

STUDIES ON VENTILATION OF *CAIMAN CROCODILUS* (CROCODILIA: REPTILIA)¹

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Abstract. The ventilatory mechanics of freely moving *Caiman crocodilus* were studied by cinefluorescopy and electromyography. The buccal oscillations serve only to flush the internal nares in olfaction. Ventilations are coincident with abdominal oscillations. The larynx ordinarily lies adpressed to the internal nares so that the posterior buccal chamber is excluded from the path of air flow during ventilation and does not contribute to respiratory dead space.

The pulmonary pressures may be variably polyphasic and the tracheal flows diphasic. Exhalation involves an anterior shift of the liver by action of the transverse abdominal muscles, while inhalation proceeds due to contraction of the diaphragmatic muscle pulling the liver caudad. The various costal muscles facilitate air flow by shifting the position of the ribs. They also play a role in fixation of the flexible rib cage so that it resists the aspirating and compressing actions of the hepatic piston.

The pattern of muscular activity shifts as the trunk is immersed; expiration becomes passive and inspiration requires increased muscular effort. The ribs, instead of changing position with each breath are comparatively fixed by the costal muscles, while changes in the volume of the pleural cavity are caused almost exclusively by movements of the hepatic piston.

Breathing pattern	Olfaction
Buccal oscillations	Rib movements
Electromyography	Ventilation
Mechanics of breathing	

The advent of simplified electromyographical techniques now permits the characterization of the mechanics of breathing in lower vertebrates. A series of studies dealing with various fishes (Ballintijn and Hughes, 1965; Ballintijn, 1969a,b; Hughes and Ballintijn, 1965; Osse, 1969; McMahon, 1969), frogs (de Jongh and Gans, 1969; Martin and Gans, 1972; West and Jones, 1975), turtles (Gans and Hughes, 1967; Gaunt and Gans, 1969b; Ireland and Gans, 1973), lizards (Hadden, 1975) and snakes

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(Rosenberg, 1973) have provided a general pattern and, as a byproduct, allowed us to modify our view of the evolution of air breathing mechanics (Gans, 1971a,b).

The senior author had carried out some pilot studies on crocodylian respiration in collaboration with A.S. Gaunt (*cf.* Gaunt and Gans, 1969a). However, their publication was delayed until after the start of the cycle of papers by Naifeh *et al.* (1970a,b, 1971a,b,c) which contain reviews of earlier literature on crocodylian ventilation. Analysis of the results obtained by these authors (which were of course ultimately aiming at different questions) pointed to certain fundamental differences from our earlier conclusions; hence, we carried out and here report on a second set of experiments. All of these experiments attempt to record from unrestrained animals under near normal circumstances, with the signals transmitted by loose leads and the animals left alone as much as possible. Where our experiments confirm the results of the earlier authors, we only note this without a further detailed report.

Methods

The experiments in the present series were carried out at approximately 23–25 °C on ten *Caiman crocodilus* (weight 400 g to 7.5 kg), out of a series of 20 used for studies of temperature control and digestive processes. Many observations made on instrumented animals could be confirmed by observing external indications of respiratory movements on members of the remainder of the population.

The animals to be instrumented were anesthetized by cooling, rarely by halothane or flaxedil therapy (Loveridge and Blake, 1972). Intratracheal pressures were monitored by means of a small (90–260 gauge), bent polyethylene tube pointing posteriorly down the trachea. The end of the tube was closed and its side opened, 'ventrally' relative to the animal. The tube was fitted to each animal, brought out through the skin, attached by sutures and adhesives to the side of the animal and capped between experiments. Statham PM 5 pressure gauges with delay times of 0.06 msec were used as transducers. Electrodes (0.003 inch silver wire, Teflon or enamel coated, variant of Basnajian and Stecko, 1962), were implanted surgically, brought through the skin adjacent to the suture, and also glued to the skin. (These non-traumatizing electrodes provide good differentiation of muscle fiber groupings; the insect pins used by Naifeh *et al.* [1970b: 341] may disturb the animal and easily pick up signals from two or more separate muscles.) A series of wires was, in each case, collected into soft polyethylene tubing leading to the preamplifiers. Up to eight muscles were monitored simultaneously. The EMG signals were passed through Grass P-15 AC, or Tectronix 122 and 26A2 preamplifiers and then stored with other records on a Honeywell 5600 intermediate band-pass tape system before being displayed on an oscilloscope and Brush 481 recorder.

Mechanical movements were recorded by fixing short mercury strain gauges across the flanks and around the buccal cavity. Other mechanical events were monitored continuously by simultaneous display of the output of pressure gauges, as well as

of the EMG preamplifiers on one half of a closed circuit television image with a view of the animal recorded on the other half. This remote control operation permitted us to avoid withdrawal bradycardia (Gaunt and Gans, 1969a), and to run long-term (24+ hours) experiments in a closed room with all manipulation proceeding by remote control from the outside.

