Rödel, 2019). (Although information of vocal sac morphology is absent for many species). In *Natalobatrachus*, the vocal sac is extremely small and posterior, and probably involves only the m. interhyoideus; vocal slits are small and posterior (Du Preez and Carruthers, 2009). In *Amietia*, *Tomopterna*, and *Strongylopus*, the vocal sac is intermediate in size; in the first two genera, it is ovoid and slightly expanded laterally (Liu, 1935; Drewes, 1984; Dubois, 1992; Channing et al., 2016). The gular skin in *Tomopterna* is differentiated and darkly pigmented anteriorly (Passmore and Carruthers, 1975; Du Preez and Carruthers, 2009; Wasonga and Channing, 2013). Sporadic underwater vocalization was reported for *Strongylopus wageri* (Wager, 1965). In *Arthroleptella*, *Cacosternum*, and *Microbatrachella*, the vocal sac is large and sub-spherical, and extends to the pectoral region (Hewitt, 1926; Du Preez and Carruthers, 2009; Channing et al., 2013). In *Cacosternum capense*, the vocal sac is large, and semicircular, and males vocalize partially submerged (Du Preez and Carruthers, 2009). Du Preez and Carruthers (2009: 387) mentioned that male *Microbatrachella capensis* have a gular disc in males, but the structure was not described in the literature (Boulenger, 1910; Hewitt, 1926).

Vocal sacs are bilobate in *Pyxicephalus adspersus* (but not *P. edulis*). Males have a bright yellow gular coloration that extends posteriorly to the sides of the body. They vocalize partly submerged in the water, exposing only the head and the anterior portion of the vocal sac generating waves in the water surface (Cook and Minter, 2004; a similar behavior as the species of *Aquarana*, Ranidae).

Three species of pyxicephalids not available for examination apparently have an external bilobate vocal sac, with a pair of longitudinal folds in the gular skin that resemble those seen in some *Leptodactylus* (Leptodactylidae). Photographs of a specimen of *Amietia nutti* deposited in the Muséum national d'Histoire naturelle in Paris (MNHN 1924.3) suggest the presence of this particular pattern of skin differentiation, but there is no reference to it in the original description (Boulenger, 1896, who reported an internal vocal sac), or in a recent revision of the genus (Channing et al., 2016, which includes an examination of this specimen). An image of a male specimen of *Amietia moyerorum*, the sister species of *A. nutti*, also appears to show longitudinal folds in the gular skin (Channing et al., 2016: fig. 15B). Moreover, paired longitudinal folds may be present in *Nothophryne ribauensis* (Conradie et al., 2018: fig. 8D).

Vocal sacs are absent in *Aubria* and *Poyntonia*, but vocalizations are known in both genera (Perret, 1966, 1994, Channing and Boycott, 1989; Channing and Rödel, 2019). Perret (1994) curiously reported "one internal median vocal sac, without mouth openings" for *Aubria subsigillata*. Moreover, they are absent in *Anhydrophryne ngongoniensis*, although present in the two other species of the genus (Bishop, 2004; Du Preez and Carruthers, 2009).

Ranidae

In terms of vocal sac morphology, Ranidae is one of the most diverse families in Anura, harboring 10 different vocal sac patterns, some of them with many independent origins (online supplementary file S3: fig. S6). This diversity is evident in the high MPD value, 0.83 (i.e., two given species have 83% probability of having different vocal sac shapes). Investigations of the vocal sac anatomy are abundant for some genera but absent for many others. Most of the information available stems from taxonomic accounts; however, the Central and North American and European genera (*Amerana*, *Aquarana*, *Boreor-*

ana, *Lithobates*, *Pelophylax*, *Rana*) in which the reproductive biology has been extensively studied are better known (Gaupp, 1899; Boulenger, 1897, 1919; Dickerson, 1907; Noble, 1931; Wright and Wright, 1949; Pace, 1974; Hayes and Krempels, 1986; Hillis and Wilcox, 2005; Wells, 2007). Relatively little is known about the vocal sac morphology of the remaining ranids, especially East Asian genera (Liu, 1935; Bourret, 1942; Inger, 1954, 1966; Perret, 1966; Yang, 1991; Dubois, 1992). Recently, Elias-Costa and Faivovich (2019) studied vocal sac structure in torrent-dwelling species and related taxa.

Separate mucosae with small (likely sphincteric) vocal slits are plesiomorphic for Ranidae and are present in all species examined, except for *Nidirana okinavana* (a species with a single spherical vocal sac and the only ranid studied here with relatively larger, elongate vocal slits.). Moreover, mucosae probably are likely fused in *Babina holsti*, *B. subaspera*, and *Clinotarsus curtipes*, the only other species in the family with a single spherical vocal sac (Inger, 1947; Tapley and Purushotham, 2011; material not available for the present study).

Paired subgular vocal sacs are synapomorphic for Ranidae and are present in most species of the basal genera *Amolops*, *Huia*, *Meristogenys*, *Sumaterana*, *Staurois*, and *Wijayarana.* This pattern is secondarily present in *Odorrana*. Adult males of most of these species have paired, diffuse patches of elastic skin (never discrete folds or pockets) and vocal sacs are internal in some of them. In some species, the m. interhyoideus has a median gap through which the mucosae protrude into the submandibular lymphatic space, which might be related to the unilateral inflation of paired vocal sacs (Elias-Costa et al., 2017; Elias-Costa and Faivovich, 2019). Secondarily, bilobate vocal sacs evolved in some species of *Amolops* (e.g., *A. larutensis*, *A. torrentis*; Yang, 1991). Underwater vocalization has been reported in species of *Amolops* lacking vocal sacs (Zheng, 2019). In *Odorrana tormota*, the inflation of the paired lobes of the vocal sacs apparently depends on the type of call emitted (Zhang et al., 2016).

The unique vocal sac of *Pelophylax* with paired, dorsally projecting lobes is described in the Results (vocal sac pattern 6B) and is synapomorphic for this genus. The greatest source of interspecific variation is the amount of subgular inflation, which reflects the variable distensibility of the internal mucosae. In a single species in the genus, *Pelophylax hubeiensis*, vocal sacs may be absent (Fei and Ye, 1982). However, these authors pointed out that the species is highly similar to *P. plancyi* (which has dorsally projecting vocal sacs), and many authors have suggested that these species are synonyms (Mou and Zhao, 1992; Zhao and Adler, 1993). Therefore, the condition of *P. hubeiensis* remains to be clarified. Male *Pelophylax* vocalize while floating in the surface of ponds during the day, and the eversible lobes project above the water level.

The genus *Hylarana* currently comprises 102 species formerly assigned to *Abavorana*, *Amnirana*, *Chalcorana*, *Humerana*, *Hydrophylax*, *Hylarana*, *Indosylvirana*, *Pulchrana*, *Papurana*, and *Sylvirana*. There is considerable taxonomic instability in this clade and phylogenetic relationships are poorly supported. Some of the characters defined here may result in useful synapomporphies for internal clades in the future because there is considerable informative vocal sac diversity (Dubois, 1992; Oliver et al., 2015). In several species of *Hylarana*, the internal mucosae of the bilobate vocal sac are disconnected but expanded medially, so that the center of the gular region is inflated. Because discrete skin folds and pouches are absent, the inflated vocal sac has a bilobate shape (fig. 3F). The vocal sacs in these species of *Hylarana* traditionally have been been termed "paired subgular." But given the overall diversity in Anura, the vocal sacs should be considered as bilobate, owing to the notable median inflation that distinguishes them from those of other ranids (i.e., lobes are not independent; Boulenger, 1882, 1920; Liu, 1935; Bourret, 1942; Inger, 1954, 1966; Yang, 1991; Dubois, 1992; Channing, 2001, Biju et al.,

2014). This pattern is present in most species of *Hylarana*, along with some members of *Glandirana* and *Nidirana* (Liu, 1935; Chuaynkern et al., 2010; Lyu et al., 2020). In other species of *Hylarana*, different vocal sac patterns evolved. All former *Hylarana* (sensu stricto), and *H. rawa* lack vocal sacs (Inger, 1954; Matsui et al., 2012; Oliver et al., 2015). The following species have well-developed, paired, subgular vocal sacs: *H. magna* (vocal sac pattern 4B; Biju et al., 2014); *H. galamensis*, *H. guentheri*; and all former *Humerana* and *Hydrophylax* (pattern 4C; Boulenger, 1892, 1920; Bourret, 1942; Perret, 1977; Padhye et al., 2015). Vocal sacs are also absent in the closely related genus *Sanguirana*.

The vocal sac morphology of the American clade composed of *Aquarana*, *Boreorana*, and *Lithobates* is diverse and has been used in the diagnoses of species groups (Hillis and de Sá, 1988; Hillis and Wilcox, 2005). Vocal sacs range from a broad subgular structure (e.g., *Aquarana clamitans*), to paired, posteriorly projecting lobes with little subgular inflation (e.g., *Boreorana sylvatica*), and include many intermediate forms (Boulenger, 1919; Liu, 1935; Wright and Wright, 1949; Pace, 1974; McCranie and Wilson, 2002). In addition, vocal sacs are absent in several species (synapomorphic of the *L. tarahumerae* and *L. palmipes* groups, although they reevolved in some species of the latter group; Hillis and de Sá, 1988; Hillis and Wilcox, 2005). This diversity stems from a variable degree of medial extension of paired mucosae (which remain disconnected in all species examined) and the lateral lobes of the m. interhyoideus, as well as the nature of the skin differentiation.

