REVIEW

The vocal apparatus: An understudied tool to reconstruct the evolutionary history of echolocation in bats?

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Abstract

Laryngeal echolocation in bats could have evolved following two scenarios: a single origin from a common ancestor or an independent acquisition inside the two clades Yinpterochiroptera and Yangochiroptera. Later, some members of Yinptero-chiroptera possibly lost their ability to echolocate. In bats, the larynx produces vocalizations for communication and, in most species, for echolocation. Here, we describe how comparative chiropteran laryngeal morphology is a novel area of research that could improve the understanding of echolocation and may help resolve the evolutionary history of bats. This review provides morphological descriptions and comparisons of the bat larynx and bioacoustics interpretations. We discuss the importance of understanding: (1) laryngeal sound production so it may be linked with the evolution of the chiropteran auditory system; and (2) the evolution of laryngeal morphology to understand the ecological and behavioural aspects of bat biology. We find that a strong phylogenetic signal is potentially the main source explaining macroevolutionary variation in laryngeal form among bats. We predict that the three parameters of sound production in echolocation (frequency, intensity, and rate of calls) are independently modulated by different laryngeal components, but this hypothesis remains understudied in terms of species diversity.

Keywords Comparative anatomy · High-frequency sound · Larynx · Mammalian nasopharyngeal morphology · X-ray microtomography · Vocal tract

Introduction

Bats are the second most diversified group of mammals (Simmons 2005), reflecting their spectacular evolutionary features: self-powered flight (Rayner 1988) and echolocation, a form of biosonar (Griffin 1944; Thomas et al. 2004). Most bats use laryngeal echolocation which requires three main capacities (Teeling 2009): production of high-frequency vocalisations with the larynx; reception of the echoes with the auditory apparatus; and processing of the acoustic information in dedicated brain areas, translating to different behaviour and feeding strategies in flight. Accordingly, these three anatomical regions should work in concert, illustrating the coevolution of how and when bats developed biosonar capabilities in their evolutionary history. The two sensory systems (nervous and auditory) that detect, transduce, and analyse echoes have already attracted considerable research interest (e.g., Baron et al. 1996; Hutcheon et al. 2002; Davies et al. 2013; Wang et al. 2017; Nojiri et al. 2021a; Sulser et al. 2022), whereas the

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evolution of the bat larynx has received far less attention. Essential anatomical and developmental work remains to be carried out on the range of laryngeal forms in bats and their close relatives.

Previous research on the bat larynx focused on understanding how bats produce laryngeal echolocation signals in general (Novick and Griffin 1961; Roberts 1972; Suthers and Fattu 1973; Griffiths 1983; Griffiths et al. 1992). Bats' requirements to accommodate high subglottic pressure for laryngeal echolocation (Suthers 2004; Frey and Gebler 2010; Metzner and Schuller 2010; Metzner and Müller 2016) suggest considerable specialisation of the organ, especially regarding its size, in the process of call production. It is also known that bats' larynges are disproportionally large compared to other mammals of similar size due to sexual dimorphism in Pteropodidae (Langevin and Barclay 1990). Despite some recent focus on the larynx (Carter and Adams 2014, 2016; Carter 2020; Nojiri et al. 2021a; Snipes and Carter 2022), we suggest that further research is needed to unravel the extent and patterning of variation in this organ as it relates to echolocation capability in bats. We hypothesise that despite a highly similar laryngeal morphology inside Orders of non-bat mammals, a variety of laryngeal forms will be observed among laryngeal echolocating bats, and these specialized laryngeal features will relate to the laryngeal echolocation strategies.

This paper reviews current knowledge and understanding of the bat larynx. We illustrate that new studies on the laryngeal morphology of bats could significantly improve the understanding of laryngeal echolocation and expand the scope of evidence that can be brought to bear on the open debate surrounding the evolutionary history of bats. The discovery and brief descriptions of laryngeal forms across bat phylogeny are essential to the assessment of a shared phylogenetic or functional relationship, potentially related to laryngeal echolocation (Dobson 1881; Robin 1881; Elias 1907; Denny 1976; Griffiths 1983; Harrison 1995). Therefore, a description of the laryngeal forms and a comparison of echolocation strategies is warranted to bring new insights into the much-debated topic of echolocation origins (Brudzynski 2010; Luo et al. 2017). Here we focus on the larynx to explain the evolutionary history of laryngeal echolocation in bats, and we acknowledge the fact that the larynx may have a different role in the evolutionary history of echolocation in non-bat mammals such as dolphins that produce echolocation 'clicks' inside the melon (e.g., Thomas et al. 2004).

New phylogeny, new evolutionary scenario

The evolutionary history of bat echolocation remains unclear. The most recent contributions debate whether laryngeal echolocation evolved once in an ancestral proto-bat and was subsequently lost in Pteropodidae (single-origin hypothesis, H1) or whether laryngeal echolocation was acquired independently at least twice in echolocating lineages (Yangochiroptera and Yinpterochiroptera) (independent origin hypothesis, H2) (e.g., Wang et al. 2017; Nojiri et al. 2021a; Sulser et al. 2022). If non-laryngeal echolocation is distinguished from laryngeal echolocation, H2 can be divided into two more sub hypotheses (H2A and H2B) (Nojiri et al. 2021a). H2A proposes that laryngeal echolocation evolved independently in Rhinolophoidea and Yangochiroptera without the emergence of non-laryngeal echolocation such as tongue-clicking or wing-beating echolocation ability in the common ancestor. H2B suggests that the common ancestor developed non-laryngeal echolocation ability, and then Rhinolophoidea and Yangochiroptera developed laryngeal echolocation independently. To date, no consensus has been reached because studies addressing this topic have focused on different areas of research (e.g., genomic, comparative anatomy, palaeontology) and have provided different perspectives and interpretations (Veselka et al. 2010; Teeling et al. 2016; Fenton 2022).

Comparisons of fossils and extant adult morphology support the conclusion that laryngeal echolocation emerged from a common ancestor (H1) (Simmons et al. 2010; Veselka et al. 2010). Wang et al. (2017) studied the prenatal development of the hearing apparatus and concluded that their evidence supported the single origin hypothesis (H1). However, more thorough developmental studies of the hearing apparatus support the independent origin hypothesis (H2) (Davies et al. 2013; Nojiri et al. 2021a). Although the origin of laryngeal echolocation is still debated, the loss of the ability to echolocate by the Pteropodidae (H1, H2B) is supported by the retention of laryngeal echolocation-associated features such as relatively large cochlea compared to other mammals and some capacity to emit social calls, in a similar manner to laryngeal echolocators (Springer et al. 2001; Nojiri et al. 2021a). Novacek (1985) posited that biosonar likely arose in Eocene bats that could echolocate in a less advanced way than extant bats families (Simmons and Geisler 1998; Wible and Davis 2000). Schnitzler et al. (2003) and later Maltby et al. (2010) proposed that the Eocene bat vocal apparatus could produce only relatively short, multi-harmonic, and narrow-frequency calls because specific calls were not needed during gliding onto vegetation and gleaning food from the surroundings. Despite its rudimentary capacities, the biosonar of primitive bats may have provided orientation, obstacle avoidance (Fenton et al. 1995), and foraging functionalities (Schnitzler et al. 2003; Jones et al. 2016). Unfortunately, some of these studies are based on fossils with damaged and possibly distorted anatomical features (Veselka et al. 2010). Additionally, the fossil record of the Pteropodidae is poorly known (Teeling et al. 2005; Eiting and Gunnell 2009), therefore reconstructing the evolutionary history of this family remains

challenging. The use of phylogenies including the different bat families' appearance ages and geographic distributions, represents an additional avenue to advance understanding of the emergence of different echolocation strategies in space and time. Bats from the Old World were likely not exposed to the same environment and climate as bats from New World, especially if they appeared at different geological times (e.g., the Phyllostomidae are a relatively recent family that lives exclusively in the New World and appeared around 37.3 Ma, and their echolocation strategy is different from some Old World bats such as the Rhinolophidae that appeared more recently, around 32.9 Ma; http://www.timetree.org/; Kumar et al. 2017).

