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The larynx of roaring and non-roaring cats

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INTRODUCTION

In most species of the cat family the hyoid bone is suspended from the skull by a series of small bones: the tympanohyal, stylohyal, epihyal, and ceratohyal. The proximal tympanohyal is embedded in the tympanic bulla whilst the distal part of the ceratohyal is attached to the basihyal (body of the hyoid). The larynx attaches to the hyoid by way of the thyrohyal bone and thyrohyoid ligament (Reighard & Jennings, 1901).

In 1834, Owen found that the lion had an incompletely ossified hyoid apparatus, with an elastic ligament 6 inches long replacing the epihyal bone; he stated that this ligament could be stretched to 8 or 9 inches, allowing the lion to move its larynx farther away from the palate, thereby gradually lengthening the pharyngeal passage. Later, Pocock (1916) confirmed Owen's observation and also found that the hyoid apparatus is incompletely ossified, with an elastic ligament replacing the epihyal, in the lion, tiger, leopard, jaguar, and snow leopard. These two authors' belief that this elastic ligament is the anatomical structure that makes roaring possible has been accepted up to the present (Ewer, 1973; Guggisberg, 1975; Neff, 1982; Nowak & Paradiso, 1983). The snow leopard also has a short ligament in its hyoid apparatus but it has never been heard to roar (Hemmer, 1972).

The ability to increase the distance between the oral pharynx and larynx, because the hyoid apparatus is not fixed, enables lengthening of the acoustic pipe, certainly lowering the pitch of voice and probably increasing its resonance. But this is not the mechanism that produces the intense amplification of sound called 'roaring'. In order to determine that mechanism, the sound generator of voice, the larynx, was studied in single specimens of most big cats and a few small felids. The results, presented in a previous short report (Hast, 1986) showed that the larynges of the four 'roaring' cats, the lion, tiger, leopard, and jaguar, can be distinguished from larynges of 'non-roaring' cats by a large pad of fibro-elastic tissue which constitutes the rostral portion of the proportionately very large vocal fold.

This paper presents a more detailed anatomical study of the larynx of all species of the big cats and a representative number of small cats. The structure of the vocal folds of the family Felidae are discussed in terms of functional morphology, with 'roaring' versus 'non-roaring' vocalisation described in principles of musical acoustics.

MATERIALS AND METHODS

A study was made, by dissection, of the morphology of 26 adult larynges of *Felis catus*, *Felis concolor*, *Felis geoffroyi*, *Felis planiceps*, *Felis manul*, *Felis marmorata*,

