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The larynx and trachea of the barking gecko, *Ptenopus garrulus maculatus* (Reptilia: Gekkonidae) and their relation to vocalization

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Since its discovery by science almost 150 years ago, *Ptenopus garrulus* has been recognized as a highly vocal gekkonid. While this ability has been the subject of ecological and ethological investigations, and while its call has been sonographically analysed, the means of sound production has remained uninvestigated. This has been partly due to a lack of context in which to place morphological investigations of the gekkonid vocal apparatus. In recent years greater attention has been paid to the functional morphology of this system, and its form in *Ptenopus* can now be evaluated in a comparative light. Herein we document the morphology of the larynx and trachea by way of dissection, histological investigation, computer-assisted three-dimensional reconstruction, and scanning electron microscopy. These investigations reveal a highly unusual structure of the laryngeal skeleton: the cricoid cartilage is a flattened plate of cartilage; the trachea is highly folded and inserted deeply into the larynx; the laryngeal constrictor muscle is asymmetrical in males; the vocal cords are horizontally disposed; the laryngeal aditus is also horizontal and is placed much more anteriorly than in any other geckos for which this relationship is known. *Ptenopus garrulus maculatus* exhibits the most anuran-like vocal apparatus yet discovered in gekkonids.

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Introduction

Most reptiles are not considered to possess 'voices', but they can produce hisses, grunts, growls, gurgles, croaks, squeaks and roars (Mertens 1946; Bogert 1953; Cott 1961; Bustard 1967; Blair 1968; Bellairs 1969; Campbell & Evans 1972; Young 1991). Lizards of the family Gekkonidae are notable among reptiles in their vocal abilities, in that the sounds they emit often have tonal or harmonic qualities (Steck 1908; Bogert 1960; Blair 1968; Werner, Frankenberg & Adar 1978; Brown 1985; Moore, Russell & Bauer 1991). As such, geckos are often described as the only reptiles with true vocal abilities (Haacke 1969), even though the vocalizations of some lacertid species have also been reported to be tonal in quality (Böhme, Hutterer & Bings 1985).

The gekkonid genus *Ptenopus* is endemic to southern Africa and currently comprises three species — *Ptenopus carpi, P. garrulus* and *P. kochi*. In many respects *Ptenopus* displays primitive characteristics when compared with the remainder of the Afro-Madagascan gekkonid radiation (Bauer 1990; Kluge & Nussbaum 1995), and certainly lacks the subdigital adhesive system associated with so many geckos. With respect to its vocal abilities, however, *Ptenopus* shows a highly derived situation (Smith 1849; Falk 1921; Fitzsimons 1935; Mertens 1946; Loveridge 1947; Brain 1962; Giess 1965; Haacke 1968; Patterson 1987; Seufer 1991). Since its discovery and description in 1849, it has been the subject of interest in this regard, from initial reports of its call volume and persistence (Smith 1849), to studies of the acoustic characteristics of its call (Haacke 1969), as the following two quotes vouchsafe:

> 'In the localities in which it occurs, many individuals may be seen peeping from their hiding places, each uttering a sharp sound somewhat like chick, chick; and the number thus occupied is at times so great and the noise so disagreeable, as to cause the traveller to change his quarters.' (Smith 1849) and
>
> 'Each call consists of a series of clicks uttered in quick succession .... A considerable variation in the number of clicks per call and the rate at which the clicks were uttered has been observed.' (Haacke 1969)

The studies of Haacke (1969, 1974, 1975) have been effective in demonstrating that *Ptenopus* is highly vocal, that these vocal signals have a social function, and that only the males are involved in this behaviour, often contributing to a chorus while standing at the mouths of their burrows. It has been postulated that the funnel-shaped burrow entrance may act as an amplifier for the call (Haacke 1969). The characteristics of the call change throughout the calling period (from sunset to darkness and sometimes through the night) and with the changing seasons, with the winter months being periods of silence.

Although significant data are now at hand to enable the calls of *Ptenopus* to be characterized and analysed, little is known of the mechanism of sound production. Haacke (1969) summarized the speculation that had been afforded this problem up to the time of his studies. He dismissed ideas that the sounds were produced by some form of 'tongue clicking' and instead favoured a laryngeal mechanism of sound production. He predicted that because *Ptenopus* is 'so exceptionally vocal' the larynx would be 'well developed' and noted that its structure had not yet been investigated.

It is now established that gekkonid vocalizations are produced by the vibrations of elastin-rich vocal cords, housed in a cartilaginous larynx (Moore, *et al.* 1991; Rittenhouse 1995). Although many lacertid taxa have been described as possessing 'membranous folds' or 'vocal cords' (Meckel 1833; Henle 1839; Wiedersheim 1876; Steck 1908; Vogel 1976), elasticized folds of the laryngeal respiratory mucosa, or true vocal cords, have only been documented in the Gekkonoidea (Paulsen 1967; Niemann 1971; Gans & Maderson 1973). The vocalizations of other reptilian species are produced by forcing air past the closely apposed edges of the arytenoid cartilages of the glottis, or by inducing vibrations in the soft tissue of the glottal lips (Henle 1839; Wiedersheim 1876; Steck 1908; Keleman 1963; Paulsen 1967; Gans & Maderson 1973; Vogel 1976; Milton & Jenssen 1979).

