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CHAPTER 1

Physiological Adaptations to Aquatic Life

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Although the first reptiles were apparently adapted to live on land (Carroll, 1969), multiple lines of reptiles have reinvaded the freshwater habitats of their amphibian relatives. The physiological adaptations for life on land permitted some reptiles to invade, not only fresh water, but also marine environments. Nevertheless, the terrestrial forms have been so successful that fewer than 8% of the nearly 6000 species of Recent reptiles are primarily aquatic.

Reinvasion of aquatic habitats by members of previously terrestrial lines is not surprising because the basic reptilian design incorporates many physiological properties that would well serve aquatic behaviour. These protoadaptations include ectothermy, pronounced capacity for anaerobic metabolism, tolerance of severe acid-base disturbances, ventilation involving breath-holding, and a circulatory system characterized by a degree of intraventricular shunting and vascular responses collectively known as the "diving response." In many cases, totally aquatic reptiles exhibit vital physiological functions that are scarcely different from those of their terrestrial relatives. However, other reptiles show modifications of their basic physiology that are clearly adaptive to aquatic life.

Some aquatic reptiles represent essentially terrestrial species that use water only as a refuge from terrestrial predators. Others rely on aquatic communities as primary sources of food, but regularly return to land to bask or to lay eggs. A few species never leave the water not even for reproduction. Turtles of all families, except the testudinids, are basically aquatic or semi-aquatic and feed on a variety of animals and plants, living and dead, that they obtain from land or water. There is a diversity of freshwater

This chapter is dedicated to Per F. Scholander (1905–1980) whose pioneering work on diving vertebrates continues to provide inspiration to comparative physiologists everywhere.

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turtles, and the seven species of sea turtles occupy several marine niches (Hendrickson, 1980). All Recent crocodilians are semi-aquatic, regularly coming on shore to bask and nest (Guggisberg, 1972). Most crocodilians favour fresh water, but some enter brackish water and occasionally venture to sea. The numerous species of snakes that take advantage of aquatic resources, range from those associated with water margins to those that never leave the water. The taxa with the greatest aquatic affinities are the natricine and homalopsine colubrids, the acrochordids, the laticaudids, and the hydrophiids, although most other snake families have at least a few aquatic representatives. The sea snakes rival the marine turtles in having the most extreme specializations for aquatic life (Dunson, 1975a; Heatwole, 1978; Voris and Voris, in press). There are no totally aquatic lizards among Recent forms, although the extinct mosasaurs were a prominent feature of Cretaceous seas. Several species of Recent lizards use water for escape and a few feed in aquatic habitats. The most familiar aquatic lizard is the Galapagos marine iguana, *Amblyrhynchus cristatus*, which feeds on coastal algae (Carpenter, 1966; Dawson *et al.*, 1977). Other lizards that often feed in water occur in the genera *Hydrosaurus*, *Shinisaurus*, *Varanus*, and *Lanthanotus*.

This chapter explores the diversity of physiological adaptations among aquatic reptiles. Life in water involves a physical environment vastly different from air. The density and viscosity of water are orders of magnitude greater than those of air, water impedes fast movement, and its buoyancy reduces the effects of gravity. The relatively high specific heat and thermal conductivity of water restrict the independence of body temperature in aquatic species. Respiration, circulation, and metabolism of aquatic organisms must be adapted to a situation in which pulmonary gas exchange is impossible and dissolved O₂ is difficult to obtain. Hydrostatic pressure affects the partial pressures of gas in the lung and causes potentially serious problems for gas transport and exchange.

II. Locomotion and Feeding in Water

In general, locomotion is energetically less demanding for animals in water than on land. Frictional energy losses incurred moving through a dense and viscous medium are more than offset by the energetic advantage of expending little or no effort supporting the body and negotiating irregularities in the terrain (Schmidt-Nielsen, 1972). Much of the work of terrestrial locomotion involves lifting and lowering the centre of gravity. In water the work load is much reduced because reptiles can be essentially weightless.

The inherent advantage of aquatic locomotion for reptiles has been demonstrated by a comparison of swimming and walking in the Galapagos

marine iguana, *Amblyrhynchus cristatus*. At similar speeds, its energy cost of swimming is about 25% of the cost of walking (Gleeson, 1979). Apparently, this lizard will swim rather than walk between two points, if offered the choice. The calculated cost of aquatic foraging for food is less than 8% of the field metabolic rate, whereas the cost of terrestrial foraging is about 30%. The combination of a low cost of locomotion and an abundant and consistent marine food source allow the marine iguana to survive when foraging only about one hour every 1–3 days.

We may observe the effect of increased locomotor specialization, including streamlining, by comparing the energetic cost of swimming in the marine iguana, which shows few morphological adaptations for aquatic locomotion (Dawson *et al.*, 1977), with that of juvenile marine turtles and sea snakes which are more streamlined. Table I shows that the marine iguana is least efficient, a green turtle intermediate, and a sea snake most efficient at transportation. The costs of transport for sea snakes and eels are similar suggesting that the similarity of shape is the critical factor. The

TABLE I
The energy cost of locomotion in three aquatic reptiles

	Marine iguana*	Green turtle**	Sea snake†
Body mass (g)	2660	735	400
Temperature (°C)	25	25	25–27
$\dot{V}_{O_2}\ddagger$, rest (ml O ₂ /g·h)	0.041	0.070	0.038
\dot{V}_{O_2} , active (ml O ₂ /g·h)	0.265	0.174	0.117
Routine swimming speed (km/h)	1.50	0.94	1.26
Cost of transport (ml O ₂ /g·h)	0.224	0.104	0.079
Cost of transport (ml O ₂ /g·km)	0.149	0.111	0.063
Cost of transport reptile eel‡	3.45	1.86	0.91

* Gleeson (1979).

** Prange (1976).

† Heatwole *et al.* (1978); Heatwole and Seymour (1975a); calculated field swimming speed (0.35 m/s) and maximum aerobic scope (0.77 ml O₂/g·h).

‡ Rate of O₂ consumption.

‡ Cost of transport in eels calculated from data of Holmberg and Saunders (cited in Schmidt-Nielsen, 1972) and corrected for body mass according to relationships described by Brett (1965). The equation used is

$$\text{ml O}_2/\text{g}\cdot\text{km} = 0.31 (\text{mass})^{-0.25}$$

differences among the reptiles are actually higher than indicated because the mass specific cost of transport decreases with body mass in animals (Schmidt-Nielsen, 1972). In fact, the reduced cost of transport in larger marine iguanas means that foraging is more economical for the adults, which swim out to the subtidal algal beds, than for the juveniles, which are restricted to feeding on or near shore (Vleck *et al.*, 1981).

Reptiles use five basic modes of aquatic locomotion: bottom-walking, paddling, flapping, sculling, and anguilliform swimming. Bottom-walking occurs in some turtles (Zug, 1971) and this form of locomotion is seen occasionally in crocodilians and lizards. A bottom-walker must be negatively buoyant or be able to hold on to the bottom with claws. Bottom-walking turtles use their well-developed webbed feet, both to push against the bottom and to propel the water.

The paddlers are exclusively turtles that move both pectoral and pelvic limbs in unison or alternatively. Primary propulsion generally comes from the rear legs (Zug, 1971). When paddling, the limbs are extended laterally and the power stroke begins with the web broadly expanded. During recovery, the feet are pulled into pockets between the carapace and plastron and thereby avoid a significant reverse stroke. Morphological change of the rear appendages swimming may be limited by their need to function in nest construction (Zug, 1971).

Marine turtles and *Carettochelys* use the anterior appendages for propulsion as they flap through the water. These turtles are considerably more streamlined than most freshwater forms, that may be limited by the need to retract the appendages. Modifications include a reduction in neck length, a smooth transition between the limbs and shell, and a flattening of the shell. The pectoral flippers have the smooth appearance of a good hydrofoil. They are moved in unison, the flipper tip delineating a figure eight (Walker, 1971, 1979), as do the wingtips of some birds, such as swimming penguins (Clark and Bemis, 1979). The angle of attack is constantly changed to provide thrust both on the up and the down stroke, although the down stroke is more effective because it is directed more posteriorly. The pelvic appendages usually provide no thrust but act as elevators and rudders. This form of locomotion is well suited for open water but, when manoeuvring at slow speeds near the bottom, marine turtles may use the limbs independently.

Sculling is the usual form of locomotion in crocodilians and lizards in open water. With the limbs pressed close to the body, the posterior trunk and tail are undulated laterally, a form of locomotion commonly seen in the marine iguana (Bartholomew *et al.*, 1976; Vleck *et al.*, 1981). The main morphological correlate to sculling is a vertical flattening of the tail, moderate in marine iguanas and some *Varanus*, but extreme in *Hydrosaurus*.

Aquatic snakes use anguilliform locomotion and apply lateral force to the water with sinusoidal waves that sweep towards the tail. Semi-aquatic snakes are good swimmers that lack obvious morphological specializations. Most sea snakes possess a severely flattened, paddle-like tail and the acrochordids possess a ventral muscle that forms the skin into a keel running almost the entire length of the body when the snake swims. The mechanics or energetics of swimming in snakes have not been studied.

Feeding in water poses physical difficulties because movement of the jaws towards a food object induces an opposing force that tends to destabilize the body of a reptile (Gans, 1969). Moreover, jaw closure tends to expel water from the mouth and push prey objects away from the gape. Turtles oppose these tendencies by paddling with their legs during the lunge or by rapidly expanding the pharyngeal cavity to suck in the prey. Some sea snakes (e.g. *Pelamis platurus*) and many crocodilians do not propel the whole body forward, but sweep the dorsoventrally flattened head rapidly sideways (Guggisberg, 1972; Pickwell, 1972). Sea snakes, other than *Pelamis*, usually do not feed in open water but forage near the bottom and search crevices (Heatwole *et al.*, 1978). Stabilization of the body during probing with the head is facilitated by a concentration of mass in the posterior part of the body in some species. The body form of sea snakes is convergent on that of some long-necked turtles and the plesiosaurs; all have a relatively stationary body platform from which a long, supple neck can move widely (Schmidt and Inger, 1957). However, a long neck is unsuitable for a fast aquatic animal as slight lateral deflections of the head tend to divert the course. Fast swimmers are better served by short necks, an adaptation epitomized by the ichthyosaurs and approached by some marine turtles.

Underwater manipulation of food can also pose problems. However, the inertia of a large food object helps to stabilize it so that portions can be twisted or pulled off (Gans, 1969). Smaller items are also manipulated to take advantage of their inertia. The object is accelerated and then suddenly released while the jaws are quickly replaced into a more advantageous position. Inertial feeding proceeds differently under water than on land; the former reduces the effect of gravity and resists quick acceleration. Some crocodilians and lizards overcome these problems by raising their heads above water to manipulate prey inertially and toss it to the rear of the mouth.

Aquatic reptiles that feed on birds and mammals can rapidly immobilize their prey by drowning it. Sea snakes use venoms quickly to subdue slippery fish in a three-dimensional environment (McCosker, 1975). Immobilization has been observed in captive snakes (Loveridge, 1946; Klemmer, 1967; Pickwell, 1972); however, several species of sea snake normally hold on to the prey after biting it and some fish can swim away if released (Heatwole *et al.*, 1978). The rear-fanged homalopsine snakes also use venom, but the

natricines and acrochordids apparently do not. Acrochordids are equipped with a muscular skin and unique conical scales with which they capture fish between the curves of their bodies (Dowling, 1960).

III. Buoyancy

In order to maintain a position below the water surface without expending energy, a reptile must be neutrally buoyant. This condition depends on matching the variable specific gravities (sp. gr.) of the water and the body. The sp. gr. is about 1.000 g/ml for fresh water and 1.025 g/ml for sea water, although these values change slightly with temperature. The sp. gr. of a submerged reptile depends on the inherent sp. gr. of the body tissues and the volume of gas in the lungs. Pulmonary volume, in turn, depends on hydrostatic pressure, so if the animal customarily travels vertically in the water column, it is rarely at neutral buoyancy. To my knowledge, there is no evidence that any reptile can resist the hydrostatic collapse of the lungs with depth or can significantly change its buoyancy by collapsing or expanding the lung by muscular action. In marine turtles, tracheal pressure nearly equals external pressure to depths exceeding 80 m at which level the gas volume is compressed to less than 8% of the volume at the surface (Berkson, 1967). Even at shallow depths, *Chelydra serpentina* cannot significantly change its sp. gr. by altering intrapulmonary pressure and volume (Gaunt and Gans, 1969a). Therefore, the only form of buoyancy control in reptiles is the adjustment of pulmonary volume at the surface and the expulsion or absorption of gas during a dive.

Several workers have attempted to assess buoyancy or pulmonary volume in various aquatic reptiles. Because lung volume is highly variable, measurements of maximal volume by filling intact or excised lungs of living or dead animals may considerably underestimate normal sp. gr. in water (Agassiz, 1857; Patterson, 1973; Heatwole and Seymour, 1975b). Measuring the body weight (in air) and volume (by water displacement) in living reptiles (Zug, 1971) is better, but the manipulation and restraint involved in the technique may result in abnormal estimates. The best data come from experiments designed to measure pulmonary volume in freely swimming and diving turtles and sea snakes. Voluntarily diving turtles have been captured under water and placed in whole body plethysmographs to measure pulmonary volume (Jackson, 1969, 1971a; Milsom, 1975). The pulmonary volume of sea snakes has been measured by the simple expedient of decapitating them under water and collecting all of the pulmonary gas (Graham *et al.*, 1975). Coupled with body weights and observations of buoyancy immediately before capture, these studies demonstrate regulation of buoyancy according to the requirements of each reptile.

