ANATOMICAL EVIDENCE FOR INTRACARDIAC BLOOD SHUNTING IN MARINE TURTLES

C W SAPSFORD
Department of Biological Sciences, University of Natal, Durban.

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ABSTRACT

Histological examination of the pulmonary arteries of four species of sea turtles revealed the presence of a muscular sphincter just distal to the origin of the ductus Botalli. This structure has not previously been described. Its presence suggests that right to left intra-cardiac blood shunts may be a feature of diving in sea turtles; the sphincter providing a mechanism for the control of blood flow through the heart.

The comparative anatomy of the pulmonary arteries of selected terrestrial reptiles suggests that a similar mechanism exists in non-diving species. The possible significance of this is discussed.

INTRODUCTION

Blood flow through the heart of the freshwater turtle during air-breathing and diving has been studied in some detail (Steggerda & Essex 1957; Millen *et al.* 1964; White & Ross 1966). Using dye dilution techniques, Steggerda & Essex (1957) demonstrated the occurrence of a substantial left to right shunt of blood through the heart during air breathing. During diving on the other hand, a marked right to left intracardiac shunt has been observed (Millen *et al.* 1964; White & Ross 1966), in which deoxygenated blood from the right atrium was pumped into the systemic arterial trunks. Millen *et al.* (1964), reported that pulmonary blood flow may cease completely under conditions of simulated diving, while White & Ross (1966), observed a marked decrease in pulmonary blood flow without complete cessation.

Right to left blood shunts associated with diving have also been reported for alligators (White 1969) and postulated for sea snakes (Seymour 1974), and it has been suggested that they may be of functional significance during periods when the lung is essentially non-functional. Under these conditions, bypassing the pulmonary circulation would result in a conservation of cardiac energy (White 1969).

The actual mechanisms involved in the control of intracardiac shunting in turtles are not clearly understood. From observations of *Pseudemys scripta,* however, it has been suggested that the direction and magnitude of the blood shunts may depend on a balance between pulmonary and systemic resistance (White & Ross 1966).

Anatomical investigations have revealed the presence of a functional bulbus cordis homologue in the freshwater turtle heart and it has been suggested that the degree of contractility of this segment of myocardial tissue at the base of the pulmonary artery is important in the regulation of pulmonary blood flow (March 1961). Woodbury & Robertson (1942) have shown this ring of cardiac muscle to be active in maintaining systemic blood flow during cases of experimentally induced haemorrhage. They demonstrated further that the wall of the pulmonary artery between the point of bifurcation and the origin of the ductus Botalli contains a substantial amount of smooth muscle. The administration of epinephrine HCL indicates that this muscle layer can influence the pulmonary reservoir through variations in pulmonary tract resistance.

Although it seems likely, no evidence has yet been obtained to suggest that intracardiac blood shunting occurs in marine turtles as well. The present study, however, indicates that right to left shunting at least may occur in these animals during diving and the mechanism whereby this may be brought about is outlined.

MATERIAL

Preserved heart-lung preparations were obtained from the following four species of marine turtle: *Caretta caretta* (loggerhead), *Chelonia mydas* (green turtle), *Eretmochelys imbricata* (hawksbill) and *Dermochelys coriacea* (leatherback). All material was from juvenile animals except in the case of *D. coriacea*, where the hearts of two large adults were studied.

RESULTS

The anatomy of the pulmonary artery in all four species is of interest. This artery arises directly from the right side of the heart in the cavum pulmonale and emerges as a stout trunk lying somewhat ventral and to the left of the systemic trunks. It then curves to the left dorsally and becomes partly obscured by the systemic branches. In all cases, the lumen of the ductus Botalli was closed. This structure arises as a thin ligament from the pulmonary artery at a point one third to one half the length of the artery from its bifurcation to the point of entry into the lung.

In all four species, the diameter of the pulmonary artery decreases abruptly just distal to the origin of the ductus Botalli and then increases gradually and progressively towards the lung. A similar narrowing of the pulmonary arteries has been reported for freshwater turtles (Woodbury & Robertson 1942). In *D. coriacea*, the external diameter decreases by a factor of 0,5.

Longitudinal sectioning of this narrow region shows a distinct and abrupt thickening of the arterial wall (Figures 1, 2; Table 1). From histological sections of this region it is clear that the increase in wall thickness is due to a remarkable thickening of the smooth muscle component of the arterial wall. Proximal to the ductus Botalli, smooth muscle fibres are present but sparsely arranged. Distal to the ductus Botalli, the layer of smooth muscle is thickest at its proximal origin, decreases in thickness distally then terminates abruptly. Distal to the muscular thickening, the histological appearance of the arterial wall is similar to that of the proximal region of the vessel where very little smooth muscle is apparent.

TABLE 1
Pulmonary arterial wall thickness in four species of marine turtle, in mm.