While geckos have long been renowned for their ability to vocalize (Hasselquist 1757; Smith 1849) and the study of their vocal apparatus began long ago (Tiedmann 1818; Meckel 1819), relatively few studies have been published that document the physical characteristics of different species' calls, the social functions they perform, or the morphological means by which they are produced (see Niemann 1971; Gans & Maderson 1973; and Moore, et al. 1991 for summaries). Of the approximately 1 000 species of geckos, only about 80 have been reported to emit sounds, and of these accounts, fewer than 30 species have had their calls analysed sonographically (Rittenhouse 1995). Furthermore, until recently descriptions of laryngeal morphology were few in number and fragmentary in nature. A survey of the laryngeal morphology of representatives of 15 genera of African and Madagascan geckos (Rittenhouse 1995) has augmented this data base. It is in the context of these findings that we examine the structure of the larynx and trachea of *Ptenopus garrulus maculatus* and interpret it in the context of the unusual vocal abilities of this taxon and its congeners.

Materials and methods

To determine the relative placement of the larynx in relation to other landmarks the following measurements were taken: snout-vent length (SVL) (measured from the anterior tip of the snout to the anterior lip of the cloaca); rostrum-clavicle length (RCL) as an estimate of head length (measured from the anterior tip of the snout to the anterior aspect of the midline abutment of the clavicles; intergirdle length (IGL) as an estimate of torso length (= SVL - RCL); and rostrum-aditus length (RAL) as an estimate of the placement of the larynx (measured from the anterior tip of the lower jaw to the anterior extremity of the glottal lips). These measurements were made on a wide array of Afro-Madagascan geckos (see Rittenhouse 1995) and were compared with the measurements obtained for *Ptenopus*.

Larynges were excised from six mature (three male, three female) formalin-fixed, ethanol preserved specimens of *Ptenopus garrulus maculatus* on loan from the California Academy of Sciences (CAS), San Francisco, California. Incisions were made around the inner margin of the mandible and through the lingual and hyoid musculature to reflect the laryngeal complex (larynx, trachea, tongue, basihyoid). The larynx and trachea were then separated from the tongue and the basihyoid by cutting the musculature and ligamentous attachments between these structures. Portions of the oral mucosa strongly adhering to the excised structures were not removed in order to prevent damage to them. Excised specimens were subsequently cleaned of connective tissue and observed with the aid of a Wild M5 dissecting microscope fitted with a *camera lucida*.

One laryngeal specimen of each sex was prepared for routine scanning electron microscopy (SEM) by isolating the larynges from their attached segments of tracheae, dividing the larynges in half longitudinally, and dehydrating each in a series of ethanol solutions of increasing concentration, over a period of 2 h. Each laryngeal specimen was placed in a 50:50 mixture of hexamethyldisilazone (HMDS) and 100% ethanol for 30 min, and then two solutions of 100% HMDS for 30 min each. After drying, the two halves of each larynx were mounted on an SEM stub cleaned with acetone, one half dorsal surface down and the other dorsal surface up. The stubs were then sputter coated, and observations were made on a scanning electron microscope at the University of Lethbridge, Lethbridge, Alberta.

The four remaining laryngeal specimens were decalcified in a 1:1 mixture of 2% ascorbic acid and 0.3M NaCl for 24 h, following the methodology of Dietrich & Fontaine (1975). Decalcified material was dehydrated and cleared, then embedded in paraffin wax using standard procedures. One larynx of each sex was sectioned in the tranverse plane, the other in the frontal plane. Section thickness varied between 8 and 10 μm. Sections were mounted in Permount on glass slides and alternate slides were stained with Milligan's trichrome, for the differentiation of muscle and collagenous connective tissues, and Verhoeff's stain for elastin fibres (Humason 1978).

The best set of transverse sections (female) was chosen to be the model for a computer-based method of reconstructing the laryngeal skeleton in three dimensions. With a projection microscope, outline drawings of the sectioned laryngeal cartilages were made at regular intervals, digitized with a flatbed scanner, and aligned using NIH Image (Version 1.54) for Macintosh computers. Once concatenated, physical connectivity between successive outlines was provided by draping a skin of rendered contours over all of the interstitial spaces in the digital template. The Application Visualization System, a general-purpose visualization package for UNIX-based computer systems, was used to visualize and render the resulting isosurfaces. A detailied description of the methodology is available elsewhere (Rittenhouse, Russell & Phillips 1996).

Infromation regarding call characteristics of *Ptenopus garruluos maculatus* and other taxa of *Ptenopus* was obtained form the publications of Haacke (1969, 1974).