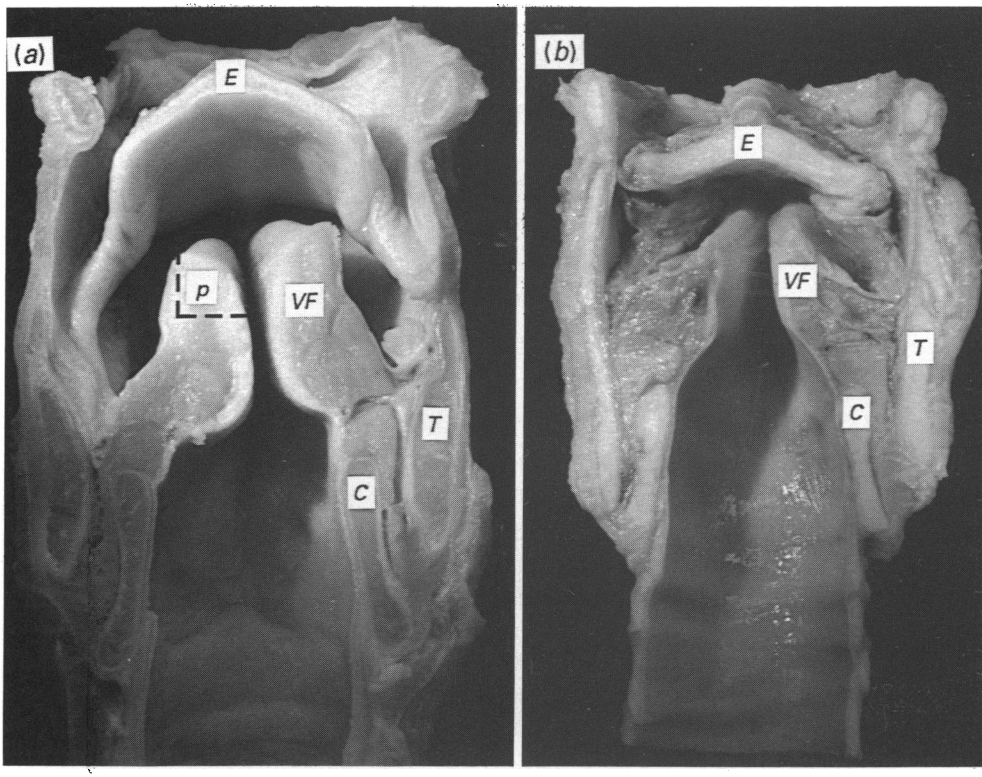

Fig. 1 (*a–b*). (*a*) Larynx of a typical *Panthera*, the jaguar (*P. onca*), viewed from the dorsal aspect and cut coronally. (*b*) Larynx of a snow leopard (*P. uncia*) from a similar point of view. The longitudinally very long vocal folds (*VF*) of the jaguar, with their large rostral pad of fibro-elastic tissue, (*p*) are readily distinguished from the proportionately shorter vocal folds of the snow leopard. Other labelled structures: *E*, epiglottis; *C*, cricoid cartilage; *T*, thyroid cartilage.

Lynx rufus, *Panthera leo*, *Panthera onca*, *Panthera pardus*, *Panthera tigris*, *Panthera uncia*, *Neofelis nebulosa*, and *Acinonyx jubatus*. With the exception of the tiger (*P. tigris*), clouded leopard (*N. nebulosa*), Pallas' cat (*F. manul*), and the marbled cat (*F. marmorata*), dissections were made of both sexes; specimens of the last-named animals were limited to females*. All postmortem specimens were taken from animals that had died of natural causes and were obtained from a number of zoological parks and museums listed later. After all cartilages, muscles, and other structures were identified, each larynx was cut vertically in a coronal section, ventral to the arytenoid cartilage. Measurements were then made of the internal longitudinal lengths of the vocal fold and infraglottic/glottal vocal tract of each larynx. Additionally, tissue was taken from the rostral portion of the vocal fold of the *Panthera*. This pad of tissue was embedded in paraffin, sectioned, and stained with haematoxylin and eosin, trichrome and elastin and reticulin stains; histological examination was done by light microscopy.

RESULTS AND DISCUSSION

It was found that all species of genus *Panthera* ('roaring cats'), with the exception of *P. uncia*, can be distinguished from 'non-roaring' cats by a large pad of fibro-elastic tissue which constitutes the rostal portion of each of the proportionately very large undivided vocal folds (Fig. 1 *a*). Sections of this pad of fibro-elastic tissue demonstrate

* Taxonomy follows Honacki *et al.* (1982).

Table 1. *Dimensions of the vocal fold and infraglottic/glottic vocal tract of female larynges of genus* Panthera *and other big cats*

PLVF is the proportion of the longitudinal length of the vocal folds to the distance from the base of the cricoid cartilage to the superior border of the vocal folds (infraglottic–glottic vocal tract).

	Longitudinal length of vocal fold (at rima glottis) (mm)	Distance from base of cricoid cartilage to superior border of vocal fold (mm)	PLVF (%)
Lion (*P. leo*)	25	62	40
Tiger (*P. tigris*)	22	55	40
Leopard (*P. pardus*)	20	50	40
Jaguar (*P. onca*)	19	46	41
Snow leopard (*P. uncia*)	9	36	25
Cheetah (*A. jubatus*)	6	31	19
Clouded leopard (*N. nebulosa*)	5	25	20
Puma (cougar) (*F. concolor*)	6	34	18

collagenous and elastic fibres, denser near the epithelial mucosal lining, with reticular fibres around the basement membrane and arteries. Because of their large mass, the *Panthera* vocal folds – the sound generating element – have a low natural frequency and, when vibrating, will produce a high acoustical energy. The design of the *Panthera* vocal folds allows for a gradual transition of sound energy from a high to a low air resistance, resulting in a better transfer of acoustical energy in an efficient sound radiator ('roaring'). Genus *Panthera* also can be distinguished from other cats by the proportionately very large cricothyroid muscle, a single rounded vocal fold with a very thick mucosal lining, a large vocalis muscle and a long and narrow median cricothyroid membrane. As in other species of the cat family, sexual differences are quantitative, with the male larynx, on the average, larger than the female.