In order to correlate pulmonary pressures with movement, the glottis and floor and roof of the pharyngeal chamber of two animals were painted with barium contrast medium and filmed at The University of Michigan cinefluoroscopy unit, utilizing a five-inch image intensifier. A few analyses of the gas composition in the posterior pharynx were taken earlier (1967) by means of the respiratory mass spectrometer of the Department of Physiology, State University of New York at Buffalo.

Results

STRUCTURE

Among Recent reptiles, crocodylians (*cf.* Chiasson, 1962, for general morphology) are unique in having a most elongate secondary palate (Iordanski, 1973). Two separate channels run from the valvular nostrils (Bellairs and Shute, 1953), located on the dorsal tip of the snout, past the olfactory chamber (Parsons, 1971) to the internal nares that open on the roof of the posterior pharynx. This pharyngeal chamber is separated from the buccal space proper by a double flap. The glottis is positioned on the large hyoid plate, immediately ventral to the internal nares. From here the trachea passes posteriorly, connecting via the bronchi to the extensive lungs within the rib cage. The narial diameter is relatively small, though the length of the internal tube is considerable. The pharyngeal chamber has a volume of an order of magnitude equivalent to the resting tidal volume.

A variety of studies (see citations in Naifeh *et al.*, 1970a, b; Gans, 1971a) document that in *Caiman* air flow is driven by three major groups of muscles: (1) various costal groupings that may increase and decrease the volume of the pleural cavity by adjusting the positions of the ribs; (2) various abdominal muscles that can (a) change the volume of that portion of the visceral cavity posterior to the liver and (b) force the liver anteriorly, thus reducing the volume of the thoracic cavity, which includes the lungs in their pleural cavity; (3) the so-called diaphragmatic muscles that (a) attach the liver to the ilia and epipubic elements of the pelvic girdle and (b) are capable of pulling the liver posteriorly, thus expanding the volume of the pleural space.

These various elements are illustrated in fig. 1, based on an animal weighing more than 4 kg. The sketches include the major costal muscles, suggesting their complex overlap and change of fiber direction along each intercostal space. The ribs are tripartite and their vertebrocostal, intercostal and sternocostal portions (Hoffstetter and Gasc, 1969) are movably articulated; the latter two portions are mainly cartilaginous in hatchlings, but later calcify (*cf.* Rathke, 1866).

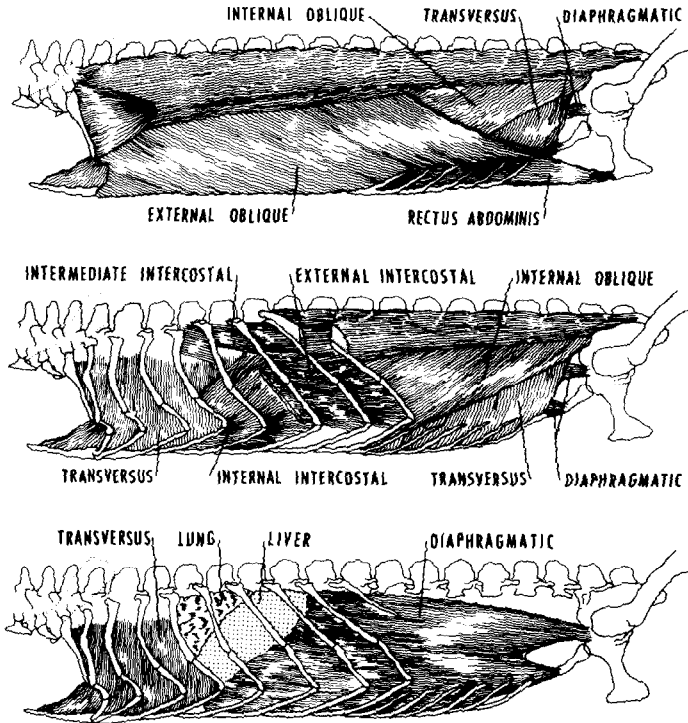


Fig. 1. *Caiman crocodilus*. Sketches of the major structures used in ventilation. The views represent successively deeper dissections of the muscles of a specimen of approximately 4 kg total weight.