The molecular basis of echolocation has also been investigated (Li et al. 2007, 2008, 2010; Liu et al. 2010, 2014; Parker et al. 2013). Two genes, *FoxP2* and *Prestin*, have yielded conflicting support for H1 or H2 (Li et al. 2007, 2008). Recently, Jebb et al. (2020) generated the first reference-quality genomes of six bat species and found three hearing-related genes that may support the single origin hypothesis (H1). To date, no specific evolutionary scenario is supported by genes related to sound production. Thus, an independent origin of laryngeal echolocation (H2A) cannot be rejected.

Ontogeny is another area that has been explored to provide evidence for the evolution of bat echolocation (e.g., Pedersen 1993; Carter and Adams 2014; Ito et al. 2021; Nojiri et al. 2021a). Modifications of the larynx during prenatal development and postnatal growth may relate to specific evolutionary pathways (Pedersen 1998, 2000; Carter and Adams 2014; Carter 2020). Recent studies have expressed the possibility that the independent origin hypothesis (H2) is a more realistic scenario than the single-origin hypothesis (H1) (Nojiri et al. 2021a; Sulser et al. 2022). Across echolocating lineages, different developmental patterns have been observed to result in similar adult morphology of the hearing apparatus, illustrating that variation in ontogeny does not necessarily get reflected in the variation of adult form, and supporting H2 (Nojiri et al. 2021a).

The conflicting hypotheses about the evolution of laryngeal echolocation express the complexity and high species diversity inside the bat phylogeny. We suggest that further testing of these hypotheses (between H1 and H2, and also H2A and H2B) would benefit from focus on the relatively under-studied larynx. Research on the vocal apparatus of bats has lagged far behind other morphological traits (e.g., the hearing apparatus) due to the non-representation in the fossil record of soft tissues such as (fibro)cartilage, ligament amd muscle that form important structures of the larynx. Additionally, prior to the advent of non-destructive soft-tissue visualization techniques such as contrast enhanced X-ray microtomography (Metscher 2009; Jeffery et al. 2011; Vickerton et al. 2013; Boyde et al. 2014; Gignac et al. 2016),

studying the larynx of bats involved destructive techniques by opening and dissecting the throat of the animals. This has constrained earlier research drastically because museums are usually reluctant to destroy or damage their specimens. As a result, the diversity of bat larynx anatomy, and its relationship to the evolution of laryngeal echolocation, remains open to further research and discoveries.

Laryngeal anatomy

Vocalisations are an essential factor in the evolution and survival of vertebrate species, as they impact sexual competition and interactions between individuals through vocal sound production (Fitch and Hauser 2003; Taylor and Reby 2010; Bradbury and Vehrencamp 2011; Wilkins et al. 2013). Mammals produce vocalisations in a great variety of frequencies and amplitudes. Understanding how sound production relates to different anatomical features is critical to understand and trace the evolutionary history and diversity of vocal communications in mammals (Borgard et al. 2020). There are two theories of sound production and control: the source-filter theory (Titze and Martin 1998; Taylor and Reby 2010) and the myoelastic-aerodynamic (MEAD) theory (van den Berg 1958; Titze and Alipour 2006; Švec et al. 2021).

The source-filter theory suggests that sound production needs independent contributions from two components. The larynx is the first component representing a source producing a fundamental frequency (F0). From the supralaryngeal space to the mouth or nose, the vocal tract forms a filter adding or cancelling harmonics and modifying the amplitude of the sound (Titze and Martin 1998; Taylor and Reby 2010; Brown and Riede 2017). In terms of the source, laryngeal morphology remains relatively constant through the different orders of mammals (Fig. 1; Negus 1949; Harrison 1995; Saigusa 2011). Five intrinsic muscles (thyroarytenoid, lateral cricoarytenoid, transverse arytenoid, dorsal cricoarytenoid, and cricothyroid) originate and insert on four principal cartilages (one thyroid, one cricoid, and a pair of arytenoids) (Figs. 2 and 3; Negus 1949; Harrison 1995; Hoh 2005, 2010; Saigusa 2011; König and Liebich 2020). These laryngeal muscles tilt the thyroid and arytenoids cartilages during phonation, adducting and abducting a pair of multi-layered membranes, the vocal folds (e.g., Harrison 1995; Metzner and Müller 2016; Brown and Riede 2017). Two branches of the vagus nerve innervate the laryngeal muscles and control phonation: the cranial laryngeal nerve (also referred to as the "superior laryngeal nerve" in physical anthropology and in some recent literature studying bats) innervates the cricothyroid muscle, and the caudal (recurrent) laryngeal nerve innervates the other intrinsic laryngeal muscles (Harrison 1995; Brudzynski 2010; Hoh 2010; König and Liebich 2020). These synapomorphies of the mammalian larynx
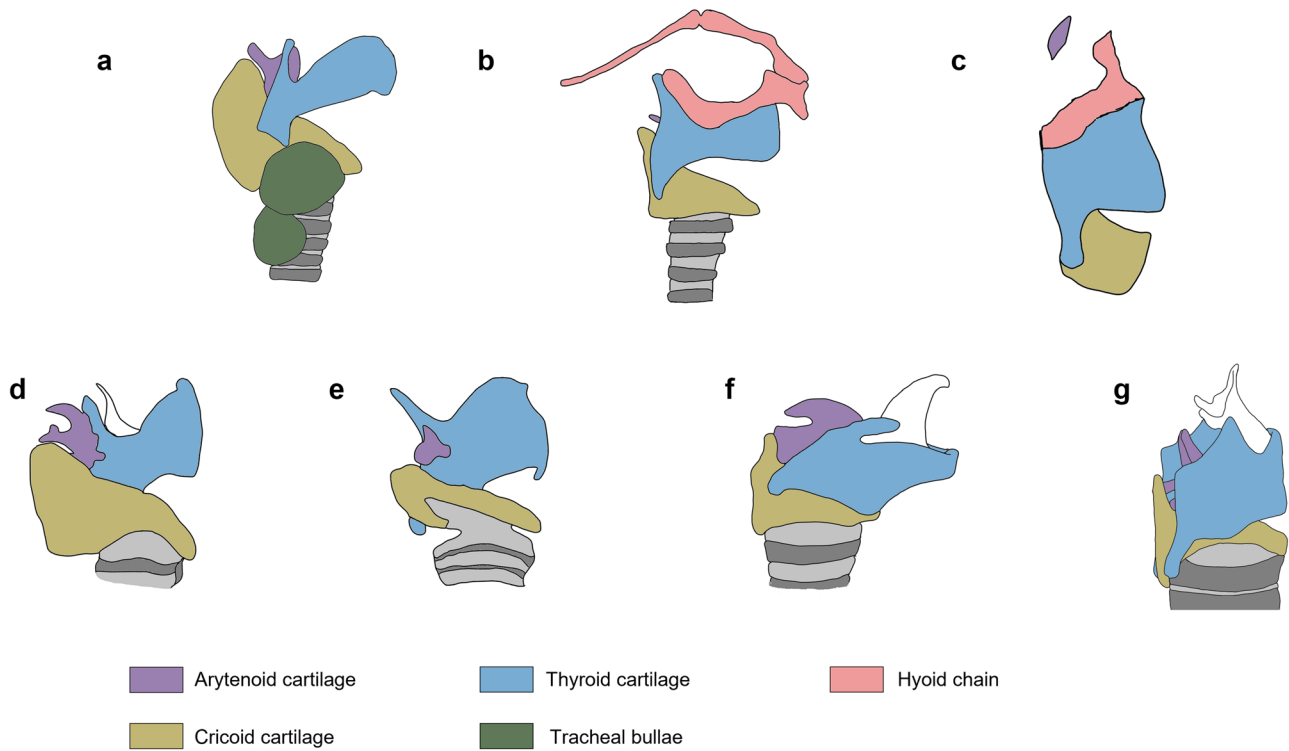
Fig. 1 Visualisation of the left lateral side of different laryngeal forms encountered in bats and mammals as schematized in the literature. **a** lesser horseshoe bat (*Rhinolophus hipposideros;* adapted from Metzner and Müller 2016); **b** cave nectar bat (*Eonycteris spelaea*); **c** hammer-headed bat (*Hypsignathus monstrosus*; adapted from Dobson 1881); **d** dhole (*Cuon alpinus*; adapted from Bowling et al 2020); **e** northern white-cheeked gibbon (*Nomascus leucogenys*; adapted from Bowling et al 2020); **f** horse (*Equus caballus*; adapted from Cook 1988); **g** house mouse (*Mus musculus*; adapted from Alli et al 2013). Larynges are not to same scale

raise questions regarding how mammals are able to produce different F0 despite having similar laryngeal morphology. Bats are a perfect example due to their production of highly specialised high-frequency vocalisations.

