

AIR FLOW IN REPTILIAN VENTILATION

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Abstract—Ventilatory air flow was measured at the nostrils of unrestrained representatives of all major surviving groups of reptiles.

1. Flow is always biphasic (out-in-pause) in resting, undisturbed reptiles.
2. Rib movements do not necessarily reflect flow.
3. Flow may become triphasic (out-in-out-pause) in excited animals.
4. Previous reports of triphasic flow during reptilian ventilation probably reflect misinterpretation of strain gauge records, use of excited animals, and utilization of closed manometric (Kopfkappe) systems (known to induce artifacts).

INTRODUCTION

An extensive series of papers (Mitchell & Morehouse, 1863; Heinemann, 1877; Dubjuga, 1882; Charbonnel-Salle, 1883; Siefert, 1896; Couvreur, 1898; François-Frank, 1909; Babak, 1914; Willem & Bertrand, 1936; Randall *et al.*, 1944; Servaty & Peyraud, 1960; Templeton & Dawson, 1963; Templeton, 1964; Bennett, 1973; Rosenberg, 1973; Gatz *et al.*, 1975; Jammes & Grimaud, 1976) has supported the idea that reptiles ventilate their lungs triphasically by an outflow-inflow-partial outflow pattern (between the variably prolonged apneustic intervals). On the other hand, there have also been many reports (Mitchell & Morehouse, 1863; Bert, 1869; Rouch, 1886; Kahn, 1902; Vos, 1936; Boelaert, 1941; McCutcheon, 1943; Gans & Hughes, 1967; Gaunt & Gans, 1969; Naifeh *et al.*, 1970; Hughes, 1973, 1974; Tenney *et al.*, 1974; Gans & Clark, 1976; Wood *et al.*, 1977) supporting the concept that ventilation proceeds biphasically, with an outflow followed by an inflow. The vast majority of such studies used indirect indicators of flow, deriving their conclusions from pressures, pulmonary or thoracic volume, movements of the thorax, impedance of the body, electromyography, and similar measures.

A series of recent studies combining electromyography and pressure recording (Gans & Hughes, 1967; Gaunt & Gans, 1969; Jongh & Gans, 1969; Gans & Clark, 1976) led to a theoretical review (Gans, 1971) suggesting that (a) the amount of work carried out in pulmonary ventilation is presumably significant to the animal, and (b) ventilation ordinarily consists of outflow followed by inflow and is hence strictly biphasic. Stimulated by this apparent conflict in the literature, we obtained a miniature flowmeter and started to measure tidal airflow directly. A first paper (Clark *et al.*, 1978) documents that flow is biphasic in snakes. We report here on direct measurements of airflow patterns in members of all other orders of currently surviving reptiles.

MATERIALS AND METHODS

Experiments were run at various temperatures, mainly between 24 and 25°C, on the animals given in Table 1,

Table 1. Species used in this study

No. of specimens	Species	Mass	Parameters monitored*
2	<i>Sphenodon punctatus</i>	720 g	F
1	<i>Boa constrictor</i>	6.0 kg	F, Pr, Th
2	<i>Python regius</i>	1.0 kg	F, Pr, Th
1	<i>Thamnophis sirtalis</i>	37 g	F
1	<i>Amphisbaena alba</i>	120 g	F
2	<i>Cordylus</i> sp.	16 g	F
1	<i>Varanus nebulosus</i>	1.1 kg	F, Th
1	<i>Crotaphytus collaris</i>	37 g	F
2	<i>Sauromalus obesus</i>	160 + 180 g	F, Th
1	<i>Chrysemys scripta</i>	230 g	F
1	<i>Caiman crocodilus</i>	2.0 kg	F

* F = air flow at nostril.
Th = diameter of thorax.
Pr = intratracheal pressure.

which also indicates supplementary manipulations carried out on each individual. In some animals the trachea was intubated with curved non-occlusive catheters, inserted through the tracheal wall as described by Gans & Clark (1976).