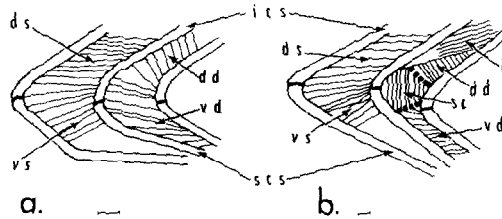


Fig. 2. *Caiman crocodilus*. Sketch to show lateral costal muscles of the right side of a small (a: 560 g) and a larger (b: 7800 g) specimen. The crossed fibers in the ventral superficial intercostal of the larger specimen suggest increased depth and complexity of the muscle architecture. The line indicates an equivalent distance to scale. DD: dorsal deep intercostal. DS: dorsal superficial intercostal. I: intermediate intercostal. ICS: intercostal segment. SC: subcostal (transversus). SCS: sternocostal segment. VD: ventral deep intercostal. VS: ventral superficial intercostal.

A very major ontogenetic change involves the development of the costal musculature (fig. 2). It is very difficult to recognize the layering of the supracostal, intercostal and subcostal muscles in small (1 kg) specimens. It is unclear whether there is a gradual ventrad shift of the margin of some of the muscles within the membranous

sheets, or if a thin layer of fibers was initially present but gradually becomes more prominent. Certainly the relative shift of fiber pattern and the change in costal elasticity and bending sites must have major effects on the mechanics of the crocodilian rib cage during ontogeny.

MOTION

Analysis confirms that *Caiman* shows independent pharyngeal and thoracic oscillations. Both are distinct cyclic movements that involve air flow through the nostrils. Except in excited animals where the glottis may be partly open, the movements of the trunk, but not those of the pharyngeal floor are reflected by pressure changes within the lung. Pharyngeal movements induce pressure oscillations of more or less equal magnitude, about atmospheric. Intratracheal (and presumably intrapulmonary) pressures remain supra-atmospheric, except for an interval during each thoracic oscillation. The pressure then drops to approximately 0.2 cm of water below atmospheric for a period of from 4 to 28 sec (typically 10 to 18 sec) confirming (with the other data) that thoracic oscillations reflect ventilatory events, while pharyngeal oscillations do not.

One of our fundamental disagreements with earlier studies concerns the relation of pharyngeal to thoracic (pulmonary) cycles. Naifeh *et al.* (1970a) suggest that the pharyngeal cavity is ordinarily distended, remaining so during respiration. Our fluoroscopic observations show quite clearly that the pharyngeal cavity is normally collapsed; the glottis then lies immediately ventral to or within the cup-shaped internal nares. Consequently buccal pumping consists of a sequence of distension-contraction (rather than contraction-distension) cycles and always ($N = 50+$) terminates with the glottis immediately adjacent to or within the internal nares. The larynx then remains in constant relation to the skull during ventilation. Air flow during breathing apparently bypasses the pharynx. No gases are ordinarily flushed through this space; consequently, the volume of the pharyngeal chamber does not represent respiratory dead space. (The slight modifications of impedance records across the pharynx observed by Naifeh *et al.*, 1970a, reflect a functionally insignificant leakage of gas into the chamber; equivalent movements were occasionally seen during fluoroscopy.) Sampling of the gas concentration in this chamber during pulmonary ventilations confirmed that there was no correlated change.

PRESSURE AND FLOW CYCLES

Figure 3 diagrams the pressures in the trachea during a single breathing cycle of an animal resting on land. The inter-breath resting level may either rise and then drop or may drop immediately at the start of a ventilatory cycle. It may pass smoothly to and then below atmospheric or show a shoulder just before this. Normally the

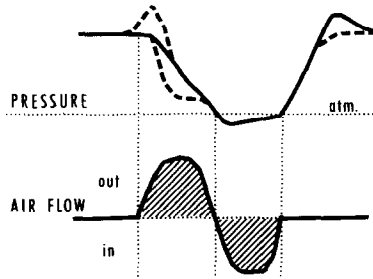


Fig. 3. Relationship between intratracheal pressure and airflow. The solid line in the pressure curve is most typically found in animals immersed in deep water, while dashed lines represent variations frequently seen in animals on dry land. Note that air flow is diphasic while pressure changes are variably polyphasic.

subatmospheric level is lower during the beginning of the first half than during the second half of the time of negative pressure. The pressure then crosses atmospheric rapidly, after which it continues to rise to, or pass and then gradually drop to, the new resting level which is almost always the same as the old one.