The MEAD theory provides complementary and detailed insights into understanding the variations of frequency in vocal production from a laryngeal source (Titze and Alipour 2006; Brown and Riede 2017; Švec et al. 2021). The theory
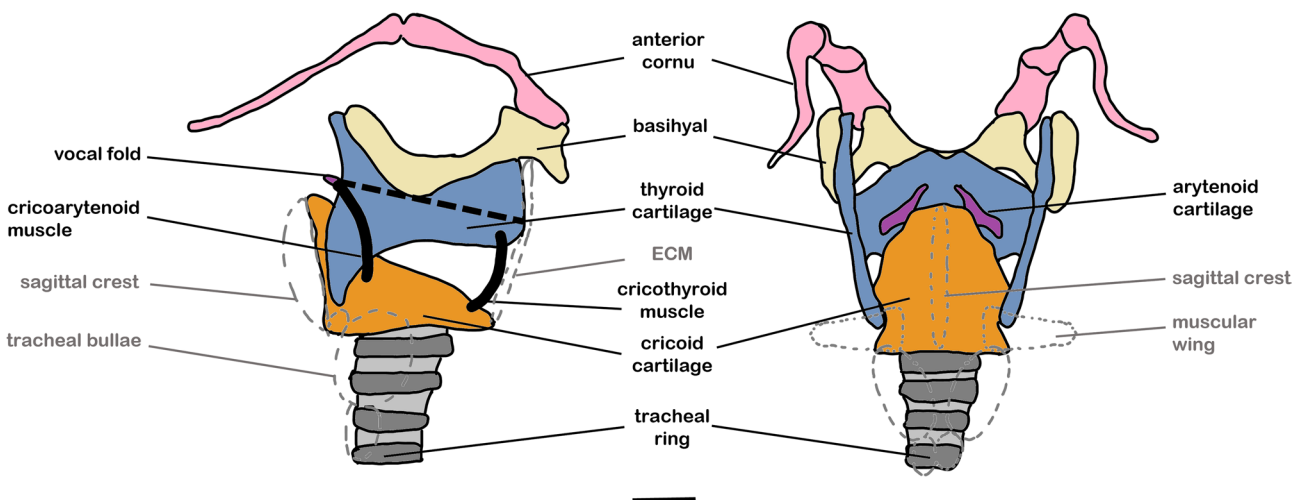

Fig. 2 Left lateral (left) and dorsal (right) views of the schematized larynx of the cave nectar bat (*Eonycteris spelaea*), belonging to the family Pteropodidae (non-laryngeal echolocators). Dashed lines represent the features observable on specific families of laryngeal echolocators. Abbreviation: **ECM**, elastic cricothyroid membrane. Scale bar equals 1 mm
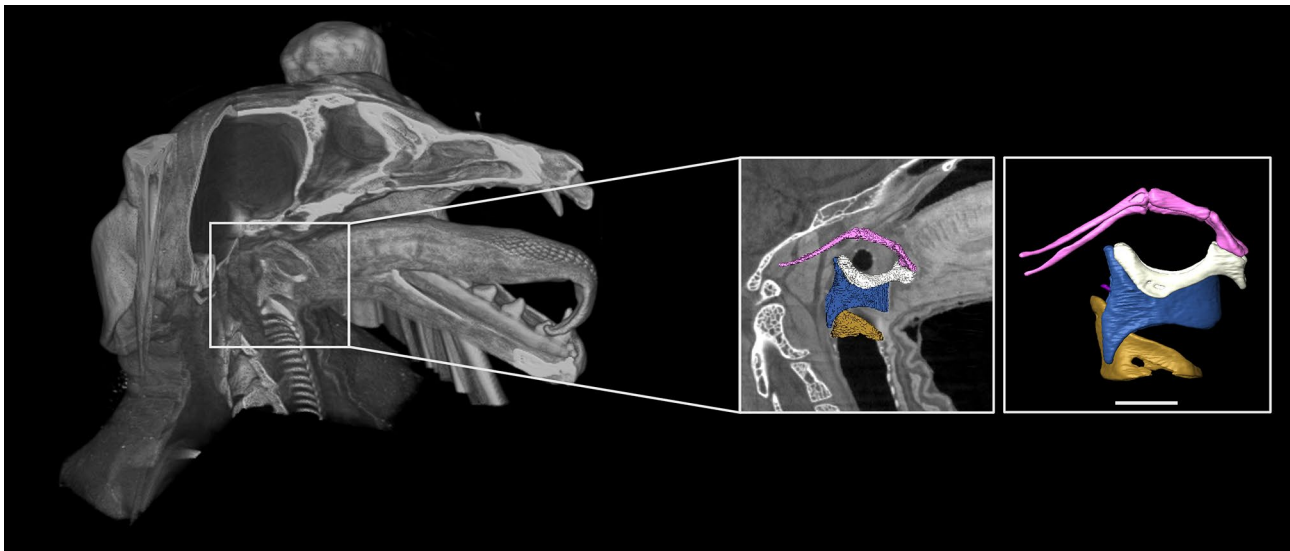
Fig. 3 Sagittal and transversal biplanar cutaway view of a 3D visualisation of the skull and neck of an adult cave nectar bat (*E. spelaea*), using diffusible iodine contrast-enhanced CT scanning, showing digital reconstruction of the larynx with the cricoid (orange), thyroid (blue), arytenoids (purple), hyoid (white), and the stylohyoid chain (pink). Scale bar equals 2 mm

states that the differential muscle activities of the larynx control the airflow needed for vocalisations by opening and closing the glottis (the vocal folds and the space between them). The elasticity and morphology of the vocal folds are also main components involved in the MEAD theory, as the vibratory properties of the membranes impact the sound produced (Brudzynski 2009; Brown and Riede 2017; Švec et al. 2021). Therefore, the differential muscle activities and the physical properties of the vocal folds identified in the source-filter, together with the MEAD theory, explain the production of different F0 in mammals (Finck and Lejeune 2010; Riede and Brown 2013; Titze et al. 2016).

Laryngeal size scales with body size in most mammalian species (e.g., Bogdanowicz et al. 1999; Bowling et al. 2020), due to adaptation links between diet and ecology. Herbivores differ from carnivores by the size of their arytenoid cartilages (e.g., Negus 1949; Harrison 1995; Berke and Long 2010; Shiba 2010). Arytenoids have an essential role in protecting ruminants, because these animals risk aspirating their food during the long rumination process. Adaptations to drastic changes in the environment are also visible in aquatic mammals, with some species having a larger larynx, air sacs, and dorsal tracheal membrane (Harrison 1995; Thomas et al. 2004; Reidenberg and Laitman 2010). Lastly, being the only true flying mammals (Frick et al. 2013), bats present unique laryngeal features, such as a reduction in length of the vocal folds and, in parallel, an extension of the posterior commissure of the glottis that allows ventilation in flight during vocalisation (e.g., Denny

1976; Harrison 1995; Thomas et al. 2004; Ratcliffe et al. 2013).

