

HOW MANY WAYS CAN A SNAKE GROWL? THE MORPHOLOGY OF SOUND PRODUCTION IN *PTYAS MUCOSUS* AND ITS POTENTIAL MIMICRY OF *OPHIOPHAGUS*

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As part of its defensive display the Indian rat snake, *Ptyas mucosus*, mediolaterally compresses the anterior portion of its body and expands its throat region ventrally. During this postural display *P. mucosus* produces a deep, rumbling defensive growl. Acoustic analysis of this growl revealed it to be a long moderately loud sound dominated by lower frequencies. Binding the neck and anterior portion of the body with surgical tape prevented the postural display; while the defensive sounds produced by bound specimens had the same duration and amplitude, their frequency increased significantly. The tracheal membrane of *P. mucosus* is unusually wide and expands away from the tracheal rings into the body cavity. We hypothesize that during the defensive postural display the expansive tracheal membrane is collapsed forming isolated pockets which have a resonance effect on the exhalent airstream. *Ptyas mucosus* may be an acoustic Batesian mimic of the king cobra, *Ophiophagus hannah*.

Key words: sound production, acoustics, Batesian mimicry, colubrids, defensive behaviour

INTRODUCTION

Snakes exhibit a wide variety of defensive behaviours (for reviews see Carpenter & Ferguson, 1977; Greene, 1988) including postural displays, expulsion of a variety of fluids, and production of a variety of defensive sounds. While some of these defensive behaviours have been extensively studied, for most the underlying mechanisms and behavioural significance remain poorly known (see Greene, 1997). Similarities in defensive displays have led to several claims of Batesian mimicry in snakes. Some of the proposed examples of Batesian mimicry are generally accepted (e.g. *Echis* and *Dasyeltis*, see Gans, 1961), while others (e.g. the coral snake complex) remain contentious (see Pough, 1988; Roze, 1996).

The Dhaman or Indian ratsnake (*Ptyas mucosus*) is a large (up to 3.5 m) colubrid that is found throughout most of southern Asia and western Indonesia. *Ptyas mucosus* is often described as a nervous snake which is both quick to strike and prone to defensive displays, including the production of a distinctive low frequency sound (e.g. Wall, 1921; Minton, 1966; De Rooij, 1917). There is substantial overlap between the geographic distribution and ecological preferences of *P. mucosus* and the king cobra, *Ophiophagus hannah* (see Smith, 1943). There are several accounts in the literature describing *P. mucosus* as resembling or mimicking that of *O. hannah*, particularly in regards to their defensive behaviours and the defensive sounds they produce (e.g. Flower, 1899; Soderberg, 1973; Whitaker, 1978; Murthy, 1986; Greene, 1997). As part of its defensive display *O. hannah* passes an exhalent airstream over a series of tracheal diverticula which act as resonating

chambers, acoustically modifying the hiss into a low frequency growl (Young, 1991). While similar tracheal diverticula are found in other snakes, including *P. korros*, they are lacking in *P. mucosus* (Young, 1992).

The reported similarities between the sounds of *P. mucosus* and *O. hannah*, coupled with the absence of resonating diverticula in *P. mucosus*, raise several questions regarding the acoustic biology of this species. Is the sound produced by *P. mucosus* really acoustically similar to the growl of *O. hannah*, and how is the sound produced without resonating diverticula? The current study examines the morphological basis of sound production in *P. mucosus* in an effort to document the acoustic properties of this defensive sound, the mechanics of sound production, and the extent of mimicry between *P. mucosus* and *O. hannah*.