Even if reptiles cannot maintain neutral buoyancy throughout the water column, it is clearly advantageous for them to be negatively buoyant when they walk on the bottom or positively buoyant if they spend much time at the surface. For example, pelagic sea snakes, *Pelamis platurus*, are usually quite positively buoyant because the pulmonary volume is normally 110–130 ml/kg and the sp. gr. is between 0.42 and 0.63 g/ml (Graham *et al.*, 1975). These snakes apparently use the resistance of their buoyant body in lieu of a solid substrate; they push against it during the lunge after prey and when restraining captured fish at the surface. When the snakes dive, they release a quantity of gas and the sp. gr. increases to about 0.77 g/ml; the snake is still positively buoyant at the surface but the sp. gr. increases as the lung collapses with depth and with gas absorption. These snakes achieve neutral buoyancy at about 4 m, and become negatively buoyant at deeper levels.

Marine iguanas, *Amblyrhynchus cristatus*, control their buoyancy by adjusting pulmonary volume. They are neutrally buoyant at about 4.6 m depth and are strongly positive buoyant at the surface where they “bob like corks” and gulp air to bloat themselves (Carpenter, 1966).

Turtles often release a portion of lung gas prior to diving and bottom-walking species (e.g. chelydrids, kinosternids, and semi-aquatic emydids) are negatively buoyant (Zug, 1971). The matamoras, *Chelus fimbriatus*, rests under water with a pulmonary volume of only 68 ml/kg (Lenfant *et al.*, 1970a). Bottom-walkers are often poor swimmers and have to struggle to reach the surface; once they reach it, they become positively buoyant while ventilating (Zug, 1971). The high pulmonary volume typically found in bottom-walkers is probably related to the need to float during breathing episodes. Thus, these turtles expend little energy maintaining position at the surface or at the bottom. The stronger swimming turtles, such as trionychids and certain emydids, typically show slight negative buoyancy (Zug, 1971). The normal sp. gr. of *Pseudemys scripta* appears to be between 1.003 and 1.006 (Jackson, 1969).

The heavy, rigid shell of aquatic turtles has important consequences for buoyancy control. In immersed *Pseudemys scripta*, the weight of the shell is 75% of that of the animal and thus requires a pulmonary volume of about 140 ml/kg to achieve neutral buoyancy (Jackson, 1969). By comparison, the pulmonary volume required for neutral buoyancy in nine species of marine snakes (*Aipysurus*, *Lapemis*, *Astrotia*, *Acalyptophis*, *Emydocephalus*, and *Acrochordus* spp.) averages 52 ml/kg (± 22 sd, $n=18$; R. S. Seymour, unpublished) which is similar to values (63–68) from *Pelamis platurus* (Graham *et al.*, 1975).

Because changes in pulmonary volume in turtles must occur within the constraints of the shell and the flexibility of the skin in the limb pockets

limits compliance in the intact lung, there is a restriction on adaptive adjustments in pulmonary volume for buoyancy control (Jackson, 1971a, 1979). Nevertheless, *Pseudemys scripta* slowly compensates for experimental changes in sp. gr. by approximating the adjustments in pulmonary volume with reciprocal changes in the volume of the urinary bladder and cloacal bursae, the bladder being most important (Jackson, 1971a). The same pulmonary compensations for experimental changes in buoyancy occur in the freshwater turtle, *Chrysemys picta*, and yearling loggerhead turtles, *Caretta caretta* (Milsom, 1975). As pulmonary volumes decline, the frequency of breathing increases in *C. caretta* (Milsom and Johansen, 1975). Although *Chrysemys picta*, like *P. scripta*, possesses cloacal bursae, *C. caretta* does not (Smith and James, 1958). Therefore, if buoyancy compensations are accompanied by changes in stored water in *C. caretta*, the urinary bladder assumes the total role. Presumably the capacity for pulmonary compensation to changes in sp. gr. evolved as an adaptation to natural changes in buoyancy caused by feeding, starvation, or reproduction. Hatchling *C. caretta* have no buoyancy control, but develop it over the first year of life (Milsom, 1975). The hatchlings are very buoyant and seem to have trouble diving. Although they may learn to dive after two to four months, complete compensation for experimental changes of buoyancy only appears after 11 months.

The lungs of reptiles are richly endowed with smooth muscle, the functions of which are obscure (Varde, 1951; Shah, 1962). The muscle may be concerned primarily with regulation of vascular resistance in the pulmonary circulation, but it may also control the orientation of a reptile in the water by shifting gas between pulmonary compartments. *Caretta caretta* can selectively shift lung gas forward or back, right or left (Jacobs, 1939). The single lung of totally aquatic sea snakes extends from the neck to the vent (George and Shah, 1956, 1965) and it supports the entire body of a floating snake. Anterior or posterior shifts in lung gas change the orientation of sea snakes, but there is no evidence that such changes are under voluntary control. When *Pelamis platurus* dives, the posterior end becomes more buoyant than the anterior end; motionless snakes often float to the surface tail first (Graham *et al.*, 1975). It may be that the shift in gas is passive, resulting entirely from the external hydrostatic pressure. When *Pelamis* is tilted head up in water-filled tubes and scanned for ^{133}Xe gas in the lung, one notes that the posterior saccular lung collapses completely, whereas some gas is retained in the anterior vascular segments when the snake is tilted head-down (Seymour *et al.*, 1981b). It is not known whether the response to head-down tilting represents active regulation of anterior lung volume or simply a mechanical retention of gas in some alveoli as the lumen of the lung collapses.

The gas exchange and hydrostatic roles of the lung appear to present two opposing selective pressures to a diving reptile. On one hand, a large lung volume facilitates O_2 storage and longer dives. On the other hand, too much buoyancy may be detrimental as it increases demands for O_2 and energy during descent. The heavy shells and relatively large pulmonary volumes of turtles compensate for both of these demands.

Stomach stones are important for buoyancy control in the Nile crocodile, *Crocodylus niloticus* (Cott, 1961). In nature, juvenile crocodiles lack these stones during their first year but ingest stones equivalent to about 1% of their body weight as they grow about 3 m long. All Nile crocodiles longer than 3 m contain stones; if the local habitat has few suitable stones it takes longer for the ballast to be acquired (Fig. 1). The stones collect in the gut ventral and posterior to the lungs; their position tends to elevate the anterior end of floating crocodile and stabilizes them against rolling. Stoneless juveniles must use limb movements to avoid rolling when floating; it may be significant that juveniles avoid deep water. The sp. gr. of Nile crocodiles is increased from about 1.08 to 1.09 by the stones. Cott (1961) suggested that this increase would allow a crocodile to resist currents and to drown prey. It would also increase the pulmonary volume and O_2 stores available to a submerged crocodile and allow a dive to be extended by about 12%.

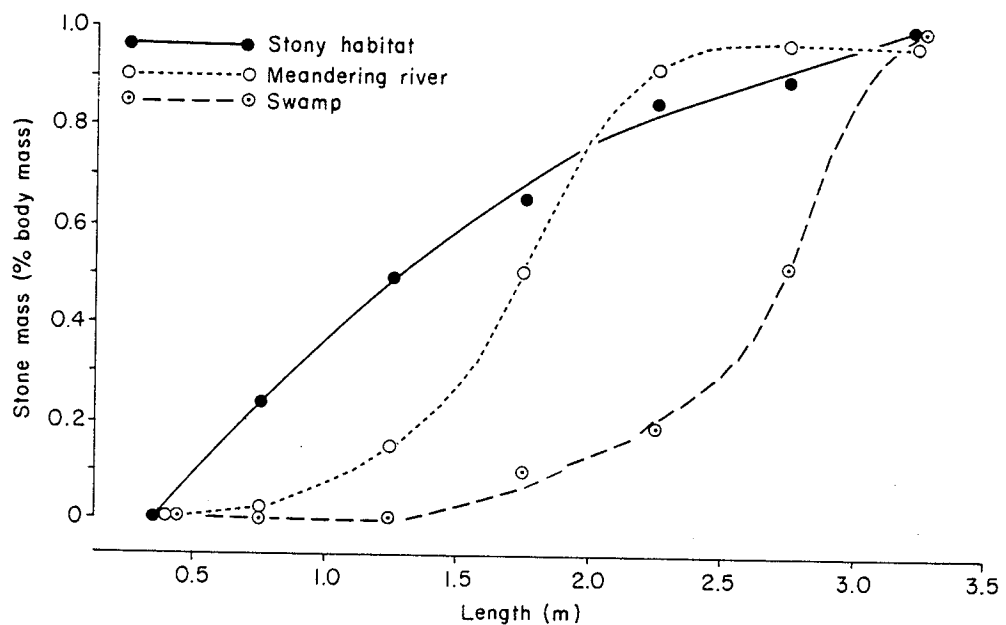


FIG. 1. Mean mass of stomach stone ballast in a large sample of Nile crocodiles, *Crocodylus niloticus*, from three habitats of different stone availability (Cott, 1961). All juveniles lack stones and, although similar loads are eventually obtained, it requires longer in the stone-poor river and swamp.

IV. Blood Pressure and its Regulation

Terrestrial animals encounter the effects of gravity on the distribution of blood and interstitial fluid. However, immersion essentially eliminates hydrostatic stresses on the cardiovascular system because the external hydrostatic pressure nearly equals the pressure caused by the blood column. Consequently, the transmural pressure becomes almost independent of postural changes. Therefore, totally aquatic animals do not need to regulate blood pressure in response to postural change, nor do they need to develop the high blood pressures otherwise necessary to work against gravity and support a column of blood above the heart.

Although small, compact reptiles are not greatly affected by postural changes, adaptive evolutionary differences in blood pressure regulation may be observed in snakes which, because of their shape and size, are significantly affected by gravity. Blood pressure and its regulation are related to habitat in snakes (Seymour and Lillywhite, 1976). Totally aquatic species have very low mean arterial blood pressure and poor regulation during tilting experiments. Mean blood pressure and the effectiveness of its regulation is higher in semi-aquatic species, still higher in the terrestrial species, and extreme in the arboreal species (Fig. 2). Moreover, there are marked difference in heart placement. In the aquatic species, the head-heart distance is 34–43% of the total body length. This decreases to 20–30% in the semi-aquatic species and 16–17% in the terrestrial and arboreal ones. A more centrally located heart may be advantageous in a gravity-free environment, because the flows and pressures necessary to perfuse the anterior and posterior parts of the body are equalized. On land, and especially in trees, a short head-heart distance ensures adequate perfusion of the brain at all body angles. It is significant that the blood pressure in the brain of the aquatic species dropped below zero and the cranial vasculature presumably collapsed during head-up tilting in air. This study demonstrates convergent physiological evolution because the semi-aquatic and aquatic species represent three, or possibly four, independent invasions of water by members of three or four families of snakes.

Scholander *et al.* (1968) investigated interstitial fluid pressure during tilting in the aquatic anaconda, *Eunectes murinus*, and the arboreal boa constrictor, *Boa constrictor*. Contrary to expectations, the water snake regulated interstitial fluid pressure well, but the tree-climber tended to develop oedema in its tail.

V. Thermal Relations

The occurrence of reptiles in or near water greatly affects the mode and success of behavioural thermoregulation. Space prohibits a review of the

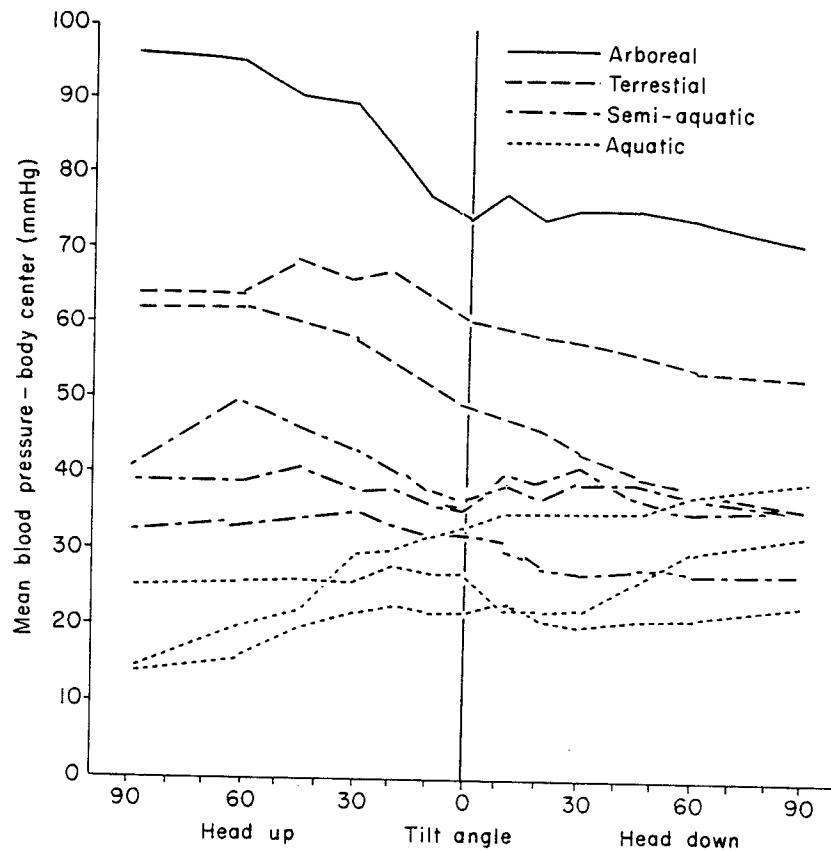


FIG. 2. Mean arterial blood pressure during tilting of nine species of snakes in air. Pressure is recorded at the body centre where changes in pressure reflect physiological factors, not physical ones. Aquatic species show poor regulation, low pressure and venous pooling, whereas terrestrial and arboreal species show good regulation and high pressure. Data from Seymour and Lillywhite (1976).

wealth of information on the thermal ecology of semi-aquatic and terrestrial reptiles that leave or enter water to adjust body temperature, but this is covered in reviews by Templeton (1970), Hutchison (1979), and by Avery and Bartholomew (volume 12). These reviews show that most reptiles generally thermoregulate by basking out of water or by selecting appropriate water temperatures in naturally occurring thermal gradients. Smith (1979) discusses this in crocodilians and Hutchison (1979) deals with turtles. Suffice it here to comment briefly on totally aquatic reptiles and the peculiar case of the marine iguana.