Bat vocalisations are high-frequency pulses used specifically in echolocation behaviour (including reception and processing of their echoes) (e.g., Griffin 1944; Vater 2000; Maltby et al. 2010; Jones and Siemers 2011; Fenton 2013). Echolocation signal production in bats comprises frequencies from 11 to 212 kHz, with most bats emitting between 20 and 60 kHz (Jones and Holderied 2007; Maltby et al. 2010; Fenton 2013). These vocalisations are one of the highest-pitched sound productions among vertebrates and may have shaped laryngeal adaptations among modern species (e.g., Jones and Holderied 2007). Reinforced cartilages supporting hypertrophied muscles are characteristic of the bat larynx (e.g., Denny 1976; Thomas et al. 2004). These features reflect the high forces needed to create and maintain the required subglottic pressure inside the larynx during intense echolocation signal production. Bats' hypertrophied muscles have been characterised as superfast muscles due to some vocalisations reaching up to 220 calls/second (Elemans et al. 2011; Moss et al. 2011; Ratcliffe et al. 2013; Grinnell et al. 2016).

Bats are governed by the same voice production theories as other mammals, notwithstanding their highly specialised frequencies and amplitudes in sound production. Correspondence in sound production is illustrated by the similarities in laryngeal anatomy between bats and other mammals, presenting only a reinforced "frame" and hypertrophied muscles (Fig. 1). Also, according to the MEAD

theory, the influence of differential muscle activities is thought to be a significant component of echolocation signal production (Roberts 1972; Griffiths 1983; Fattu and Suthers 1981; Pedersen 2000; Kobayasi et al. 2012; Metzner and Müller 2016). However, assessment of variation in size and morphology of the different structures constituting the larynx could reveal new knowledge on the different echolocation types in bats (Brudzynski 2009; Kobayasi et al. 2012). Indeed, it has been shown that variations in subglottal air pressure could explain some changes in the frequency and amplitude ranges of the social vocalisations and echolocation calls produced by bats. Through the biomechanical properties of the larynx (undescribed in the mentioned paper), some vocalisations could be produced without direct neuromuscular activity (Kobayasi et al. 2012). Lastly, since echolocation behaviour, diet, ecology and the larynx of bats are intercorrelated (e.g., Schnitzler et al. 2003; Denzinger and Schnitzler 2013), we can expect some adaptation of the larynx in relation to diet (as for other mammals; Harrison 1995) and, by inference, to the different echolocation strategies. As such, it is essential to investigate the laryngeal morphology on a macroevolutionary scale in bats to evaluate the extent to which features other than the muscle activity parameters could be responsible for the evolution and development of high-frequency sound production.

Research on vocal communication in mammals initially focused on the behavioural aspects of emitted sounds (e.g., McComb 1991; McElligott et al. 1999). Early research in bats also focused on analyses of echolocating signals, such as rate of calls by species, whereas a few studies addressed morphofunctional aspects of bioacoustics (e.g., Griffin 1944; Novick 1971; Roberts 1972; Suthers and Fattu 1973; Pye 1979; Hartley and Suthers 1987). Understanding the specific laryngeal morphology of bats and comparing these laryngeal forms to understand echolocation strategies

remains a complex exercise as there exist few publications on the topic.

Literature review

Literature selection was carried out using the free web search engine Google Scholar. The use of specific keywords such as "bat larynx", "laryngeal anatomy", "echolocation", and "vocal folds" narrowed the search. For inclusion in this review, we considered sixteen publications from Dobson (1881) to Carter (2020) as being sufficiently informative about the different laryngeal forms that can be seen in bats (Table 1). We selected papers dating back to 1881 as there are few recent papers that provide enough information about laryngeal anatomy in bats Most of the literature sources were written in English (fourteen out of sixteen papers), one in French (Robin 1881) and one in German (Elias 1907). The following criteria were used to include papers in this review: (1) studies with a clear description of an entire larynx from one or several species, (2) studies with a brief overview and/or comparison of different laryngeal forms encountered in bats, (3) anatomical studies mentioning the morphology of bat larynges. The small number of papers that met these three criteria, compared to the 2914 articles mentioning bats echolocation on the Web of Science from 1970 to 2021 (Cao et al. 2022), illustrates how modest the research on bat larynges has been and how underappreciated this topic remains. Additionally, the studies selected herein describe the larynges of bats by mainly reporting general aspects of the morphology in all species (e.g., Robin 1881; Denny 1976) or focusing on one or two species or families (Griffiths works between 1978 and 1994). Some publications also focused on the hyoid region and make only brief references to laryngeal morphology (Sprague 1943).

Table 1 Overview of descriptive studies of laryngeal anatomy in bats

Level of Morphological Description	Families	References
Generally Described: The study describes broadly or fully the larynx of a species, a group of species, a family, or of several families	Emballonuridae, Hipposideridae, Megadermatidae, Molossidae, Mormoopidae, Noctilionidae, Nycteridae, Phyllostomidae, Pteropodidae, Rhinolophidae, Rhinopomatidae and Vespertilionidae	Dobson (1881), Robin (1881), Elias (1907), Sprague (1943), Denny (1976), Griffiths (1978, 1982, 1983, 1994), Griffiths and Smith (1991), Griffiths et al. (1991, 1992), Harrison (1995), Giannini et al. (2006), Carter and Adams (2014), Carter (2020)
Poorly Described: The study briefly mentions the larynx and the descriptions are really succinct, but it brings some relevant information	Miniopteridae, Natalidae and Thyropteridae	Elias (1907), Sprague (1943)
Not Described	Cistugidae, Craseonycteridae, Furipteridae, Mystacinidae, Myzopodidae and Rhinonycteridae	None

Published data on the anatomy of bat larynges is extremely limited. Out of 21 families of bats, only 12 have been described at the family level in terms of general morphology, with some details on particular traits (Table 1). Three other families (Table 1) have simply been briefly mentioned in one or two studies but are not described (Elias 1907; Sprague 1943). Lastly, the remaining six families (Table 1) have not been mentioned in descriptive or comparative studies of the larynx to date. All figures of laryngeal schematisations in this review are based on previous published illustrations, except for the larynx of *Eonycteris spelaea,* which has been reconstructed by x-ray computed tomography (Fig. 3).

Comparative anatomy

Bat larynx morphology is similar to that of other mammals but with hypertrophied muscles supported by reinforced cartilages, an evolutionary tendency that concentrates within bats (Fig. 1; Harrison 1995). Compared to mammals of the same body size (rodents, shrews), bat larynges are larger, and in most species cartilages mineralise early in ontogeny to resist the forces generated by the well developed muscles involved in the production of high-frequency calls. Despite