MATERIALS AND METHODS

ACOUSTICS

Eight specimens of *Ptyas mucosus* (mean SVL = 136.4 cm, SD = 14.8) were caught in the wild in the vicinity of the Madras Crocodile Bank Trust, India. Individual specimens were placed in a large quiet room and their defensive behaviour elicited by the presence of the investigator. The defensive sounds were recorded using a ND 757B (ElectroVoice) microphone (frequency response 50-22 000 Hz), positioned approximately 20 cm from the head of the snake, and a FOSTEX X-18 recorder (frequency response 20-12 000 Hz). Amplitudes of the hisses were determined using a 840029 Digital Sound Meter (SPER Scientific), positioned approximately 30 cm away from the snake's head. At least five defensive sounds were recorded from each specimen. Acoustic analyses were performed by inputting the recordings into an Instrunet Analog/Digital converter (GW Instruments) coupled to a Power Macintosh 6500 (Apple Computers) which supported the

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SoundScope software (GW Instruments), and WLFDPAP 1.0 digital filter (Zola Technologies).

Once a series of defensive hisses had been recorded, the animal was restrained and porous surgical tape (Leukopor) was wrapped around the snake's body, beginning just caudal to the head and extending for approximately one-quarter of the snake's length. The surgical tape was applied tightly enough to prevent vertical expansion of the neck region, but was not so tight as to interfere with ventilatory airflow. Once the tape was in place, the animal was released and a second series of defensive sounds was recorded as described above. Following this second series of defensive sounds, the animals were again restrained, the surgical tape was removed, and small plugs of sterile cotton were packed into the external nares and sealed in place with surgical tape. The animals were again released and their defensive sounds invoked and recorded. After this third series of recordings the narial plugs were removed and the snakes returned to the wild.

MORPHOLOGY

The upper respiratory tract was examined in three adult specimens of *P. mucosus* from the private collection of the senior author. In one specimen the trachea and larynx were dissected. In the second specimen segments of the trachea were removed, dehydrated in an ethanol series, cleared in Hemo-De (Fisher), embedded in paraffin, and 10 μm sections were cut in both the parasagittal and transverse planes. The head of the third specimen was bisected sagittally, decalcified in Cal-Ex (Fisher), dehydrated in an ethanol series, cleared in Hemo-De (Fisher), embedded in paraffin, and 12 μm sections were cut in the parasagittal plane. Slides were stained with a modified form of Van Gieson's stain (Young *et al.*, 1995); Verhoff's elastin stain (Luna, 1968) was also used to test for elastin in the sections through the trachea.

RESULTS

DEFENSIVE BEHAVIOUR

Adult specimens of *Ptyas mucosus* are alert diurnal snakes which are quick to respond to provocation. When provoked *P. mucosus* adopts a defensive posture in which approximately the anterior fifth of the body is held horizontally several centimetres off the ground. The neck and anterior portion of the body expands ventrally and narrows in width, this expansion is most pronounced immediately behind the head (Fig. 1). These postural behaviours are normally accompanied by multiple open-mouth strikes. In between these defensive strikes, while the neck region is still expanded ventrally, *P. mucosus* produces a low raspy hiss which is best described as a growl. This defensive sound is produced during exhalation while the mouth is closed – little sound is produced during inhalation.

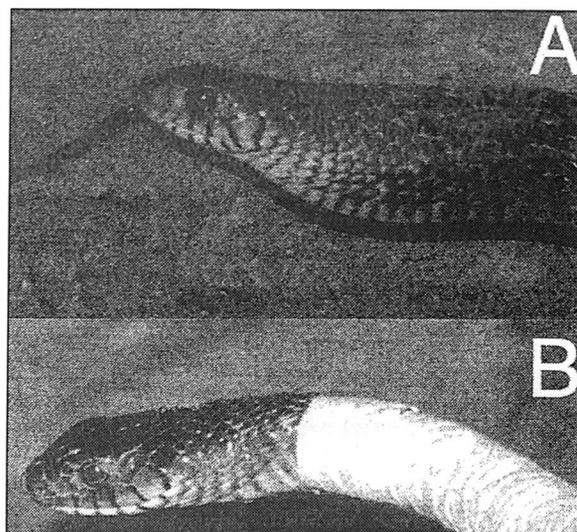


FIG. 1. Defensive posture of a 120 cm SVL specimen of *Ptyas mucosus*. Unbound state showing the ventral expansion of the throat region during growling (top); same specimen following binding of the anterior portion of the body with surgical tape (bottom).