Basal species of *Aquarana* have relatively well-developed, paired lobes and cream-colored throats (*A. virgatipes* and *A. septentrionalis*; Dickerson, 1907). In the other species, there is less lateralization of vocal sacs and considerable subgular inflation, as well as a bright yellow gular pigmentation unique to the genus (*A catesbeiana*, *A. clamitans*, *A. grylio*; Dickerson, 1907). Paired lobes are retained in the m. interhyoideus of these species, but they are smaller and more ventral than in other species of the genus, and the distensible portion of the skin does not form any conspicuous folds or pouches (the vocal sacs inflate "inside the body wall" as opposed to forming discrete lobes). The species of *Aquarana* with yellow throats usually vocalize during the day, whereas those with cream-colored throats are mostly nocturnal; thus, color may play a role in visual communication (Dickerson, 1907; Wright and Wright, 1949; Given, 1987).

Most species of the diverse *Lithobates pipiens* complex have well-defined, paired lobes of the m. interhyoideus that vary in their degree of development. These range from paired spheres behind the angles of the jaw (e.g., *L. blairi*; Pace, 1974) to elongate, posterior projections above the arms (e.g., *L. pipiens*; Dickerson, 1907; also present in *B. sylvatica*, not belonging to this species complex). In some species, paired spherical lobes are oriented posterodorsally, somewhat resembling the condition seen in *Pelophylax* (e.g., *L. areolatus*, *L. berlandieri*, *L. kauffeldi*, and *L. sphenocephalus*, but potentially in other poorly known species as well). The gular skin in these *Lithobates* has a distensible pouch supported ventrally by a more rigid portion, which likely enables dorsal projection. However, in these species—unlike *Pelophylax*—the elastic pouches are less clearly delimited (i.e., the contrast with the unmodified skin is neither as evident nor as localized); thus, the inflated lobes are less defined. The lobes do not completely fold within themselves when deflated, but instead hang loosely at the sides of the head. This may be because the m. interhyoideus is not closely associated with the dermis, which pulls the pouches inward (fig. 9).

In the few species of *Rana* with vocal sacs, gular skin differentiation is absent. All the species examined have paired subgular lobes in the m. interhyoideus, which are much smaller than those in *Lithobates*, with the exception of *Rana arvalis* and *R. temporaria*, in which they are well developed (Wright and Wright, 1949; Hayes and Krempels, 1986). In *Amerana boylii*, lateral development is negligible, and the

inflated vocal sac is practically single subgular (Stebbins, 1985).

Most *Amerana*, *Aquarana*, *Lithobates*, and *Rana* vocalize from the surface of shallow ponds, while either floating or partially submerged at the edges of the water body (Dickerson, 1907; Wright and Wright, 1949; Zweifel, 1955; Savage, 2002). Waves produced on the water surface during vocalization play an important role in intraspecific communication in some species (Höbel and Kolodziej, 2013). Additionally, in *Aquarana catesbeiana*, sound is radiated through the partially submerged vocal sac, as well as through the tympanic membrane, which produces airborne sound waves (Purgue, 1997). The tympanum is considerably larger in male bullfrogs than in the females; this suggests that sound transmission through it may also occur in other species also in which there is a sexually dimorphic difference in the size of the tympanum (Wright and Wright, 1949).

In Ranidae vocal sacs were lost several times during the evolutionary history of the clade. We identified between 11 and 19 losses, depending on the optimization. These transformations are distributed throughout the family, but are concentrated in the genera *Amolops*, *Lithobates*, and *Rana*, in which the presence of vocal sacs has complex evolutionary histories (online supplementary file S3: fig. S5). Moreover, there is polymorphism in the presence and number of vocal slits in some species (Hayes and Krempels, 1986; Hillis and de Sá, 1988). Some species without vocal sacs are not known to vocalize, whereas others do so but at low volumes and often below the surface of the water (Hillis and de Sá, 1988; Asimakopoulos et al., 1990: Northen, 1993; Platz, 1993; Hillis and Wilcox, 2005; Wells, 2007; Sanguila et al., 2016; Zheng, 2019, and references therein). With the exception of (at least) *Lithobates palustris* and *Amerana boylii*, which call from both above and below the surface, most ranids that vocalize underwater lack vocal sacs (MacTague and Northen, 1993; Given, 2005; Wheeler and Welsh, 2008). The evolution of advertisement calls and vocal sac loss in ranids and comparison of the repertoires of closely related species that vocalize in air and underwater are beyond the scope of this paper, but clearly deserve further study.

Ranixalidae

Vocal sacs are plesiomorphically absent in the family (obtained as a synapomorphy of Ranixalidae + Dicroglossidae). This condition is retained in several species of the family (*Walkerana diplosticta*, *W. leptodactyla*, *W. phrynoderma*, *Indirana beddomii*, *I. brachytarsus*, *I. leithii*, *I. semipalmata*; Boulenger, 1882, 1920; Modak et al., 2018). In several others (*Walkerana muduga*, *Indirana bhadrai*, *I. duboisi*, *I. longicrus*, *I. paramakri*, *I. salelkari*, *I. sarojamma*, *I. tysoni*, *I. yadera*; Dahanukar et al., 2016; Garg and Biju, 2016; Modak et al., 2018; Dinesh et al., 2020), there are no explicit mentions of the lack of vocal slits in the literature and vocal sacs probably are absent. The natural history of most ranixalids is poorly known; however, despite lacking vocal sacs, some of these species have been observed to call and even to have diverse vocal repertories (e.g., *I. duboisi*; *I.* cf. *tysoni*; *I.* sp.; Gaitonde and Giri, 2014; Mudke and Thunga, 2020; Mudke and Tapley, 2021); while at least one species apparently does not vocalize (e.g., *I. leithii*; Modak et al., 2018).

Vocal sacs have been reported in two species of *Indirana*. In *I. chiravasi*, the vocal sac is single, subgular, and internal, and probably scarcely distensible (Dahanukar et al., 2016). Paired, subgular vocal sacs were reported for *I. gundia* by Dubois (1986), who included this condition (so far reported for this species only) as a diagnostic character of the family. However, these species are deeply nested inside the genus (Dahanukar et al., 2016; Garg and Biju, 2016; Portik et al., 2023), so their presence does not affect the inference of the plesiomorphic state of the family.

Rhacophoridae

Plesiomorphically, vocal sacs in the family are spherical, internal, and lack sexually dimorphic

pigmentation—a condition retained by most genera (e.g., *Beddomixalus*, *Buergeria*, *Gracixalus*, *Kurixalus*, *Leptomantis*, *Mercurana*, *Philautus*, *Polypedates*, *Rhacophorus*, *Taruga* and *Zhangixalus*, and some species of *Chirixalus*, *Feihyla*, *Gracixalus*, *Liuixalus*, *Nasutixalus*, *Philautus*, *Pseudophilautus*, *Rohanixalus*, and *Theloderma*; online supplementary file S3: fig. S8; Boulenger, 1882; Liu, 1935; Inger, 1954, 1966, Malkmus et al., 2002; Abraham et al., 2013; Biju et al., 2020; Wang et al., 2018; Munir et al., 2021). In several groups there are external, single, subgular vocal sacs, in which skin modification usually is moderate and widespread across the gular region (e.g., some members of *Feihyla*, *Gracixalus*, *Ghatixalus*, *Liuixalus*, *some Nasutixalus*, *Philautus*, *Pseudophilautus*, *Raorchestes*, and some *Rohanixalus*; Malkmus et al., 2002; Manamendra-Arachchi and Pethiyagoda, 2005; Biju and Bossuyt, 2009; Rowley et al., 2011; Yang and Chan, 2018; Biju et al., 2020; Garg et al., 2021). In almost all species, inflation of the spherical vocal sac—regardless of its size—involves the entire gular region (i.e., the anterior limit of the sac is the mandibular symphysis). In contrast, several *Raorchestes* (e.g., *R. akroparallagi*, *R. bombayensis*) inflate only that part of the gular region corresponding to the m. interhyoideus, whereas the portion underlain by the m. intermandibularis remains constricted/not expanded (fig. 12E). This pattern, not observed in any other member of the family, is observed both during calls (when the vocal sac is fully inflated), as well as between calls when males retain large volumes of air in the resting vocal sac (a feature typical of the genus).

A few rhacophorids evolved vocal sacs that are not spherical. In at least two species of *Chiromantis* (*C. xerampelina* and *C. rufescens*), vocal sacs are bilobate, but internal and poorly developed (with separate mucosae in the specimen examined of the genus). Other species have been reported to have internal, paired vocal sacs (*Polypedates colleti*, *Rhacophorus omeimontis*, *R. pardalis*; Liu, 1935, Inger, 1966). However, it is not clear whether the authors are referring to paired lobes of the inflated vocal sac or paired internal cavities (i.e., separate mucosae). We observed the latter in *Rhacophorus reinwardtii* and *Zhangixalus dennysi*, in which the paired mucosae are in contact in the midline and likely produce a single or bilobate vocal sac when inflated. For instance, in *Polypedates megacephalus*, vocal sacs were described as paired, lateral, and internal (Liu, 1935), although they inflate as a subgular spherical (this study). Images of fully inflated vocal sacs were not available for these three species; thus, their condition is not clear. Tentatively, we accept the terminology of these authors; however, a more suitable term (e.g., single or bilobate, according to the classification provided here) might be applicable. Anatomical dissections of a more inclusive sample and images of vocalizing frogs are needed to clarify this matter.