When the experimental animals were permitted to swim in 25 cm of water the pressure curves showed less variability (solid curve in fig. 3). The subatmospheric pressures of an individual ventilatory event remained the same. However, (a) the interventilation resting pressure stabilized at a level reflecting the hydrostatic pressure onto the thoracic cavity (fig. 4); (b) the start of a ventilation cycle did not show a

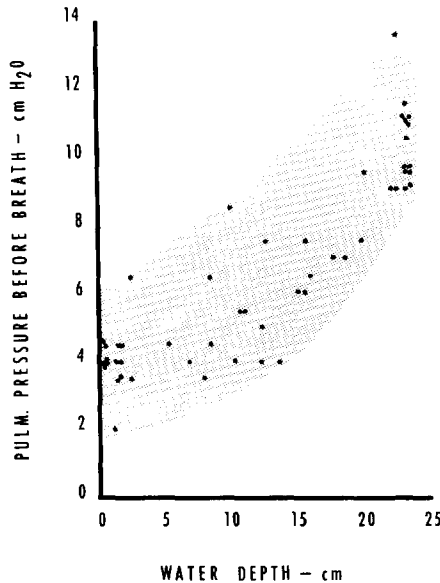


Fig. 4. *Caiman*. Graph of intrapulmonary pressure of a freely moving specimen (weight 4.8 kg) sampled over 6 hours of a 30 hour run during which the water in the tank was repeatedly raised and lowered.

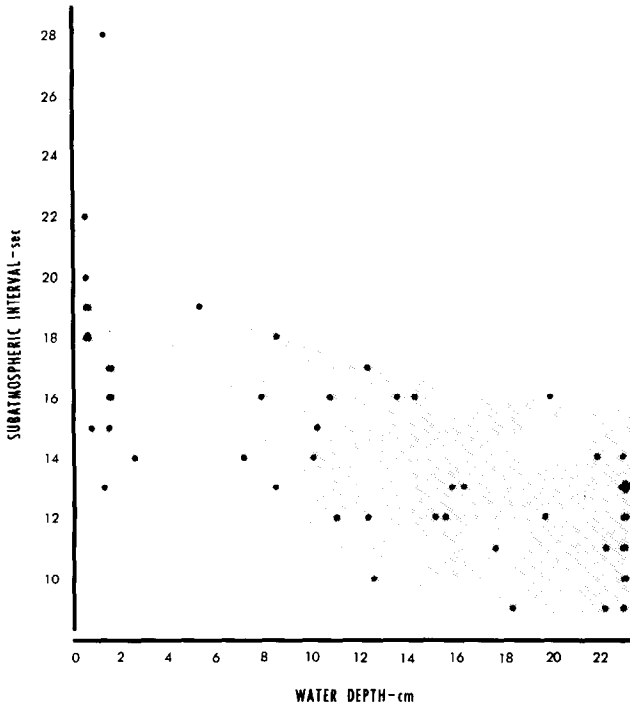


Fig. 5. *Caiman*. Graph of the duration of the subatmospheric interval for the same breathing sequence shown in fig. 4.

preliminary rise in the pulmonary pressure; (c) the shoulder in the curve during the fall of pressure toward atmospheric disappeared or became less obvious; (d) when rising again, the pressure tended to overshoot the previous resting level and then, more or less slowly, return to it; and (e) the duration of the subatmospheric interval decreased significantly (fig. 5).

Gas flows only down a pressure gradient, from zones of high to those of low pressures. As the caiman lacks a buccal pump, the inhalatory phase of respiration must be defined by the interval of subatmospheric pressure in the trachea (and lung). Exhalation theoretically could occur at any time at which the lung is at supra-atmospheric pressure and the glottis remains open. These two events are coincident only during the beginning of each breath. Consequently breathing involves exhalation followed by inhalation and is diphasic. The pressure changes are at least triphasic (fall, hold, rise), but as shown by Naifeh *et al.* (1970b) and confirmed by us, the terminal rise in pressure occurs after glottal closure and only involves a repositioning of the visceral mass.

Several variations occur in the ventilatory pressure curves of excited animals. When on land, agitated individuals may prematurely fire intercostal and abdominal pressurizing muscles (before the glottis opens), resulting in a drastic rise of intrapulmonary pressure prior to exhalation. If an excited animal fires its pressurizers

strongly during exhalation, the normally smooth descent of the pressure curve is interrupted by a brief rise. In resting animals isolated for several (5–20) hours, ventilatory pressure curves usually lose the initial and terminal rises above inter-breath baseline (fig. 3).

The pharyngeal oscillations flush the narial tubes and pharyngeal space. They can provide a continuing supply of gas to the olfactory chambers. However, they do not contribute significantly to a flushing (or reduction) of the respiratory dead space. Each exhalation still fills the internal narial canal with waste gas and leaves it full at the start of inhalation. The volume of the tubes from nares to larynx consequently must represent part of the respiratory dead space. On the other hand, this tube could be bypassed should the animal manage to breathe through the open mouth. Such a function of the gape does not seem previously to have been considered; it remains to be seen whether gaping animals actually open the pharyngeal partition. (A large excited *Crocodilus palustris* apparently had the pharynx distended while gaping; however, while some air could be observed to burst forth, the buccal flaps remained overlapping.)