MORPHOLOGY OF THE UPPER RESPIRATORY TRACT

The trachea of *P. mucosus* is located near the ventral surface of the body, displaced slightly to the left-hand side (Fig. 2A,C). The tracheal membrane, which connects the opposing tips of the cartilaginous rings, is expansive and extends to the right-hand side of the animal and then dorsally (Fig. 2B,C). Although this tracheal membrane is quite wide, it neither supports diverticula nor is it compressed into distinct pleats. The tracheal rings of *P. mucosus* show a gradation of cartilage types: the distal tips of the tracheal rings are hyaline cartilage; however, the majority of the tracheal ring is composed of elastic cartilage, as evidenced by differential reaction with Verhoff's elastin stain (Fig. 2D). The tracheal membrane supports a simple cuboidal epithelium and does not show any specializations for gas exchange. Between the basement membrane of the epithelium and the surrounding connective tissue, there is a distinct layer of longitudinally arranged smooth muscle fibres (Fig. 2E). The larynx of *P. mucosus* does not include any septa, partitions or diverticula.

The choana and nasopharyngeal duct of the specimens examined were large, owing to the large size of adults of this species; however, other than a constriction at the cranial end of the nasopharyngeal duct, they show no anatomical specializations. The cavum nasi proprium is also large, particularly the choanal tube. The concha is distinct, as is the expansive dorsolateral choanal zone. The choanal tube opens into the dorsomedial portion of the nasal vestibulum, which lacks any distinctive anatomical specializations. The external nares do not support an occluding flap or sphinctered valve.

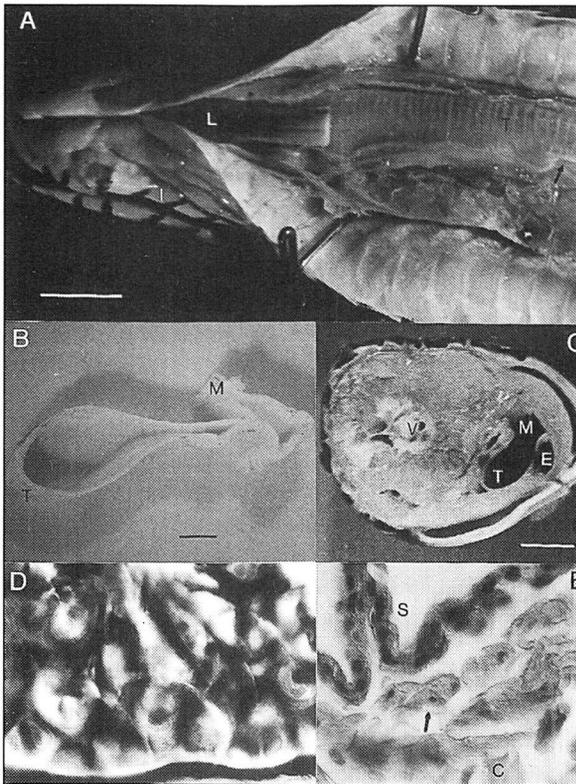


FIG. 2. Morphology of the trachea of *Ptyas mucosus*. A - ventral view of the throat region following removal of the oesophagus and caudal portion of the tongue: note the lateral displacement of the larynx and the dorsolateral position of the tracheal membrane (arrow) (scale bar = 1 cm); B - transverse section of the excised trachea showing the relative expansion of the tracheal membrane (scale bar = 1 mm); C - cranial view of a transverse section through the throat region showing the position of the trachea and the expansion of the tracheal membrane (scale bar = 5 mm); D - transverse section through the tracheal cartilage stained with Verhoff's elastin stain: note the dark basement membrane and the black elastic fibers among the chondrocytes (scale bar = 0.1 mm); E - transverse section through the tracheal membrane stained with a modified Van Gieson's stain: note the presence of smooth muscle fibres (arrow) between the luminal epithelium and the surrounding connective tissue (scale bar = 0.1 mm). Abbreviations: C - loose irregular connective tissue; E - oesophagus; I - infralabial scale; L - tongue; M - tracheal membrane; S - luminal epithelium of the tracheal membrane; T - tracheal rings; V - vertebra.