Several species of freshwater turtles and all marine turtles only come ashore at nesting time and are generally assumed to have body temperatures near ambient water temperature. Sea turtles floating in shallow tidepools may warm with the water, and loggerhead turtles may achieve a 3.75°C difference between body and water temperatures (Sapsford and van der

Riet, 1979). Captive juvenile green turtles, *Chelonia mydas*, may bask on land, but it is doubtful that terrestrial basking plays any significant role in nature (Balazs, 1974; Mrosovsky, 1980).

Living reptiles generally have low rates of metabolic heat production and poor insulation compared with birds and mammals. Thus the proposition of significant endothermy is implausible, especially in aquatic species living in an environment of high thermal conductance and heat capacity. However, the warm-bodied fish (Carey and Teal, 1969; Dizon and Brill, 1979) attest to the errors of our preconceptions. Leatherback turtles, *Dermochelys coriacea*, may be able to raise their body temperatures as much as 18 °C above water temperature by endogenous heat production (Frair *et al.*, 1972). This capability may rest in a favourable surface-volume ratio, a thick layer of insulating fat under the carapace, and the elements of a countercurrent heat exchanger in the fins (Greer *et al.*, 1973). The rates of heat production of active adult green turtles (Prange and Jackson, 1976; Jackson and Prange, 1979) and rates of heat loss measured in leatherbacks resting in cold water (Frair *et al.*, 1972) allow one to calculate that a 134-kg marine turtle may maintain a 12°C difference between the body temperature and that of the sea. Telemetred body temperatures of the green turtle, *Chelonia mydas*, show that this moderately sized species can raise its body temperature as much as 8°C above the ambient water (Standora *et al.*, 1979; Spotila *et al.*, 1979). Mrosovsky and Pritchard (1971) calculated similar differences based on other data and showed that small turtles such as olive ridleys, *Lepidochelys olivacea*, were incapable of developing large gradients. Endothermy in *Dermochelys* may enable it to extend its range into cold water to feed and digest. Leatherbacks are quite active in water with temperatures of 6–8°C, a level that appears to be lethal to smaller species (Mrosovsky, 1980). Body temperatures of leatherbacks at tropical nesting beaches have been shown (often from egg temperatures) to be only a few degrees warmer than those of the sea (Mrosovsky and Pritchard, 1971; Sapsford and Hughes, 1978; Mrosovsky, 1980). This may indicate active thermoregulation to achieve body temperatures between 25°C and 33°C, the range preferred by most turtles (Hutchison, 1979). The higher body temperatures of large species are correlated with shorter periods between egg laying during the breeding season (Mrosovsky, 1980). However, this may not represent a significant selective advantage for the larger species, because the larger species tend to lay fewer eggs per season (Hirth, 1980).

It has been proposed that some sea snakes, especially the black-backed *Pelamis platurus*, bask while floating on the surface and dive to cool off, but no significant thermoregulatory behaviour has been demonstrated (Graham, 1974a; Kropach, 1975). At best, *Pelamis* will be only 2.4°C above ambient water temperature (Dunson and Ehlert, 1971). Because most sea

snakes tend not to leave the water and none is known to hibernate, they are restricted to relatively warm tropical waters (Dunson, 1975a). The most widespread species, *Pelamis*, is rarely found in water cooler than 18–20°C at the surface and its upper lethal temperature is about 33°C which is surprisingly low (Dunson and Ehlert, 1971; Graham *et al.*, 1971).

Marine iguanas bask on land and then maintain selected body temperatures of about 35–37°C (Bartholomew, 1966; Bartholomew *et al.*, 1976). However, during foraging trips at sea, the body temperature drops nearly to water temperature (about 25°C) and the rate of drop depends on body size (Mackay, 1964; Bartholomew, 1966). Unlike most reptiles, this lizard thus becomes most active at temperatures considerably below the preferred temperature. Nevertheless, foraging activity is thought to require a relatively small fraction of its time (Gleeson, 1979).

VI. Energetics and Metabolism

A. ROLE OF ANAEROBIOSIS UNDER NATURAL CONDITIONS

As they have metabolic rates appropriate to low energy exchange (Pough, 1980b), reptiles seem well-suited for long periods of breath-holding. Long dives may be accomplished aerobically and the diver avoids long lasting acid–base disturbances and less efficient intermediary metabolic pathways such as gluconeogenesis. Anaerobic dives can also be energetically wasteful because lactate may be lost in the urine (Jackson and Silverblatt, 1974). Therefore, if a reptile dives repeatedly, it incurs a selective advantage in aerobiosis. Until recently much of the work on reptiles has been clouded by preconceptions based on diving birds and mammals and there has been little effort to relate laboratory experiments to the natural history of the various species. Thus the long, forced, experimental dives caused circulatory and metabolic responses that may only rarely occur in nature.

Only a few studies have assessed the role of anaerobiosis during naturally occurring activities of reptiles. These rely on analysis of blood or whole body lactate which, in reptiles, is almost the only anaerobic end-product (Hochachka *et al.*, 1975; Bennett, 1978).

There is now good evidence that hibernating turtles engage in significant anaerobic metabolism under undisturbed laboratory and quasi-field conditions. Total body lactate is uniformly low (about 1–3 mmol/kg) in *Chrysemys picta* resting in air and diving voluntarily in laboratory and outdoor pools in summer at about 25°C (Gatten, 1981). However, turtles placed in an outdoor pool in winter, progressively build up extremely high body lactate (over 62 mmol/kg) over the period of about two months when the water temperatures may range from 0 to 8°C and ice may cover the water

for much of the time. The turtles do not breathe but occasionally move about on the bottom. These results confirm the postulated adaptive value for extreme tolerance of anaerobiosis by turtles. Several other species of freshwater turtles are known to hibernate for protracted periods under ice or buried in mud (Carr, 1952; Wood *et al.*, 1975; Carroll and Ehrenfeld, 1978), conditions under which hypoxia may be severe enough to prevent non-pulmonary O₂ uptake. However, *C. picta* shows a distinct shift towards anaerobiosis during the winter regardless of whether they are in water or air. It is likely that marine turtles (*Chelonia agassizi*, *Caretta caretta*, and possibly others) engage in anaerobiosis when dormant, but there are no supporting physiological data (Felger *et al.*, 1976; Carr *et al.*, 1980/81).

The role of anaerobiosis in sea snakes has been assessed from blood samples from four species that were swimming and diving in the Philippine seas (Seymour, 1979). In 16 specimens, the lactate concentration (0.5–3.8 mmol/l) was characteristic of resting snakes, but two *Laticauda laticaudata* had exceptionally high values (12.2 mmol/l). In light of data on diving frequency and the persistence of lactate in the body, these two snakes provide evidence that dives involving severe anaerobiosis do occur naturally, but infrequently, possibly every 100–200 dives. The circumstances associated with those dives and the cause of the anaerobiosis, anoxia or strenuous activity are unknown. Field records show that submergence times of sea snakes average about 15 min at 23–28°C (Heatwole, 1975) and voluntary dives of this duration are aerobic in the laboratory (Seymour and Webster, 1975).

Cruise swimming in the Galapagos marine iguana, *Amblyrhynchus cristatus*, appears to be supported aerobically, but experimental burst swimming and forced submersion results in a lactate burden (Bartholomew *et al.*, 1976). However, field-captured marine iguanas, returning to shore from foraging areas beyond the surf, had blood lactate levels similar to those in resting animals (1.5 mmol/l; Gleeson, 1980a). Normal foraging dives in the marine iguana last about 2–6 min (Hobson, 1965, 1969; Carpenter, 1966; Bartholomew *et al.*, 1976). The lungs of the marine iguana contain enough O₂ to satisfy aerobic metabolism during these short foraging dives (White and Ackerman, MS), but escape dives of 20–30 min might involve anaerobiosis. The capacity for aerobic or anaerobic metabolism of the marine iguana is no greater than are those of wholly terrestrial lizards (Bennett *et al.*, 1975) and if a lactate load is acquired, there is no special mechanism for its quick removal, although basking behaviour helps (Gleeson, 1980b).

Anaerobiosis during swimming and diving in marine turtles is unknown but the exertion associated with nesting in the green turtle, *Chelonia mydas*, results in moderate lactate loads (6.5 mmol/l), although the work is often

broken by periods of rest and the blood remains well oxygenated (Jackson and Prange, 1979). Aerobic metabolic rate increases about tenfold during this terrestrial activity.

Several species of lizard may naturally seek refuge by diving into water and enduring anoxic anaerobiosis. *Iguana iguana*, for example, may remain submerged for 50–270 min and tolerate blood lactate loads up to about 35 mmol/l (Moberly, 1968).

It has been suggested that some water snakes (*Nerodia rhombifera*) employ anaerobic metabolism during escape activity but not during normal feeding behaviour which does not appear to be very strenuous (Gratz and Hutchison, 1977).

The total metabolic rate of reptiles appears to remain fairly constant during tranquil aerobic dives. The rate of heat production by *Pseudemys scripta*, measured by direct calorimetry, remains stable during the first 20–25 min of a forced submersion at 24°C (Jackson and Schmidt-Nielsen, 1966; Jackson, 1968). During this time O₂ is available in the lung and blood. However, when the O₂ supply runs low, anaerobic metabolism becomes important and heat production quickly declines to about 40% of the aerobic value. Thereafter, heat production slowly drops to about 15% during dives lasting as long as 7 h. Interestingly, a low and constant level of O₂ is maintained in the body throughout the latter part of the dive. These turtles can maintain aerobiosis until lung P_{O₂} drops to very low values (12–35 mmHg) and stable rates of O₂ consumption are maintained at inspired P_{O₂} above 38 mmHg (Jackson, 1973).

Although Irvine and Prange (1976) suggested that metabolism is reduced during voluntary breath-holding in water snakes, *Nerodia taxispilota*, their data for O₂ consumption are difficult to interpret. When Gatten (1980) compared the rate of O₂ consumption of the snapping turtle, *Chelydra serpentina*, during voluntary breathing in air and in water, there was no difference in cold acclimated animals but a slight (about 16%) decrease in warm acclimated animals in water. The difference might be accounted for by differences in behaviour or costs of ventilation.

In forcibly submerged alligators, pulmonary O₂ content dropped to about 70 mmHg in the first 20 min (Andersen, 1961). This is near the critical limit for stable O₂ consumption in alligators (Boyer, 1966). Because normal field diving times of alligators are 5–7 min (Smith *et al.*, 1974), it is clear that routine dives are aerobic. The Nile crocodile, *Crocodylus niloticus*, normally dives for 7–15 min in the field (Cott, 1961) and is probably also aerobic most of the time.

B. ADAPTATION TO ANAEROBIOSIS

Although routine dives appear to be aerobic, some reptiles inevitably

engage in anaerobic metabolism during long or strenuous dives. Anaerobiosis is almost completely supported by glycolysis; poisoning of the glycolytic pathway with iodoacetic acid results in the quick death of anoxic turtles (Belkin, 1962; Jackson, 1968). Anaerobiosis due to prolonged anoxia in turtles is supported by endogenous and exogenous sources of carbohydrate. Cardiac glycogen stores of *Chrysemys picta*, although ten times the levels in mammals, are quickly exhausted and heart activity is supported by blood glucose, presumably formed from liver and skeletal muscle glycogen reserves which decline much more slowly (Daw *et al.*, 1967). Continued circulation is essential for long survival during experimental anoxia because it either supplies exogenous substrate or carries away toxic metabolites (Belkin, 1968b). In *Pseudemys scripta*, liver glycogen is ultimately used anaerobically (Clark and Miller, 1973) and in some species, blood lactate can exceed 100 mmol/l (Johlin and Moreland, 1933).

Lactate may be held in the muscles by local ischaemia and released during recovery or it may leak into the circulation during a dive (Andersen, 1961; Murdaugh and Jackson, 1962; Robin *et al.*, 1964; Berkson, 1966; Hochachka *et al.*, 1975; Seymour and Webster, 1975). During the several hours of recovery, the lactate declines in the blood. There is little information on the fate of this lactate. In *Nerodia rhombifera*, much of it appears to be converted into glucose (gluconeogenesis) in the liver (Gratz and Hutchison, 1977). The glucose then travels back to the muscle where it is stored as glycogen.

Analysis of the activities of glycolytic enzymes supports the contention that reliance on anaerobic metabolic pathways is not closely related to diving behaviour in reptiles. Because analytic techniques differ, it is impossible to compare the results of different studies. However, two studies involve identical techniques to examine lactate dehydrogenase, hexokinase, phosphorylase, and phosphofructokinase activities in 11 species of snakes from different habitats (Baldwin and Seymour, 1977; Seymour *et al.*, 1981a). Totally aquatic snakes appear on both ends of a wide range of anaerobic capability; the highly active and deep diving sea snakes (*Hydrophis* spp.) have the highest capability and the extremely sluggish file snakes (*Acrochordus* spp.) have the lowest. Thus, patterns of behavioural activity are best reflected in enzyme activity.

The capacity for aerobic or anaerobic energy production (metabolic scope) is not well correlated with diving behaviour. For example, terrestrial reptiles rely greatly on anaerobic energy metabolism during strenuous activity in air (Bennett, 1978). Aerobic and anaerobic metabolic scope are similar in aquatic and terrestrial turtles (Gatten, 1974). Tolerance of anoxia in reptiles is not related to diving behaviour in any consistent way (Belkin, 1963; Baeyens *et al.*, 1980).