Species	Proximal	Sphincter	Distal	Sphincter: Proximal ratio
D. coriacea	1,5	3,9	1,0	2,6
E. imbricata	0,7	1,0	0,7	1,4
C. mydas	1,0	2,0	1,0	2,0
C. caretta	0,8	2,5	0,7	3,1

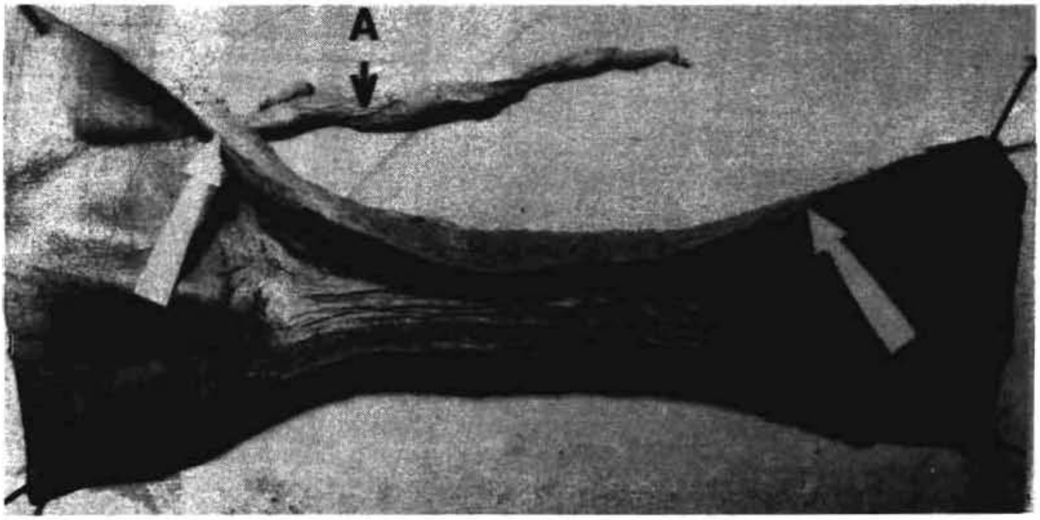
Thus in these species, there is a distinct and well-defined sphincter muscle surrounding the pulmonary artery which is clearly visible to the naked eye as a reduction in vessel diameter and which is situated just distal to the origin of the ductus Botalli.

For comparison, pulmonary artery anatomy was examined in two species of land tortoise, *Chersine angulata* (angulate tortoise) and *Testudo gigantea* (Galapagos tortoise), the snake, *Haemachatus haemachatus*, and the lizard, *Agama atricolis*. In both tortoises a similar abrupt decrease in pulmonary artery diameter was observed at the ductus Botalli. As for the sea turtles, the lumen of this structure is occluded and it is in the form of a ligament. Longitudinal sections of this region in the Aldabra tortoise showed a thickening of arterial wall for approximately one centimetre distal to the origin of the ductus Botalli (Figure 3). Similar though less-marked reductions in vessel diameter were observed in both the snake and the lizard. Microscopic examination of the inner wall of the pulmonary artery of the snake indicated the possible presence of a distinct sphincter in the narrow region. However no histological confirmation has yet been undertaken.

DISCUSSION

From the above observations it is apparent that marine turtles possess a mechanism for reducing or preventing pulmonary blood flow, since the contraction of the pulmonary sphincters would undoubtedly result in a considerable increase in pulmonary tract resistance. As occurs in the freshwater turtle (Millen *et al.* 1964; White & Ross 1966), it is proposed that a right to left shunt of blood through the heart occurs during diving in marine turtles as a consequence of constriction of a pulmonary sphincter muscle and in this respect the mechanism may differ from that reported for freshwater turtles (Millen *et al.* 1964; White & Ross 1966) and alligators (White 1969).

In alligators it has been shown that right to left intracardiac blood shunting may be induced in air-breathing animals on administration of acetylcholine (White 1969). It would now be of interest to determine whether the pulmonary sphincter muscles observed in sea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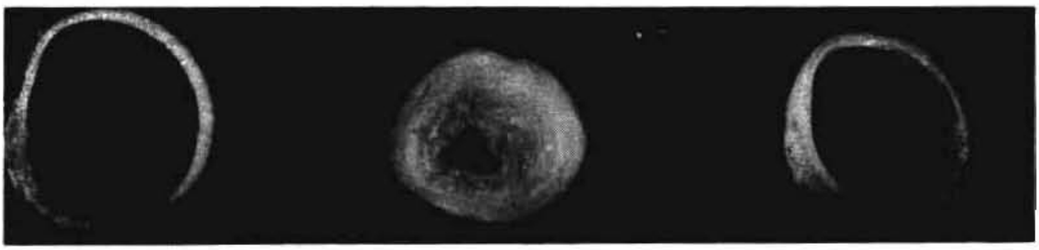