ACOUSTICS OF THE DEFENSIVE HISS

When initially approached all eight specimens produced a deep growling sound. This growl had a mean duration of 1.98 sec (SD = 0.53, range = 1.10-2.90, $n = 8$) and a mean amplitude of 53.9 dB SPL (SD = 2.67, range = 50.2-57.0, $n = 8$). Acoustic analyses (Fig. 3) revealed the growls to have a mean dominant frequency of 1019 Hz (SD = 250, range = 722-1619, $n = 8$), a mean maximum frequency of 6370 Hz (SD = 180, range = 6103-6803, $n = 8$), and a mean minimum frequency of 414 Hz (SD = 62, range = 262-546, $n = 8$). The growling sound showed neither temporal patterning, regular amplitude modulation, frequency modulation, nor distinct harmonics (Fig. 3).

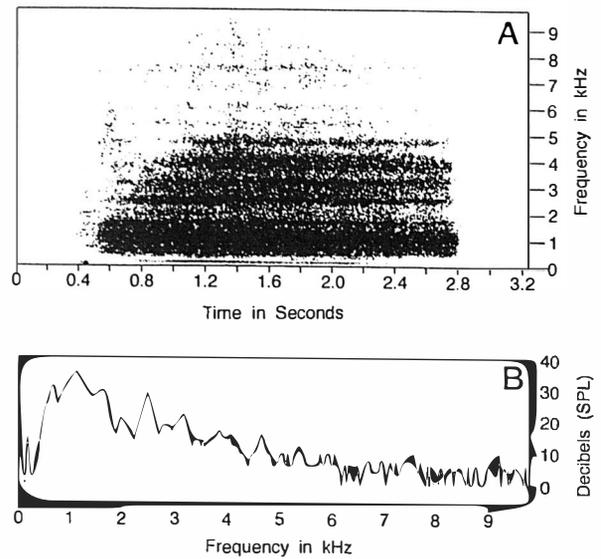


FIG. 3. Acoustic analysis of the "growl" of *Ptyas mucosus*. A - sonogram of a 2.3 sec growl: note the absence of frequency or amplitude modulation; B - power spectral analysis (FFT of 2048 points) of the same growl: note the dominance of low frequency sounds and the absence of any prominent harmonics.

Wrapping the neck and anterior portion of the body in surgical tape prevented the snake from ventrally expanding its throat region (Fig. 1). However, the specimens still produced defensive sounds. Qualitatively, these sounds were quite distinct from the growl of the unbound snake in lacking the low frequency rumbling quality of the growl, and may be more properly referred to as a hiss. The hisses recorded had a mean duration of 1.78 sec (SD = 0.5, range 1.17-3.11, $n = 8$).

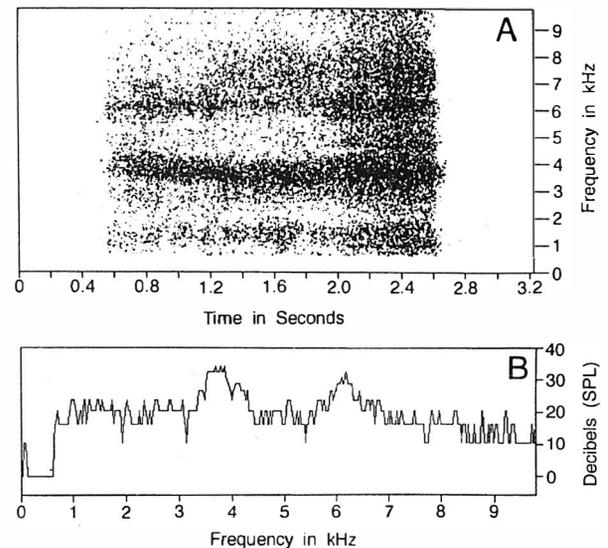


FIG. 4. Acoustic analysis of the hiss of *Ptyas mucosus*; these sounds were recorded after binding surgical tape around the anterior portion of the body of the same specimen analysed for Fig. 3. A - sonogram of a 2.0 sec hiss; note the absence of frequency or amplitude modulation and the shift to higher frequency when compared to the growl (Fig. 3); B - power spectral analysis (FFT or 2048 points) of the same hiss: note the shift in dominant frequency following the binding of the throat region.