VII. Respiration and Circulation

A. VOLUNTARY DIVING

1. *Patterns of Ventilation*

Ventilation in aquatic and terrestrial reptiles has received considerable attention. Wood and Lenfant (1976) review the characteristics of ventilation in reptiles and point to considerable variability, both within and among individuals. Breathing in most reptiles may be generally described as apneic; episodes of diaphasic air flow are separated by breath-holding of variable duration (Randall *et al.*, 1944; Gans and Clark, 1978). Most patterns of ventilation may be described as terrestrial or aquatic (Fig. 3). Breathing rhythm is generally faster and more regular in terrestrial species. The apneic periods tend to be longer in aquatic species and this, of course, is valuable because it reduces the breathing effort in a submerged reptile that must travel to the surface. Many aquatic species take several breaths in a breathing episode (McCutcheon, 1943; Belkin, 1964; Lenfant *et al.*, 1970a; Naifeh *et al.*, 1970a; Jackson, 1971b; Pough, 1973; Burggren, 1975; Glass and Johansen, 1976, 1979; Heatwole, 1977b; Lucey and House, 1977; Glass *et al.*, 1978; Gratz, 1978; Burggren and Shelton, 1979; Seymour *et al.*, 1981a; among others), but this is not always the case. Marine turtles and sea snakes commonly take only one breath on each trip to the surface (Tenney *et al.*, 1974; Heatwole, 1975; Jackson *et al.*, 1979; Seymour *et al.*, 1981b). In some aquatic species, the pattern of long apneic periods and multiple breaths is maintained both in and out of water (McCutcheon, 1943; Gaunt and Gans, 1969a; Burggren, 1975; Heatwole, 1977b; Jackson *et al.*, 1979),

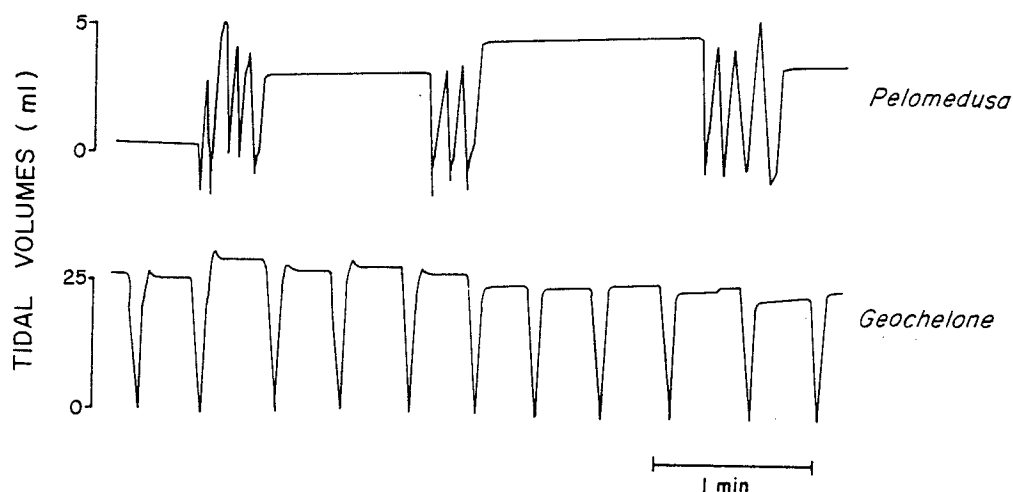


FIG. 3. Patterns of ventilation in an aquatic (*Pelomedusa subrufa*) and a terrestrial (*Geochelone pardalis*) turtle. From Glass *et al.* (1978).

but in others, such as semi-aquatic snakes, breathing may switch from an aquatic to a terrestrial pattern as appropriate (Heatwole, 1977b; Gratz, 1978).

Both inspiration and expiration are active processes in turtles (Gans and Hughes, 1967), snakes (Rosenberg, 1973), and crocodilians (Naifeh *et al.*, 1970b; Gans and Clark, 1976). In water, the hydrostatic pressure facilitates expiration and hinders inspiration. Breathing in *Chelydra serpentina* is shallow and rapid when the body is at the surface but is deep and infrequent when the body is deeper in the water (Gaunt and Gans, 1969a). Hydrostatic pressure also affects ventilation in *Caiman crocodilus* (Gans and Clark, 1976).

The deeper a reptile dives, the more likely it is to show prolonged apneic periods. A summary of diving times of aquatic reptiles indicates that submergence tends to be long in deep diving sea snakes (Heatwole, 1975). Sea snakes in the laboratory and the field commonly remain submerged for 5–30 min, but on occasion dives lasting up to about 2 h have been observed. Some of these snakes may spend about 10 min just travelling between the bottom and the surface of the sea (Heatwole and Seymour, 1975b).

Some aquatic reptiles exhibit high tidal volumes. In *Acrochordus javanicus* the tidal volume averages over 50% of the lung volume (Standaert and Johansen, 1974; Glass and Johansen, 1976). It is about 33–90% in the marine turtle, *Chelonia mydas* (Tenney *et al.*, 1974; Jackson *et al.*, 1979), and up to about 80% in some sea snakes (Seymour and Webster, 1975; Seymour *et al.*, 1981b). On the other hand, tidal volumes are often low (about 10% of lung volume) in many freshwater turtles (Jackson, 1971b; Jackson *et al.*, 1974; Glass *et al.*, 1978) and crocodilians (Naifeh *et al.*, 1970a).

Long breath-holding sometimes correlates with generally high extraction coefficients in aquatic reptiles. *Pseudemys scripta* may extract 52% of the inspired O₂ (Jackson, 1971b) and *Acrochordus javanicus* about 35% (Glass and Johansen, 1976). This compares with 14–30% in terrestrial snakes and lizards (Dmi'el, 1972; Bennett, 1973a). However, the air convection requirements (alveolar ventilation rate/O₂ consumption rate) are similar in aquatic (*Pelomedusa subrufa*) and terrestrial (*Geochelone pardalis*) turtles (Glass *et al.*, 1978).

2. Cardiovascular Changes during Intermittent Ventilation

Gas exchange is more effective and is accomplished with the least energy expenditure if the convection of gases to and from both sides of the respiratory surface are well matched (West, 1977). Thus the pronounced periodicity of ventilation in some aquatic reptiles is accompanied by large changes in pulmonary perfusion (White and Ross, 1966; Johansen *et al.*, 1970; Shelton and Burggren, 1976; Burggren, 1977a; Burggren *et al.*,

1977a). Variation in pulmonary blood flow is less evident in terrestrial reptiles that breathe more regularly (Burggren *et al.*, 1977a; Burggren, 1977b). The response is often related to changes in cardiac rate but not necessarily so. There is evidence of resistance changes in the pulmonary outflow tract of the turtle and snake heart (Burggren, 1977a, 1977b), which are possibly responsive to different patterns of ventricular depolarization controlled by the vagus (White, 1968, 1969; Burggren, 1978). Alternatively, pulmonary resistance might be controlled more distally in the large pulmonary arteries of turtles (White, 1976) or in the small arteries or arterioles of aquatic snakes (Fig. 4). Although the response is mediated cholinergically, the stimulus is unclear. Pulmonary blood flow increases with ventilation even when there is no O₂ in the inspired gas (Boyer, 1963; White and Ross, 1966). Stretch receptors in the lung have been implicated in *Pseudemys scripta*, but they do not provide the complete answer. Thus almost identical changes in cardiac rate and pulmonary blood flow can be achieved by withdrawing about 50% of the lung volume through a catheter or by collapsing the lung only 7% during submergence in 75 cm of water (Johansen *et al.*, 1977). Reversible changes in cardiac rate occur with changes in the pulmonary volume of crocodilians and sea snakes (White, 1968; Seymour, 1978). Changes in cardiac rate and, presumably, pulmonary blood flow are often observed before the animal breathes or even moves towards the surface (Boyer, 1963; Belkin, 1964; Gaunt and Gans, 1969b; Johansen *et al.*, 1970; Pough, 1973; Burggren, 1975; Heatwole, 1977a). Such "anticipatory" changes suggest the possibility of voluntary control.

The increase in heart rate, tachycardia, that often accompanies breathing episodes should not be confused with the release of bradycardia after forced dives. Both terms describe changes relative to the normal heart rate. In aquatic reptiles, however, it is difficult to specify the normal rate. Discussion of this problem by various authors (Belkin, 1964; Gaunt and Gans, 1969a, b; Burggren, 1975; Heatwole, 1977a, 1978; Heatwole and Seymour, 1976) leads to these operative definitions: (1) "tachycardia" describes the increase in heart rate accompanying ventilation or muscular activity in reptiles during voluntary and usually aerobic dives, (2) "bradycardia" is reserved for pronounced slowing of the heart during forced or anaerobic dives when there is severe peripheral vasoconstriction and muscle ischaemia. The normal rate, therefore, is that prevailing during voluntary apnea.

Ventilation tachycardia is common, but not universal, among aquatic reptiles. It has been measured in various turtles (Gaunt and Gans, 1969a; Burggren, 1975; Shelton and Burggren, 1976; Johansen *et al.*, 1977; Kinney *et al.*, 1977; Lucey and House, 1977; Ackerman and White, 1979), lizards (Bartholomew and Lasiewski, 1965; Millard and Johansen, 1974; Wood and Johansen, 1974), snakes (Pough, 1973; Heatwole and Seymour, 1975b,

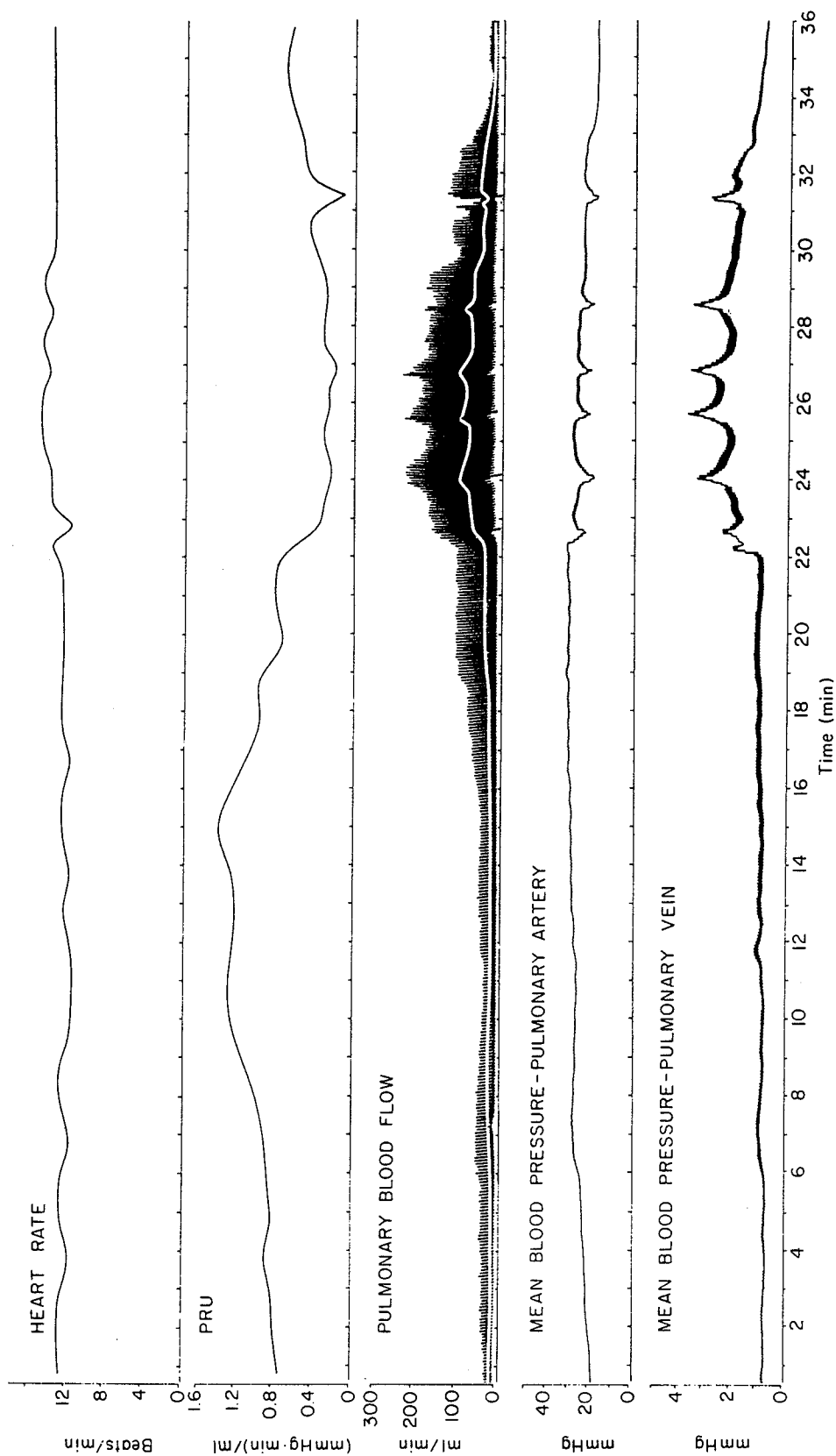


FIG. 4. Cardiovascular changes in the aquatic snake, *Chersydrus arafurae*, during voluntary apnea and ventilation. Blood pressures were measured in the pulmonary vessels distal to the common artery and vein. Pulmonary flow (mean in white) was measured by a Doppler flow cuff on the common pulmonary artery. Peripheral resistance units (PRU) and heart rate were calculated from the flow and pressure records. Six breaths were taken during the breathing episode (R. S. Seymour, unpublished).

1976; Irvine and Prange, 1976; Jacob and McDonald, 1976; Heatwole, 1977a; Heatwole *et al.*, 1979; Baeyens *et al.*, 1980), and crocodilians (Andersen, 1961; Huggins *et al.*, 1969, 1970; Gaunt and Gans, 1969b). However, in some species it is not obvious (Burggren, 1975, 1977b; Shelton and Burggren, 1976; Burggren *et al.*, 1977a; Fig. 4).