The sensing elements—paired Fenwall GC32L8 bead thermistors—of a bidirectional flowmeter (Hill & Givens, 1969) were placed in a tube, the end of which could be positioned over the reptile's nostril by means of individually shaped extensions of polyethylene tubing. This configuration was necessary because the unshielded unit is so sensitive that its response to convection currents would otherwise produce a very high noise level. The thermistors are coupled to yield positive and negative deflections from a baseline value, in this case reflecting exhalation and inhalation via the nostrils, respectively. The time-constant of the flowmeter is approximately 0.2 sec (undriven decay from 71 to 26% of full scale deflection).

Small pieces of velcro plastic were glued onto the skin of the head or back of the animals and matching pieces on the body of the flowmeter. The flowmeter and its extension tubing and cable (with matching pieces of velcro) could then be positioned to cause minimal restriction of the activity of the animal. A mercury strain gauge around the trunk indicated body wall movements. These were monitored in parallel with airflow and occasionally with fluctuations of pressure in the trachea. All leads were long

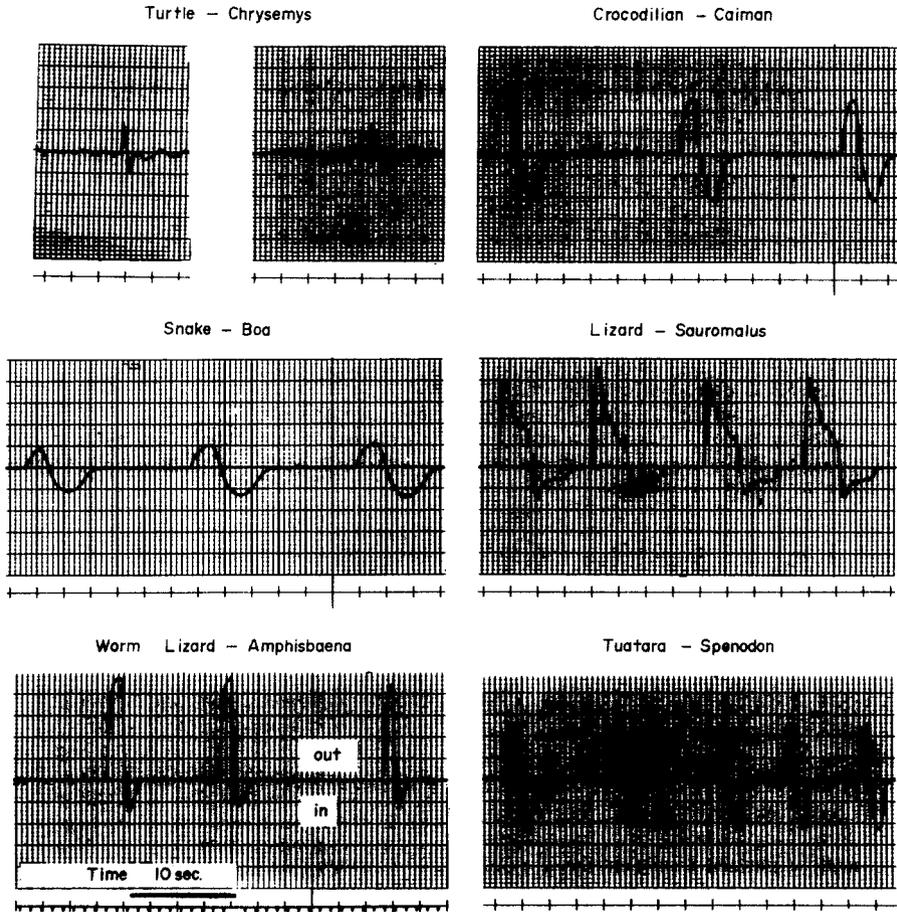


Fig. 1. Records of airflow from the nostrils of resting, undisturbed representatives of the six major groups of surviving reptiles. Airflow is biphasic in every case, although in *Chrysemys* pulmonary ventilation is interspersed between periods of buccal flushing.

enough to permit free movement of the animals within an enclosure.