MYOGRAPHIC RECORDS

Our observations (fig. 6) confirm that it is primarily the activity of the diaphragmatic

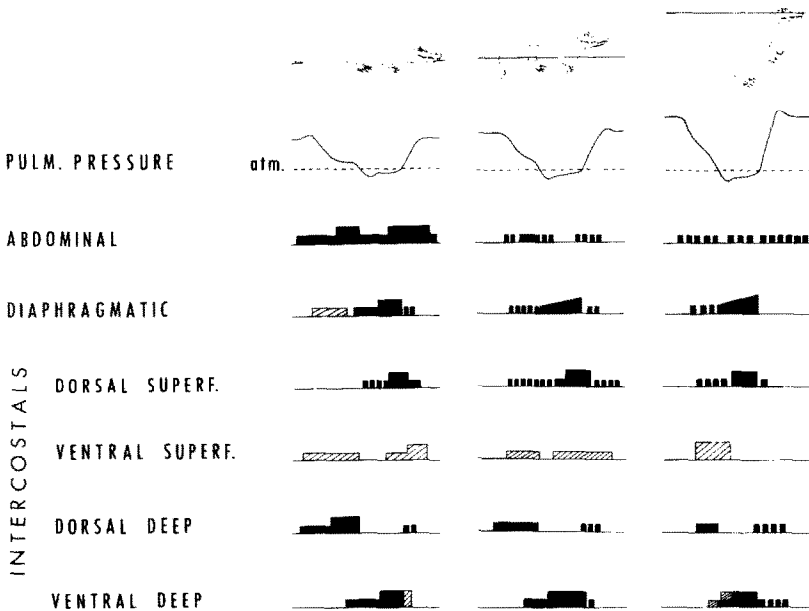


Fig. 6. *Caiman*. Activity patterns of various muscle groupings at different depths of immersion. Combined from a series of animals observed over a four-month period. The activity recorded from any intercostal layer depends on the site of electrode implantation.

muscle that is coincident with the drop of pulmonary pressure below atmospheric, though we did observe significant inhalatory activity in the section of the deep intercostals attaching mainly to the sternocostal rib segments. Those deep intercostals attaching to the intercostal and vertebrocostal segments generally act during the exhalation and again during the repressurization phases.

The superficial intercostals fire in a more complex fashion. Activity at any site is relatively constant with respect to the phase of the breathing cycle. There is an indication of a marked shift in activity with elevation along an intercostal space, as well as between cycles that show differences in the pressure curves. The dorsal superficial intercostals fire mainly during periods of negative pressure, though they often continue during the rise to resting level; particularly when the animal is immersed, the muscle may also show low intermittent activity before inhalation. Records from the ventral superficial intercostals, located near the junction between intercostal and sternocostal segments of the rib show more irregular activity, mainly during supra-atmospheric phases, but with some overlap into the action periods of the more dorsal portions of these muscles.

The abdominal wall musculature fires when the pressure in the pulmonary cavity is decreasing. It tends to cease activity at the shoulder in the descending pressure curve. The magnitude of this firing correlates well with the rate of the pressure change. Less regular activity was observed during repressurization. In general, the more active the animal the more extensive the firing. All of the muscles used in ventilation, including the diaphragmatic, also fire during locomotion.

Another and major set of changes occurs as the animal enters the water. The deeper the water the less and more irregular the activity of those muscles that increase pulmonary pressure. Here again there are intercycle differences.

The ventral portion of the deep intercostal and the diaphragmatic muscles fire mainly during the period when the pulmonary contents are at subatmospheric pressure. They increase their activity when the trunk of a resting animal becomes flooded; instead of starting to fire during the first portion of the subatmospheric period, the ventral deep intercostal muscles delay onset of full firing until the middle of the subatmospheric period; they then fire strongly. After flooding, a period of lower-level, intermittent activity precedes the period of maximum activity. This is followed in turn by a series of short, high intensity bursts. Perhaps this shift in the activity of intercostal muscles reflects the observed reduction in rib movement. The intercostals may act to move the ribs during ventilation on land and to stabilize them during ventilation in water.

The diaphragmatic muscle generally starts and ceases activity earlier in the flooded animal. It fires at a constant, low level during the initial subatmospheric phase, builds up to a steady high level after about 30% of the subatmospheric interval, and then remains there until just prior to the rise in atmospheric pressure, when it suddenly becomes silent; very rarely does it show intermittent activity thereafter. The inhalatory muscles show only sporadic activity during the terminal phase of repressurization, as do the pressurizing muscles.