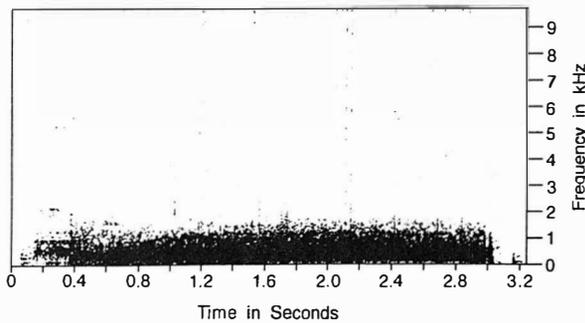


FIG. 5. Sonogram of the growl produced by a nine foot king cobra (*Ophiophagus hannah*) recorded and analysed in the same fashion as described for *P. mucosus*: note the lower frequency of the growling sound of *O. hannah* compared to *P. mucosus*.

= 8) and a mean amplitude of 53.9 dB SPL (SD = 2.67, range 50.2–57.0, $n = 8$). Sonogram and spectral analyses (Fig. 4) show that the hiss has a dominant frequency of 2,322 Hz (SD = 1037, range 897–3675, $n = 8$) a maximum frequency of 6500 Hz (SD = 371, range = 5775–7568, $n = 8$) and a minimum frequency of 566 Hz (SD = 169, range = 306–875, $n = 8$). The hiss of *P. mucosus* is an acoustically simple sound lacking modulation, harmonics, or temporal patterning (Fig. 4). Plugging the external nares eliminated defensive sound production and appeared to impede the overall activity pattern of the snake.

Statistical analysis revealed no significant regression between body size and the quantified features of the defensive sounds. Student's *t*-test revealed significant differences between the growls and the hisses in both the dominant ($t = 5.36$, $df = 17$, $P = 0.0001$) and minimum ($t = 3.47$, $df = 17$, $P = 0.0029$) frequencies. The duration, amplitude, and maximum frequency of the hiss of *P. mucosus* were not significantly different (using Student's *t*-test with a $P = 0.05$ level) from the corresponding features of the growl.

DISCUSSION

Any claim of mimicry or close resemblance between *Ptyas mucosus* and *Ophiophagus hannah* must be placed in a very restricted context. While these are both large, thick-bodied species, there are several distinctive features including the prominent occipital shields of *O. hannah*. While the general body features of *P. mucosus* are distinct from those of *O. hannah*, it is the defensive repertoire that is frequently cited as being similar (e.g. Flower, 1899; Soderberg, 1973; Whitaker, 1978; Murthy, 1986; Greene, 1997). A brief inventory of defensive behaviour makes the distinction between these two species clear: (1) body posture—*P. mucosus* holds the anterior portion of its body horizontally; *O. hannah* holds the anterior portion of its body vertically: (2) throat expansion—*P. mucosus* expands the throat region ventrally causing a mediolateral compression; *O. hannah* expands the throat region laterally into a small hood causing dorsoventral compression: (3) strike—*P.*

mucosus is quick to strike (even while the harasser is well out of range, most strikes are performed with the mouth open, and multiple strikes are common); *O. hannah* is more inclined to maintain a postural stance, (most strikes are performed with the mouth closed, and multiple strikes are not as common); and (4) sound production—both species produce a low rumbling growl.