At least two rhacophorid species have paired subgular vocal sacs with two patches of modified skin: *Kurixalus bisacculus* (Taylor, 1962; Zug and Mulcahy, 2020: fig. 6) and *Rhacophorus vampyrus* (Rowley et al., 2010). Vocal sacs in these species probably inflate as independent lobes, a very rare feature in the family.

Rhacophorids have a relatively complex pattern of vocal slit evolution. Several species have small, circular apertures located posteriorly near the angles of the jaw; these apertures often are surrounded by a thickened buccal mucosa. This condition, frequent in Natatanura, is plesiomorphic for Rhacophoridae + Mantellidae. In these two families, small vocal slits cooccur with single vocal sacs. In contrast, elongate, slitlike apertures evolved in several taxa (e.g., recovered as a synapomorphy of *Buergeria*, but also present in some *Chirixalus*, *Chiromantis*, *Gracixalus*, *Philautus*, and *Rhacophorus*), as did large, gaping holes (synapomorphy of a clade of *Leptomantis*). This diversity in vocal slit morphology is not associated with changes in the external vocal sac morphology, because almost all taxa have single, subgular spherical vocal sacs.[1]

[1] Drewes (1984) reported muscle fibers surrounding the vocal slit in *Philautus acutirostris*, likely indicating a sphincter. However, this species was not listed in the examined material, and perhaps he meant *Phrynobatrachus acutirostris*, which would make more sense considering his African sampling. No species of *Philautus* was examined for this paper.

Vocal sacs are absent in some members of the family, although most of the transformations occurred in single species. They were lost in *Nyctixalus* + *Theloderma* (but regained independently in *T. horridum* and the *T. asperum* group sensu Poyarkov et al., 2015). Vocal sacs are absent in *Polypedates hecticus*, *P. macrotis* (although the species calls loudly), and *P. mutus*, *Rhacophorus nigropalmatus*, and *Zhangixalus prominanus* (Inger, 1954, 1966; Harvey et al., 2002; Pauly, 2008; Kuraishi et al., 2013; Rujirawan et al., 2013). This pattern of taxonomic distribution raises questions about the selective pressures that cause reduction of the vocal sacs in a few isolated species while their ecologically similar sister species retain them.

Rhinodermatidae

Darwin's frogs of the genus *Rhinoderma* are the only known tetrapods to possess oral incubation. This unique reproductive mode, whereby males incubate larvae in their highly modified vocal sacs, was first documented by Jiménez de la Espada (1872) and is a form of pseudoviviparity known as neomelia (Pflaumer, 1936; Cei, 1962; Crump, 2002; Busse, 2002; Wells, 2007). Some interesting peculiarities have been reported for the structure of the vocal sac in *Rhinoderma darwinii*. Tyler (1971b) noticed the absence of the pectoral lymphatic septum in this species, which is present in all other Anura. This thin connective tissue membrane connects the pectoral musculature with the ventral skin; it separates the pectoral and abdominal lymphatic sacs and is a physical barrier impeding the caudal extension of the vocal sac. Because this septum is absent in *R. darwinii*, the vocal sac can expand to occupy the whole abdominal region (Howes, 1888). Additionally, the m. interhyoideus is sexually dimorphic, having two strips in males but only one in females (Manzano and Lavilla, 1995). Garrido et al. (1975) reported the presence of a secretory epithelium lining the lumen of the vocal sac. The histological structure of this epithelium appears to be related to the presence or absence of larvae in the vocal sac. In *Rhinoderma darwinii*, nonfeeding tadpoles are retained in the vocal sac for up to 52 days while they complete metamorphosis before leaving the sac as froglets through the very large vocal slits (i.e., gaping holes; Cei, 1962; Busse, 1970; Jorquera et al., 1972; Goicoechea et al., 1986). In *Rhinoderma rufum* (likely extinct), exotrophic, free-living tadpoles emerge before metamorphosis and complete development in the water (Formas et al., 1975; Jorquera et al., 1982, Formas, 2013).

Vocal sacs in the other genus of the family, *Insuetophrynus*, are internal and very poorly developed. Mucosae are rudimentary and remain mutually disconnected, resembling the morphology shown in figure 4B. They are present only in larger males (which have relatively well-defined, very long vocal slits), suggesting that evagination of the buccal floor occurs very late in postmetamorphic growth, after other structures (such as spines in hands or pectoral patches) are well developed. Barrio (1970) reported that males have "single, paired or absent vocal sacs," likely referring to vocal slits. We found no other reference to the presence of vocal sacs in the literature, so we ignore the shape of the fully inflated vocal sac, either appearing externally as a poorly inflated single subgular or slightly bilobate vocal sac (Penna and Veloso, 1990; Diaz et al., 1983). The rudimentary vocal sacs in *Insuetophrynus* raises interesting questions about the evolutionary origin of the greatly developed vocal sacs in *Rhinoderma*. These two genera have been consistently recovered as sister taxa with high support in all major recent analyses (Correa-Quezada et al., 2006; Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011; Blotto et al., 2013; Fouquet et al., 2013; Zhang et al., 2013; Streicher et al., 2018; Jetz and Pyron, 2018; Hime et al., 2021; Portik et al., 2023).

Rhinophrynidae

The vocal sac and highly derived submandibular musculature of *Rhinophrynus dorsalis* were described by several authors (Walker, 1938; Tyler, 1974b; Trueb and Gans, 1983, Elias-

Costa et al., 2021). Vocal slits are small, round and posterior. In adult males, the m. interhyoideus is projected dorsolaterally, thereby extending the vocal sac cavity above the head (fig. 15C). The lateral skin is not differentiated; thus, the two dorsal lobes seem to inflate "inside the body wall" while males vocalize floating in the surface of small temporary ponds (Foster and McDiarmid, 1983; Sandoval et al., 2015; similar to the condition described for *Trachycephalus mesophaeus*; Moura et al., 2021). While the frog vocalizes, the large volume of air stored in the lungs is displaced anterodorsally; this shifts the frog's center of mass rotating the body of the frog temporarily before it returns to the horizontal position.

Scaphiopodidae

Vocal sacs are plesiomorphically single, subspherical, and internal in the family, and vocal slits are elongate. This condition is retained in all *Scaphiopus*, in which the mucosae are fused. Males *Scaphiopus* vocalize while floating in the surface of ponds; the frogs strongly bend their trunks dorsally when they call, so that the bright white subgular vocal sac is inflated out of the water (Dickerson, 1907; Wright and Wright, 1949; McAlister, 1959). Curiously, as the body is contracted during sound production, the frogs close their eyes, a highly atypical behavior among anurans. McAlister (1959) noticed that in *Scaphiopus holbrooki* and *S. hurterii*, a thin membrane divides the vocal sac cavity sagittally (probably the surface of contact of paired mucosae), but the membrane has a round perforation that connects both contralateral cavities. In *Scaphiopus couchii*, however, this membrane is absent (i.e., mucosae are fused). Moreover, in this species, the posterior margin of the inflated vocal sac is not strictly transverse; laterally, it has a small projection toward the base of each arm (Dickerson, 1907).

External bilobate vocal sacs are a synapomorphy of the genus *Spea* (Smith, 1934; McAlister, 1959). Morevoer, the disconnection of mucosae, present in all species, is plesiomorphic for the genus. Males also vocalize while floating in small ponds and bend their trunks dorsally but not as strongly as male *Scaphiopus*. All species of the genus have external vocal sacs (Wright and Wright, 1949; McAlister, 1959).

Sooglossidae

Vocal sac morphology in the family was treated by Tyler (1985). More recently, Elias-Costa et al. (2021) reported on the submandibular musculature of some species. Vocal sacs in all species are single, subgular, and subspherical; they are relatively small and posterior in position (Tyler, 1985; van der Meijden et al., 2007). Vocal slits are small and posterior. In *Sechellophryne gardineri* (the only species of the family examined here), the vocal sac mucosa is not entirely covered by the m. interhyoideus, which is present as a thin, transverse band, and the posterior half of the mucosa lies free in the lymphatic sacs.

Strabomantidae

Although vocal sacs are plesiomorphically present in the family (online supplementary file S3: figs. S13–S15), they were lost several times and show an astounding amount of homoplasy. This results in a relatively high MPD value (0.49), particularly considering that vocal sacs are single subgular in all species in which they are present (i.e., disparity does not stem from differences in vocal sac shape). Most genera have representatives with and without vocal sacs, regardless of clade size (*Bryophryne*, *Lynchius*, *Niceforonia*, *Noblella*, *Oreobates*, *Phrynopus*, *Pristimantis*, *Serranobatrachus*, and *Strabomantis*). Thus, the occurrence of a vocal sac is not as useful as a diagnostic character for these genera as it is in other families. The distribution of vocal slits in *Pristimantis* was reviewed by García-Gómez et al. (2022); plesiomorphically, the vocal slits are present, but they are inferred to have been lost at least 21 times, and in many cases, in single species (Lynch and Ruiz-Carranza, 1983; González-

Durán et al., 2017; García-Gómez et al., 2022; Ortega et al., 2022).

Vocal sacs are present in all species of *Bahius*, *Barycholos*, *Microkayla*, *Psychrophrynella*, *Qosqophryne*, *Tachiramantis*, and *Yunganastes* included here, whereas they are absent in all sampled *Holoaden*. We found no reports of vocal sacs in *Euparkerella*; thus, the genus may lack them. Despite being plesiomorphic for these genera, it is impossible to recognize the absence of vocal sac as synapomorphic for any of them given the complex taxonomic distribution of this character state and the poorly supported relationships among them.