All of these statements apply primarily to quiescent animals. The firing amplitudes generally increase markedly when the caimans are excited, and the range of firing is somewhat extended. One curious and significant observation concerns the activity of the ventral superficial intercostals. On land these fire much more strongly during exhalation, then become silent to start again weakly some time after the dorsal superficial and ventral deep intercostals and to increase, gradually reaching a peak almost equivalent to their earlier rate by the end of inhalation.

CORRELATIONS

The electromyographic patterns correlate well with the pressures and movements observed in the intact animal. The activity of the dorsal deep intercostals apparently adducts the ribs to the vertebral column, rotating them into a generally more acute angle. The ribs may also be adducted by other forces, for instance, by the effect of the body's weight pressing down on the sternum. This presumably explains the positive pulmonary pressure when the animal rests on land. The exhalation occurs primarily by the action of the transverse abdominal muscles; these shift the liver anteriorly and thus reduce the volume of the pulmonary chamber. Simultaneously the deep dorsal and superficial ventral intercostals change the position of the ribs and further reduce pulmonary space. This volumetric shift causes the air to flow outward through the patent glottis. When the several muscles fire more strongly or precede the activity of the glottal and narial dilators, they may pressurize the pulmonary contents and thus lead to their more rapid discharge.

The reversal of visceral movement which leads to inhalation is hardly instantaneous; a second or so may pass before the diaphragmatic muscle fires intensively. Even minor activity in this muscle causes an initial shift of the pulmonary pressure to below atmospheric. Maintenance of the subatmospheric pressure level apparently requires ever greater activity; in any case the muscle fires most strongly just prior to return to supra-atmospheric pressure in the lung. Activity in the ventral deep intercostal generally accompanies that in the diaphragmatic muscle, but lags behind the latter. It clearly helps to maintain the patency of the pulmonary cavity.

In quiet animals, activity in glottal dilator and constrictor muscles indicates that airflow is diphasic (outflow-inflow). The glottal dilator fires at the onset of the cycle, and shows low level activity until the end of the subatmospheric phase; the constrictor then fires strongly. Excited animals often show irregular firing patterns in the glottal dilator; when glottal and ventilatory muscles fire out of phase, abnormalities appear in the intratracheal pressure curves.

As the water becomes deeper and covers the animal's flanks, the pressurizing muscles become inactive, and the initial pressure peak as well as the shoulder in the pressure curve become irregular and then disappear altogether. Apparently the action of hydrostatic pressure (Gaunt and Gans, 1969b) is by itself sufficient to cause the initial outflow of air: the pressure seems to act on the abdomen and shift the

liver further into the rib cage. The configuration of the rib cage and the ligamentous ties of the liver keep the pleural cavity from collapsing; consequently the lung remains patent even when the open glottis permits the pulmonary contents to drop toward atmospheric pressure without interruption; this explains the disappearance of the shoulder in the pressure curve of immersed animals. As the water becomes deeper, the dorsal superficial intercostal is active earlier; it then fires intermittently during the fall of pressure.

The firing pattern of the diaphragmatic muscle correlates well with the development and maintenance of the subatmospheric level. The activity of the ventral deep intercostals is delayed during immersion. The increasingly antagonistic firing of the ventral superficial intercostals during excitement suggests a stabilizing rather than a distending function. Apparently the intercostals fix the movable frame, thus maintaining the subatmospheric pressure against which the diaphragmatic acts in shifting the liver.

BREATHING SEQUENCES

A number of long term (24+ hours) records of freely moving caimans, exposed to rising and falling water levels and normal (14-10 hour) day-night cycles were recorded from animals tethered by long cables and observed by closed-circuit television. Isolation was necessary because some animals dive when disturbed while others, more habituated and used to being fed by hand, rise to the surface when one of us enters the chamber. In general, the animals would breathe in sets of two or occasionally three ventilatory cycles when their body was in the air. They would shift to single ventilatory cycles interspersed with pauses of one or more minutes when the water became deep enough to cover their trunk. When undisturbed for long periods the caimans showed a generally inversely weight-dependent breathing rate (table 1). Our highest values for resting animals are less than one half those reported by Huggins *et al.* (1969) for 'minimally stimulated' animals of equivalent size. We only observed (by TV) rates equivalent to theirs when our animals were moving about the tanks.

TABLE 1
Respiratory rates of *Caiman* at 23-25 °C

Mass	Breaths/min	Period monitored
5.0 kg	0.167	24 hrs
4.8 kg	0.144	12 hrs
4.8 kg	0.250	180 min
650 g	0.574	500 min
290 g	0.633	450 min
180 g	0.580	550 min

Many of the animals dived voluntarily, staying beneath the water for 15 to 25 minutes at a time. Upon emergence they would breathe deeply, perhaps five to eight times in a row, with the intervals between initial breaths on the order of one minute and this period increasing to three to four minutes during the next half hour. In general, the data confirm the observations of Gaunt and Gans (1969a) and Huggins *et al.* (1970) that each breath is accompanied by a slight tachycardia.