The growl produced by *P. mucosus* is acoustically similar to that of *O. hannah* (compare Figs. 3 and 5). The growl produced by *O. hannah* is of a lower frequency range (Young, 1991), but the frequency ranges of the two sounds overlap extensively. The growl of *O. hannah* is produced by a series of connective tissue diverticula which extend off the tracheal membrane and are continuous with the lumen of the trachea; airflow through the trachea produces resonance within these tracheal diverticula which results in the growling sound (Young, 1991, 1992). *Ptyas mucosus*, although lacking these tracheal diverticula (Fig. 2), is capable of producing a similar growling sound which differs acoustically from most exhalatory sounds made by snakes (Young, 1991, 1997; Young, Sheft & Yost, 1995; Young & Lalor, 1998).

The nasal passageway of *P. mucosus* has a large diameter, presumably reflecting the large head and body size of this species. Other ophidians with large heads (e.g. *Bitis arietans*) produce higher frequency exhalatory sounds (Young *pers. obs.*), as do even larger monitor lizards (Young, *et al.*, 1998). Although the larynges of some ophidian species have anatomical specializations associated with sound production (Young *et al.*, 1995), no such features were observed in the larynx of *P. mucosus* (Young, 1998). When standing close to a growling *O. hannah*, it is easy to localize the growling sound as emanating from the throat, not the head; similarly, the growl of *P. mucosus* appears to emanate from the throat region. For these reasons, we concentrated our manipulations on the throat region of *P. mucosus*.

The amplitude and duration of the hisses produced by *P. mucosus* when the anterior portion of its body was wrapped with surgical tape were not significantly different from the amplitude and duration of the growls produced by the snake in its natural state. This similarity of amplitude and duration indicates that the surgical tape did not interfere with the exhalatory airflow. The significant differences in the acoustic properties of the hiss and the growl (Figs. 3 and 4), coupled with no significant differences in the amplitude and duration of these sounds, support our contention that the nasal passageway and larynx do not play a key role in producing the growl (since they were unaffected by the surgical tape) and further indicate that the growl is dependent on changes in the state of the trachea associated with the ventral expansion of the throat.

The structure and position of the trachea are such that at rest, both the tracheal lumen and the space de-