The snow leopard (*P. uncia*) also possesses an incomplete hyoid apparatus with an elastic ligament, undivided thyroarytenoid folds, and its larynx is similar in size to that of a small jaguar. However, the snow leopard has no pad of fibro-elastic tissue to increase the length and mass of its vocal fold (Fig. 1*b*), and it does not roar. In the sound-producing mechanism of the snow leopard and other non-pantheran cats, transfer of energy is less efficient, and the ability to radiate sound is poorer because of the form of the vocal folds. With the snow leopard's longitudinally shorter vocal folds (Table 1), a lower resistance to airflow is developed subglottally and there is an abrupt change in the diameter of the tube or horn when the acoustic energy becomes supraglottic; the result is a poorer transfer of sound energy and an inability to 'roar'.

Using the larynx as an anatomical character supports the snow leopard's classification as a separate genus *Uncia uncia* (Guggisberg, 1975; Hemmer, 1972; Neff, 1982; Pocock, 1917) not as *Panthera uncia* (Corbet & Hill, 1980; Honacki, Kinman & Koeppl, 1982). Peters (1978) also favours the former classification, and he believes that there is no relationship between the vocalisation of a cat species and the structure of its hyoid apparatus or body size.

Genus *Felis* possesses a larynx with divided thyroarytenoid folds, with a depression between the rostral and caudal folds that varies from a slight fossa to a deep ventricle, and a vocal fold with a sharp edge. The larynx of the male puma (*F. concolor*), the largest of the genus *Felis*, is similar in size to a small *Panthera*, but its divided thyroarytenoid folds are even shorter in their longitudinal dimension than those of the snow leopard (Table 1). The puma can purr, growl or scream with its sharper-edged vocal folds, but it does not possess a larynx designed for roaring. The dimensions of a male cheetah's larynx also place it close to that of a small *Panthera* but it, too, has felis-like vocal folds and does not roar. The structure of the larynx of two other cats, the clouded leopard (*N. nebulosa*) and the bobcat (*L. rufus*), also resembles genus *Felis* and they are not capable of roaring.

The entire vocal mechanism of the roaring *Panthera*, i.e. subglottic larynx, vocal folds, supraglottic larynx, pharynx and open mouth, is analogous to the brass trumpet. The *Panthera* vocal folds simulate the form of a trumpet mouthpiece. The mouthpiece, when added to one end of the tube (supraglottic larynx and pharynx), adjusts frequencies of the harmonics. The result is to increase slightly the effective length of the tube and to cause the instrument to behave acoustically like an open tube with a new length; the instrument (vocal mechanism) will then produce a set of resonances which includes all the notes of the overtone series (Berg & Stork, 1982). The wide open mouth of the cat is analogous to the bell of the trumpet. Adding a bell or wide open mouth to the cat's trumpet-like vocal apparatus provides the correct match between instrument and outside air to transfer the sound most efficiently; a bell also modifies the frequency and stability of the harmonics, increasing their production and radiation (Bachus, 1977; Berg & Stork, 1982).

The configuration of an instrument employing a mouthpiece at one end of a straight tube and a bell at the other end will produce a sound that is louder, and a tone that is brighter and more 'trumpet-like' than any instrument that lacks either a mouthpiece or a bell (Holmes, 1985). Finally, the replacement of the epihyal by an elastic ligament in genus *Panthera* allows the larynx to be moved a greater distance from the tympanic bulla and is analogous to the modern valve brass trumpet or slide trombone, where every lengthening of the instrument by 6% will result in a decrease in pitch of one semitone i.e. about 6% in frequency (Bachus, 1977).

SUMMARY

Dissections were made of the larynges of 14 species of the cat family, with representative specimens from all *genera*. It was found that the vocal folds of the larynx of genus *Panthera* (with the exception of the snow leopard) form the basic structure of a sound generator well-designed to produce a high acoustical energy. Combined with an efficient sound radiator (vocal tract) that can be adjusted in length, a *Panthera* can use its vocal instrument literally to blow its own horn with a 'roar'. Also, it is proposed that laryngeal morphology can be used as an anatomical character in mammalian taxonomy.

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