RESULTS

The results are clear and unequivocal. Figures 1-3 show samples of the flow patterns observed. The flow trace always shows an exhalation followed by an inhalation unless the animals are excited, in which case a minor tertiary exhalation is occasionally observed. Movements of the polyethylene sampling tube occasionally produced asymmetry of the inflow and outflow curves, apparently reflecting differential leakage, as the tube generally did not occlude the nasal aperture. Other reasons for asymmetry of responses to inflow and outflow streams are (a) slight shifts of the position of the paired thermistors in the airstream, (b) variable saturation of the gases with moisture, and (c) the tendency for outflow to be exaggerated because its jet is directed toward the sampling tube. (The latter effect is important as it emphasizes that terminal outflow—the so-called E_2 phase—would have been recognized if it had indeed occurred.)

The flow readings also correlate excellently with records of intratracheal pressure. There is certainly

no indication that the flowmeter readings reflect anything but mechanical events.

The readings obtained from strain gauges reflect rib movements, but are also affected by other factors such as position of the gauge, the way the trunk of the animal is curved, and the depth of ventilation. Figure 2, recorded from a small monitor lizard, illustrates that airflow is not necessarily correlated with rib movement. While airflow is biphasic (out-in), the ribs often move triphasically (in-out-in). Figure 3 illustrates the effect of excitement on the ventilatory pattern, indicating a shift of the strain gauge output at rest (due to inflation of the trunk), a marked increase in the tidal volume, and a slightly secondary exhalation after the inhalation.

DISCUSSION

The results here reported support the earlier observations that resting reptiles normally use biphasic ventilation. It appears that some of the earliest reports, suggesting that ventilation is triphasic, reflect the nature of the recording apparatus. However, incidental observations during our investigations indicate that more recent authors might consider ventilation

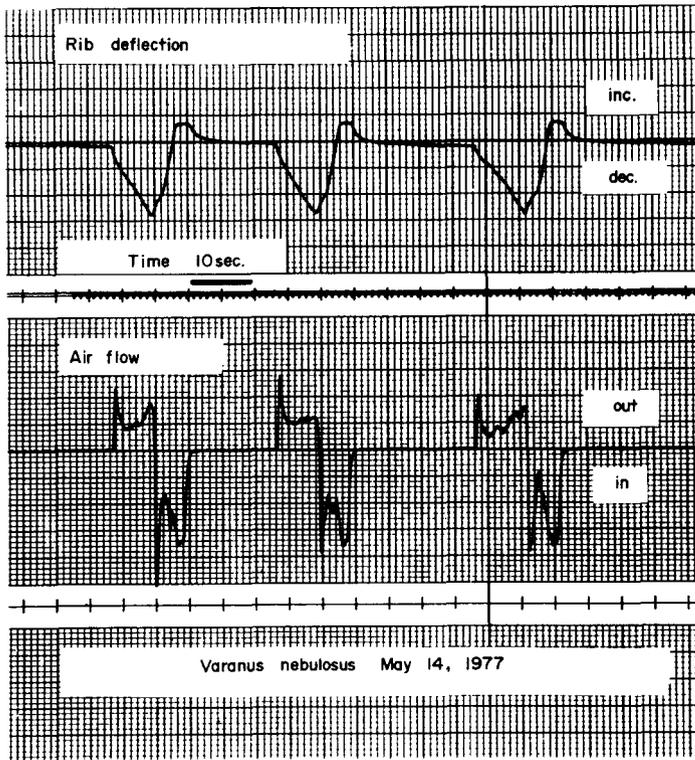


Fig. 2. Simultaneous records of airflow and thoracic diameter in a resting monitor lizard. Airflow is biphasic while movements are triphasic.