The degree of development or relative size of the fully inflated vocal sac could be informative for some clades. For instance, Padial et al. (2012) noticed that one important characteristic of *Oreobates* is the strong reduction (to near absence) of the vocal sac, a state that also seems to be shared with *Lynchius*, its sister group. Nevertheless, this kind of fine-scale information is unavailable for most species.

Some species of *Noblella* (e.g., *N. coloma*, *N. mindo*, *N. worleyae*) have an expanded gular skin with a pair of longitudinal folds, similar to those found in the eleutherodactylid genus *Diasporus*. In some specimens, the folds converge in the pectoral region to form a discoidal fold (Reyes-Puig et al., 2020, 2021). This character might prove useful for the taxonomy of the genus, which, as currently defined, is likely not monophyletic.

A "weakly bilobed" vocal sac was reported for *Pristimantis crenunguis* (Lynch, 1976). We tentatively score it as bilobate; however, we examined neither specimens nor images of vocalizing males. Deformation of the spherical vocal sac is extremely rare in Brachycephaloidea, the only other example known being some *Eleutherodactylus* (see account for Eleutherodactylidae). Of the few strabomantids dissected for this study, disconnected mucosae were found in *Oreobates barituensis*, *O. quixensis*, *Pristimantis palmeri*, and *Serranobatrachus sanctaemartae*. However, in all cases, the mucosae are well developed medially and there is no evidence in the m. interhyoideus or the gular skin that suggests that vocal sacs in these species inflate as bilobate. In *Strabomantis zygodactylus*, vocal slits are small and posterior, and the mucosae are separate, projecting through a gap in the m. interhyoideus. This pattern strongly resembles that described for hylodids (Elias-Costa et al., 2017) but the functional implications of the morphology in this species are uncertain.

Telmatobiidae

Vocal sacs are absent in all members of the family, representing the largest radiation of anurans in which the structure is lost and not regained subsequently (online supplementary file S3: fig. S9). Calls were traditionally considered to be absent in the genus (Trueb, 1979; Penna and Veloso, 1987), but a few studies have identified this behavior in at least some species (Blancas Sanchez, 1959, Laurent, 1973; De la Riva, 1994; Brunetti et al., 2017). Moreover, underwater vocalizations have been characterized in the genus. These relatively simple, low-pitched calls are likely perceived through extratympanic pathways, as these species have very reduced tympanic middle ears (Brunetti et al., 2017).

CONCLUSIONS

After their early origin in the evolutionary history of anurans, vocal sacs have diversified into a wide array of forms. Moreover, even though mostly related to acoustic behavior, vocal sacs have been coopted in several clades to perform a broader function in multimodal displays. Curiously, despite the presence of vocal sacs in most species and their highly conspicuous structures, their diversity has been quite underestimated.

This study has revealed a great deal of variation in each layer of the vocal sac. The most internal one, the vocal sac mucosa, is the one that shows the least variation. Nevertheless, the ability to project the buccal cavity into the submandibular space—and even fuse these lobes in the midline to form a single

cavity—is unique among vertebrates. In contrast to amniotes, which have more sophisticated mechanisms for lung inflation, frogs recycle air by vocalizing mostly with the closed mouth. This necessity to save both air and elastic energy likely represented an important selective pressure that favored the expansion and rearrangement of the buccal cavity.

Additionally, the diversification of submandibular muscles was crucial for the evolution of vocal sacs. A previous study (Elias-Costa et al., 2021) indicated that submandibular muscles (particularly the mm. intermandibularis and interhyoideus) are extremely variable in Anura. These muscles—the homology of which can be traced back to those of early gnathostomes or even cyclostomes—provide ventral support to the head, with little variation across vertebrates. Particularly relevant to this study is the plasticity of m. interhyoideus. In most vertebrates, this muscle forms a layer of transverse fibers, but in many anurans it expands ventrally, posteriorly, or dorsally, often forming well-defined lobes. Moreover, its extracellular matrix is rich in elastic fibers that form highly organized tridimensional networks and allow for great variation in size during inflation. This morphological and functional diversification of the m. interhyoideus with respect to other vertebrates (possibly enabled by changes in the hyoid, the reduction of the vertebral column, and with it, the absence of a cervical region and proximity of the pectoral girdle and the jaws, the relative expansion of the mandibular arch, the flexion of the mandible, etc.) boosted the diversification of vocal sacs.

It is also interesting that several species have independently evolved similar vocal sac morphologies. For example, semicircular or paired vocal sacs, which displace air from the gular region to the sides of the head, permit vocalization while floating on the surface of the water. A similar effect is observed in species that project the vocal sac anteriorly while being half submerged. Moreover, some distantly related species that breed in noisy environments have evolved complex behaviors like the unilateral sac inflation. Such convergences suggest that vocal sac shape is likely affected by environmental conditions.

On the other hand, despite the relevance of vocal sacs for the biology of many species, we inferred an astounding number of independent losses (between 146 and 196) during the evolutionary history of anurans. The question of whether secondary losses of the vocal sac coevolved with reductions in calling activity is open for future studies. However, considering the diversity of life histories among species that lack a vocal sac, it seems clear that many different selective pressures (e.g., underwater vocalization, reproduction in reduced spaces like phytotelmata, high altitude, etc) are responsible for vocal sac reduction.

Our study provides many new synapomorphies and a large dataset that are available for future taxonomic studies. It is hoped that knowledge of vocal sac anatomy, diversity, and evolution will pave the way for future assessments of the evolutionary processes that underlie the loss of vocal sacs and the origin of different vocal sac morphologies; the interplay of vocal sac shape, calling behavior, microhabitat of vocalization, and acoustic parameters; and the evolution of sexual dimorphism in anurans.

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APPENDIX 1

List of Specimens Examined

Institutuional abbreviations follow Sabaj (2022). All specimens are adult males unless indicated with f (adult female) or juv (juvenile). Specimens marked with * (asterisk) were examined only externally. Specimens marked with "+" (plus) were studied histologically.

ALLOPHRYNIDAE: *Allophryne ruthveni* MZUSP 78207.

ALSODIDAE: *Alsodes gargola* MACN 38937 (f); *Alsodes neuquensis* MACN 41370, 48996; *Alsodes verrucosus* MACN 41388 (f); *Eupsophus calcaratus* MACN 41444; *Eupsophus roseus* MACN 49594, 52414; *Eupsophus vertebralis* CENAI 3747; *Limnomedusa macroglossa* JF 3064 (MACN), MACN 40642.

ALYTIDAE: *Alytes obstetricans* MZUSP 11472; *Discoglossus galganoi* ZFMK 61040; *Discoglossus pictus* MZUSP 94898; *Discoglossus sardus* ZFMK 96965.

AROMOBATIDAE: *Allobates femoralis* ZFMK 85548; *Allobates marchesianus* MZUSP 51237 (f); *Anomaloglossus stepheni* MZUSP 67883 (f); *Mannophryne herminae* CENAI 2617.

ARTHROLEPTIDAE: *Arthroleptis adelphus* ZFMK 69254; *Arthroleptis poecilonotus* MZUSP 114613 (f); *Arthroleptis stenodactylus* ZFMK 44842; *Arthroleptis variabilis* ZFMK 78413; *Astylosternus diadematus* ZFMK 77965; *Astylosternus fallax* ZFMK 81609; *Astylosternus montanus* ZFMK 69170; *Astylosternus perreti* ZFMK 81000; *Astylosternus robustus* USNM 571059; *Astylosternus schioetzi* ZFMK 89473; *Cardioglossa elegans* ZFMK 67735; *Cardioglossa gracilis* ZFMK 69195; *Cardioglossa leucomystax* ZFMK 81627; *Leptodactylodon blancyi* MNHN-RA-1996.8876* (MNHN Online database); *Leptodactylodon boulengeri* ZFMK 69188; *Leptodactylodon mertensi* ZFMK 69396; *Leptodactylodon ornatus* ZFMK 67369; *Leptodactylodon ovatus* ZFMK 81712; *Leptopelis bocagii* ZMH A 06243; *Leptopelis brevirostris* ZFMK 28842, 61305 (f); *Leptopelis karissimbensis* ZFMK 87997; *Leptopelis kivuensis* ZFMK 87993; *Leptopelis millsoni* ZFMK 87708; *Leptopelis natalensis* MACN 53610; *Nyctibates corrugatus* ZFMK 81156; *Scotobleps gabonicus* ZFMK 87775.

ASCAPHIDAE: *Ascaphus truei* MACN 39148.

BATRACHYLIDAE: *Atelognathus patagonicus* MACN 37883, MACN w/o No.; *Atelognathus nitoi* MACN 41332; *Batrachyla antartandica* BB 2134 (MACN); *Batrachyla leptopus* MACN 48995; *Batrachyla taeniata* MACN 41265; *Chaltenobatrachus grandisonae* BB 2341 (f, MACN); *Hylorina sylvatica* MACN 42530.

BOMBINATORIDAE: *Bombina bombina* ZMH A 05109; *Bombina orientalis* MACN 42130; *Bombina pachypus* ZMH A 06205.

BRACHYCEPHALOIDEA incertae sedis: *Geobatrachus walkeri* ICN 20347 (f).

BRACHYCEPHALIDAE: *Brachycephalus ephippium* CFBH 16836, MZUSP 100304; *Ischnocnema guentheri* MACN 17058.