Associated with the changes in pulmonary blood flow during intermittent ventilation are variations in the pattern of flow through the heart. There can be variable amounts of mixing in the heart; left-to-right and right-to-left shunting often relates to the state of ventilation in aquatic species (White, 1970, 1976). Although estimates of shunting vary tremendously among studies, the common response seems to be one of considerable left-to-right shunting during ventilation (whereby some oxygenated blood is recirculated to the lung) and the appearance and increase of right-to-left shunting during apnea (Steggerda and Essex, 1957; Millen *et al.*, 1964; White and Ross, 1966; Shelton and Burggren, 1976; Burggren *et al.*, 1977a; Burggren and Shelton, 1979). Changes in shunt pattern may be more extreme in aquatic turtles than in terrestrial ones (Burggren and Shelton, 1979), but variability in the data prevents a definite conclusion. The adaptive value of right-to-left shunting may be that it metres O_2 out of the lung at rates appropriate to the metabolic demands of the animal and allows the heart to expend less energy perfusing the lung. The role of left-to-right shunting has not been adequately explained. While it may favour complete oxygenation of that part of the blood affected by diffusion limitation and anatomical shunts in the lung (see Crawford *et al.*, 1976; Seymour, 1978), surely the replenishment of O_2 stores in the body would be more quickly attained if the most deoxygenated blood were exclusively supplied to the lung (Johansen, 1972).

Despite some intraventricular shunting during the ventilation cycle, there is now good evidence for a high degree of separation of oxygenated and deoxygenated blood and reasonable equality of flow in the systemic and pulmonary circuits in most reptiles breathing voluntarily (Lenfant *et al.*, 1970a; White, 1970, 1976; Shelton and Burggren, 1976; Kinney *et al.*, 1977; Seymour, 1978). Large right-to-left shunts, including complete pulmonary bypass, normally develop only during long asphyxic dives when there is little O_2 to be gained from the lung (Millen *et al.*, 1964; White and Ross, 1966; White, 1969). However, the totally aquatic sea snakes consistently show right-to-left shunts that amount to about 50–70% the total systemic cardiac output, even when there is considerable O_2 in the lung. The distribution of blood flow in sea snakes has been measured with techniques involving dissolved gases in the blood (Seymour and Webster, 1975; Seymour, 1978) and injected radioactive particles (Seymour *et al.*, 1981b). The magnitude of pulmonary bypass observed in sea snakes has been linked

with cutaneous gas exchange (Section X). These snakes may be exceptional also because the pulmonary bypass appears to diminish when the O_2 supply in the lung becomes too low to saturate the blood (Seymour and Webster, 1975).

3. Cyclic Gas Exchange

A major consequence of intermittent ventilation is that the changes in the composition of lung gases during apnea progressively reduce the gradients of respiratory gases across the lung. Aquatic reptiles with characteristically long apneic periods, therefore, show changes in the exchange of O_2 and especially of CO_2 during the interbreath period. Because CO_2 is quite soluble in blood, it tends to build up there during apnea and the rate of O_2 recruitment from the lung does not parallel the rate of CO_2 loss into the lung. This inequality is observed as a decline in the gas exchange ratio measured by analysing pulmonary P_{CO_2} and P_{O_2} (Fig. 5). The effect is an

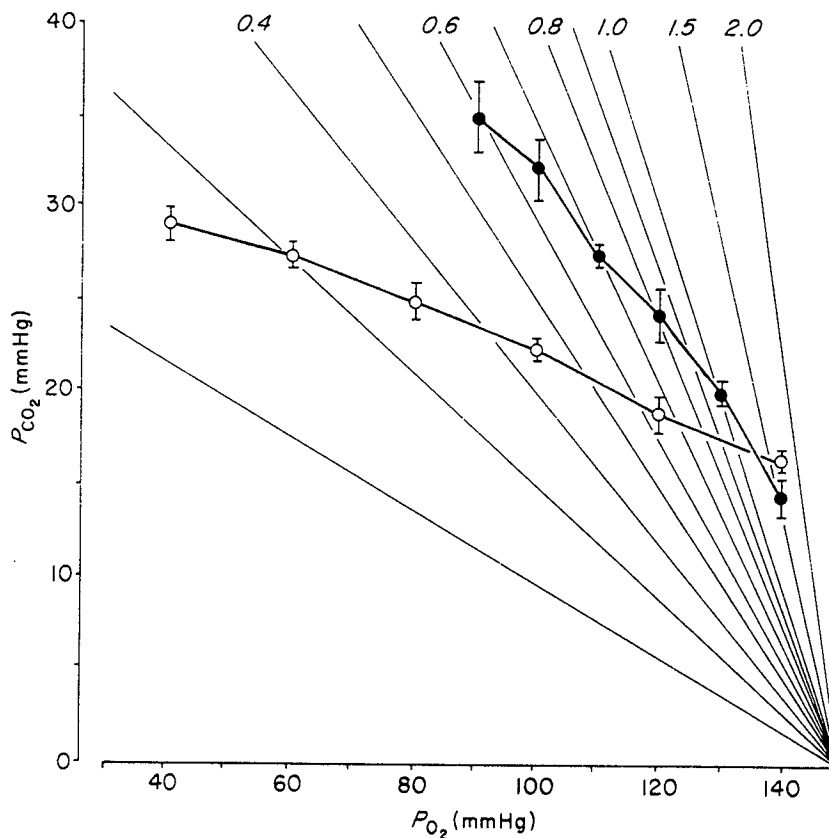


FIG. 5. Pulmonary gas tensions during voluntary ventilation and apnea in *Pseudemys scripta* (open circles) and *Testudo graeca* (solid circles). The gas exchange ratio (evaluated by the numbered lines) is initially high after ventilation and progressively declines during apnea. Lower exchange ratio in *P. scripta* is attributed to higher cutaneous CO_2 loss in this species. Data from Burggren and Shelton (1979).

inevitable consequence of breath-holding in vertebrates (Mithoefer, 1965), but it becomes particularly obvious in aquatic reptiles such as turtles (Wilson, 1939; Berkson, 1966; Lenfant *et al.*, 1970a; Ackerman and White, 1979; Burggren and Shelton, 1979), crocodilians (Andersen, 1961; Glass and Johansen, 1979), snakes (Seymour and Webster, 1975; Seymour *et al.*, 1981a), and marine iguanas (White and Ackerman, 1981a). The effect is analysed in detail by Ackerman and White (1979) and Burggren and Shelton (1979).

The removal of O_2 from the lung tends to concentrate the CO_2 in the pulmonary gas. This may reverse the CO_2 gradient across the lung and the P_{CO_2} may be higher in the pulmonary vein than in the pulmonary artery. Such a reversal has been observed in *Chelus fimbriatus* (Lenfant *et al.*, 1970a) and *Acrochordus arafurae* (Seymour *et al.*, 1981a).

Because so much CO_2 is held in the blood and tissues and a single breath only rids the animal of the CO_2 in the lung, we can see the value of multiple breaths within a single breathing episode (Fig. 3). In *Acrochordus arafurae* the breathing episodes are co-ordinated with pulmonary blood flow so that almost all of the blood volume of the snake is passed through the lung during the episode (Seymour *et al.*, 1981a). During the conspicuous pauses between the breaths of each episode, CO_2 is allowed to build up in the lung. Meanwhile the arterial and venous O_2 stores are replenished and the snake may begin a long apnea with both the lung and blood rich in O_2 . Analysis of end-tidal gas in the Nile crocodile, *Crocodylus niloticus*, and the aquatic turtle, *Pelomedusa subrufa*, show that the respiratory exchange ratio increases from breath to breath of a given episode; this indicates that the rate of O_2 exchange varies much more than the rate of CO_2 exchange during ventilation (Glass *et al.*, 1978; Glass and Johansen, 1979).

Some aquatic reptiles appear to be capable of adding urinary CO_2 loss to pulmonary and cutaneous loss. *Crocodylus porosus* in fresh water can eliminate over one-third of its total CO_2 production as urinary ammonium bicarbonate (Grigg, 1978). This accounts for a low respiratory quotient in *C. porosus* and possibly in *C. niloticus* (Glass and Johansen, 1979). It is not clear whether this could occur in salt water reptiles that have low rates of urine production.

4. Oxygen Reserves and Breathing Stimuli

It is often inferred that diving reptiles use most of their O_2 stores before being stimulated to rise to the surface and breathe. However, there is little evidence from voluntarily diving reptiles to support this idea. In fact, most species breathe with a surprising amount of O_2 remaining in the lung and blood. *Pseudemys scripta* breathes when the lung P_{O_2} is above 80 mmHg and uses much less than one-half of its reserve (Burggren and Shelton, 1979).

Hydrophiid sea snakes use about one-half of their reserves (Seymour and Webster, 1975). Although the pulmonary P_{O_2} may drop to 30 mmHg in *Acrochordus javanicus* (Standaert and Johansen, 1974), the high Hb- O_2 affinity of the blood and the large blood volume indicate that less than one-half of the reserve is used (Seymour *et al.*, 1981a; Feder, 1980). In *Chelus fimbriatus*, breathing occurs when the blood is more than 80% saturated (Lenfant *et al.*, 1970a). The pulmonary reserves are always high in *Crocodylus niloticus* (Glass and Johansen, 1979). However, O_2 reserves in *Varanus niloticus* are severely depleted during laboratory dives (Wood and Johansen, 1974). In the last case, the pattern may be characteristic of "escape" and "threat" dives that also occur in *Iguana iguana* (Moberly, 1968) and *Amblyrhynchus cristatus* (Bartholomew *et al.*, 1976).

In view of the relatively high O_2 reserves in the blood and lung, it seems doubtful that myoglobin could ever be a functional O_2 source during normal dives. Low concentrations of myoglobin in the skeletal muscles of diving reptiles have been inferred from the colour of the muscles (Berkson, 1966; Dawson *et al.*, 1977). Myoglobin concentration is much lower in *Chersydrus arafurae* (0.22 mg/g) (Seymour *et al.*, 1981a) than in three species of terrestrial snake (0.38–1.85 mg/g; Ruben, 1976). Myoglobin concentration appears to be related to aerobic metabolic scope and is known to facilitate O_2 uptake by the tissues (Scholander, 1960).

Both aquatic and terrestrial reptiles are sensitive to O_2 and CO_2 (Wood and Lenfant, 1976) but it is not known which gas is primarily responsible for stimulating breathing. In some aquatic species, such as *Chelus fimbriatus* and *Acrochordus javanicus*, hypoxia is implicated because high inspired P_{CO_2} did not increase ventilation rate and dives are prolonged following breaths of pure O_2 (Lenfant *et al.*, 1970a; Glass and Johansen, 1976). Other aquatic species respond to changes in both CO_2 and O_2 in the experimental breathing mixture (Frankel *et al.*, 1969; Jackson, 1973; Jackson *et al.*, 1974; Glass *et al.*, 1978; Glass and Johansen, 1979; Gratz, 1979). Jackson *et al.* (1974), however, suggested that little correlation existed between the responses to inspired CO_2 and the buildup of CO_2 in the lung during a dive. Indeed, in some sea snakes, pulmonary and arterial P_{CO_2} are remarkably constant during voluntary breath-holds because of buffering of CO_2 in the body and non-pulmonary CO_2 loss (Seymour and Webster, 1975). This observation indicates that an hypoxic stimulus is important in sea snakes.

B. FORCED DIVING

Forced dives may be artificial extensions of voluntary dives or immediate involuntary submersions of restrained animals. The differences between voluntary and forced dives are so striking that it is no longer valid to assume

that submergence *per se* results in a uniform suite of responses in reptiles. In fact, the mere presence of investigators can dramatically alter the pattern of circulatory and respiratory responses to so-called voluntary dives in the laboratory (Gaunt and Gans, 1969b; Irvine and Prange, 1976). The role of these forced responses in the natural history of aquatic reptiles is not known. They may be reserved for crucial circumstances involving escape, conflict, or predation under water.

The literature on cardiovascular physiology associated with forced and voluntary dives in reptiles has recently been reviewed (White, 1976). In brief, forced dives are usually accompanied by severe bradycardia, increased peripheral resistance, muscle ischaemia, and anaerobic metabolism as indicated by high blood lactate persisting hours after the dive. The development of these aspects of the "diving response" varies from species to species and from dive to dive. Bradycardia may occur quickly or slowly and lactate may appear in the blood during the dive or after the first breath. Right-to-left intraventricular shunting increases and can lead to a complete pulmonary bypass.

Although more emphasis has been placed recently on voluntary dives, a few studies have confirmed the picture of forced diving (Jackson and Silverblatt, 1974; Seymour and Webster, 1975; Irvine and Prange, 1976; Baeyens *et al.*, 1980). Free ranging alligators equipped with radio transmitters to monitor heart rate show severe diving bradycardia when disturbed by man, but no bradycardia during natural dives (Smith *et al.*, 1974).

VIII. Diving Depths and Hydrostatic Pressure

Most diving reptiles inhabit the margins of water bodies and probably do not dive very deep. However marine turtles and snakes are known to dive to depths that have profound effects on the pressures of lung gases and the fluxes of dissolved gas in the body. Hydrostatic pressure increases approximately one atmosphere (ATA) every 10 m of depth and therefore the marine species that dive with air in the lung cannot avoid exceptionally high pulmonary gas tensions. Loggerhead turtles, *Caretta caretta*, and Pacific green turtles, *Chelonia mydas*, have been captured or observed at depths ranging to 290 m (Landis, 1965; Berkson, 1967). Some species of sea snakes have been observed at about 40 m, and others are presumed to dive to about 100 m because they feed on fish at that level (Heatwole *et al.*, 1978; Heatwole and Seymour, 1975b).

In comparison to the bulk of information on the physiological changes associated with deep diving in mammals, there is little comparative information from other vertebrates. Experimental work from reptiles is

limited to two studies which involved subjecting Pacific green turtles and sea snakes to high hydrostatic pressure in hyperbaric chambers. Nevertheless these studies are sufficient to identify pronounced differences among mammalian and reptilian divers.

In green turtles compressed to as much as 19 ATA, P_{O_2} and P_{N_2} were always considerably less in the blood than in the lung (Berkson, 1967). Similarly, P_{O_2} in the systemic arterial blood of three sea snake species was far from levels in the lung (Seymour, 1978). This non-equilibrium between lung and blood apparently results from right-to-left shunting of systemic venous blood past the gas exchange surface. At surface pressure the high shunt in hydrophiid sea snakes results in the aortic blood being only 30–70% saturated with O_2 (Seymour and Webster, 1975; Seymour, 1978).