Results

In order to provide a contrast for the conditions found in *Ptenopus* it is necessary to describe first the morphological features of a more 'typical' gekkonid, the tokay gecko, *Gekko gecko* (Figure 1). Here the larynx is a pyramid-like elevation arising from the floor of the mouth, lying posterior to the tongue and medial to the orbits (Figure 1a) (Moore, *et al.* 1991). It occupies a concavity in the palate. The anterior opening of the larynx is the glottis and at rest this opening is tilted slightly dorsally. The lips of the glottis have a somewhat lobular appearance and isolate the larynx form the oral cavity (Figure 1b).

The laryngeal skeleton is cartilaginous, its main body composed of a ring-shaped cricoid that bears a pair of lateral processes (Figure 1c). A pair of arytenoid cartilages articulate anteriorly with the dorsolateral parts of the cricoid and extend anteriorly and medially to support the glottal lips. Posteriorly

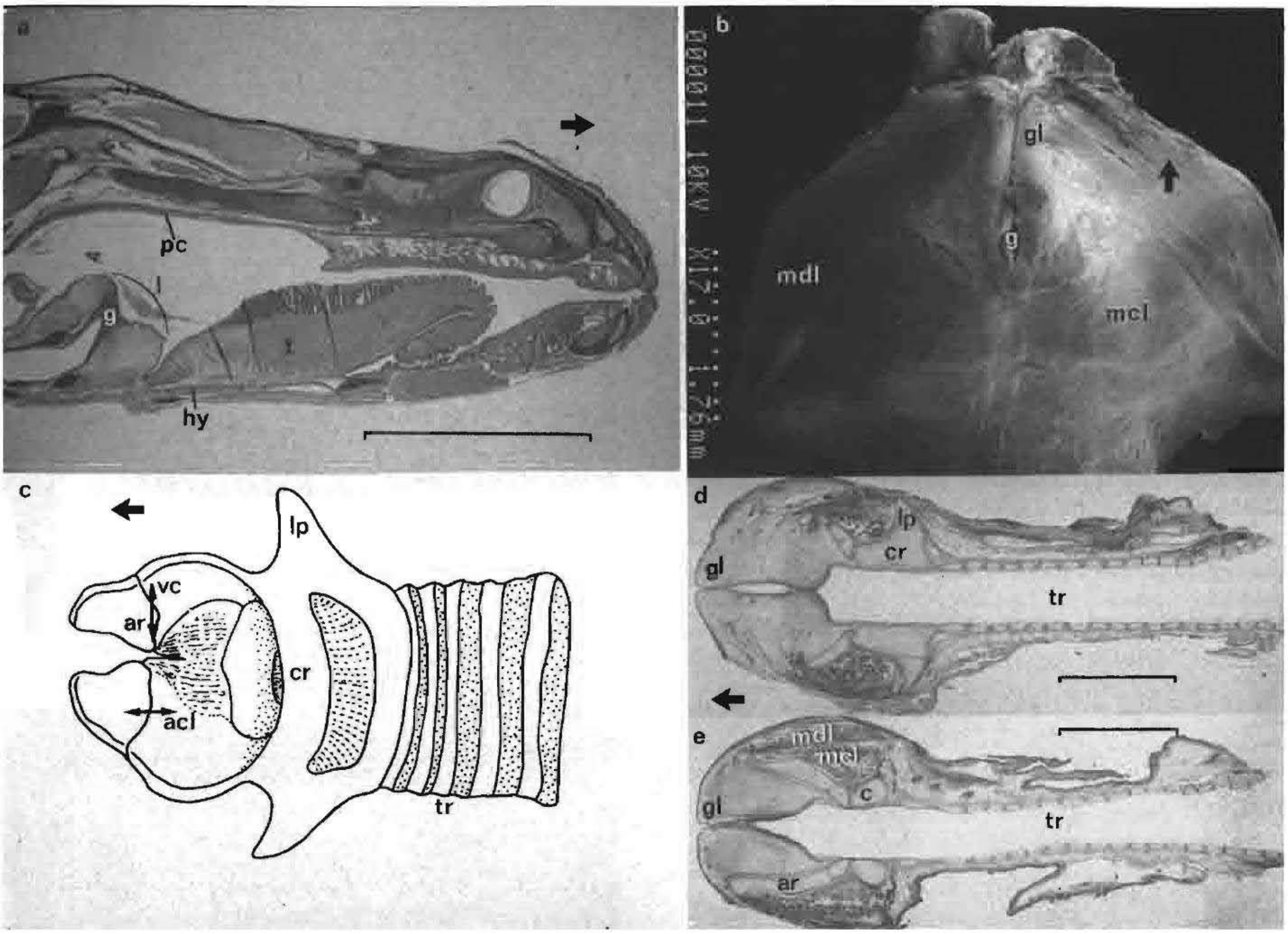

Figure 1 Laryngeal structure and position in a juvenile tokay gecko (*Gekko gecko*). (a) Parasagittal section through the rostrum of a tokay indicating the positional relationships and orientation of the larynx within the oral cavity: scale bar = 5 mm; (b) scanning electron micrograph of the dorsal view of the larynx of the tokay showing the major muscles and the glottal lips; (c) diagram of the laryngeal cartilages and trachea, showing the courses of the arytenoid-cricoid ligaments and the vocal cords; (d) frontal section through the trachea and larynx at the level of the lateral processes of the cricoid cartilage: scale bar = 2 mm; (e) frontal section though the trachea and larynx at the level of the main body of the arytenoid cartilages: scale bar = 2 mm. Abbreviations: acl, course of the arytenoid-cricoid ligament; ar, arytenoid cartilage; cr, cricoid cartilage; g, glottis; al, glottal lips; hy, hyoid skeleton; l, larynx; lp, lateral process of cricoid cartilage; mcl, *constrictor laryngis* muscle; mdl, *dilator laryngis* muscle; pc, concavity in roof of palate; t, tongue; tr, trachea; vc, course of vocal cords. Large arrow indicates anterior. For (a), (d) and (e) the stain employed was Milligan's trichrome.

the lumen of the larynx is continuous with the trachea (Figure 1d,e). The larynx is supported in the floor of the mouth by muscular and ligamentous attachments to the hyoid apparatus (Figure 1a).

Embracing the anterior end of the laryngeal skeleton are two muscles (Figure 1b), the *m. constrictor laryngis* that runs from the basihyoid to the dorsal aspect of the cricoid, and the *m. dilator laryngis* that runs from the lateral processes of the cricoid to insert on the arytenoid cartilages.