BREVICIPITIDAE: *Breviceps adspersus* ZFMK 21915; *Breviceps mossambicus* ZMB 83243; *Callulina kreffti* ZMB 23341.

BUFONIDAE: *Adenomus kelaarti* ZFMK 85842; *Amazophrynella minuta* ICN 46770 (f); *Anaxyrus cognatus* ZFMK 96294; *Anaxyrus woodhousii* MACN 42131, 42123; *Ansonia hanitschi* ZFMK 80741; *Ansonia longidigita* ZFMK 80678; *Atelopus flavescens* ZFMK 36524; *Atelopus ignescens* ZFMK 35397; *Atelopus pastuso* ICN 26587; *Atelopus pulcher* ZFMK 50685; *Atelopus spumarius* ICN 46839 (f); *Atelopus varius* ICN 31488 (f), ZFMK 85045; *Bufo bufo* ZMH A 09102; *Bufo gargarizans* ZFMK 94953; *Bufotes viridis* ZMH 14716; *Dendrophryniscus leucomystax* CFBH 22328; *Didynamipus sjostedti* ZMB 77471; *Duttaphrynus aturokalei* ZFMK 85833; *Duttaphrynus dhufarensis* ZFMK 29059; *Epidalea calamita* MACN 36530 (f), ZFMK 97180; *Incilius coccifer* ZFMK 85120; *Incilius melanochlorus* ZFMK 85112; *Ingerophrynus galeatus* ZFMK 88978; *Leptophryne borbonica* CENAI 7615-7; *Melanophryniscus altroluteus* MACN 39994; *Melanophryniscus devincenzii* MACN

39960; *Melanophryniscus klappenbachi* MACN 49593; *Melanophryniscus krauczuki* MACN 39957; *Melanophryniscus moreirae* CFBH 297; *Melanophryniscus pachyrhinus* BKT 3387; *Melanophryniscus rubriventris* MACN 50937; *Melanophryniscus setiba* CFBH 15737; *Melanophryniscus stelzneri* MACN 47819; *Nannophryne cophotis* KU 211710; *Nannophryne variegata* MACN 52417; *Nectophryne batesi* ZFMK 78237; *Nectophrynoides tornieri* ZMB 48547; *Nectophrynoides viviparus* ZMB 48555; *Nimbaphrynoides occidentalis* ZMB 73883; *Osornophryne bufoniformis* ICN 12254; *Peltophryne empusa* MACN 39143; *Phrynoidis asper* ZFMK 61861; *Rentapia hosii* ZFMK 48606; *Rhaebo guttatus* ICN 34808 (f); *Rhaebo hematiticus* ICN 32925, ICN 55281 (f); *Rhinella arenarum* MACN 15867; 43405, MACN S/D 1 (f), MACN S/D 2 (f); *Rhinella fernandezae* MACN 39370; *Rhinella major* MACN 39100, without no. (f); *Rhinella margaritifera* ZFMK 85222; *Rhinella rumbolli* MACN 43713; *Rhinella spinulosa* MACN 41859; *Rhinella veraguensis* ZFMK 80578; *Schismaderma carens* CENAI 5984; *Sclerophrys capensis* CENAI 6851; *Sclerophrys garmani* ZMH 14694 (juv); *Sclerophrys pardalis* CENAI 5694; *Strauchbufo raddei* ZFMK 9674; *Vandijkophrynus angusticeps* CENAI 6194 (f), ZFMK 85730; *Werneria mertensiana* ZFMK 69139.

CALYPTOCEPHALELLIDAE: *Calyptocephalella gayi* MACN 45818; *Telmatobufo australis* ICMLH 579*.

CENTROLENIDAE: *Cochranella nola* ZFMK 83336; *Espadarana prosoblepon* ICN 19657; *Nymphargus chamai* MAR 2912; *Vitreorana parvula* MACN 49000.

CERATOBATRACHIDAE: *Alcalus baluensis* FMNH 231091; *Cornufer guentheri* CENAI 7553; *Cornufer papuensis* MCZ A-2441* (as *Platymantis corrugatus rubstriatus*; obvserved in the MCZ online database); *Cornufer trossulus* ZMH A 00671; *Cornufer vertebralis* ZMH A 00650; *Platymantis* cf. *corrugatus* FMNH 274231.

CERATOPHRYIDAE: *Ceratophrys aurita* MZUSP 56463; *Ceratophrys cornuta* MZUSP 151382, 151492, CFBH 20082 (juv); *Ceratophrys cranwelli* MACN 42339; *Ceratophrys joazeirensis* MZUSP 126203; *Ceratophrys ornata* CENAI 6834; *Chacophrys pierotti* CENAI 10940; *Lepidobatrachus asper* CENAI 2990; *Lepidobatrachus laevis* MACN 52418 (f), *Lepidobatrachus llanensis* MACN 38505 (f).

CONRAUIDAE: *Conraua goliath* USNM 571269.

CRAUGASTORIDAE: *Craugastor fitzingeri* MACN 39163 (f); *Craugastor gollmeri* MZUSP 85552; *Craugastor hobartsmithi* MZUSP 5319; *Craugastor raniformis* ICN 10758; *Haddadus binotatus* MACN 17042.

CYCLORAMPHIDAE: *Cycloramphus acangatan* CFBH 10005; *Cycloramphus asper* MACN 17030 (f); *Cycloramphus boraceiensis* CFBH 2258 2260, 17297 (f); *Cycloramphus eleutherodactylus* MACN 17041; *Thoropa taophora* CBFH 12734.

DENDROBATIDAE: *Adelphobates galactonotus* MZUSP 147784 (f); *Ameerega flavopicta* MZUSP 90635; *Ameerega trivittata* ZMH 2786, 2796; *Dendrobates tinctorius* ZFMK 67165; *Hyloxalus subpunctatus* ICN 11023, 26928; *Oophaga histrionica* MZUSP 100070; *Ranitomeya fantastica* ZFMK 41503.

DICROGLOSSIDAE: *Euphlyctis cyanophlyctis* USNM 266858; *Euphlyctis ehrenbergii* USNM 249112; *Fejervarya cancrivora* USNM 580823; *Fejervarya iskandari* MNHN-RA-1997.4916* (MNHN Online database); *Fejervarya limnocharis* USNM 520448; *Fejervarya vittigera* USNM 513084; *Hoplobatrachus occipitalis* USNM 576587; *Hoplobatrachus rugulosus* USNM 520480; *Limnonectes acanthii* USNM 556097; *Limnonectes blythii* USNM 587656; *Limnonectes doriae* USNM Zug field No. 282047; *Limnonectes hascheanus* ZFMK 80298; *Limnonectes* aff. *kuhlii* USNM 68075; *Limnonectes magnus* USNM 228820; *Minervarya nilagirica* MNHN-RA-1984.2340* (MNHN Online database); *Minervarya rufescens* MNHN-RA-1984.2348* (MNHN Online database); *Nannophrys ceylonensis* ZFMK 61090; *Nan-*

norana liebigii FMNH 195726; *Nannorana pleskei* ZFMK 58097; *Occidozyga baluensis* FMNH 77107; *Occidozyga laevis* USNM 228532; *Occidozyga lima* USNM 278613 (f); *Quasipaa boulengeri* FMNH 233022; *Quasipaa spinosa* ZFMK 92843.

ELEUTHERODACTYLIDAE: *Diasporus gularis* ICN 36835; *Eleutherodactylus auriculatus* ZMH A 14692; *Eleutherodactylus johnstonei* ICN 42263; *Eleutherodactylus martinicensis* ZFMK 42468; *Eleutherodactylus nubicola* CENAI 8487.

HEMIPHRACTIDAE: *Fritziana ohausi* CFBH 14819; *Fritziana* sp. CENAI 2221; *Gastrotheca christiani* CENAI 3204 (f); *Gastrotheca riobambae* ZMH A 05665; *Hemiphractus* sp. without no. (f); *Stefania evansi* MZUSP 150734.

HEMISOTIDAE: *Hemisus marmoratus* MACN 39130, ZMB 79848*.