Surprisingly, the Hb- O_2 saturation in the aortic blood of *Hydrophis belcheri* and *H. ornatus* is independent of depth. Despite compression up to 5.1 ATA, a pressure causing the pulmonary P_{O_2} to rise above 500 mmHg, the blood P_{O_2} remains below 50 mmHg and the saturation less than 80%. Progressive lung collapse causes the difference in P_{O_2} between the lung gas and the pulmonary veins to increase. Aside from the development of these intrapulmonary shunts, there exists the possibility that increased pulmonary resistance leads to increased intraventricular shunts in *Hydrophis*. Thus the collapse of the lung with hydrostatic pressure not only increases the pulmonary gas tensions but also increases pulmonary bypass in proportion, the result being virtual independence of arterial P_{O_2} and depth. The extent to which this effect is strictly mechanical or mediated neurophysiologically is not known, but the adaptive value is clear in these sea snakes that can take up O_2 cutaneously. Because the skin is supplied with systemic arterial blood and the diffusion of dissolved gases is related to the partial pressure gradient across the skin (Section X), cutaneous O_2 uptake is possible only if the internal P_{O_2} is less than the P_{O_2} in the sea water. The low saturation of arterial blood passing to the skin maintains a low internal P_{O_2} as O_2 is taken up. If the arterial blood became saturated by hydrostatic compression of the lung, cutaneous uptake would decrease and, indeed, O_2 could be lost to the sea water. Deep diving behaviour and cutaneous gas exchange would be incompatible was it not for the effect observed in these snakes.

The isolation of arterial blood from lung gas may protect deep diving reptiles from formation of bubbles in the blood during decompression. A lungful of air contains enough N_2 to saturate the tissues to dangerous levels and, in any case, repeated breath-hold dives to depths below about 25 m can gradually build up N_2 concentration in blood and tissues (Paulev, 1965). Berkson (1967) demonstrated lower P_{N_2} in the blood than in the lung of green turtles and suggested that lung collapse somehow reduced the

invasion rate of N_2 into the blood, possibly by venous shunting or by thickening of the lung walls or by compression of the gas into the non-exchange areas of the lung, as in marine mammals. Nevertheless he produced fatal decompression sickness following compressions to about 19 ATA when the blood P_{N_2} reached 8–10 ATA. This effect is understandable because the threshold for bubble formation is about 3.4 ATA in sea snakes (Seymour, 1978), and about 3.3 ATA in cats (Harvey *et al.*, 1944). The data of Berkson relating blood P_{N_2} to pulmonary P_{N_2} shows that the bubble threshold would be reached at depths just less than 50 m. We do not know how these turtles are able to dive deeper.

The deep diving sea snakes might be at risk of decompression sickness were it not for their cutaneous gas exchange capability and their large right-to-left shunt that increases with depth. Both mechanisms are required to prevent buildup of N_2 in the body during the long and repeated dives of foraging snakes (Seymour, 1974). The shunt dilutes N_2 -rich blood from the lung with N_2 -poor blood from the systemic veins. Unlike O_2 which is continuously taken up by the systemic tissues, N_2 would eventually build up in the systemic veins but cutaneous N_2 loss prevents this. If either the shunt or the loss of N_2 is altered experimentally, bubbles can form in the blood. With values of shunting and cutaneous gas permeability, one can estimate the maximum possible N_2 concentrations at various depths in the shallow diving *Laticauda colubrina* and the deep diving *Hydrophis belcheri* (Fig. 6). In *Hydrophis*, a conspicuously high shunt and a high cutaneous gas permeability keeps blood N_2 considerably below the bubble threshold, even at 100 m. With its lower shunt and cutaneous permeability, *Laticauda* is in danger at depths below about 30–70 m, but it is unlikely that this species dives that deep (Heatwole and Seymour, 1975b).

There remain several unanswered questions concerning deep diving reptiles: why do green turtles die of decompression sickness in hyperbaric chambers (Berkson, 1967) at pressures (depths) less than those encountered in nature? Why does the sea snake, *Emydocephalus annulatus*, die after being brought to the surface from a depth of 20 m (M. E. Feder and G. C. Gorman, pers. comm.)? Although *Laticauda colubrina* and *Hydrophis belcheri* do not die after N_2 bubbles are experimentally produced in the blood (Seymour, 1978), do they suffer any damage? Is surface seeking behaviour, which occurs in sea snakes when the blood P_{O_2} is relatively high (Seymour and Webster, 1975), adaptive because it prevents extreme pulmonary hypoxia during decompression? How do these reptiles avoid pulmonary damage resulting from the so-called squeeze when the gas is compressed into the bronchi and trachea? What are the mechanisms by which cardiac rate and pattern of blood flow are altered by hydrostatic pressure (Berkson, 1967; Johansen *et al.*, 1977; Seymour 1978)?

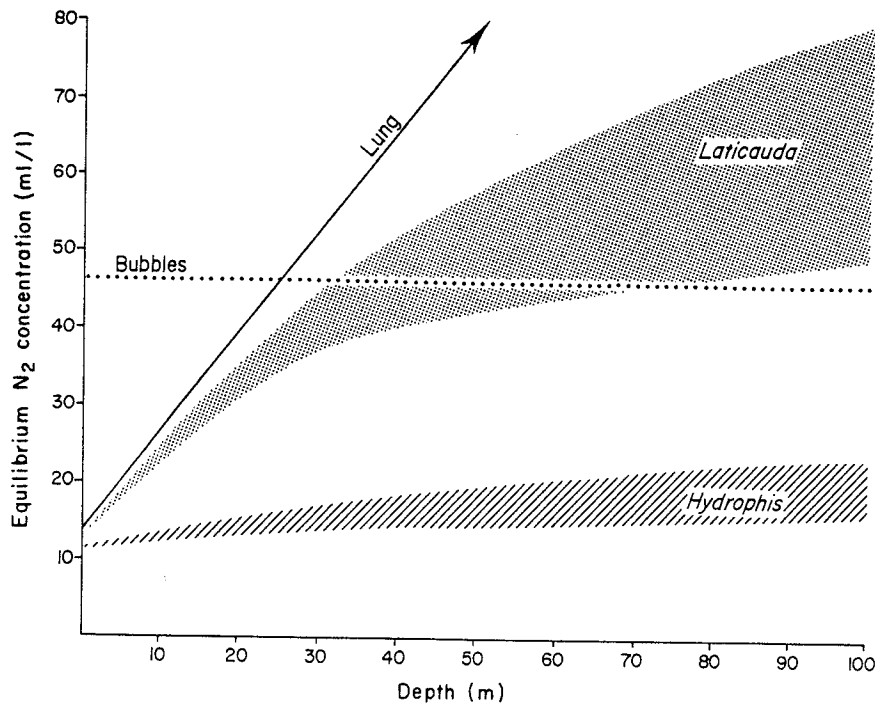


FIG. 6. Calculated maximum N_2 concentrations in the lung (diagonal line) and systemic blood (shaded ranges) of *Laticauda colubrina* and *Hydrophis belcheri* at increasing depth. The threshold for bubble formation during decompression in sea snakes and cats is near the dotted line. *Laticauda* probably dives no deeper than about 20 m but *Hydrophis* may dive to 100 m. Data from Seymour (1978).

IX. Respiratory Properties of the Blood

A. OXYGEN STORAGE

The capacity to store O_2 in the blood has an obvious advantage to any diving animal. Endothermic divers appear to store more O_2 than their terrestrial relatives (Andersen, 1966; Lenfant, 1969; Lenfant *et al.*, 1970b). Among endotherms, blood volume, O_2 capacity, and muscle myoglobin concentration tend to be significantly higher in divers. However, aquatic reptiles generally do not show these adaptations.

Data on O_2 capacity of reptilian blood show no statistical differences separating divers from non-divers (Pough, 1979). Although the mean values from crocodilians and aquatic and semi-aquatic snakes are higher than the average from all reptiles, the mean from aquatic and semi-aquatic turtles is lower than the average and lower than that of terrestrial turtles. There are no values for O_2 capacity of the blood of marine iguanas but its haematocrit of 31.5% is almost identical to the mean (32.0%) of 27 species of terrestrial iguanas (Dawson *et al.*, 1977).

Oxygen capacity is only partly useful for assessing O_2 storage in the blood. Data on the volumes of blood and the saturation in the venous and arterial sides of the systemic circulation are required but are not generally available. Dunson (1975b) suggested that the blood volumes may be higher in sea snakes than in other reptiles but the data for sea snakes (Graham, 1973, 1974b; Dunson, 1975b; Feder, 1980) overlap considerably with those for terrestrial snakes (Thorson, 1968; H. B. Lillywhite, pers. comm.). Even if sea snakes have a higher than normal blood volume, they do not take advantage of it because the saturation of the arterial blood rarely exceeds 80%, even immediately following a breath (Seymour and Webster, 1975; Seymour, 1978).

Some acrochordid snakes appear to be exceptional in their high capacity for O_2 storage. Although the blood O_2 capacity of *Acrochordus javanicus* (93 ml O_2 /l; Johansen and Lenfant, 1972) and *Chersydrus arafurae* (about 83 ml O_2 /l; Seymour *et al.*, 1981a) is near the mean for all reptiles (87 ml O_2 /l; Pough, 1979), it is about twice this value in *A. granulatus* (162 ml O_2 /l; Feder, 1980). Moreover, the blood volume of *A. granulatus*, estimated by exsanguination, is 133 ml/kg. This is probably an underestimate but it is still about twice the values for other reptiles (Feder, 1980). This high blood volume is probably contained in the conspicuously expanded veins of the body cavity (Heatwole, 1978). Because the "venous" blood is typically more than 95% saturated in *C. arafurae* (Seymour *et al.*, 1981a), it is clear that these snakes store considerable O_2 in both sides of the circulatory system.

With the possible exception of *A. granulatus*, the failure of most diving reptiles to show high O_2 capacity may be related to the effect of blood viscosity (Seymour, 1976). Because O_2 capacity is usually tied to haematocrit in reptiles, raising the haematocrit becomes disadvantageous when the accompanying viscosity reduces blood flow and O_2 transport (Snyder, 1971). The acrochordids may tolerate high haematocrits because they are typically very sluggish snakes with low O_2 demands (Heatwole and Seymour, 1975a) and low rates of blood flow (Seymour *et al.*, 1981a).

The occurrence of methaemoglobin in the blood of reptiles further confounds an analysis of O_2 storage. However, the significant amounts of this inactivated haemoglobin reported in turtles (Sullivan and Riggs, 1964), snakes (Prado, 1946), and lizards (Pough, 1969) may have been artefacts from an inappropriate technique (Gruca and Grigg, 1980). With a slight modification of technique, blood from terrestrial and aquatic reptiles shows consistently negligible methaemoglobin; furthermore the methaemoglobin reductase in reptilian erythrocytes is ample to maintain low levels (Board *et al.*, 1977).

B. Hb-O₂ AFFINITY

There has been much speculation about the adaptiveness of the position of Hb-O₂ equilibrium (dissociation) curves of terrestrial and aquatic reptiles and, as Pough (1980a) recognized, there is a tendency for physiologists to defend any value of affinity as being adaptive. The same is true for the magnitude of the Bohr effect. However, for the proper evaluation of affinity it is worthwhile to remember two facts. On one hand, a high affinity increases the P_{O_2} difference across the pulmonary exchange surface and therefore increases the rate of oxygenation of the blood. Even if blood flow through the lung is relatively rapid, as during activity or ventilation, a high affinity ensures that the blood leaving the lung has obtained the maximum amount of O₂ possible. Furthermore, with declining P_{O_2} in the lung during long breath-holding, a steep gradient for O₂ diffusion is maintained until a large fraction of O₂ has been removed from the lung. On the other hand, a low affinity tends to increase the blood-mitochondrion P_{O_2} difference and promotes a rapid rate of diffusion into the active tissues at times when the demand for O₂ is high. Thus a diving reptile might find advantage in both a high and a low affinity; the former is valuable when the P_{O_2} falls in the lung and the latter is valuable when the blood O₂ stores decline. A highly sigmoid equilibrium curve tends to maximize diffusion gradients in both the lung and body tissues. A large Bohr effect is also beneficial in this way. Nevertheless, it is clear that the Hb-O₂ affinity represents a compromise and we may view affinity as adaptive to gas transport difficulties that potentially occur at the level of the lung or the body tissues in reptiles with various life-styles.

The available evidence suggests that O₂ transport at the tissue level is severely diffusion limited in reptiles. The capillary surface area of reptilian muscle is less than one-fifth that of mammals and the average diffusion distance is about 2.5 times as great (Pough, 1980a). High levels of muscle lactate in exercising reptiles, despite abundant O₂ in the arterial and venous blood (Seymour *et al.*, 1981a), attest to diffusion limitation in the tissue. On the other hand, the thickness of the gas-blood barrier in the lungs of reptiles is similar to that in mammals and differences in the pulmonary surface area are offset by differences in rates O₂ consumption such that the mean P_{O_2} difference across the pulmonary tissue layer is similar in reptiles, birds, and mammals (Perry, 1976, 1978). Compared to resistances to pulmonary gas exchange caused by shunts and inhomogeneity of ventilation-perfusion ratio, the effect of diffusion limitation is minor (Seymour, 1978). It has been hypothesized that the generally low affinity of reptilian blood compensates for diffusion limitation in the tissues (Pough, 1980a). If this is true, and if there is no other form of compensation,

one should see a tendency for lower affinity in reptiles having high rates of O_2 consumption and high aerobic metabolic scopes. However, one must be careful when looking for trends in this direction in the available literature. Variations in experimental technique, often involving inappropriate pH or temperature, and lack of data on gas tensions and pH in the blood make comparisons between studies difficult (Wood and Lenfant, 1976). Nevertheless, the following studies employing similar techniques suggest that affinity is indeed better correlated with patterns of activity and metabolic rate than to diving behaviour.