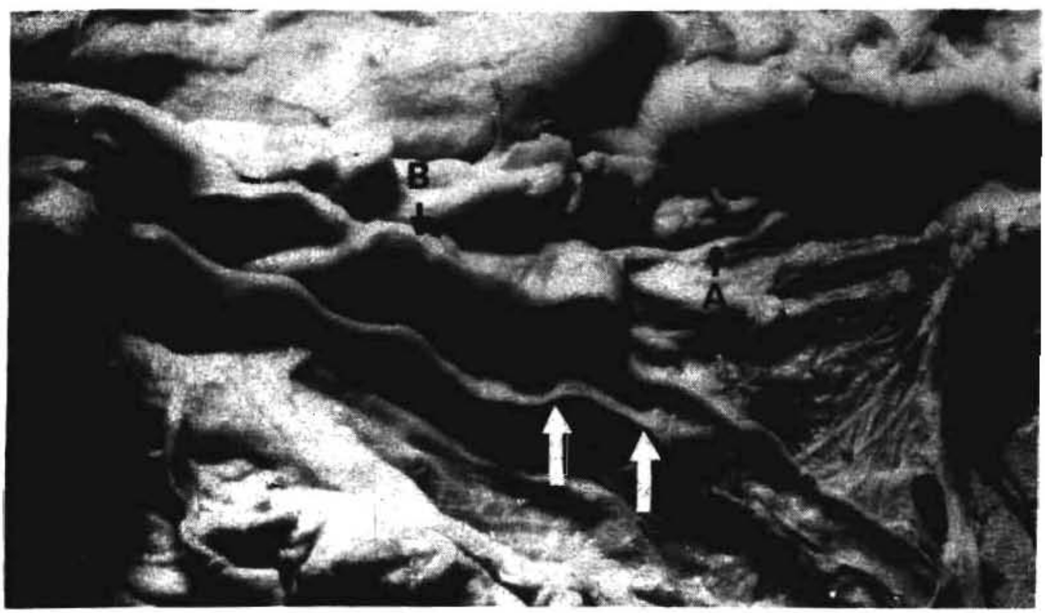
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turtles are innervated by the parasympathetic nervous system and whether right to left shunting during diving may be associated with the low heart rates observed during submersion (Berkson 1966).

The narrowing of the pulmonary arteries in the terrestrial species examined and the possibility of pulmonary sphincter muscles in these animals as well, strongly suggests that the phenomenon may not represent a particular and peculiar adaptation to an aquatic mode of life. It is possible that right to left blood shunting may occur in response to the activity of this sphincter muscle in terrestrial reptiles as well.

Right to left intracardiac blood shunting has been observed in lizards in response to heating and it has been suggested that these shunts may be important in controlling heat loss to the environment at the air: blood interface in the lung (Tucker 1966). It has further been suggested that the lung may act as a heat exchanger in reptiles and that right to left blood shunts in diving reptiles may provide a means of thermally isolating the peripherally situated lung from the deep core tissues and aid in the retardation of heat loss to the environment while the lung is essentially non-functional as a gas exchanger. The degree of blood shunting would regulate and determine the rate of heat exchange with the environment across the carapace in Chelonia by altering the heat transport capacity of the pulmonary circulation (Sapsford, unpublished data).

In view of the above observations and the anatomical evidence concerning the possible occurrence of pulmonary sphincter muscles in terrestrial reptiles, it seems reasonable to suggest that right to left intracardiac blood shunting in terrestrial species relies on the same mechanisms which are operative in marine turtles during diving. Equally, the significance of right to left shunting in both groups may be in the regulation of heat flux with the environment. Due to the acute heat loss problems associated with immersion in water, the ability to control pulmonary blood flow in diving reptiles may be more marked. However, their secondarily aquatic history suggests that they may have elaborated on and exploited a mechanism which existed in their terrestrial ancestors and one which on land may be associated with temperature regulation.

FIGURE 1 (Opposite page, top)

Longitudinal section of the pulmonary artery of the leatherback turtle, *D. coriacea*, showing the presence of a distinct sphincter commencing just distal to the origin of the ductus Botalli (A). The extent of the sphincter is indicated by the arrows.

FIGURE 2 (Opposite page, centre)

Transverse sections of the pulmonary artery of the green turtle, *Chelonia mydas*. Left: proximal to the sphincter; centre: through the sphincter, and right: distal to sphincter.

FIGURE 3 (Opposite page, bottom)

Dissected pulmonary artery (B) of the Galapagos tortoise, *Testudo gigantea*, showing an abrupt decrease in diameter just distal to the origin of the ductus Botalli (A). The arrows indicate a muscular thickening of the arterial wall and the extent of the pulmonary sphincter.

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