HYLIDAE: *Acris crepitans* MACN 39139 (f); *Agalychnis asper* MNRJ 42550; *Agalychnis lemur* ZFMK 39444; *Aplastodiscus perviridis* MACN 52420; *Boana tepuiana* AMNH 131377; *Boana cordobae* MACN 52410; *Boana curupi* MACN 42589; *Boana faber* MACN 45274; *Boana pulchella* MACN 40485; *Boana punctata* MACN 40114; *Boana raniceps* MACN 45053; *Boana riojana* MACN 43664; *Bokermannohyla ibitiguara* CFBH 17318; *Bokermannohyla saxicola* MACN 40563-6; *Corythomantis greeningi* CFBH 16129; *Cruziohyla calcarifer* ZFMK 21525; *Dendropsophus counani* MNHN-RA-2015.101* (MNHN Online database); *Dendropsophus gaucheri* MNHN-RA-1999.8621* (MNHN Online database); *Dendropsophus leali* USNM 201989; *Dendropsophus marmoratus* USNM 568134; *Dendropsophus microps* CFBH 22025; *Dendropsophus minutus* MACN 43286, 45095; *Dendropsophus nanus* MACN 43436, 43441; *Duellmanohyla uranochroa* ZFMK 38442; *Hyla arenicolor* USNM 238965; *Hyla cinerea* MACN 39136; *Hyla meridionalis* ZMH A 06852; *Hyloscirtus colymba* USNM 572631; *Hyloscirtus palmeri* MAR 1472; *Isthmohyla graceae* USNM 297652; *Itapotihyla langsdorffii* CFBH 12724, MZUSP 134848; *Julianus camposseabrai* MHNJCH 000569; *Julianus pinimus* LGE 094, UFMG-AMP 20178; *Litoria caerulea* ZMH A 14695; *Litoria eucnemis* MZUSP 36185; *Litoria thesaurensis* ZMH A 00551; *Lysapsus limellum* MACN 21342, 52419; *Nyctimantis brunoi* CFBH 002715; *Nyctimantis siemersi* CENAI 3435; *Ololygon* aff. *cardosoi* UFMG-AMP 19944, 10320, 19942; *Ololygon* aff. *flavoguttata* UFMG-AMP 19978; *Ololygon* aff. *tupinamba* UFMG-AMP 19970; *Ololygon agilis* CFBH 22808; *Ololygon albicans* CFBH 35542; *Ololygon arduoa* CFBH 17988; *Ololygon argyreornata* CFBH 26368; *Ololygon belloni* CFBH 33313 (f), UFMG-AMP 19950; *Ololygon berthae*, MACN 49150, 51591; *Ololygon canastrensis* CFBH 17356; *Ololygon catharinae* CFBH 08499; *Ololygon* cf. *cosenzai* UFMG-AMP 19933, 19935; *Ololygon cosenzai* UFMG-AMP 16412; *Ololygon insperata* UFNG 19963; *Ololygon littoralis* CFBH 35296; *Ololygon littorea* UFMG-AMP 19956; *Ololygon longilinea* CFBH 36916; *Ololygon melanodactyla* MNRJ 75123 (f); *Ololygon perpusilla* CFBH 19508; *Ololygon rizibilis* CFBH 35077; *Ololygon tupinamba* UFMG-AMP 19971; *Ololygon v-signata* MNRJ 44573, UFMG-AMP 19974; *Osteocephalus buckleyi* USNM 166016; *Osteocephalus leprieurii* USNM 588699; *Osteocephalus planiceps* USNM 567460; *Osteocephalus taurinus* MZUSP 143815; *Osteocephalus verruciger* USNM 286415; *Osteopilus dominicensis* USNM 329681; *Osteopilus ocellatus* USNM 327232; *Osteopilus pulchrilineatus* USNM 65064; *Osteopilus septentrionalis* USNM 503652 (f), 503625; *Osteopilus vastus* MACN 45309; *Osteopilus wilderi* USNM 327190; *Phasmahyla exilis* ZFMK 54361; *Phrynomedusa marginata* ZFMK 54365; *Phyllodytes luteolus* CFBH 36888, CFBH 890; *Phyllodytes melanomystax* CFBH 35707; *Phyllomedusa azurea* MACN 52422; *Phyllomedusa tetraploidea* MACN 42319; *Phyllomedusa sauvagii* MACN 38136; *Pseudis cardosoi* CFBH 78, *Pseudis minuta* MACN 39253, 40867 (f), w/o No. 1, w/o No. 2+; *Pseudis platensis*, MACN 24004, 52421; *Scarthyla goinorum* CFBH 24814, 24817; *Scarthyla vigilans* ICN 27085; *Scinax acuminatus* MACN 36957 (f), 38076; *Scinax alter* CFBH

001442; *Scinax caldarum* CFBH 43852; *Scinax crospedospilus* MNRJ 44658; *Scinax cruentomma* MZUSP 34873; *Scinax curicica* CFBH 30904; *Scinax cuspidatus* CFBH 24626; *Scinax duartei* MNRJ61095; *Scinax eurydice* CFBH 35327; *Scinax flavoguttata* CFBH 08415; *Scinax fuscomarginatus* CFBH 24363; *Scinax fuscovarius* MACN 36918, 43393; *Scinax granulatus* CFBH 3867, MACN 41197; *Scinax hayii* CFBH 0137; *Scinax imbegue* MNRJ 8300; *Scinax nasicus* JF02, MACN 36934, 39445 (f), 39445; *Scinax nebulosus* CFBH 03644; *Scinax pachycrus* CFBH19519; *Scinax perereca* MACN 35100; *Scinax rogerioi* MNRJ 87280; *Scinax ruber* CFBH 10286; *Scinax squalirostris* CFBH 35249, JF1230; *Scinax staufferi* USNM 559218; *Smilisca baudinii* MACN 36861; *Smilisca phaeota* USNM 523225; *Sphaenorhynchus lacteus* MACN 46691, ZUEC 5853; *Sphaenorhynchus prasinus* MZUFV 2633; *Sphaenorhynchus surdus* MNRJ 4407; *Tepuihyla edelcae* USNM 550336; *Trachycephalus* cf. *typhonius* MZUSP without no.; *Trachycephalus jordani* USNM 283290; *Trachycephalus nigromaculatus* MZUSP 121472; *Trachycephalus resinifictrix* MZUSP 091910; *Trachycephalus typhonius* MACN 49595; *Trachycephalus venezolanus* ICN 40219; *Triprion spinosus* ZFMK 41134; *Xenohyla truncata* CFBH 23532.

HYLODIDAE: *Crossodactylus aeneus* MNRJ 39369, 39364+, 47765 (f)*; *Crossodactylus boulengeri* MZUSP 111020 (f)*, 111051; *Crossodactylus cyclospinus* MNRJ 40220, 40222*; *Crossodactylus dantei* MNRJ 39444 (f)*, 39446; *Crossodactylus dispar* MZUSP 23578(m)*, 23587; *Crossodactylus gaudichaudii* MNRJ 74088 (f)*, 74089; *Crossodactylus grandis* MNRJ 48356 (f)*, 48357+; *Crossodactylus lutzorum* MNRJ 4761 (f, paratype), 4762 (?, paratype)*; *Crossodactylus schmidti* MACN 42159*, 42188*, 42415 (f), JF853 (f)+, JF1976+, JF1142+, JF3124+; *Crossodactylus timbuhy* USMN 200449*, 200450 (?)*; *Crossodactylus trachystomus* UFMG-AMP 5355 (f), USNM 98017 (?)*,98018 (f)*; *Crossodactylus werneri* MZUSP 69099 (f), 69100 (f)*; *Hylodes amnicola* MZUSP 141746*, 141747; *Hylodes asper* MZUSP 112639, 112641*, 157462 (f)*, 157499+, 157464*; *Hylodes babax* USNM 222553*, 239938*, 239939*; *Hylodes cardosoi* MZUSP 112578, 112579 (f)*; *Hylodes charadranaetes* MZUSP 112841, 112843 (f)*, USNM 245901 (m, paratype)*; *Hylodes fredi* MNRJ 35217 (f, paratype)*, 38936 (m, paratype)*; *Hylodes glaber* AMNH 103902(m)*, USNM 245940*, 245943*; *Hylodes heyeri* MZUSP 093246(m)*, 093248, USNM 541344*; *Hylodes lateristrigatus* CENAI 8413, USNM 207680*, 208557*, 208558*, *Hylodes magalhaesi* AMNH 74425 (m, paratype)*, MZUSP 112661 (f)*, 112662, USNM 565123*; *Hylodes nasus* AMNH 72456*, USNM 164112 (f)*, 164113 (f)*; *Hylodes perplicatus* MTR 26735, USNM 101716 (f)*, 101717*; *Hylodes ornatus* AMNH 103914(m)*, USNM 245929 (f, subadult)*, MZUSP 60845*; *Hylodes phyllodes* USNM 243491 (m, paratype)*, MACN 17252, MZUSP 133184+, 137532*, TG 3603+; *Hylodes pipilans* MNRJ 35990 (f, paratype)*, MNRJ 39374 (m, paratype)*, *Hylodes sazimai* MZUSP 136796*, 136797; *Hylodes uai* MZUSP 23861 (m, subadult), 23863*; *Hylodes vanzolin*i USNM 222554 (?)*; *M. goeldii* CFBH 23800*, 23801*; *Phantasmarana apuana* MTR 26059 (f), UFMG-AMP 13536.

HYPEROLIIDAE: *Acanthixalus spinosus* ZFMK 67598; *Afrixalus fornasini* MZUSP144227 (f); *Afrixalus paradorsalis* ZFMK 97301; *Heterixalus madagascariensis* ZFMK 62890; *Heterixalus variabilis* ZFMK 53605; *Hylambates leonardi* ZFMK 73198; *Hylambates maculatus* MACN 39173 (f), ZMB 5508; *Hylambates verrucosus* ZFMK 64608; *Hyperolius acuticeps* ZFMK 81749; *Hyperolius argus* MZUSP144350; *Hyperolius castaneus* ZFMK 87984; *Hyperolius concolor* ZFMK 86147; *Hyperolius hypsiphonus* MNHN-RA-1999.5564* (MNHN Online database); *Hyperolius jynx* MNHN-RA-1999.5561* (MNHN Online database); *Hyperolius kivuensis* ZFMK 86150; *Hyperolius marmoratus* ZMH 09533; *Hyperolius pusillus* USNM 153348; *Hyperolius tuberilinguis* CENAI 6701, 7071; *Kassina cochranae* ZMB 86656; *Kassina decorata* ZFMK 67830; *Kassina senegalensis* CENAI 5932, ZFMK 70815; *Morerella cyanophthalma*

ZFMK 42354; *Opisthothylax immaculatus* ZFMK 87796; *Semnodactylus wealii* CENAI 5712; *Tachycnemis seychellensis* ZFMK 62860.