Internally the larynx is lined with respiratory mucosa. Elastin-rich ligaments run longitudinally between the arytenoid and cricoid cartilages (the arytenoid-cricoid ligaments) and vertically, medial and lateral to the point of articulation, between the arytenoids and cricoids (Figure 1c). The latter form the core of the vocal cords, but both sets of ligaments may result in folds protruding into the laryngeal lumen and may be continuous with one another.

The laryngeal skeleton of *Ptenopus garrulus maculatus*

The cricoid of *Ptenopus garrulus maculatus* is a plate of cartilage which, with its extremely large, transversely oriented lateral processes, is diamond-shaped (Figure 2a,c,d). It is obliquely oriented within the frontal plane, angling dorso-posteriorly from the floor of the buccal cavity. In both sexes a large foramen exists about its longitudinal midline (Figure 2c,d; Figure 3b,d) extending from the level of the lateral process to a point near the posterior border of the *aditus laryngis*. This foramen has a transverse width equivalent to that of the trachea. In the female, this space appears somewhat rectangular, and in the male is triangular. The posterior portions of these foramina could not be observed macroscopically because they are occupied by the anterior ends of the tracheae. This occurs because of the cricoid's oblique angle of inclination relative to the trachea. The trachea does not articulate with the cricoid cartilage so much as it inserts into the lumen of the cricoid (Figure 4a).

Figure 2 Isosurfaced reconstructions of the cricoid and right arytenoid of a female *Ptenopus garrulus maculatus* (CAS 167739) in (a) anterior, (b) lateral, (c) dorsal, and (d) perspective views. Shaded and stippled areas with dashed borders and the open arrow depict the position and orientation of the fibers of the right half of the *m. constrictor laryngis* in lateral and dorsal views. a, arytenoid; c, cricoid; cf, cricoid foramen; lp, lateral process of cricoid. Scale bar = 1 mm.

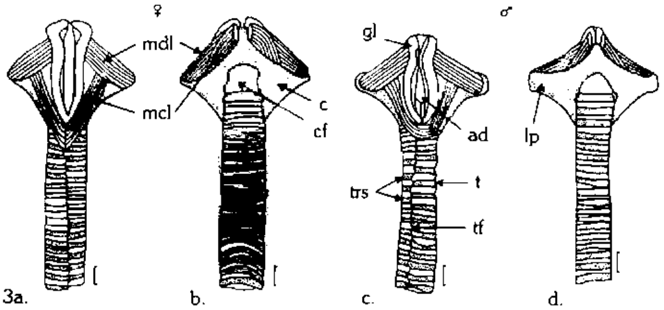

Figure 3 *Camera lucida* drawings of the dorsal and ventral views of the larynx and trachea of (a, b) female, and (c, d) male *Ptenopus garrulus maculatus* (CAS 167749, CAS 167747). ad, *aditus laryngis*; gl, glottal lip; mcl, *m. constrictor laryngis*; mdl, *m. dilator laryngis*; t, trachea; tf, tracheal fold; trs, tracheal rings. Other abbreviations as in Figure 2. Scale bar = 1 mm. Note sexual differences in the symmetry of the *m. constrictor laryngis* and in the shape of the cricoid foramen.