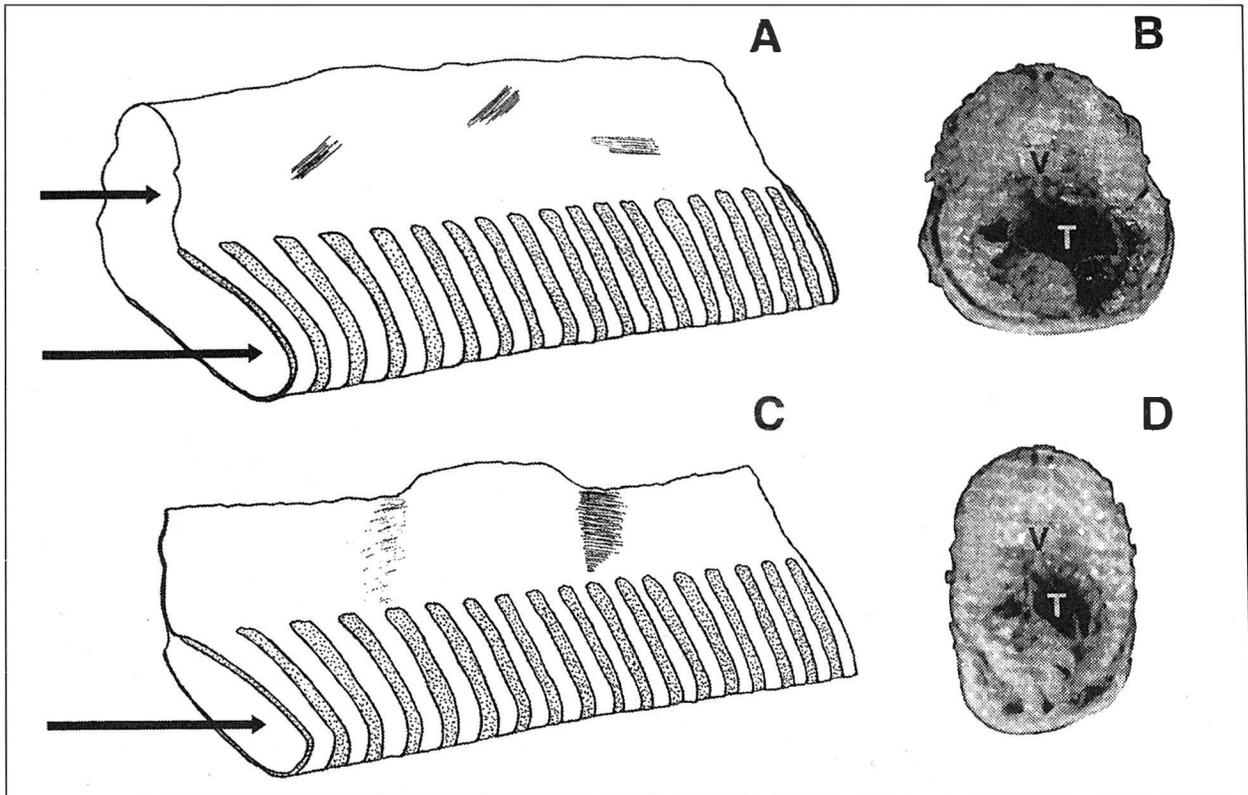


FIG. 6. Illustration of the hypothesized morphological basis of growling in *Ptyas mucosus*. A - illustration of a patent trachea and tracheal membrane allowing for complete airflow; B - transverse section near the middle of the throat showing the patent trachea and membrane; C - illustration of the trachea upon compression of the throat region showing distortion of the tracheal rings, collapse of the tracheal membrane, and localized expanded regions in the tracheal membrane; D - same transverse section used in B but with pressure applied to the lateral surfaces to produce compression and ventral expansion, note the alteration in the size and shape of the tracheal lumen. Abbreviations: T - tracheal lumen, V - vertebra.

finned by the expanded tracheal membrane should be patent (Fig. 6). Mediolateral compression of the throat region results in two changes in the trachea: the tracheal cartilages flex slightly (which brings the opposing tips of the trachea together), and the expanded tracheal membrane is collapsed down by the body wall (Fig. 6). We hypothesize that this collapse of the tracheal membrane is incomplete, particularly in the neck region, and that isolated portions of the tracheal membrane remain patent. Localized expansions of the tracheal membrane may be promoted by contraction of the longitudinal smooth muscle in the tracheal membrane. These isolated patent segments of the tracheal membrane would then function like tracheal diverticula, producing the resonant growling sound (Fig. 6). When the snake calmed down and the mediolateral compression stopped, the elastin in the cartilage would enable the trachea to return to its original state, the spreading of the opposing tips of the tracheal rings serving to expand the tracheal membrane.

There is considerable morphological variation in the structure of the tracheal membrane in ophidians, including narrow membranes, expanded membranes, diverticulae, and tracheal lungs (see Young, 1992; Wallach, 1998). The acoustic role of many of these morphological features has been explored (Young,

1997), and the tracheal membrane may also play a role in some postural displays by allowing the snake to expand its throat region (Noble, 1921; Young, 1992). If our hypothesis for sound production in *P. mucosus* is correct, it would represent the first example of a dynamic shape change in the trachea associated with sound production, and a strong example of a functional interrelationship between postural display and sound production (see Kinney, Young & Abishahin, 1998).

At the very least, our analyses document the acoustic similarities between the growls produced by *P. mucosus* and *O. hannah*. Since these sounds are only produced during defensive displays, these animals have considerable overlap in geographic range and habitat preference, and *O. hannah* has a highly toxic venom, this defensive growl would appear to be an example of acoustic Batesian mimicry.