a similar, roughly rounded shape of the cricoid cartilage, the presence of a sagittal crest in most bat families (nearly absent on Pteropodidae; Figs. 1, 2, 4a, and 5) is a character usually found in much larger mammals, and this could explain the necessity for echolocating bats to support larger laryngeal muscles than in mammals of the same body size (e.g., Harrison 1995). Another key feature of bat larynges is the reduction in length of the vocal folds coupled with the extension of the posterior commissure in the glottis, allowing flight and vocalization to occur simultaneously (Harrison 1995). The vocal folds are attached to the thyroid and arytenoid cartilages like most other mammals. Bats are unlike rodents, which generate high-frequency calls from vocal folds that are fixed to the cricoid cartilages (Harrison 1995). Also, when compared to the other mammalian orders of the clade Scrotifera (Tsagkogeorga et al. 2013), it is not clear whether bats present larger arytenoids as in the majority of the cetartiodactyls or smaller arytenoids as in carnivorans (e.g., Harrison 1995; Thomas et al. 2004). Lastly, one characteristic of some bat families that differs from most mammals (except for some marsupials and primates; Schneider 1964; Harrison 1995) is the presence of tracheal pouches or bullae that may be involved in echolocation (Figs. 1a, 2, 4a, and 5; Roberts 1972; Denny 1976; Griffiths 1994; Harrison 1995).
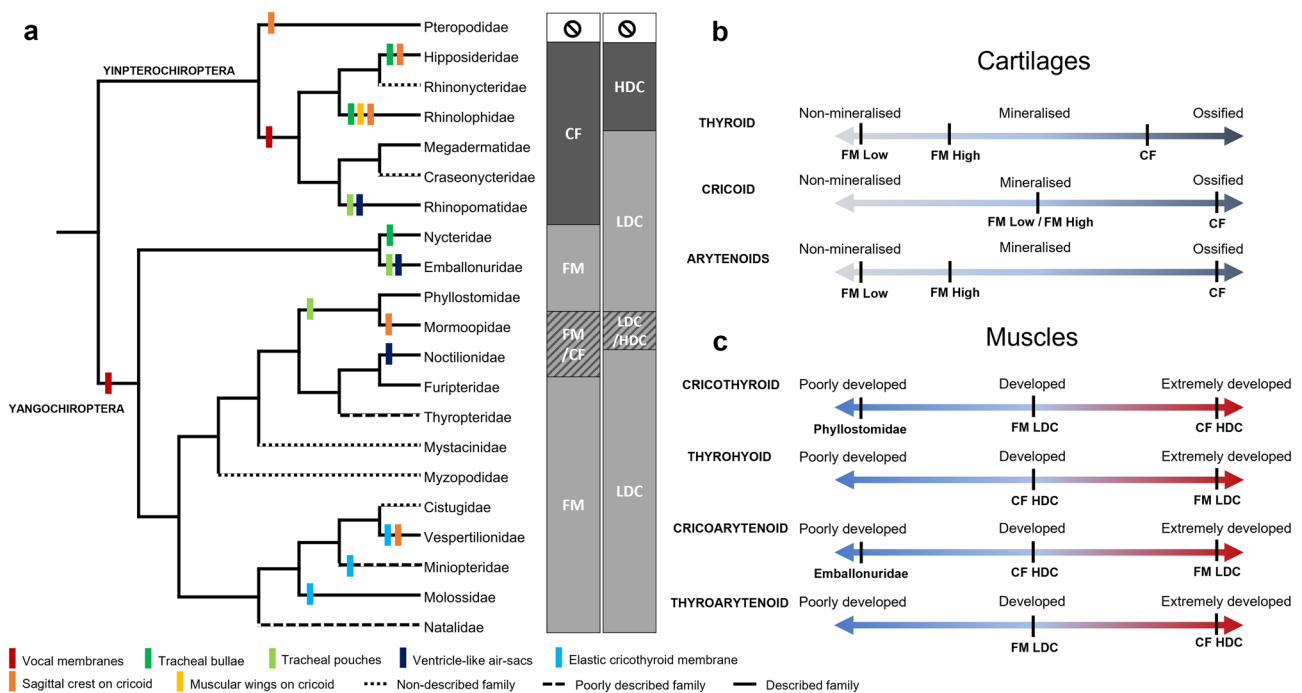

Fig. 4 Visual summary of the different laryngeal forms in bats described in the literature. **a** Distribution along the bat phylogeny of the different traits observed in bat larynges; **b** Characterisation of the different echolocation strategies regarding the degree of mineralisation of each laryngeal cartilage; **c** Characterisation of the different echolocation strategies regarding the development of the different laryngeal muscles involved in echolocation. Abbreviations: **CF**, constant frequency; **FM High**, frequency modulated with high intensity; **FM Low**, frequency modulated with low intensity; **HDC**, high-duty cycle; **LDC**, low-duty cycle
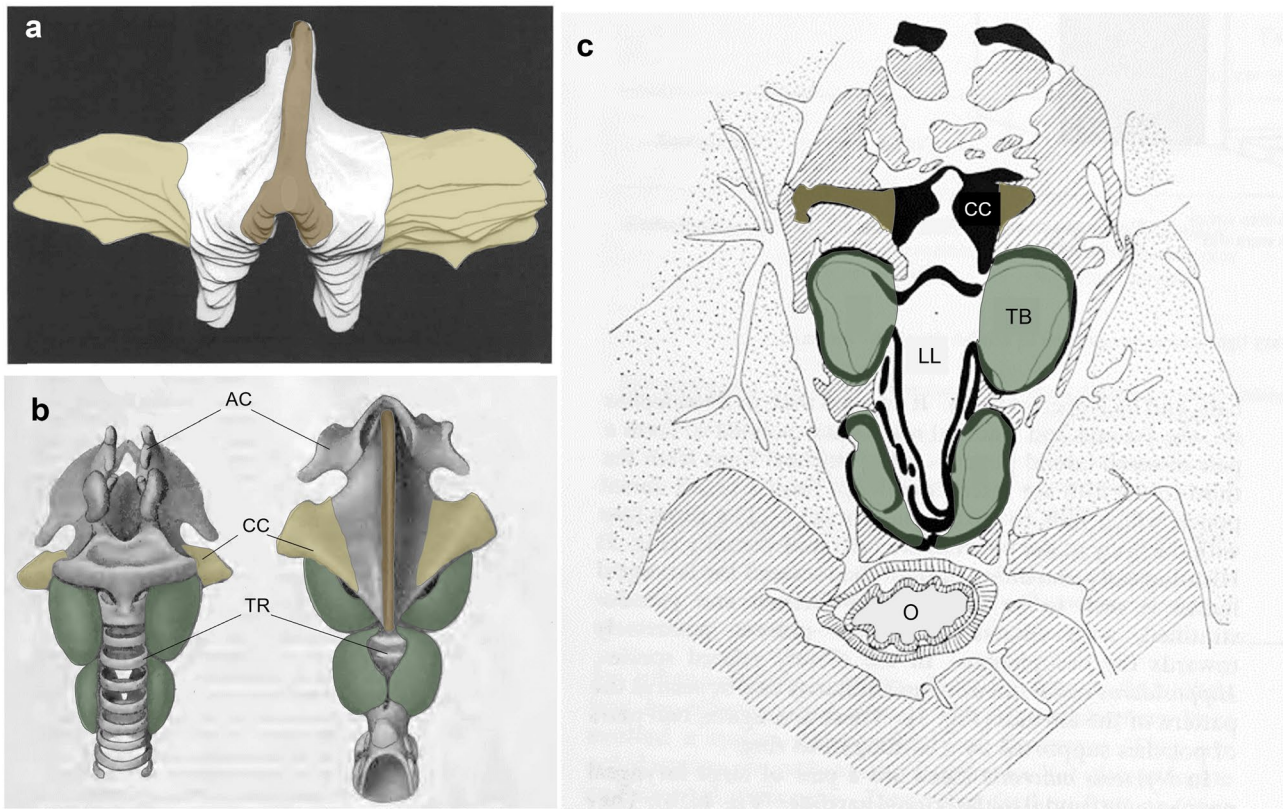
Fig. 5 Visualisation of the specific laryngeal components of *Rhinolophus* species described in the literature. **a** Reconstruction from cardboard sections of the dorsal view of the cricoid cartilage of *R. hipposideros* (adapted from Harrison 1995); **b** Drawings of the ventral (left) and dorsal (right) views of the larynx of *R. hipposideros* (adapted from Elias 1907); **c** Schematic coronal section of the larynx of *R. ferrumequinum* (adapted from Denny 1976). Colour identification: green for tracheal bullae; yellow for lateral wings on cricoid; brown for sagittal crest on cricoid. Abbreviations: **AC**, arytenoid cartilages; **CC**, cricoid cartilage; **LL**, laryngeal lumen; **O**, oesophagus **TB**, tracheal bullae; **TR**, tracheal rings

For many decades, research involving echolocation in bats considered differential muscle activity as the main factor influencing variation in sound production. A detailed, macroevolutionary examination of how laryngeal anatomy varies in relation to ecology and echolocation has been neglected, although such relationships are likely to be present. Morphological variations have been reported in 15 out of 21 families of bats (Table 1), and similar results could be expected from the six non-described families. These morphological variations are crucial to understand in the context of how different echolocation strategies may related to laryngeal anatomy and the evolutionary history of echolocation.