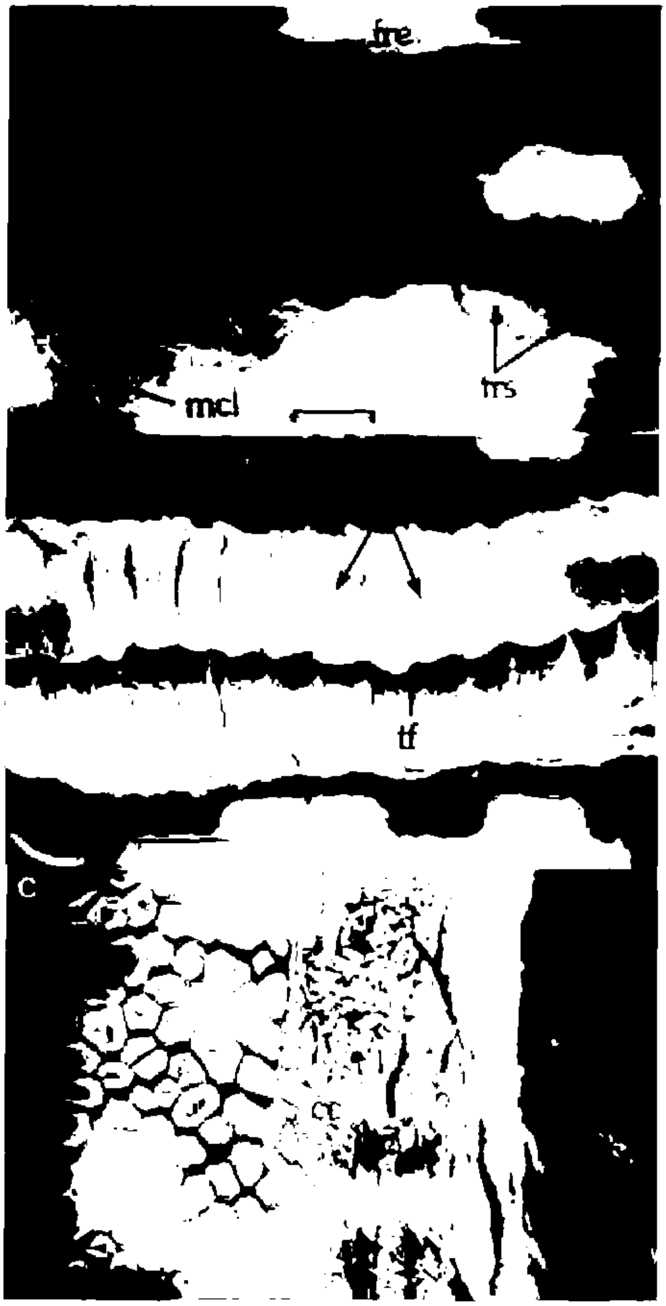

Figure 4 Scanning electron micrographs of the trachea of *Ptenopus garrulus maculatus*. (a) Sagittal view of the right half of the larynx of *P. g. maculatus* (CAS 167741), illustrating the manner in which the trachea inserts into the larynx. Dorsal is at the top of the figure and the open arrow in this and subsequent figures points anteriorly. fre, fold in the respiratory epithelium of the laryngeal mucosa; ll, laryngeal lumen. Other abbreviations as in Figure 3. Scale bar = 250 µm. (b) Dorsal view of the fold evident in the trachea of *P. g. maculatus* (CAS 167741), such that the left half of the trachea folds over the right. Abbreviations as in Figure 3. Dorsal is up. Scale bar = 0.5 mm. (c) Enlargement of the fold observed in Figure 4(a) depicting a distinct transition in the epithelial structure over this mucosal fold. The dorsal region of the larynx is to the left. cc, ciliated cells; gc, goblet cells. Scale bar = 10 µm.

The reconstructions of the arytenoids (Figure 2a,c,d) indicate that these cartilages are rod-shaped and project antero-medially such that their anterior ends converge over the dorso-anterior surface of the cricoid. The posterior ends of the arytenoids angle ventro-laterally to articulate with the dorso-medial surface of the cricoid at the level of the posterior border of its lateral processes (Figure 2c). The arytenoids are positioned such that their points of articulation with the cricoid are immediately adjacent to the cricoid foramen and lie in close proximity to the anterior end of the trachea.

The trachea of *Ptenopus garrulus maculatus*

The trachea of *P. garrulus* is folded in on itself, producing a longitudinal invagination, in which the left side of the trachea covers the right; a condition unique among gekkonid lizards (Figures 3a,c; 4b). The tracheal rings are incomplete in this fold, along the entire length of the excised portion of the trachea. In both sexes, the tracheal rings are relatively uniform in terms of their anterior-posterior length. Those of the female exhibit some intertracheal ring fusion (Figure 3b). The intertracheal ring spaces are of variable thickness, dorsally and ventrally, relative to the rings that bound them. The anterior end of the trachea inserts deeply into the larynx (Figure 4a) and does not simply abut its posterior end.