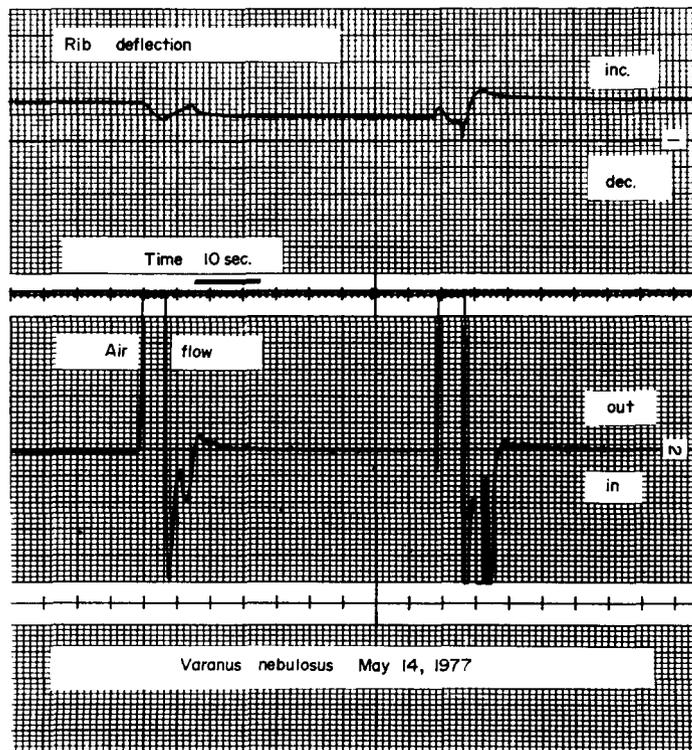


Fig. 3. Same animal (and amplifier settings) as in Fig. 2. Here the experimenter entered the room, exciting the animal and inducing it to inflate (note change in baseline of the rib deflection curve). The magnitude of tidal flow increased and a slight secondary exhalation is apparent. The diminished rib oscillations reflect a slight shift in the posture of the lizard.

to be triphasic for three distinct reasons. These are (1) that they derived flow patterns from a limited number of indirect measurements of pressure or body movement, (2) that they used closed manometric techniques to monitor breathing, and (3) that the animals were physically restrained or hyperexcited for other reasons.

(1) The amount of gas passing via the nostrils presumably reflects shifts in the arrangement of the thoracic elements (and consequently of the impedance across them), changes of thoracic diameter, and the differences between intrapulmonary and ambient pressures. However, flow is modified by the condition of the glottal (and possibly of the narial) valves. A change in pulmonary pressure or impedance, or in thoracic diameter would only correspond to airflow if the glottis and nares were open (Fig. 2); partial restriction of these valves would have graded effects on the flow rate. Consequently the output of plethysmographs (Randall *et al.*, 1944; Bennett, 1973; Rosenberg, 1973), records of intrapulmonary pressure (Charbonnel-Salle, 1883; Templeton, 1964), or of body wall excursions (Bert, 1869; Babak, 1914; Templeton & Dawson, 1963) cannot immediately be used to predict flow, unless the configuration of the glottis is monitored simultaneously (as effected by Gans & Clark, 1976).

The position of the lungs within the visceral cavity becomes important in this connection. Displacement of the postero-ventral aspect of the lung involves displacement of the remainder of the visceral tissues, which are elastic, non-homogeneous, and only loosely restrained with respect to each other. Consequently, they do not move as a uniform piston, but show relative displacements both during and after ventilatory muscular activity.