Variations in the size and shape of the laryngeal cartilages are visible when comparing the different families of bats. The Rhinopomatidae have larynges with a relatively basic morphology, with the caudal parts of the thyroid (cornus), as well as the ventral part of the cricoid, relatively narrow and reduced in length (Robin 1881; Denny 1976). The Emballonuridae are similar in morphology to the Rhinopomatidae and Vespertilionidae but more specialised than the former and less specialised than the latter (Robin 1881; Elias 1907;

Denny 1976). This is illustrated by larger arytenoids than the Vespertilionidae and wider cornus and cricoid than the Rhinopomatidae (Elias 1907). It must be noted that some genera of Emballonuridae, such as *Taphozous,* possess a cricoid with a "trunk" or "cone" shape that differentiates them from the other families of bats (Robin 1881; Elias 1907). The Vespertilionidae show the most specialised laryngeal morphology of all the laryngeal echolocating families, with laryngeal cartilages being generally thinner than the Rhinolophidae and with a thyroid that is divided into two parts for each lateral side of the cartilage, the most caudal part presenting a vertical wing shape (Robin 1881; Elias 1907). Two other families with a close phylogenetic position to Vespertilionidae, Miniopteridae and Molossidae (Teeling et al. 2012), have a laryngeal cartilage morphology similar to the one found in vespertilionids bats, and the Thyropteridae have a similar hyoid form to the three aforementioned families (Robin 1881; Elias 1907; Sprague 1943).

Rhinolophidae and Hipposideridae families have a similar but shorter and more robust larynx than the Vespertilionidae, with a more prominent cricoid cartilage (e.g., Elias

1907; Denny 1976; Griffiths and Smith 1991). The latter contrasts with the families of Vespertilionidae, Miniopteridae, Molossidae, Emballonuridae and Rhinopomatidae, which share similar form. Specifically, the prominence of the cartilages is due to the development of lateral "muscular wings" on the cricoid of the Rhinolophidae and a large sagittal crest on the dorsal aspect of the cricoid for both Rhinolophidae and Hipposideridae, which provide muscle attachment sites (Figs. 2 and 5; Robin 1881; Elias 1907; Denny 1976; Harrison 1995). The Phyllostomidae have a larynx that is similar in shape to that of Rhinolophidae but thinner, especially in relation to thyroid and arytenoid cartilages (Robin 1881; Denny 1976; Carter 2020). Nycteridae, Megadermatidae, and Rhinolophidae have similar laryngeal morphology except that the larynx of the Nycteridae seems slightly longer and smoother than the larynx of the Rhinolophidae (Robin 1881; Sprague 1943; Denny 1976). In Megadermatidae, the larynx is more robust than in Nycteridae. The cricoid ring does not seem to present some notched or thin ventral part in Megadermatidae, which contrasts with all other laryngeal echolocators (Robin 1881; Denny 1976).

The larynges of three other families have been described relatively to those of other laryngeal echolocating bats. The Natalidae larynges are not currently known, but the hyoid region is similar to that in Phyllostomidae (Sprague 1943). Conversely, the larynx of Mormoopidae has been described as very different to that in Phyllostomidae, especially regarding the oval cricoid and the diamond shape of the thyroid (Griffiths 1978, 1983). The larynx of Mormoopidae appears unique in the form of its cricoid and thyroid when compared to other families. The Noctilionidae larynx seems to exhibit traits that are a combination of different families already described (Robin 1881; Denny 1976). The Noctilionidae larynx is shorter and larger than Emballonuridae and is similar to the Rhinolophidae in this aspect (Robin 1881), while some features (see Additional features below) like the ventricle-like air sacs below the vocal folds, are shared with the Rhinopomatidae and the Emballonuridae (Denny 1976).

The Pteropodidae being non-laryngeal echolocators have a larynx similar to the common mammalian morphology (Fig. 1; Harrison 1995). Their larynx has a relatively smooth sagittal crest on the cricoid (Giannini et al. 2006) and some species of the Epomophorinae are the only ones known to present a laryngeal sexual size dimorphism (Dobson 1881; Robin 1881; Langevin and Barclay 1990). *Hypsignathus monstrosus* possess a large thyroid in a shield shape and some pharyngeal air-sacs which make the larynx of this species the most dimorphic among bats (Langevin and Barclay 1990). Apart from *H. monstrosus* and others Epomophorinae, the rounded shapes of the thyroid and cricoid ring observed in Pteropodidae are like those found in carnivorans or cetartiodactyls and contrast with the more compact and narrow cartilages of the laryngeal echolocating bats (Figs. 1, 2, and 3).

Carter (2020) distinguished among three main patterns of laryngeal cartilage calcification and ossification linked to bioacoustic requirements. The first pattern contains bat larynges with mineralised cricoid cartilage but no mineralisation of the thyroid and arytenoids. The Phyllostomidae are the main family belonging to this group (Fig. 4; Denny 1976; Griffiths 1978, 1982; Carter and Adams 2014; Carter 2020). The second group of families comprises the Rhinopomatidae, Mormoopidae and Vespertilionidae. Their cricoid is calcified like the Phyllostomidae, and their thyroid contains some important patches of mineralisation (Elias 1907; Griffiths 1978, 1983; Carter 2020). However, some modifications are present, such as the lateral border of the cricoid remaining uncalcified in *Pteronotus parnellii* (Griffiths 1978, 1983). Lastly, the third pattern includes the Hipposideridae, Rhinolophidae and Emballonuridae. They possess a fully ossified, bony, cricoid and a partially ossified thyroid (Robin 1881; Elias 1907; Denny 1976; Carter 2020) in contrast to the larynx of the other two groups being fully cartilaginous with only some mineralisation of the cricoid and sometimes patches within the thyroid (Harrison 1995; Carter 2020).

Pteropodidae are non-laryngeal echolocators and they have a larynx similar to the third pattern of mineralisation with an ossified cricoid and thyroid (Dobson 1881; Carter 2020). However, pteropodids possess a fully ossified thyroid, unlike the laryngeal echolocators of the third group that still have some patches of calcified cartilage. Pteropodids arytenoids are not mineralised, in contrast to the heavily mineralised arytenoids of the third group of bat families. Unfortunately, the families Megadermatidae, Miniopteridae, Molossidae, Natalidae, Nycteridae and Noctilionidae have not been described at a level of detail that would permit evaluation of the degree of mineralisation or ossification of their laryngeal cartilages.

Some laryngeal traits appear to be prominent in the more derived echolocators, apart from the general morphology of the three laryngeal cartilages. First, the "muscular wings" present on the cricoid of the Rhinolophidae (Harrison 1995) and second, the sagittal crest on the dorsal part of the cricoid in families like Rhinolophidae (e.g., Robin 1881), Hipposideridae (Denny 1976), Mormoopidae (*P. parnellii*; Griffiths 1983), Vespertilionidae (Robin 1881; Elias 1907), as well as the non-echolocating family Pteropodidae (Giannini et al. 2006). Although these two features are morphological variations of the cricoid cartilage, they should be considered as anatomical entities distinguishing laryngeal forms (Figs. 2 and 5; Robin 1881; Elias 1907; Harrison 1995).