The laryngeal musculature of *Ptenopus garrulus maculatus*

The laryngeal musculature of *Ptenopus garrulus maculatus* consists of dilators which arise from the dorsal surface of the lateral processes of the cricoid and insert on the arytenoids, and constrictors that arise from the basihyoid and meet at the dorsal midline of the cricoid (Figure 3). In this species, the *m. dilator laryngis* has a larger mass than the *m. constrictor laryngis*. The fibres of the dilator muscles are transversely oriented (Figure 3a,c) and insert into the glottal lips which delineate a dorsally-oriented *aditus laryngis*. The *m. constrictor laryngis* is longitudinally oriented and extends posteriorly over the trachea (Figure 3a,c) but inserts on the caudal border of the cricoid. Dorsally, the constrictor muscle is divided by a thin raphe. In the female, this strip is located in the dorsal midline of the posterior region of the cricoid (Figure 3a) whereas in the male it is offset (Figure 3c), appearing on the right side of the specimen. Ventrally, the fibres of the constrictor muscles run parallel to one another and are directed antero-medially. From a histological perspective, the *m. constrictor laryngis* of *P. garrulus* is composed of a deep layer and a superficial layer (Figure 5a), an apparently unique situation for geckos.

Histology and SEM of the larynx of *Ptenopus garrulus maculatus*

The glottal lips are positioned dorsally in *Ptenopus garrulus maculatus* (Figure 4a), medial to the dorsal halves of the arytenoid cartilages, and extend from the anterior tips of the arytenoids to the anterior, mid-dorsal margin of the dorsal-posterior part of the cricoid. The glottal lips, compared to the condition of other geckos (Moore, *et al.* 1991), contain a moderate amount of loose connective tissue (Figure 5b). A random distribution of longitudinally-oriented elastin fibers is present in the loose connective tissue of each glottal lip. The few venous spaces that are present indicate that the glottal lips of *Ptenopus garrulus maculatus* do not have the structural characteristics of erectile tissue, as is evident in certain other geckos (Moore, *et al.* 1991; Rittenhouse 1995).

The arytenoid-cricoid ligaments are located between the ventral surface of the arytenoids and the dorsal surface of the cricoid, and are elasticized along their medial sides.

The vocal cords are prominent, horizontal bands of elastin that run the entire length of the ventral aspects of the glottal lips (Figure 5a). As such, the vocal cords are situated dorsal to, rather than anterior to, the arytenoid-cricoid ligaments, the entire larynx having been rotated dorsally relative to the 'typical' condition. There is no continuity between the elastin present in the vocal cords and the arytenoid-cricoid ligaments. The elastin fibres in the vocal cords are dense and longitudinally oriented, and lie beneath the *lamina propria* of the laryngeal mucosa (Figure 5a).

The examination of the laryngeal mucosa by scanning electron microscopy revealed a distinct horizontal fold in the respiratory epithelium along the ventro-medial border of the glottal lips (Figure 4a). A distinct epithelial transition was seen on the cord-like structures found in *Ptenopus garrulus*. The respiratory mucosa directly over these structures consists entirely of goblet cells, but adjacent to these folds, both dorsally and ventrally, the goblet cells are interspersed with numerous ciliated cells (Figure 4c). The epithelium consists of a glandular stratified cuboidal type medially, a pseudostratified type ventro-medially, and simple cuboidal epithelium along the ventral border of the vocal cords.