The pressure in the lungs did not change regularly between breaths, however, the pulmonary pressures reflect movements and other activity of the animal. When accidentally disturbed, the animals might inflate themselves or raise pressure by inducing peak firing of the pressurizing muscles. As the trunk musculature is also used in locomotion, it is inappropriate to correlate all pulmonary pressure changes with breathing events.

THE PRESSURE-VOLUME CURVE

We attempted to obtain an estimate of tidal volume in ventilation by the standard technique of inflating and then deflating an animal and mapping the pressure-volume curve for the crocodylian lung (fig. 7). Catheterized animals (under deep anesthesia or freshly killed) were alternately inflated and deflated by stages in varying depths of water. The observations document the standard pressure-volume curve hysteresis (Hills, 1971; Gil and Weibel, 1972). The curve for submerged animals always showed some mid-level rearrangement of the trunk as the animal started to float. Further restraint might have eliminated this but would also have introduced artifacts by modifying the compliance of the animal's body. We consequently limited the caiman's movements only by placing it beneath a brick that just touched (but did not press upon) the fully inflated trunk. The hysteresis was very large. When covered by 7

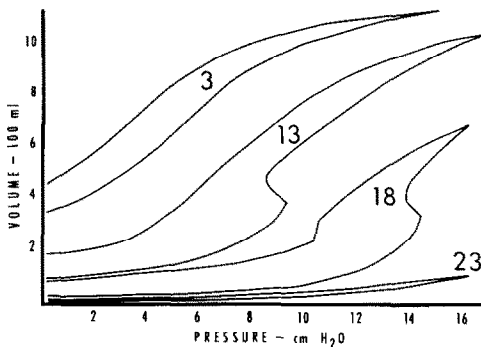


Fig. 7. *Caiman*. Selected pressure-volume curves measured on a freshly-killed specimen (weight 5 kg). The cusps of the curve represent volumes at which the animal passed neutral density and the carcass floated within a confining, but not resisting space. The numbers within or by the loops indicate water depths (in cm) at which measurements were taken.

inches of water this amounted to up to a 40 % increase in pressure for a particular volume. The tidal volumes estimated from these curves are greater by almost an order of magnitude (85 ml/kg in 3 cm of water compared with 12 ml/kg) than those reported by Naifeh *et al.* (1970a) from plethysmographic techniques. Possibly our approach changed the compliance of the rib cage; this may be more stiffly elastic in animals that have the costal muscles in tonic condition.

A couple of incidental observations suggest some reasons for the observed hysteresis. When a caiman that has been partially inflated under water is then manually squeezed, the pulmonary relations shift from the inflation to the deflation curve and remain there. If the animal is then inflated further intermediate points are obtained until another squeezing sequence returns things to the deflation curve. If the pressure is then permitted to drop it proceeds along the deflation curve. The effect of squeezing is greatest when the pressure is applied to the thoracic rib cage rather than to the abdominal portion of the animal. When a transient pressure peak is applied to the inside of the lung the curve shifts only part way. The observations suggest that the hysteresis may be due to the intrinsic frictional resistance between the shifting components of the crocodilian body. As pressure on the rib cage is more effective in shifting the animal between the sides of the hysteresis loop than is pressure on the abdominal wall, one can furthermore state that it is primarily the mechanical friction intrinsic to the rib system that is responsible for the effect. We have no evidence to evaluate the possible occurrence of changes in alveolar configuration (*cf.* Weibel *et al.*, 1973) in this system. The hepatic piston floats more or less freely in a fluid-filled space and is apparently more compliant than are the costal articulations.

Figure 8 shows a simple mechanical model of such a pulmonary system. Increase in the volume occupied by the lung (L) requires that work be exerted to compress an elastic spring (E) and possibly a plastic component (P). The deformation of the pulmonary constraints also involves some structural rearrangements and apparently incorporates frictional resistance (F) between the mechanical components. Once the pressure in the pulmonary chamber is increased by driving air into it, the system will shift until the air pressure is just equivalent to the sliding friction. On the other hand, if the pressure is dropped the force on the piston must again be just slightly greater than the static friction before the piston will move. During the transition from

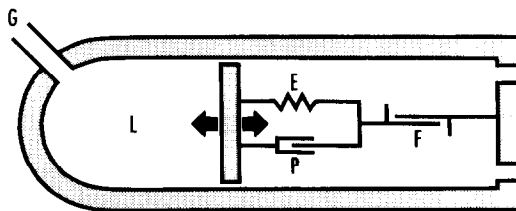


Fig. 8. Model illustrating some aspects of ventilatory mechanics. The piston is intended to represent all movable and compliant portions of the system. See text for details. E: elastic resistance. F: frictional resistance. G: glottis. L: pulmonary cavity. P: plastic resistance.

just enough force to keep distending to just enough force to start collapsing the volume remains constant (except for volumetric expansion as the pressure drops). This explains the shift from the inhalatory to the exhalatory curve after the rib cage has been squeezed.