Possibly the most important anatomical trait that should be discussed in bat laryngeal forms is the enlargement of the laryngeal lumen, as it may play the largest role in the variety of echolocation signals found in laryngeal bats (e.g., Denny 1976; Harrison 1995). This enlargement has been achieved

through various morphological forms in laryngeal echolocating bats. It should be noted that an increase in laryngeal volume is not specific to laryngeal echolocation but to all types of vocalisations (such as for communication) as it can be seen in the extremely developed laryngeal lumen of some Epomophorinae (Langevin and Barclay 1990). Laryngeal lumen enlargement is achieved in some echolocating bats by modification of the tracheal rings at the junction of the cricoid cartilage into a pair of cartilaginous bullae. The Rhinolophidae and Hipposideridae larynges possess a pair of tracheal bullae on the first and second tracheal rings and third bullae in the dorsal position between the third and the fifth ring (Figs. 1a and 5; Robin 1881; Denny 1976; Harrison 1995). The larynx of the Nycteridae also possesses a pair of large tracheal bullae that extend to the tenth ring (*Nycteris macrotis*; Denny 1976). Separately, the first tracheal rings can be enlarged under the cricoid cartilage, increasing the volume of the larynx lumen. This morphology can be found in the Rhinopomatidae from the 5th to the 15th ring and in the Emballonuridae from the 2nd to the 10th ring (Sprague 1943; Griffiths and Smith 1991). Tracheal enlargement into so-called "tracheal pouches" is also visible for some Phyllostomidae and Mormoopidae from the cricoid to the 5th or 8th first rings (Denny 1976; Griffiths 1978, 1983). The larynges of the Rhinopomatidae and Emballonuridae also possess a pair of ventricle-like air-sacs below the vocal folds, to which they are partially fused (Denny 1976). Noctilionidae larynges do not possess tracheal pouches, but ventricle-like air-sacs have been described (Denny 1976). Another aspect of laryngeal morphology is the elastic cricothyroid membrane (ECM), also called the saccus intercartilaginous anterior (Elias 1907), which is an elongation of the cricothyroid membrane composed of collagen and elastic fibres (Fig. 2; Robin 1881). The elastic cricothyroid membrane appears to be a morphological adaptation of the Vespertilionidae and potentially of the phylogenetically related Miniopteridae and Molossidae (Robin 1881; Elias 1907). This membrane stretches from the cranial lip of the cricoid cartilage to the thyroid cartilage and hypothetically plays the same role as the tracheal bullae or pouches (Robin 1881). Lastly, the vocal folds of all laryngeally echolocating bats possess thin extensions called vocal membranes that allow faster vibrations and the production of high-frequency vocalisations (Novick and Griffin 1961; Fitch 2006).

Bats commonly possess strong and well-developed laryngeal muscles (e.g., Harrison 1995). However, some qualitative differences have been noted. The Hipposideridae and Rhinolophidae laryngeal muscles are similar and extremely powerful with large insertion areas, especially the thyroarytenoid and cricothyroid muscles that cover the entire ventral part of the larynx (Robin 1881; Elias 1907). The Megadermatidae and Nycteridae larynges present similar forms with a complex cricothyroid (Griffiths and Smith 1991). The

Rhinopomatidae only differ in the cricothyroid's attachment, which is more medial on the cricoid cartilage than on the Rhinolophidae (Elias 1907). The main difference between the laryngeal muscle morphology of certain families appears to be the relative size of different laryngeal muscles. Hypertrophied thyroarytenoids in Rhinolophidae differ from the hypertrophied cricoarytenoids in Vespertilionids (Fig. 4a). Indeed, the Vespertilionidae, Mormoopidae, and potentially the Miniopteridae and Molossidae have strongly developed dorsal cricoarytenoids on the dorsal side of the cricoid (Elias 1907; Griffiths 1978, 1983). The Pteropodidae possess muscles most similar to those of Vespertilionidae larynges but less developed when compared to all other bat families (Robin 1881). In contrast to these hypertrophied cricoarytenoid muscles, the laryngeal musculature of the Emballonuridae shows relatively underdeveloped and weak cricoarytenoid muscles even though the cricothyroid remains hypertrophied (Elias 1907; Griffiths and Smith 1991; Griffiths et al. 1991). Lastly, the Phyllostomidae have a relatively simple cricothyroid muscle that is weaker (smaller in mass) than all other bat families, which might relate to the lack of mineralisation observed in their laryngeal cartilages (Griffiths 1978, 1982).

The precise location and shape of the intrinsic muscle attachments to the laryngeal cartilages have not been described, and nor has the composition in terms of muscle fibres, despite being essential to understanding the physiology and function of the laryngeal muscles for echolocation (Hoh 2005). Six out of 21 families of bat (Teeling et al. 2016) are lacking laryngeal description and most of the other families involved in anatomical studies are only briefly described. For example, the larynx of Nycteridae has been described in terms of hyoid morphology and drawings of the larynx were published in Griffiths study, but no description was provided (Griffiths 1994). Several families have been linked to each other by similar or different laryngeal forms and their biological adaptations. However, the studies are few and date back at least 50 and sometimes over 100 years (e.g., Robin 1881; Elias 1907; Denny 1976). Also, clear comparison of the laryngeal form of the different families, as detailed for the hyoid bone (Sprague 1943), should be considered. Indeed, it is unknown whether the families similar to Rhinolophidae (e.g., Megadermatidae) have larynges with a sagittal crest on the cricoid cartilage because the descriptions are limited in terms of relative size, degree of mineralisation and some additional features that stand out.

Bioacoustic implications

The distribution of morphological variation in size and shape for the three intrinsic cartilages appears to reflect a phylogenetic signal in bats. Indeed, most families that are

phylogenetically close to the Vespertilionidae show a relatively similar laryngeal morphology, and the same applies for the families related to the Rhinolophidae. Potentially, two morphotypes would be identified regarding the conclusions brought from the studies describing bat larynges – one more related to Rhinolophoidea and a second form illustrated in a majority of Yangochiroptera. Nevertheless, some families present independent characteristics like the "trunk" shape of the cricoid of some Emballonuridae or the diamond shape of the thyroid of the Mormoopidae (Elias 1907; Griffiths 1978).

A link with sound production appears to be the most probable influence on the degree of mineralisation (Fig. 4). Bats producing vocalisations at a higher intensity and with higher rates (High Duty Cycle, High Intensity; e.g., Fenton 2013) possess the most mineralised or ossified larynges, whereas bats with the lowest intensity and rate of calls (Low Duty Cycle; e.g., Fenton 2013) have a weaker laryngeal structure with cartilages that are partially mineralised or unmineralised (Carter 2020). From a macroevolution perspective, the Phyllostomidae have the weakest laryngeal structure. This lack of mineralisation is linked to their use of echolocation for obstacle avoidance and not insect hawking, in addition to their reliance on other senses (e.g., Denzinger and Schnitzler 2013). Therefore, their larynx does not require strong cartilages and muscles as they have reduced their use of echolocation (Griffiths 1982). In contrast, the Rhinolophidae and Hipposideridae cartilages have, through ossification, been replaced by bone to support hypertrophied muscles that produce high-rate calls of constant frequencies (Fenton et al. 2012).

Some laryngeal features like the tracheal bullae may be adaptations to vocalisation requirements (Fig. 5; Denny 1976; Harrison 1995; Metzner and Müller 2016), but this hypothesis remains unexplored. These structures could be interpreted as Helmholtz resonators that function to produce higher intensity calls (Roberts 1972; Denny 1976). The added air volume in the larynx could allow more pressure on the glottis and a higher rate of flow through the vocal fold to produce louder sounds (Roberts 1972). The elastic cricothyroid membrane could be employed for the same purpose in Vespertilionidae (Robin 1881). Additional features or elasticity of the membranes might relate to the variation of intensity in sound production. Moreover, the extreme increase in laryngeal volume of the non-echolocating Epomophorinae is linked to a courtship behaviour, allowing the male *H. monstrosus* to attract the female with high-intensity vocalisations during the mating period.

The extreme development of the laryngeal muscles in bats seems to be related to the high requirements to produce high frequency echolocation signals (Fig. 4). The three main structural variables of echolocation signals in bats are frequency (constant frequency CF or frequency modulated FM, Vater 2000; Fenton et al. 2012), intensity, and the rate of calls. The capacity to modify intensity has been explained by potential gain in laryngeal volume thanks to added features such as the tracheal bulla, the tracheal pouches, the elastic cricothyroid membrane or the ventricle-like air-sacs (e.g., Robin 1881; Denny 1976; Griffiths 1983). Although the larynx is the principal component responsible for sound production, the coordinated action of the flight muscles and other musculature in the thoracic cage are responsible for the high subglottic pressure generated in bats (Metzner and Schuller, 2010). The rate of call seems not only related to the reinforcement of the cartilage but also to muscle activity. High Duty Cycle (HDC) bats have both branches of the cricothyroid muscle lying in the same direction but working with antagonistic movement, one branch pulling the thyroid close to the cricoid cartilage (adduction) and the other one pulling it back (abduction) (Griffiths 1983). This coordinated action allows rapid creation and release of tension in the vocal folds. The thyrohyoid muscle is relatively weak in HDC bats presumably because the action of the two branches of the cricothyroid are sufficient to regulate vocal fold tension. These antagonistic movements of the cricothyroid branches are important for the control of the third variable of echolocation, frequency. Bats emitting in constant frequency use the antagonistic movement of the cricothyroid branches for fine control of call frequency (Griffiths 1983). In FM bats, the cricothyroid pulls in only one direction, and it is the thyrohyoid muscle that releases the tension on the vocal folds and produces the drop in frequency. Therefore, differences in cricothyroid development and thyrohyoid size potentially impact echolocation strategies (Griffiths 1983).