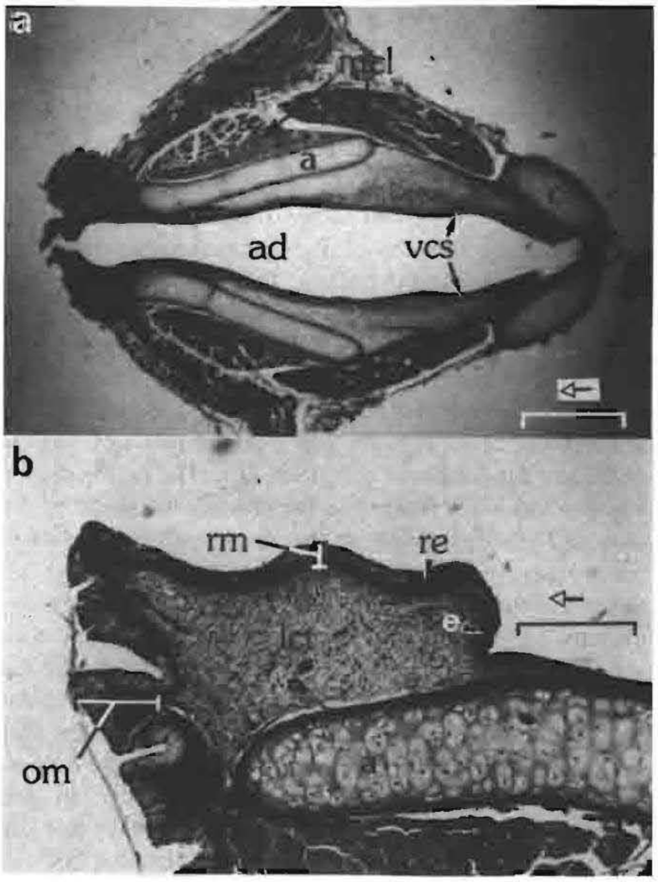

Figure 5 (a) Frontal section of the larynx of *P g. maculatus* (CAS 167749) at the level of the dorsal-most point of the cricoid. Note the horizontally oriented vocal cords and the closure of the laryngeal aditus anteriorly. vcs, vocal cords. Other abbreviations as in Figures 2 and 3. Verhoeff's elastin stain. Scale bar = 500 µm. (b) Transverse section of the left glottal lip of *P. g. maculatus* (CAS 167739), half-way along the length of the arytenoid. e, elastin; om, oral mucosa; re, respiratory epithelium of the larynx; rm, laryngeal respiratory mucosa. Verhoeff's elastin stain. Scale bar = 150 µm.

Discussion

The laryngeal morphology of *Ptenopus garrulus maculatus* differs markedly from that of all other geckos examined. From a phylogenetic perspective perhaps the most appropriate taxa for comparison are members of the large radiation of African and Madagascan geckos that appears to constitute the sister group of *Ptenopus*. The exact make-up of this sister group is debatable, as *Ptenopus* may have its closest affinities either with a southern African-Madagascan clade (Joger 1985; Bauer 1990) or with a more broadly construed Pan-African clade as a whole (Kluge & Nussbaum 1995). In practical terms, however, the implications for the interpretation of laryngeal morphology are identical; the character states illustrated by *Ptenopus* are virtually all autapomorphic, and consequently the larynx and trachea of *Ptenopus* are no more similar to closely-related taxa than they are to those of more distantly allied forms.

The cricoid of *Ptenopus* is not ring-like but has instead become flattened into a broad plate. Its posterior end receives rather than abuts with the trachea. The vocal cords, owing to the flattened nature of the cricoid and its articulation pattern with the arytenoid cartilages, are horizontally rather than vertically oriented in the resting position. The *m. dilator laryngis* is extremely large, and it is this muscle that is responsible for the dorso-lateral rotation of the arytenoid cartilages on the cricoid and the parting of the glottal lips. The *m. constrictor laryngis*, which is responsible for altering the shape of the *aditus* and placing tension on the vocal cords, is unusual in several respects. Firstly, it extends posteriorly as far as the anterior extremity of the trachea. Secondly, its fibres are significantly longitudinally oriented. Thirdly, this muscle consists of two distinct parts on each side. Fourthly, where the left and right neighbours of this pair unite there is apparent sexual dimorphism. In the female, the muscles of the two sides meet in the sagittal plane, where they abut onto a tendinous raphe, whereas in the male the belly of the left side crosses the sagittal plane so that the abutment of the pair lies slightly to the right of the body long axis. In taxa, such as *Gekko gecko* the *m. constrictor laryngis* and the *m. dilator laryngis* probably work in concert to carry out dorso-lateral rotation of the arytenoids, parting of the glottal lips, alteration of the shape of the aditus, and tensing of the vocal cords. The morphology of the situation in *Ptenopus garrulus*, however, suggests that the *m. dilator laryngis* dominates in elevating the vocal cords dorsally and placing the glottal lips into apposition.

In *Ptenopus garrulous maculatus* the *aditus laryngis* lies in the horizontal plane, such that air exhaled from the respiratory tract is directed dorsally. In this way, the sound that is produced may have more opportunity to resonate within the oral cavity than it would if the air flow was directed more anteriorly. Consequently, the musculature of the larynx and the buccal cavity may contribute to the production of the voice, especially if taut (Steck 1908). The elongated, plate-like cricoid cartilage is unique amongst geckos and is significant in the horizontal alignment of the vocal cords in the resting position of the larynx.

Additionally, *Ptenopus garrulus maculatus* has a longitudinal invagination along the dorsal surface of its trachea. This suggests that the trachea is capable of being inflated, and of containing a relatively large volume of air that could be used to create more forceful exhalations. Also, the large membrane of the fold that separates the ends of tracheal rings could initiate vibrations that are amplified in the larynx and oral cavity of this species.

How *Ptenopus garrulus maculatus* expands this fold is not known. One possibility is that the contraction of the longitudinally-oriented fibres of the *m. constrictor laryngis* could cause the cricoid to rotate anteriorly, such that it, the arytenoids and the vocal cords become vertically oriented, lying at a near right angle to the trachea. Because the membrane lining the laryngeal lumen is continuous with that present within the tracheal invagination, this rotation could cause the expansion of the tracheal fold as the larynx becomes more upright. The unique cricoid-tracheal 'articulation' in this species, the almost spherical shape of the head that is relatively short when compared to postcranial body length (Figure 6a), the relatively anteriorly-displaced *aditus laryngis* (Figure 6b), the free posterior end of the cricoid, and the large foramen that represents the lumen of this cartilage, would all seem to allow this anuran-like (Gans 1973), laryngeal gyration to occur. Paulsen (1967) has stated that the cricoid of the tokay (*Gekko gecko*) is drawn forward and into a more upright position just prior to vocalization. Future *in vivo* laboratory observations are needed to determine if this is also the case in the *Ptenopus*.