The model also suggests why pressures produced by aspiration breathing may be lower than those for pulse-pumping equivalent amounts of gas in a particular animal. If flow is induced by movements of the pulmonary wall, thus increasing and reducing the pressures as the result of a primary change of the volume, the process should move along the deflation curve. However, when the gaseous medium has to serve both as a carrier of respiratory gases and as a mechanical transmission medium, inflation requires greater pressures to maintain forces sufficient to keep the non-ideal piston moving. Part of the difference between the inflation and deflation curves will then represent the cost of pulse-pumping.

Finally the model suggests an advantage for the terminal overshoot of pulmonary pressure during repressurization prior to return to base line. A temporary overshoot will permit the animal to store the gas at a lower apneic pressure.

Discussion

The present results confirm earlier observations (de Jongh and Gans, 1969; Gans and Hughes, 1967; Gaunt and Gans, 1969b) that the respiratory activities of amphibians and reptiles seem closely matched to the normal environmental circumstances of the animals. The aspiration breathing patterns seen in the several Recent reptiles presumably arose independently from each other, and probably from the pattern seen in mammals; consequently they must be analyzed by themselves. The key to this basic conclusion is again confirmed by the present studies which document that the undisturbed caiman utilizes minimal respiratory muscle activities, *i.e.* does minimal work, to move the air necessary for absorption and release of respiratory gases. The studies also show that the cup and socket connection between larynx and internal nares reduces the respiratory dead space and with this again increases the efficiency of ventilation.

The spacing of breathing cycles furthermore reflects the animal's capacity to dive for prolonged periods. Post-dive emergence is accompanied by repeated breathing movements, which discharge the accumulated lactate and gradually reoxygenate the tissues.

The buccal oscillations in this sense are interpreted as serving one major function, namely to flush gas along the olfactory epithelium. The observations of Naifeh *et al.* (1970a) that ventilation cycles were often preceded by one to three pharyngeal oscillations suggests a sensory function; there is no direct association of these pharyngeal movements with gas exchange. The possible role of gaping in ventilation remains to be checked.

We confirm results of Naifeh *et al.* (1970a, b) regarding artifacts generated when

animals are excited, particularly when being handled. An excited state may well occur in animals in the wild; it is difficult to quantify or to compare. Consequently we emphasize study of isolated *Caiman* that are free to move but happen to be resting.

The diaphragmatic muscles are neither homologous nor analogous to a mammalian diaphragm. Inward movement of the abdominal wall does not 'serve to push the abdominal contents up against the diaphragm, thus assisting in evacuation of air from the lungs' (Naifeh *et al.*, 1970b); it does shift the liver anteriorly, thus reducing the space within the thoracic cavity.

We are able to confirm that the various trunk and diaphragmatic muscles fire either to reduce the pulmonary pressure or to increase it. No muscle does both. Our records do suggest that an insect pin would at most intercostal sites record from at least two layers, one of them active during inhalation and another active during exhalation and/or repressurization. There is presumably no selective advantage for the maintenance of pulmonary contents at a particular supra-atmospheric level between breaths. (There would be a disadvantage if the glottal closers would have to fire continuously to keep the gas from escaping as suggested by Naifeh *et al.*, 1970a; however, 1970b would suggest that this was only occasionally observed; our records do not show it.)

The various intercostal muscles span the intercostal spaces. No matter what their angle of origin or insertion, such muscles can only act to bring a pair of adjacent ribs more closely together. Whether this results in abduction or adduction of a particular rib depends on the forces (active and elastic) resisting displacement and on the relative moments imposed on the two ribs. The secondary firing of the ventral superficial intercostals in excited animals may then be conceived of as bringing a mechanically ineffective muscle into action at a critical time, thus increasing the stability of the rib cage during deep inhalation. Consequently some of the activity of the costal muscles serves to maintain the patency of the cylinder so that shifts of the hepatic piston may cause maximal changes of pressure. This effect is most pronounced when the trunk is flooded. The postventilatory firing of the pressurizers presumably serves a repositioning function, particularly when the animal is on land and thus without the benefit of hydrostatic pressure against its trunk. Such costal activity may be the inevitable price of a ventilatory pattern that involves a major shift of the viscera with each breath.

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