There is no consistent relationship between affinity of whole blood and aquatic behaviour in several species of turtles (Gaumer and Goodnight, 1957; Burggren *et al.*, 1977b; Palomeque *et al.*, 1977), although selected aquatic species have low affinity (Lenfant *et al.*, 1970a; Wood and Lenfant, 1976). Data from *in vitro* solutions of turtle haemoglobin can be misleading because the values may bear no relation to affinity *in vivo* (McCutcheon, 1947; Sullivan and Riggs, 1967; Sullivan, 1974). Another source of error involved in previous comparisons among turtles is that affinity is probably related to body mass and the aquatic species examined tend to be large. In most animal groups, mass-specific metabolic rate decreases, and affinity increases, with increasing body mass.

Data from the lizards and snakes reveal a similar picture. Hb- O_2 affinity is related to body size in squamates. Affinity increases with size in lizards (Pough, 1977a) but it decreases with size in snakes (Manwell, 1960; Pough, 1977b, c, d, 1980a). Superimposed on these relationships is a clear tendency for the more behaviourally active species to have a lower affinity (Pough, 1980a), but there is no relationship between affinity and diving behaviour.

There are no data on Hb- O_2 affinity in the marine iguana, *Amblyrhynchus cristatus*, which is probably the lizard best adapted for diving. However, in other lizards that commonly use diving as an escape measure, the blood is not exceptional (Wood and Moberly, 1970; Wood and Johansen, 1974; Courtice, 1981b).

Seven species of sea snake show affinities within the 95% confidence interval for terrestrial snakes measured with the same technique (Seymour and Webster, 1975; Pough, 1977d). However, the sea snake data are all higher than the mean predicted by the terrestrial species. This indicates a weak tendency for high affinity in the hydrophiids (Heatwole and Seymour, 1975b). This tendency must be viewed cautiously because of differing blood acid-base status in the two groups. A careful comparison of the semi-aquatic sea snake, *Laticauda colubrina*, and the terrestrial elapid, *Pseudechis porphyriacus*, shows no significant difference in affinity at normal values of arterial pH (7.52 and 7.68 respectively) although at a common pH (7.6) the affinity in the sea snake is higher (Seymour, 1976).

Extremely high affinity has been found in whole blood of *Acrochordus javanicus* (Johansen and Lenfant, 1972), *A. arafurae* (Seymour *et al.*, 1981a), and *Chersydrus granulatus* (Seymour and Webster, 1975). At a circulating pH of 7.5 and at 25°C, the P_{50} is only 18 mmHg in *C. arafurae*. These extremely sluggish aquatic snakes have resting metabolic rates that are the lowest for any snake (Standaert and Johansen, 1974; Heatwole and Seymour, 1975a; Glass and Johansen, 1976) and their aerobic metabolic scope is exceptionally low (Seymour *et al.*, 1981a). Apparently these snakes do not require a high blood-tissue P_{O_2} gradient and have evolved a high affinity that is useful for quick replenishment of blood O_2 stores during their typically infrequent breathing episodes. Juvenile water snakes, *Nerodia sipedon*, and garter snakes, *Thamnophis sirtalis*, also show a moderately high affinity that decreases gradually as the snakes grow in size (Pough, 1977b, c, d, 1978). Because the young snakes are incapable of sustained activity (Pough, 1977c, 1978), their aerobic metabolic scopes are probably low.

The Bohr effect is equally difficult to interpret in relation to diving behaviour in reptiles. The aquatic acrochordid snakes, on one hand, show what may be the highest fixed-acid Bohr shifts among vertebrates, $0.94\text{--}1.47 \Delta \log P_{50}/\Delta \text{pH}$ (Johansen and Lenfant, 1972; Seymour *et al.*, 1981a), but on the other hand, the sea snakes have low or negligible Bohr shifts (Seymour and Webster, 1975; Seymour, 1976). Direct comparison of Bohr coefficients among species (Pough, 1979), however, is dangerous because the coefficients depend on the level of saturation of the Hb (R. B. Reeves, Pers. comm.; Lapennas and Lutz, MS) and on the absolute range of P_{50} over which the reptile usually operates (i.e. animals with inherently high affinity tend to yield high Bohr coefficients). Furthermore, the Bohr effect, like affinity, may vary in an unpredictable way in response to acclimation to different temperatures (Wood *et al.*, 1978; Johansen and Lykkeboe, 1979), and it is now important to distinguish between the CO_2 Bohr effect and the fixed-acid Bohr effect (i.e. the individual direct effects of CO_2 and pH on affinity). In crocodilians and marine turtles, CO_2 is a significant direct modifier of affinity (Bauer and Jelkmann, 1977; Grigg and Cairncross, 1980; Lapennas and Lutz, MS), but in other species pH is most important.

The difference between the CO_2 Bohr effect and the fixed-acid Bohr effect may be important for diving reptiles. If a diver endures a long or strenuous dive resulting in the production of CO_2 and lactic acid in the muscles, a large fixed-acid Bohr effect is beneficial because during recovery there is an increase in the rate of O_2 diffusion into the tissues (e.g. liver and muscle) in which the lactate is oxidized. At the same time, there is some decrement in O_2 gradient at the lung. However, those diving reptiles that have high Bohr effects (e.g. crocodilians and acrochordid snakes) also tend to have high inherent Hb- O_2 affinity, so that there is probably no danger of

failing to load the blood in the lung. On the other hand, if diving is totally aerobic and CO_2 is the only metabolite building up in the blood, a high CO_2 Bohr effect is beneficial because during and after the dive, the high tissue P_{CO_2} favours O_2 unloading there. During recovery, the rapid diffusion of CO_2 into the lung increases the affinity and favours O_2 loading.

The interaction between CO_2 , pH, and organic phosphates (especially ATP and GTP in reptiles) on Hb- O_2 binding needs to be studied *in vivo* during diving. All of these modifiers are related to intermediary metabolism and their values may change in the course of a dive. The curious reliance of crocodilians on CO_2 rather than pH to modify affinity may be related to their notably low concentrations of red cell organic phosphates (Bauer and Jelkmann, 1977; Bartlett, 1978, 1980; Grigg and Gruca, 1979). At high concentration, organic phosphates can inhibit the specific effect of CO_2 on affinity, but at low concentrations they may reduce the effect of pH (Duhm, 1976).

Reptiles have multiple haemoglobins (Dessauer, 1970) and differences in inherent affinity and susceptibility to the action of extrinsic modifiers are thought to account for the "unusual" shapes of equilibrium curves of whole blood. Previously, reptilian curves have been forced into the Hill and Bohr paradigms in which the Hill and Bohr coefficients, both measured at the P_{50} , are assumed to be constant throughout most of the range of saturation. Careful work on *Pseudemys scripta* (R. B. Reeves, pers. comm.) and marine turtles and snakes (Lapennas and Lutz, MS; Seymour and Webster, 1975; Seymour, 1976) shows that both coefficients may vary throughout the range of saturation. The adaptiveness of these saturation-dependent perturbations of the equilibrium curves has been proposed for aquatic reptiles (Lapennas and Lutz, MS). A lower Bohr shift and a Hill coefficient near 1 at low saturation values favour continued O_2 extraction from the lung during long dives when O_2 stores become low. Lapennas and Lutz (MS) hypothesize that this is important in divers that store most of their O_2 reserves in the lung rather than the blood, but there is no evidence from naturally diving reptiles to evaluate the importance of the effect.

C. BLOOD BUFFERS

The possible advantages of the fixed-acid Bohr effect raise questions about the adaptiveness of a high blood buffer capacity in diving reptiles. There may in fact be no adaptive value since there is no significant difference in non-carbonic blood buffer values among terrestrial ($\bar{x}=20.5 \pm 10.1$ Slykes) and aquatic and semi-aquatic ($\bar{x}=19.5 \pm 18.1$ Slykes) reptiles (Table II). Furthermore, diving turtles, which are known to withstand forced anoxia for much longer periods than do other reptiles

TABLE II

Blood buffer capacity (non-carbonate) in reptiles from terrestrial, semi-aquatic, and aquatic habitats

Species	Habitat	Buffer value (Slykes)*	Buffer** [Hb]	Reference
Turtles				
<i>Geochelone denticulata</i>	T	5.2	—	Lenfant <i>et al.</i> , 1970a
<i>Geochelone denticulata</i>	T	8.3	—	Rahn and Garey, 1973
<i>Chelus fimbriatus</i>	A	11.0	0.17	Lenfant <i>et al.</i> , 1970a
<i>Podocnemys expansa</i>	A	12.3	—	Rahn and Garey, 1973
<i>Pelomedusa subrufa</i>	A	19.0	0.27	Wood and Johansen, 1974
<i>Pseudemys scripta</i>	A	20.3	0.27	Wilson, 1939
Crocodylians				
<i>Crocodylus acutus</i>	SA	18.5	0.28	Dill and Edwards, 1931
<i>Crocodylus porosus</i>	SA	37.0	0.43	Grigg and Cairncross, 1980
<i>Alligator mississippiensis</i>	SA	20.8	0.25	Dill and Edwards, 1935
Lizards				
<i>Amphibolurus barbatus</i>	T	37.8	0.54	Wilson, 1971
<i>Egernia cunninghami</i>	T	35.1	0.43	Wilson, 1971
<i>Heloderma suspectum</i>	T	14.4	0.19	Edwards and Dill, 1935
<i>Iguana iguana</i>	T	25.0	0.30	Wood and Moberly, 1970
<i>Physignathus lesueurii</i>	T	18.5	0.25	Wilson, 1971
<i>Sauromalus hispidus</i>	T	30.7	0.42	Bennett, 1973b
<i>Sauromalus obesus</i>	T	15.2	0.19	Dill <i>et al.</i> , 1935
<i>Tiliqua scincoides</i>	T	32.0	—	Wilson, 1971
<i>Trachydosaurus rugosus</i>	T	16.1	0.24	Wilson, 1971
<i>Varanus niloticus</i>	T	18.9	0.27	Wood and Johansen, 1974
Snakes				
<i>Boa constrictor</i>	T	12.0	—	Rahn and Garey, 1973
<i>Pseudechis porphyriacus</i>	T	17.6	0.20	Seymour, 1976
<i>Laticauda colubrina</i>	SA	19.4	0.32	Seymour, 1976
<i>Acalyptophis peronii</i>	A	12.0	0.11	Seymour and Webster, 1975
<i>Acrochordus arafurae</i>	A	27.6	0.47	Seymour <i>et al.</i> , 1981a
<i>Aipysurus laevis</i>	A	14.4	0.22	Seymour and Webster, 1975
<i>Emydocephalus annulatus</i>	A	34.6	0.47	Seymour and Webster, 1975
<i>Hydrophis elegans</i>	A	19.6	0.14	Seymour and Webster, 1975
<i>Hydrophis melanocephalus</i>	A	8.8	0.10	Seymour and Webster, 1975
<i>Lapemis hardwickii</i>	A	17.6	0.15	Seymour and Webster, 1975

* mmole $\text{HCO}_3^-/\text{l} \cdot \text{pH}$.

** mmole $\text{HCO}_3^-/\text{g Hb} \cdot \text{pH}$.

(Belkin, 1963), tend to have the lowest buffer values. The buffer values of diving mammals and birds are higher than those of diving reptiles (Wood and Johansen, 1974). Most reptiles have buffer values similar to those of man (Davenport, 1969) but only one-half the haemoglobin concentration. This indicates that reptilian blood probably contains other important buffer systems, as yet unspecified. The variable importance of these systems is indicated by the variation in the haemoglobin-specific buffer value in reptiles (Table II).

The carbonic buffer system, measured as blood and body bicarbonate concentration, is available to buffer metabolic acids produced during bouts of anaerobiosis. Plasma bicarbonate tends to be considerably higher in turtles than in other reptiles, but this is true in terrestrial species as well as in divers (Dessauer, 1970). Higher plasma bicarbonate is associated with higher blood P_{CO_2} caused by infrequent breathing (Howell and Rahn, 1976).

It has been suggested that the high concentrations of bicarbonate in the large volumes of peritoneal and pericardial fluids of turtles buffer metabolic acids during anaerobiosis (Smith, 1929; Murdaugh *et al.*, 1962). However the bicarbonate accounts for only a small fraction of the total buffer capacity of the body in *Pseudemys scripta* (Jackson and Silverblatt, 1974).

X. Non-pulmonary Gas Exchange

The ability to exchange gases with water is of such significant adaptive value that it appears in aquatic representatives of practically every major animal group (except the endotherms). Because an effective aquatic gas exchanger must have the appropriate area and thickness to meet the metabolic demands of the animal, the thick, cornified skin that has contributed to the success of terrestrial reptiles at first appears to prevent aquatic gas exchange and make all reptiles obligate air breathers. Permeability of the integument is doubtless an evolutionary compromise between many selective forces. On one hand, high permeability to dissolved gas lengthens the dives and reduces the energy required for breathing. On the other, a thin integument potentially imposes osmotic and ionic stresses and offers less protection than a hard armour. The interrelationships between these factors and others, such as temperature, metabolic rate, diving depths and times, ambient gas tensions, and availability of air, have not been adequately examined.