LEPTODACTYLIDAE: *Adenomera* cf. *andreae* MZUSP 58203; *Crossodactylodes* sp. MTTS 554 (field number of M.T.T. Santos, to be accessioned in CFBH); *Edalorhina perezi* MACN 39142; *Engystomops petersi* MZUSP 87875; *Hydrolaetare caparu* MZUSP 151495; *Leptodactylus bufonius* MACN 38169+, 38173, 52862; *Leptodactylus discodactylus* MZUSP 24785; *Leptodactylus elenae* MACN 40902*, 40903, 40905*; *Leptodactylus fragilis* USNM 572972 (f); *Leptodactylus fuscus* MACN 41505, 50952*; *Leptodactylus gracilis* MACN 38386*, 38387*; *Leptodactylus laticeps* MACN 42547*; *Leptodactylus luctator* MACN 51864, MACN w/o No. (f); *Leptodactylus macrosternum* MACN 40440 (f), 52908*; *Leptodactylus podicipinus* MACN 51432*; *Leptodactylus rhodomystax* USNM 531560; *Lithodytes lineatus* MZUSP 95546; *Paratelmatobius cardosoi* CFBH 22130; *Paratelmatobius poecilogaster* CFBH 9879; *Physalaemus biligonigerus* MACN 52413; *Physalaemus cuvieri* MACN 52423; *Pleurodema borellii* MACN 50187, 53545*, 53546*; *Pleurodema bufoninum* MACN 38306; *Pleurodema cinereum* MACN 42034*, 45890*; *Pleurodema diplolister* MACN 41789*; *Pleurodema kriegi* MACN 46272*; *Pleurodema marmoratum* MACN 42036*; *Pleurodema nebulosum* MACN 38753; *Pleurodema thaul* MACN 41316*, 54279*, MACN w/o No.; *Pleurodema tucumanum* MACN 50006; *Pseudopaludicola bolviana* MACN 38524; *Pseudopaludicola falcipes* MACN 44616.

LIMNODYNASTIDAE: *Adelotus brevis* ZFMK 28264; *Heleioporus albopunctatus* CENAI 8502; *Lechriodus fletcheri* KU 175512; *Limnodynastes peronii* CENAI 8537, KU 179939; *Limnodynastes tasmaniensis* KU 186903; *Neobatrachus aquilonius* KU 93576 (f); *Notaden bennetti* KU 175516 (f); *Notaden nichollsi* MACN 39158; *Philoria frosti* KU 186907 (f); *Platyplectrum melanopyga* KU 133626 (f); *Platyplectrum ornatum* CENAI 8544 (f).

MANTELLIDAE: *Aglyptodactylus madagascariensis* ZFMK 53612; *Blommersia wittei* ZFMK 52612; *Boophis albilabris* ZFMK 59906; *Boophis doulioti* ZFMK 59863; *Boophis luteus* ZFMK 52645; *Boophis microtympanum* ZFMK 53654; *Gephyromantis boulengeri* FMNH 261388; *Gephyromantis luteus* AMNH A23876, USNM 499526; *Gephyromantis rivicola* AMNH A157201; *Gephryomantis tandroka* MNHN-RA-1973.924* (MNHN Online database); *Guibemantis bicalcaratus* ZFMK 17651*, 52738, 78768*; *Laliostoma labrosum* USNM 149301; *Mantella baroni* ZFMK 46056; *Mantella betsileo* ZFMK 51818; *Mantidactylus lugubris* ZFMK 60130; *Mantidactylus opiparis* ZFMK 60097; *Spinomantis aglavei* ZFMK 60002.

MEGOPHRYIDAE: *Leptobrachella oshanensis* FMNH 232908; *Leptobrachella picta* ZFMK 80747; *Leptobrachium abbotti* ZFMK 85390; *Leptobrachium chapaense* ZFMK 79869; *Leptobrachium pullum* ZFMK 95646; *Ophryophryne hansi* ZFMK 82916; *Pelobatrachus* cf. *nasutus* MACN S/D; *Pelobatrachus nasutus* ZFMK 85381; *Xenophrys major* ZFMK 95638.

MICROHYLIDAE: *Anodontohyla boulengeri* ZFMK 52781; *Asterophrys marani* ZMB 63879; *Asterophrys pullifer* ZMB 64165; *Asterophrys turpicola* ZMB 64105; *Austrochaperina macrorhyncha* ZMB 85615; *Callulops wondiwoiensis* ZMB 58675; *Chaperina fusca* KU 321413 (m, juv), 329496; *Choerophryne laurini* ZMB 65132; *Choerophryne microps* ZMB 70358; *Cophixalus balbus* ZMB 62595; *Cophixalus riparius* ZMH A 00749; *Cophixalus tridactylus* ZMB 63159; *Cophyla phyllodactyla* ZFMK 53732; *Cophyla tuberifera* ZFMK 53725; *Copiula derongo* ZMB 70334; *Copiula major* ZMB 62077; *Copiula* cf. *pipiens* ZMB 64111; *Dermatonotus muelleri* JF 2146 (juv, MACN), MACN 37330+, 37313, 37335 (f), 40153 (f)+, 40160, 51724 (juv); *Dyscophus antogilii* ZFMK 43825; *Elachistocleis bicolor* MACN 52935; *Gastrophryne carolinensis* MZUSP 14409; *Glyphoglossus guttulatus* ZFMK 90169; *Glyphoglossus molossus* USNM 520318; *Hamptophryne boliviana* MZUSP 153072; *Hoplophryne ulugurensis* ZMB 76680;

Hylophorbus tetraphonus ZMB 70323; *Hylophorbus wondiwoi* ZMB 70317; *Kalophrynus interlineatus* AMNH A 27012; *Kaloula pulchra* MACN 39169 (f), 39671; *Oninia senglaubi* ZMB 74608; *Oreophryne* aff. *atrigularis* ZMB 70300; *Oreophryne celebensis* ZFMK 100874; *Oreophryne clamata* ZMB 62327; *Paradoxophyla palmata* ZFMK 60009; *Phrynomantis bifasciatus* MACN 42120; *Plethodontohyla guentheri* KU 336961; *Plethodontohyla notosticta* ZFMK 52766; *Rhombophryne testudo* ZFMK 28409; *Scaphiophryne brevis* ZFMK 59993; *Scaphiophryne calcarata* ZFMK 59996; *Scaphiophryne madagascariensis* ZFMK 52758; *Scaphiophryne marmorata* ZFMK 50148; *Stumpffia psologlossa* ZFMK 52530; *Uperodon systoma* MNHN-RA-0.5040 (MNHN Online database); *Xenorhina bouwensi* ZMB 62632; *Xenorhina similis* MCZ A-28501.

MYOBATRACHIDAE: *Crinia riparia* KU 175519; *Geocrinia laevis* KU 186930; *Geocrinia victoriana* KU 186877 (f); *Mixophyes fasciolatus* KU 179957; *Mixophyes iteratus* KU 179963; *Pseudophryne coriacea* KU 179979; *Pseudophryne guentheri* CENAI 9594; *Rheobatrachus silus* KU 179995 (f); *Taudactylus diurnus* KU 179999 (f); *Uperoleia variegata* KU 181003 (f, paratype).

NYCTIBATRACHIDAE: *Nyctibatrachus humayuni* ZMH 10299; *Nyctibatrachus major* FMNH 218234 (f).

ODONTOBATRACHIDAE: *Odontobatrachus natator* ZMB 78229.

ODONTOPHRYINIDAE: *Macrogenioglottus alipioi* MZUSP 126264; *Odontophrynus americanus* MACN 49002+, S/D; *Odontophrynus cultripes* MZUSP 141197; *Odontophrynus occidentalis* MACN 2973, 43318; *Proceratophrys avelinoi* MACN 36849; *Proceratophrys boiei* MZUSP 143563.

PELOBATIDAE: *Pelobates fuscus* CENAI 7548 (f), ZFMK 86757; *Pelobates syriacus* ZFMK 98529.

PELODYTIDAE: *Pelodytes caucasicus* ZFMK 72202; *Pelodytes punctatus* ZMH A 07255.

PETROPEDETIDAE: *Petropedetes cameronensis* ZFMK 81154; *Petropedetes juliawurstnerae* ZFMK 88867; *Petropedetes palmipes* ZFMK 94815*, ZFMK 94816*, ZFMK 94817*; *Petropedetes parkeri* ZFMK 61342; *Petropedetes perreti* ZFMK 69218*, ZFMK 69219*, ZFMK 75532;*; *Petropedetes vulpiae* ZFMK 88860.

PHRYNOBATRACHIDAE: *Phrynobatrachus acridoides* USNM 231659; *Phrynobatrachus auritus* ZFMK 81694; *Phrynobatrachus calcaratus* ZFMK 77151; *Phrynobatrachus cricogaster* ZFMK 81088; *Phrynobatrachus gutturosus* MNHN-RA-1999.8258* (MNHN Online database); *Phrynobatrachus krefftii* CENAI 7623 (f); *Phrynobatrachus maculiventris* MNHN-RA-1958.346* (MNHN Online database); *Phrynobatrachus manengoubensis* MNHN-RA-1939.113* (MNHN Online database), *Phrynobatrachus sandersoni* ZFMK 78494.