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REFERENCES

- Carpenter, C. C. & Ferguson, G. (1977). Variation and evolution of stereotyped behavior in reptiles. In *Biology of the Reptilia*, Vol 7, pp. 335-554. Gans, C. and D. Tinkle (Eds.). New York: Academic Press.
- De Rooij, N. (1917). *The reptiles of the Indo-Australian archipelago*. II. Ophidia. E.J. Brill, Leiden (reprinted 1970 by A. Asher, Vaals).
- Flower, S. S. (1899). Notes on a second collection of reptiles made in the Malay peninsula and Siam, from November 1896 to September 1898, with a list of the species recorded from those countries. *Proc. Zool. Soc. London* **1899**, 600-696.
- Gans, C. (1961). Mimicry in procryptically colored snakes of the genus *Dasypeltis*. *Evolution* **15**, 72-91.
- Greene, H. W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia*, Vol. 16, pp. 1-152. Gans, C. and Huey, R. (Eds.). New York: Alan R. Liss, Inc.
- Greene, H. W. (1997). *Snakes: The evolution of mystery in nature*. Berkeley: University of California Press.
- Kinney, C., Young, B. A. & Abishahin, G. (1998). Hissing in rattlesnakes: Redundant signaling or inflationary epiphenomenon? *J. Exp. Zool.* **280**, 107-113.
- Luna, L. (ed.) (1968). *Manual of the histological staining methods of the armed forces institute for pathology*. New York: McGraw-Hill.
- Minton, S. A. (1966). A contribution to the herpetology of West Pakistan. *Bull. Amer. Mus. Nat. Hist.* **134**, 1-184.
- Murthy, T. S. N. (1986). *The snake book of India*. Dehra Dun: R. P. Singh Gahlot.
- Noble, G. K. (1921). Snakes that inflate. *Nat. Hist.* **21**, 167-171.
- Pough, F. H. (1988). Mimicry and related phenomena. In *Biology of the Reptilia*. Vol. 16, pp. 153 - 234. Gans, C. and R. Huey (Eds.). New York: Alan R. Liss, Inc.
- Roze, J. A. (1996). *Coral snakes of the Americas: Biology, identification, and venoms*. Florida: Krieger Publishing.
- Smith, M. A. (1943). *The fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region*. Vol. 3, Serpentes. London: Taylor and Francis.
- Soderberg, P. (1973). On eleven Asian elapid snakes with specific reference to their occurrence in Thailand. *Nat. Hist. Bull. Siam Soc.* **24**, 203-217.
- Wall, F. (1921). *Ophidia Taprobanica or the snakes of Ceylon*. Colombo: H. R. Cottle.
- Wallach, V. (1998). The lungs of snakes. In *Biology of the reptilia*, Vol. 19, pp. 93-295. Gans, C. and A.S. Gaunt (eds.) Ohio: SSAR.
- Whitaker, R. (1978). *Common Indian snakes: A field guide*. New Delhi: MacMillan Comp. of India.
- Young, B. A. (1991). The morphological basis of "growling" in the King Cobra (*Ophiophagus hannah*). *J. Exp. Zool.* **260**, 275-287.
- Young, B. A. (1992). Tracheal diverticula in snakes: possible functions and evolution. *J. Zool., Lond.* **227**, 567-583.
- Young, B. A. (1997). A review of sound production and hearing in snakes, with a discussion of intraspecific acoustic communication in snakes. *J. Penn. Acad. Sci.* **71**, 39-46.
- Young, B. A. (1998). The comparative morphology of the ophidian larynx. ms sub. to *Acta Anat.*
- Young, B. A. & J. Lalor (1998). Sound production in the eastern hognose snake, *Heterodon platyrhinos* (Serpentes: Colubridae): Does it snore? *Amphibia-Reptilia* **19**, 407-418.
- Young, B. A., Sheft, S. & Yost, W. (1995). Sound production in *Pituophis melanoleucus* (Serpentes: Colubridae) with the first description of a vocal cord in snakes. *J. Exp. Zool.* **273**, 472-481.
- Young, B. A., Abishahin, G., Bruther, M., Kinney, C. & Sgroi, J. (1998). Acoustic analysis of the defensive sounds of *Varanus salvator* with notes on sound production in other varanid species. *Hamadryad* **23**, 1-14.

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