There is now good evidence that certain turtles and snakes can satisfy a significant portion, if not all, of their gas exchange requirements through non-pulmonary means. Despite variations in experimental technique, the differences in total non-pulmonary O_2 uptake among reptiles are obvious (Fig. 7). Sea snakes and highly aquatic turtles, such as *Trionyx* and

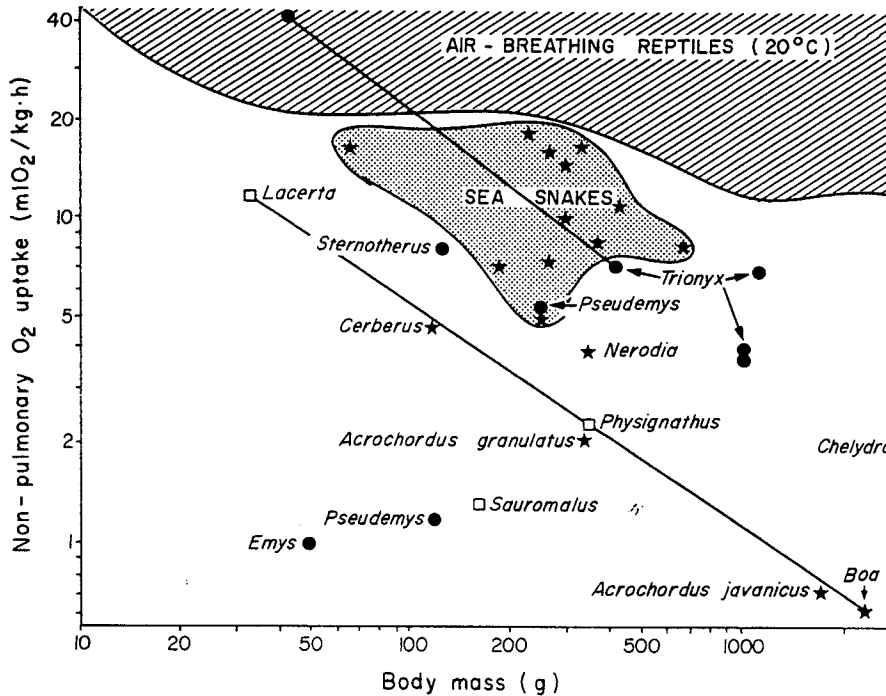


FIG. 7. Rates of non-pulmonary O_2 uptake in aquatic and terrestrial reptiles at 20–30°C compared with the range of pulmonary O_2 uptake rates in reptiles at 20°C. The data are means from turtles (closed circles) (Gage and Gage, 1886; Krogh, 1904; Root, 1949; Dunson, 1960; Girgis, 1961; Jackson and Schmidt-Nielsen, 1966; Belkin, 1968a; Gatten, 1980), snakes (stars) (Graham, 1974b; Standaert and Johansen, 1974; Heatwole and Seymour, 1975a, 1978; Gratz, 1978), and lizards (squares) (Crawford and Schultetus, 1970; Jammes and Grimaud, 1976; Courtice, 1981a). The envelope containing the pulmonary uptake was determined by Bennett and Dawson (1976).

Chelydra, show consistently high rates of uptake; those of other turtles and snakes are much lower. Only for *Trionyx spiniferus* has aquatic gas exchange in a single species been examined over a great enough range of body mass to demonstrate conclusively the effect of surface area (Dunson, 1960). The data show that the total O_2 uptake from water (\dot{V}_{O_2} , ml/h) increases with body mass (m , g) according to the equation

$$\dot{V}_{O_2} = 0.72m^{0.23}$$

over the body mass range of 40–400 g. Data from larger specimens fall very close to this line (Gage and Gage, 1886). The exponent of this equation (0.23) indicates that aquatic uptake falls short of the increase in surface area which is related to mass to the 0.67 power. This difference may be caused by relatively thicker exchange surfaces in the larger reptiles (Maderson and Lillywhite, volume 12). For example, thickness of alligator skin scales to the 0.38 power of body mass (Smith, 1979).

A similar correlation of non-pulmonary gas exchange and body mass

appears when we compare the terrestrial squamates. Non-pulmonary O_2 uptake in the lizards, *Lacerta* and *Physignathus*, and the snake, *Boa*, fit the line

$$\dot{V}_{O_2} = 0.123m^{0.32}$$

which again shows a decreasing effectiveness of non-pulmonary gas exchange in large animals. Another lizard, *Sauromalus obesus*, from a xeric habitat, has a somewhat lower rate. In this case, there is probably a tremendous advantage to reducing cutaneous water loss and little or no advantage to cutaneous gas exchange.

It is interesting that the three aquatic snakes, *Cerberus rhynchops*, *Acrochordus granulatus*, and *A. javanicus*, all have rates of cutaneous O_2 uptake similar to the rates of terrestrial species, thus disagreeing with earlier inferences (Standaert and Johansen, 1974). It is significant that these snakes usually inhabit relatively shallow coastal waters, often in mangroves or freshwater swamps, where high temperature, thermal stratification, and significant respiration by aquatic organisms can lower the dissolved O_2 content (Heatwole and Seymour, 1978; Dunson and Minton, 1978; Feder, 1980; Voris and Glodek, 1980; Seymour *et al.*, 1981a).

Some studies of aquatic turtles indicate low rates of non-pulmonary O_2 uptake. Early work on *Emys* sp. yielded very low rates, but this may have been caused by the experimental design as discussed below (Krogh, 1904). Measurements on *Pseudemys scripta* are equivocal, indicating both high (Jackson and Schmidt-Nielsen, 1966) and low values (Belkin, 1968a; Ackerman and White, 1979; Robin *et al.*, 1964), and this discrepancy has not been resolved.

Non-pulmonary CO_2 loss is also related to habitat in turtles, the more aquatic species losing more CO_2 (Jackson, 1976; Jackson *et al.*, 1976). The terrestrial *Geochelone denticulata* loses only 2.9% of its total CO_2 production to the water but *Trionyx* loses 64%. The absolute rates of CO_2 loss among the six species studied differ by a factor of 3.7.

There are several lines of evidence indicating that non-pulmonary gas exchange in most aquatic reptiles is severely diffusion limited and under little physiological control. Within the normal range of ambient P_{O_2} , the rate of O_2 uptake is linearly related to ambient P_{O_2} in the turtle, *Sternotherus minor* (Belkin, 1968a) and the sea snake, *Pelamis platurus* (J. B. Graham, pers. comm.). Cutaneous O_2 uptake increases in *Nerodia rhombifera* when it breathes hypoxic gas mixtures (Gratz, 1979). Thus the rate of O_2 uptake changes according to variations in P_{O_2} across the skin. Moreover, O_2 uptake in the sea snake, *Lapemis hardwickii*, appears independent of cutaneous blood flow because the rate does not change following cessation of the heart beat 2 h after death (Heatwole and Seymour, 1975a). The twofold

increments in cutaneous O_2 uptake in active sea snakes may indicate some physiological control or may result from better ventilation of the skin in respiratory chambers.

A diffusion-limited system is consonant with the relative rates of cutaneous O_2 and CO_2 exchange within species. The non-pulmonary respiratory exchange ratio is 4.4 in *Trionyx* sp., 3.5 in *Acrochordus javanicus*, and 3.2 in *Pelamis platurus* (Gage and Gage, 1886; Graham, 1974b; Standaert and Johansen, 1974). Because the amount of CO_2 diffusing through tissues is about 21 times that of O_2 in response to the same partial pressure difference (Comroe, 1965), the average respiratory exchange ratio in these three species indicates that the P_{O_2} difference is about 4.8–6.6 times the P_{CO_2} difference. This is reasonable because in diving turtles and snakes arterial P_{CO_2} is typically 15–30 mmHg and arterial P_{O_2} about 40–80 mmHg (Lenfant *et al.*, 1970a; Rahn and Garey, 1973; Jackson *et al.*, 1974; Jackson and Silverblatt, 1974; Seymour and Webster, 1975; Donnelly and Woolcock, 1977, 1978; Burggren *et al.*, 1978; Seymour, 1978; Ackerman and White, 1979; Burggren and Shelton, 1979; Seymour *et al.*, 1981a).

Finally, temperature changes within the physiological range have relatively small effects on a diffusion-limited system. Cutaneous O_2 uptake is lower at 4°C than at 20°C in *Chelydra serpentina*, but the Q_{10} (2.01) is considerably below that for pulmonary O_2 uptake (3.44) over this range of low temperature (Gatten, 1980). Between 15 and 30°C, the slopes of the log-transformed data for cutaneous O_2 and CO_2 exchange in *Physignathus lesueurii* are not significantly different from zero (Courtice, 1981a). A low sensitivity to temperature justifies direct comparison of aquatic gas exchange in species studied at temperatures ranging from 20 to 30°C (Fig. 7).

Non-pulmonary gas exchange in sea snakes appears to be limited to the skin (Graham, 1974b), but some turtles exchange gas through the walls of the pharynx and cloaca. Some species of *Trionyx* possess filamentous projections on the inside of the pharynx (Agassiz, 1857; Girgis, 1961; Winokur, 1973). In *T. triunguis*, 30% of the non-pulmonary O_2 uptake occurs through the mouth; only 7.4% occurs through the cloaca (Girgis, 1961). In *T. spiniferus*, pharyngeal uptake can increase to equal the total non-pulmonary uptake if the flux through the skin and cloaca is blocked (Dunson, 1960). If the pharynx is blocked, the cloaca and skin are able to take up only about one-half the total rate. These data from *T. spiniferus* are suggestive of physiological regulation of pharyngeal gas exchange, possibly by adjusting the rate of ventilation. Pharyngeal O_2 uptake in *Sternotherus odoratus* accounts for about 35% of the total non-pulmonary exchange (Root, 1949). In some species, the role of the cloaca seems insignificant but in others it may be the major gas exchanger. A recently described species of

Australian turtle, *Rheodytes leukops*, has well-developed cloacal bursae lined with highly vascularized, thin-walled villi (Legler, 1979; Legler and Cann, 1980). These turtles swim with the cloaca widely open and they ventilate the bursa at rates of 15–80 times per min. They rarely breathe air. Steen (1971) reported data of Peterson and Bellamy demonstrating that cloacal respiration in a South American aquatic turtle, *Podocnemis* sp., also can be substantial.

It has been proposed that cloacal bursae function in respiration, ionic balance, fluid storage, and buoyancy control. Many turtles move water in and out of the cloaca (and possibly the cloacal bursae) synchronously with pulmonary ventilation (Steen, 1971), and in *Pseudemys scripta*, cloacal ventilation stops during submersion (Belkin, 1968a). Although Smith and James (1958) opined that cloacal bursae were valuable for respiration in some turtles that hibernate under water, subsequent experiments were not able to demonstrate an effect on the duration of underwater survival in *Chrysemys picta* and *Pseudemys scripta* (Smith and Nickon, 1961).

There is still no unequivocal proof that any reptile can remain aerobic indefinitely without using the lungs, although this has been suggested for *Trionyx* sp. (Dunson, 1960; Girgis, 1961). As shown in Fig. 7, however, the data for small specimens of *Trionyx spiniferus* invade the envelope enclosing the data for total O_2 consumption of air-breathing reptiles at 20°C. Because metabolism is related to temperature with a Q_{10} of between 2 and 3 (Bennett and Dawson, 1976) and gas exchange through a diffusion-limited system should have a Q_{10} near 1, it is possible that even large turtles hibernating on the bottoms of cold, but well-oxygenated water bodies could remain aerobic without resorting to pulmonary gas exchange. However, the metabolism of *Chrysemys picta* becomes decidedly anaerobic during hibernation in water at low temperature (Gatten, 1981). In this case, unfortunately, the ambient P_{O_2} is not known. It would be particularly interesting to examine metabolism of *Chelonia mydas* which becomes dormant during winter on the floor of the Gulf of California at 15°C (Felger *et al.*, 1976), or *Caretta caretta* which apparently hibernates in aggregations off Florida at similar temperatures (Carr *et al.*, 1980/81). Non-pulmonary gas exchange would appear to be relatively unimportant in these large, thick-skinned turtles that lack cloacal bursae (Smith and James, 1958). Some of the turtles are found partially buried in a muddy and sandy substrate with only the top of the carapace visible, but others are buried, sometimes head-first, in anaerobic mud.

We do not know the extent to which sea snakes rely on cutaneous gas exchange under natural conditions. It is clear that they use pulmonary gas exchange during normal activity because they return to the surface to breathe, an event that sometimes requires considerable swimming effort

(Heatwole, 1975; Heatwole *et al.*, 1978). In the laboratory, resting sea snakes also routinely breathe in shallow aquariums; cutaneous O_2 uptake accounts for up to 33% of the total O_2 consumption (Graham, 1974b; Heatwole and Seymour, 1975a). Thus, cutaneous gas exchange can make a significant contribution and some species may be able to reduce their metabolic demands sufficiently to survive continuously beneath the well-stirred and oxygenated seas of the tropics. Sea snakes are not very tolerant of anoxia but may voluntarily allow arterial P_{O_2} to drop to about 10 mmHg which would facilitate cutaneous O_2 uptake (Seymour and Webster, 1975). The ability to depend exclusively on cutaneous gas exchange would account for the conspicuous absence of certain snakes from the surface during the day or night when they can be found resting on the bottom (Dunson and Minton, 1978). Cutaneous gas exchange may be important during swallowing of fish which may require up to 20 min in *Pelamis platurus* (Graham, 1974b). However, a 2-m *Disteira major* can ingest a 1.5-m eel in about 6 min, a relatively short breath-hold for a sea snake (Heatwole *et al.*, 1978).

Further work on non-pulmonary gas exchange in reptiles should be rewarding. However, the data can be more valuable if taken under uniform and ecologically relevant conditions. Factors not recognized by previous workers can have a significant effect on rates of non-pulmonary gas exchange and a few, easily obtained peripheral data can make measurements of gas exchange more valuable in an analytical sense. In future work, it will be worthwhile (1) to control precisely temperature and ambient gas tensions, (2) to measure ambient gas tensions in the field, (3) to mix the experimental water to avoid the development of a stagnant layer near the skin, (4) if possible, to measure blood gas tensions to evaluate the gradients through which the gases move, (5) to measure pulmonary gas exchange in order to partition bimodal exchange, (6) to eliminate or correct for the metabolism of micro-organisms in the water, (7) to remember that pH affects the solubility of CO_2 in water and hence the rate of diffusion, and finally (8) to present the body weights with the weight-specific rates of exchange so that the allometric relationships may be more accurately determined.

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