(2) Clark *et al.* (1978) have shown that the application of an externally imposed back-pressure may, in snakes, produce major intrapulmonary pressure fluctuations and indirectly modify the periods of glottal closure. This explains results such as those of Rosenberg (1973) in which a closed *Kopfkappe* with inadequate volume led to triphasic flow recordings, presumably because of delayed glottal closure. It also raises some questions as to the mechanisms by which the closure of the glottis is monitored. It appears that in the caiman (Gans & Clark, 1976) opening is initiated via a burst of activity of the *M. dilator* and is maintained by its low level activity, while closing involves a sharp burst of activity in the glottal constrictors, with closure apparently maintained by the intrinsic elasticity of the glottal cartilages, possibly coupled with adhesion of the glottal lips. It seems likely that stretch receptors within the lung (Gatz *et al.*, 1975; Milsom & Jones, 1976; Fedde *et al.*, 1977; Scheid *et al.*, 1977) provide sensory feedback to the glottis, so that artificially high back-pressures might prove to be the proximate cause of abnormal glottal activity.

(3). Turtles and caimans, implanted with chronic EMG electrodes and left undisturbed for days, often breathe very shallowly and slowly, seemingly with minimal muscular activity. If they are disturbed, and particularly if they have been handled (and in some cases when food is offered), they breathe much more deeply, and the pressure levels, particularly of exhalation,

rise markedly (Fig. 3). Whenever the ventilation cycles of animals run into each other there may be a tendency for the glottis to remain open beyond the inhalatory period. As most reptiles appear to let their viscera droop when resting and consequently maintain a positive pulmonary pressure during apneusis, any delay in closure will induce a secondary exhalation. Forced distension of the buccal cavity may cause such an effect (Mitchell & Morehouse, 1863) and already Bert (1869) (also François-Frank, 1909) had observed that the glottis sometimes remains open in excited animals.

The time required for airflow may have further advantages to the animal. As the rate of ventilation is increased, forcible displacement of ribs and viscera may have to be maintained until, or slightly beyond the instant that the glottis closes. When animals snorkel while swimming, the duration of ventilation is affected by the depth of water over the trunk, and presumably also by the excitatory state of the animal. Reptiles that are diving generally shift from a breathing sequence in which each ventilation is interrupted by a prolonged apneusis to one in which there is a short series of two or more ventilatory cycles before the next apneustic period (and dive). Presumably such animals flush out the respiratory dead-space and thus facilitate an increased length of apneusis and a more prolonged dive. There may be some selective advantage to breathing more rapidly in order to reduce the length of time that the animal remains exposed at the surface.

The importance of the apneustic period as an integral portion of the reptilian ventilatory rhythm must be stressed. Presumably it is not equivalent to the exceptional event described as apneusis in mammals (Sears, 1977), and discussions whether apneusis occurs during the inhalatory or the exhalatory phase of reptilian ventilation probably lack meaning. Gas is continuously exchanged from the pulmonary contents throughout the apneustic period (Lenfant *et al.*, 1970). This suggests that exhalation of this low O_2 -high CO_2 gas must logically proceed before fresh air is aspirated. The relative length of the apneustic and ventilatory periods will reflect the metabolic rate, the ratio of tidal volume to ventilatory dead space, and such ecological factors as the cost a diving animal incurs for each trip to the surface. The latter is presumably reflected in the series of multiple breaths between apneustic periods seen in diving reptiles.

The external gas exchanger also serves secondary functions in permitting distension of the body and hissing as part of a threat display (Gans & Maderson, 1973; Martin & Huey, 1971). For instance, disturbed or excited crocodylians will engage in repeated inhalation-exhalation cycles and some species of crocodylians will even inhale air through the nostrils and exhale by forcing it through the posterior pharyngeal fold (Garrick & Lang, 1977). Similar excitatory conditions may be reflected in the reports that turtles such as *Emys orbicularis* (Lüdicke, 1936) and *Sauromalus* (Salt, 1943; Templeton, 1964) tend to inflate their body by buccal pumping rather than by aspiration. Until such systems are analysed with a combined approach based on experiments involving simultaneous pressure records, electromyograms and flow measurements, discussion seems futile.

As far as can be determined, all reports of triphasic ventilation involve one of the three experimental variants here described. Consequently, it appears that reptiles ordinarily ventilate with a purely biphasic flow pattern, departing from this only when they are highly excited or when utilizing airflow for the production of warning signals or in social communication.

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