Unfortunately, as illustrated herein, knowledge about bat larynges is still partial and lacks understanding concerning the functional implications of structural variations with respect to echolocation. Additionally, no research hypotheses have been proposed to test the different associations (potential morphotypes, pattern of mineralisation, muscle development) and morphology observed. All these studies present another major issue: they all report qualitative results. Except for one study on Pteropodidae (Giannini et al. 2006), no quantitative descriptions have been published. As such, illustration of a potential phylogenetic or functional signal in laryngeal morphology through statistical analyses remains a challenge due to the absence of measurement data.

This information serves to highlight the opportunity for further quantitative research to uncover form-function relationships within laryngeal features and to assess their evolutionary patterning.

Evolutionary development and ontogeny

During recent decades, research on the ontogeny of echolocation has been conducted through two main fields of expertise: bioacoustics and anatomy. In terms of bioacoustics, several studies have focused on describing the postnatal development of the emitted sound for echolocation (e.g., Gould 1975; Brown and Grinnell 1980; Habersetzer and Marimuthu 1986; Moss 1988; Moss et al. 1997; Vater et al. 2003; Carter et al. 2014; Engler et al. 2017; Smarsh et al. 2021). Those studies state that bats vocalize immediately post-partum and that FM and CF bats develop echolocation in different ways (Gould 1975; Brown and Grinnell 1980; Carter et al. 2014). FM bat pups develop echolocation by increasing the frequency and the rates of sound pulses, but the duration of these pulses is reduced during ontogeny (some being described as constant frequency signals; Gould 1975; Brown and Grinnell 1980; Habersetzer and Marimuthu 1986; Moss 1988; Moss et al. 1997; Carter et al. 2014). These low-frequency, low-rate calls might illustrate an immaturity of the larynx at birth and during the first postnatal week (Moss 1988). The same does not apply to the pups of CF bats, such as Rhinolophidae and Hipposideridae, whose calls have the same constant frequency and rates as adult CF bats, with the duration of call pulses increasing with age (Brown and Grinnell 1980; Habersetzer and Marimuthu 1986). Variation observed in CF pups after several days concerned specifically the bandwidth and the suppression of the different harmonics to concentrate the energy of the sound on the second harmonic, resulting in production of less variable constant frequency pulses (CF_2; Habersetzer and Marimuthu 1986; Vater et al. 2003; Carter and Adams 2016). Notably, only one CF echolocator bat species in the Yangochiroptera, *Pteronotus parnellii* (Mormoopidae), is unable to echolocate with CF during the first week, producing only some CF vocalizations similar to the other FM species of Mormoopidae (Vater et al. 2003). After several days these vocalisations are tuned on CF_2 and the pups can echolocate by maintaining this CF component that other FM pups losedue to reduction of pulse duration (Vater et al. 2003). Therefore, the ontogeny of *P. parnellii* might explain the evolutionary convergence of echolocation strategies with the Rhinolophoids. Carter et al. (2014) and Engler et al. (2017) argued that social calls and echolocation signals do not have the same developmental pattern in bats, and therefore have separate evolutionary histories. *Rousettus* bats do not change the frequency or duration of their clicks during ontogeny due to early development of tongue morphology and innervation (Smarsh et al. 2021). These observations of development in bioacoustics need to be compared with the ontogeny of the larynx itself to assess how the development of sound production relates to organ development in laryngeal echolocators.

Only a few studies have been published regarding the relationship between anatomy and echolocation (e.g., Pedersen 1995; Carter et al. 2014; Nojiri et al. 2021b). Some of that research considered the evolutionary aspect of laryngeal echolocation (e.g., Nojiri et al. 2021a), whereas the laryngeal aspect of sound production and its implications for laryngeal echolocation development has received attention only recently (e.g., Carter and Adams 2014; Carter et al. 2019; Carter 2020). The ontogeny of the skull (Pedersen 1995) and of the cochlea (Carter and Adams 2016; Nojiri et al. 2021b) was found to be constrained, to some extent, by the demands of vocalisations in bats. By using a model that integrates bats' cochlear development (evo-devo), larynx, sound production and flight, Carter and Adams (2016) argued that hearing sensitivity evolved before the production of high-frequency calls. Further, they suggested that sensitivity and high-frequency production both appeared before the ability to fly and then the three capacities coevolved through time. The ontogeny of the cochlea has been described as accelerated compared to non-echolocator mammals (Nojiri et al. 2021b) and among bats, specific developments of the hearing apparatus have illuminated several evolutionary pathways (Nojiri et al. 2021a). The ontogeny of the hyoid apparatus and the intrinsic laryngeal cartilages are correlated with the development of echolocation. The different echolocation strategies relate to the reinforcement by postnatal mineralisation or ossification of some parts of the cartilages (Carter et al. 2019; Carter 2020). These reinforcements during bat development illuminate potential evolutionary scenarios (Carter et al. 2014). Understanding the development of laryngeal morphology is essential because sound production, and hence evolution of laryngeal echolocation, may be inferred from it. Unfortunately, as for the adult morphology, little is known about the different developmental forms of the laryngeal anatomy in bats. Future work on the ontogeny of the larynx across bat families could provide new insights into echolocation development and evolution, as well as resolution of the previous hypotheses tested on the ontogeny of the hearing apparatus (e.g., Nojiri et al. 2021a).

Conclusion: The larynx as a potential new proxy to elucidate the evolutionary history of echolocation

This review has assembled different sources of information from over 140 years of publications to draw conclusions regarding the morphology of the bat larynx, the potential variations of form encountered, and the factors influencing variations. A phylogenetic signal has been found to potentially impact the forms of the laryngeal cartilages with two main morphotypes, illustrated in the two main superfamilies of bats (Rhinolophoidea and Verspertilionoidea). Three

parameters of sound production for echolocation are correlated with different aspects of the laryngeal morphology. The differences in emitting calls associated with CF or FM appear to be related to muscle activity and the size of the muscles involved. The antagonist branches of the cricothyroid are the principal feature involved in the different frequencies emitted. The rate of calls (HDC/LDC) correlates with muscle volume and the degree of reinforcement (mineralisation or ossification) of the laryngeal cartilages. Lastly, the intensity of the calls found in bats appears to be driven by modified features like the tracheal bullae or an elastic cricothyroid membrane in some Yangochiroptera. Unfortunately, these data are partial, being based on a few species only, and a comprehensive description and comparison among the high species diversity of bats remains to be undertaken. Such work will provide insights in the fields of bats bioacoustic and behaviour by illuminating the morphofunction of the larynx and the special traits visible in bats.

The evolutionary history of bats remains largely unclear, and this also holds true for the origins of bat echolocation. Improving descriptions and comparisons of laryngeal forms to a level that matches that available for the hearing apparatus, represents a potentially fruitful avenue of further research that would advance our understanding of mammalian sensory evolution. Such an agenda would profit from the use of new technologies, allowing anatomical structures to be imaged, analysed, and visualised in a more detailed way. Data on the development of the larynx are also missing, despite the unique value of ontogenetic comparison in identifying instances of convergent evolution and for resolving phylogenetic relationships. Further research into laryngeal morphology will likely yield novel insights into the evolutionary history of echolocation and the correlations between morphology and echolocation strategies in bats.

Declarations

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