The above-mentioned features of the larynx and trachea and the potential results of the movements between them can be related to field observations. It has been noted that in association with calling, the throat is expanded and deflated (Brain 1962; Haacke 1964) and the mouth is opened and

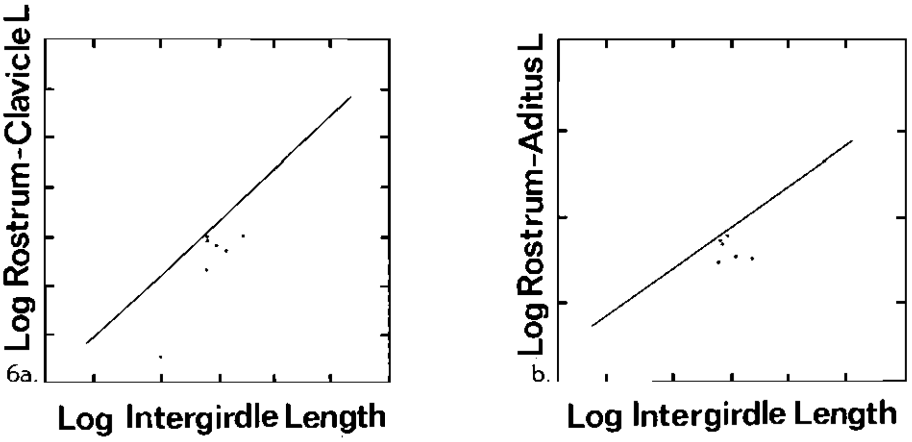

Figure 6 Geometric Mean Regressions representing the isometric relationships of (a) head size to body size, and (b) laryngeal position with the buccal cavity to body size across 15 Afro-Madagascan genera (n = 123; taken from Rittenhouse 1995). The positions of the scatter plots for *Ptenopus garrulus maculatus* relative to the GMR axes illustrate that the head of this species is comparatively short, and that the *aditus laryngis* is displaced anteriorly.

closed in a rhythmic fashion for the emission of each click. This is accompanied by small jerks of the head. The sound emitted is very loud, especially for the size of the animal involved, and 'under ideal conditions can be heard for several hundred yards' (Haacke 1969). It is evident that considerable force is needed to generate a call of such volume, and the combination of an inflatable trachea and elongated vocal cords borne within a larynx capable of pivoting could well be significant in this regard. The jerking of the head could be involved with the explosive emission of air from a pre-pressurized trachea. Further observations on the lungs and the complete airway system are necessary to evaluate this hypothesis further.

The fact that only male *Ptenopus* seem to call spontaneously (Haacke 1969) is suggestive that there might be significant sexual dimorphism in laryngeal structure. There are, however, only two features that are noticeably sexually dimorphic — the location at which the posterior ends of the *m. constrictor laryngis* meet; at the midline in the females, somewhat offset from the midline in males, and the anterior extremity of the cricoid foramen is squared off in the female but triangular in the male (Figure 3a,c). These differences are not, in themselves, suggestive of a major difference in function. The morphology of the larynx and trachea, as far as we can ascertain, is constructed in such a way as to allow phonation. That the females do not do this may be determined either by social interactions that inhibit it, or it may be reflective of as yet unidentified anatomical dimorphism in terms of the motor control of central pattern generators. Such neurologically-based sexual differences have been shown to be responsible for differential vocal abilities between male and female *Xenopus laevis* (Tobias & Kelly 1988).

The combination of the circumstantial correlation between the highly modified vocal apparatus, the exceptionally well-developed vocal abilities of *Ptenopus*, and the model of how sound production may be developed by such a system strongly supports the contention of Haacke (1969) that the source of vocalization is the larynx. Further, it appears that the trachea and laryngotracheal connection of *Ptenopus* are also highly derived, and that the highly developed vocal capabilities of this taxon are almost certainly associated with such a specialized system as a whole.

Why such a system should have evolved uniquely in *Ptenopus*, or more broadly why a social system of this complexity should exist still remains unknown. Although hypotheses may be put forth for such evolutionary questions they will be difficult to test because phylogenetic patterns remain poorly resolved and because no putative relatives appear to exhibit similar morphologies or behaviours from which those of *Ptenopus* might be reasonably derived. Alternatively, the model of phonation outlined in this paper can be tested by the application of dynamic morphological methods, in particular a combination of electromyography, force and pressure transduction recording, sonograms, and high speed videography. If our model of phonation is correct then the situation found in *Ptenopus* may be the closest to an anuran type of vocalization system yet identified in gekkonids. The considerable progress made in the study of anuran vocalization could then be adopted to further the understanding of gekkonid phonation.

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