PIPIDAE: *Hymenochirus boettgeri* ZMH A 14691; *Pipa carvalhoi* MZUSP 82005; *Pipa pipa* MZUSP 142753; *Pseudohymenochirus merlini* ZFMK 96287; *Xenopus borealis* ZFMK 81733; *Xenopus laevis* MACN S/D; *Xenopus muellerli* ZFMK 96252; *Xenopus tropicalis* MZUSP 144234; *Xenopus wittei* ZFMK 55077.

PTYCHADENIDAE: *Ptychadena* cf. *nilotica* MACN 39150+; *Ptychadena retropunctata* MNHN-RA-1951.225* (MNHN Online database); *Ptychadena submascareniensis* MNHN-RA-1951.205* (MNHN Online database); *Ptychadena subpunctata* USNM 200265.

PYXICEPHALIDAE: *Amietia angolensis* USNM 153051; *Amietia nutti* MNHN 1924.3* (MNHN Online database); *Cacosternum boettgeri* ZMH A 05013; *Cacosternum capense* CENAI6426; *Strongylopus grayii* ZFMK 33095; *Tomopterna delalandii* ZMH 14693.

RANIDAE: *Amolops chunganensis* FMNH 232961; *Amolops cremnobatus* FMNH 258374; *Amolops marmoratus* FMNH 187460; *Amolops panhai* FMNH 268356; *Amolops spinipectoralis* ZFMK 92862; *Aquarana catesbeiana* MACN 41799; *Aquarana clamitans* USNM 590492; *Aquarana virgatipes* USNM 541251; *Boreorana sylvatica* MZUSP 36251; *Glandirana rugosa* USNM 300632; *Huia cavitympanum* ZFMK 79845; *Hylarana albolabris* USNM 163207; *Hylarana chalconota* USNM 197714; *Hylarana erythraea*

ZFMK 90285; *Hylarana grandocula* USNM 228877; *Hylarana guentheri* USNM 78262; *Hylarana lateralis* USNM 524000; *Hylarana latouchii* USNM48369; *Hylarana malabarica* AMNH A38088; *Hylarana maosonensis* ZFMK 92850; *Hylarana mortenseni* ZFMK 90292; *Hylarana nigrovittata* USNM 583177; *Hylarana papua* USNM 212947; *Hylarana signata* ZFMK 79802; *Hylarana temporalis* USNM 67854; *Lithobates berlandieri* USNM 226226; *Lithobates montezumae* USNM 113727; *Lithobates palmipes* USNM 562589; *Lithobates palustris* USNM 531804; *Lithobates pipiens* USNM 531816; *Lithobates sphenocephalus* USNM 539081; *Lithobates vaillanti* USNM 496615; *Meristogenys jerboa* USNM 197684; *Meristogenys kinabaluensis* ZFMK 79807; *Meristogenys orphocnemis* ZFMK 80681; *Meristogenys* sp. 1 ZFMK 46765; *Meristogenys* sp. 2 ZFMK 85379; *Nidirana okinavana* USNM 160129; *Nidirana pleuraden* FMNH 49462; *Odorrana andersonii* USNM 76234; *Odorrana bacboensis* ZFMK 80110; *Odorrana graminea* ZFMK 95659; *Odorrana hosii* USNM 586985; *Odorrana livida* ZFMK 80191; *Pelophylax nigromaculatus* USNM 248431; *Pelophylax ridibundus* MZUSP 5109, USNM 249391; *Pelophylax saharicus* USNM 520728; *Rana arvalis* ZMH R 09684; *Rana boylii* USNM 52913; *Rana cascadae* USNM 62427; *Rana chensinensis* USNM 68650; *Rana dalmatina* ZMH A 07901; *Rana temporaria* USNM 590971; *Sanguirana everetti* USNM 318615; *Staurois guttatus* FMNH 238911, ZFMK 97998; *Staurois latopalmatus* FMNH 235780; *Staurois natator* USNM 228903, ZFMK 28975; *Staurois tuberilinguis* ZFMK 47919;.

RANIXALIDAE: *Indirana beddomii* FMNH 217966; *Indirana brachytarsus* FMNH 217954.

RHACOPHORIDAE: *Buergeria japonica* USNM 291617; *Chiromantis rufescens* USNM 199436; *Feihyla palpebralis* ZFMK 94930; *Kurixalus eiffingeri* USNM 66027; *Leptomantis angulirostris* ZFMK 85316; *Philautus bunitus* ZFMK 79833; *Polypedates leucomystax* MACN 39174 (f), ZFMK 92563; *Pseudophilautus leucorhinus* ZFMK 38347; *Pseudophilautus microtympanum* USNM 67912, ZFMK 39511; *Raorchestes gryllus* ZFMK 94222; *Rhacophorus reinwardtii* ZFMK 80368; *Taruga eques* ZFMK 9002; *Theloderma asperum* ZFMK 95234; *Zhangixalus dennysii* ZFMK 83874.

RHINODERMATIDAE: *Insuetophrynus acarpicus* CENAI 3694–3699, 7239; MACN 54820, 54827, 54829, 54830; *Rhinoderma darwinii* CENAI 5370, 5469 (f), 5472, 5473, 5478, 5489; *Rhinoderma rufum* CENAI 1240.29, 1240.52, ZFMK 8345.

RHINOPHRYNIDAE: *Rhinophrynus dorsalis* MACN 39131.

SCAPHIOPODIDAE: *Scaphiopus holbrooki* MZUSP 5699; *Spea bombifrons* MACN 39156; *Spea multiplicata* USNM 114044.

SOOGLOSSIDAE: *Sechellophyne gardineri* ZFMK 62868.

STRABOMANTIDAE: *Bahius bilineatus* MZUSP 132291; *Barycholos pulcher* MZUSP 114763; *Barycholos savagei* MZUSP 69765; *Barycholos ternetzi* CFBH 13451 (f), MZUSP 152237; *Euparkerella brasiliensis* MZUSP 95932 (f); *Holoaden bradei* MZUSP 94660; *Holoaden luederwaldti* MZUSP 94403; *Hypodactylus nigrovittatus* MZUSP 24842 (f); *Lynchius nebulanastes* MHNSM 15438; *Lynchius parkeri* MHNJP 1571; *Noblella myrmecoides* QCAZ 41171; *Oreobates barituensis* BB 1732 (MACN); *Oreobates berdemenos* MACN 45635, 45684; *Oreobates heterodactylus* MZUSP 79836; *Oreobates quixensis* MZUSP 74463; *Pristimantis erythropleura* ICN 18726 (f); *Pristimantis nervicus* ICN 41459; *Pristimantis nicefori* ICN 21027; *Pristimantis palmeri* ICN 28537; *Pristimantis permixtus* ICN 36132; *Pristimantis platydactylus* ZFMK 60231; *Serranobatrachus carmelitae* MZUSP 54565; *Serranobatrachis sanctaemartae* MZUSP 54998; *Strabomantis anomalus* ICN 32598; *Strabomantis cornutus* MZUSP 13440; *Strabomantis zygodactylus* ICN 27482; *Tachiramantis prolixodiscus* ICN 10105; *Yunganastes fraudator* CENAI 4759.

TELMATOBIIDAE: *Telmatobius oxycephalus* MACN 49004; *Telmatobius rubigo* MACN 41608.

APPENDIX 2

Mean Pairwise Distance within Major Anuran Clades

Mean pairwise distance (MPD) is a measure of the internal disparity of a clade. It represents the probability that two random terminals within a clade will have different phenotypes (0 = all terminals are equal; 1 = all terminals are different). In this case, MPDs were calculated using a single character, the 20-state vocal sac classification, such that each value indicates the degree of vocal sac shape variation in each clade.

Clade	MPD
Anura	0.57
Acosmanura	0.57
Neobatrachia	0.57
Ranoides	0.63
Afrobatrachia	0.3
Natatanura	0.72
Notogaeanura	0.53
Australobatrachia	0.3
Nobleobatrachia	0.53
Allophryinidae	0
Alsodidae	0.75
Alytidae	0
Aromobatidae	0.03
Arthroleptidae	0.47
Ascaphidae	0
Batrachylidae	0.48
Bombinatoridae	0.25
Brachycephalidae	0
Brevicipitidae	0.17
Bufonidae	0.49
Caligophrynidae	0
Calyptocephalellidae	1
Centrolenidae	0.08
Ceratobatrachidae	0.67
Ceratophryidae	0.39
Ceuthomantidae	1
Conrauidae	0
Craugastoridae	0.45
Cycloramphidae	0.54
Dendrobatidae	0.08
Dicroglossidae	0.77
Eleutherodactylidae	0
Heleophrynidae	0
Hemiphractidae	0.47
Hemisotidae	0
Hylidae	0.47
Hylodidae	0.47
Hyperoliidae	0.3
Leiopelmatidae	0
Leptodactylidae	0.71
Limnodynastidae	0.61
Mantellidae	0.4
Megophryidae	0.47
Micrixalidae	0
Microhylidae	0.3
Myobatrachidae	0.08
Nasikabatrachidae	0
Neblinaphrynidae	0
Nyctibatrachidae	0.07
Odontobatrachidae	0
Odontophryinidae	0.1
Pelobatidae	0
Pelodytidae	0
Petropedetidae	0.46
Phrynobatrachidae	0
Pipidae	0
Ptychadenidae	0
Pyxicephalidae	0.24
Ranidae	0.83
Ranixalidae	0.42
Rhacophoridae	0.24
Rhinodermatidae	0.67
Rhinophrynidae	0
Scaphiopodidae	0.57
Sooglossidae	0
Strabomantidae	0.49
Telmatobiidae	0