

SALT GLANDS IN MARINE REPTILES

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"SO they went up to the Mock Turtle, who looked at them with large eyes full of tears"¹; "for I am the Crocodile," and he wept crocodile-tears to show it was quite true"². Frequent literary references to a propensity for tear production in reptiles have not sufficiently challenged scientific imagination, and an interesting chapter in the physiology of excretion has remained unnoticed.

The finding that marine birds depend on a gland in the head rather than the kidney for the excretion of salt^{3, 4} suggested an investigation of their reptilian relatives, the marine turtles, crocodiles, snakes and lizards. These animals have maintained the terrestrial habit of air-breathing, and have an integument practically impermeable to salt and water. In these respects their physiology is essentially that of a terrestrial animal, but an important difference is that their food often has a high salt content, and the only drinking water available contains 3.5 per cent salt. Thus, their problems of osmo-regulation are comparable to those of marine birds.

Marine birds can tolerate the ingestion of sea water because the salt gland can excrete sodium chloride in a concentration almost twice as high as in sea water. Thus, marine birds do not suffer from the intake of sea water, in spite of the inability of their kidney to produce a urine more than about half as concentrated as sea water. The concentrating ability of the reptilian kidney is even lower, and marine reptiles could therefore be expected to have a mechanism for salt excretion similar to that in marine birds.

Marine reptiles. Reptiles with a marine habitat are found in four different orders: turtles, crocodiles, snakes and lizards.

Five species of turtles are strictly marine, going on land only to lay their eggs in the sand of tropical beaches. Their food consists of fish, some invertebrates, or seaweed. While the fish have a relatively low salt content, invertebrates as well as seaweed

have the same osmotic concentration as sea water. These latter types of food, therefore, impose a heavy burden on the processes of osmo-regulation. Other turtles are found in brackish water, such as the diamond-back terrapin, *Malacolemys terrapin*. This animal is never found in truly fresh water⁵.

One species of crocodile, the salt water crocodile (*Crocodylus porosus*), is estuarine in its habits, but has occasionally been found far out at sea in the Indian and Pacific Oceans. It is a carnivore, subsisting mainly on fish.

The sea-snakes, Hydrophidae, are common in the Indian Ocean. Some of the more primitive (*Laticauda*) lay their eggs on land, while the more specialized bear living young. They are all excellent swimmers and live on fish. Probably many other snakes are able to live in brackish water, an example being *Natrix sipedon compressicauda*, which is reported from brackish swamps in Florida⁶.

One lizard, the Galapagos sea iguana (*Amblyrhynchus cristatus*), is well known for its appearance as well as its habits. It lives in the surf of the Galapagos Islands, where it climbs on rocks and eats seaweed exclusively⁶. A few other lizards also have been reported from a marine habitat⁵.

Head glands. Several different kinds of head glands are found in the four reptilian orders mentioned. There are glands in the orbit of the eye (Harderian gland and lachrymal glands), glands opening into the nasal cavity (nasal glands), and glands opening into the mouth (salivary glands, poison glands, etc.).

In order to find whether marine reptiles are provided with salt glands we used two approaches, studies of (1) the histological structure of the head glands, and (2) the secretion obtained after a salt load, or after stimulation of the glands with the drug methacholine, a drug which stimulates glandular secretion in general.

Turtles have a large gland on each side of the head, located in the orbit of the eye. In the logger-

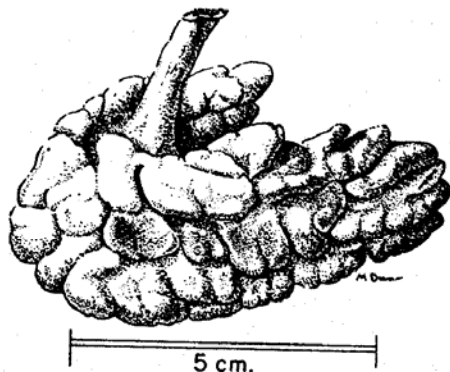


Fig. 1. Salt gland of the loggerhead turtle, *Caretta caretta*

head turtle, *Caretta caretta*, this gland (Fig. 1) is large, reddish-brown, and divided into about one hundred lobes separated by blood vessels and connective tissue. It connects to the exterior via a short, wide duct that opens in the posterior corner of the eye. The two glands weighed 60 gm. in a turtle of 130 kgm., which is 0.05 per cent of the body-weight. The relative weight of the gland was similar in the diamond-back terrapin. In the herring gull we have found the salt gland to be almost 0.1 per cent of the body-weight, and in the brown pelican 0.03 per cent.

The loggerhead gland consists of closely packed branching glandular tubules (Fig. 2) radiating from central ducts or canals in the lobes. This characteristic histological structure, which has previously been observed in the large 'lachrymal' gland of *Chelonia mydas*⁷, is similar to the structure of the avian salt gland⁸. The structure of the terrapin gland is similar but less regular.

Crocodyles have well-developed nasal and Harderian glands^{9,10}, but the functions of these glands are not known. The nasal gland in *Crocodylus porosus* has been described as a rather large acinous gland¹¹.

Several sea-snakes, for example *Enhydria*, have a well-developed nasal gland¹². It is, however, missing in one sea-snake, *Pelamis*. According to our own observations on a sea-snake (*Hydrophis ornata*) there is a gland above the eye with a histological structure resembling that of the salt gland of the terrapin. The gland consists of closely packed glandular tubules.

The marine iguana has a large nasal gland which in a specimen of 490 gm. weighed about 300 mgm. (0.06 per cent of the body-weight). Histologically the structure of this gland resembles that of the avian salt gland. The gland opens, via a short duct, into the lateral nasal cavity, which seemingly can

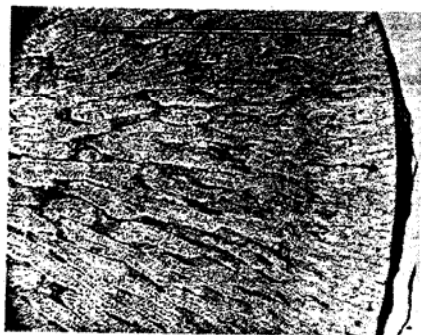


Fig. 2. Microscopic structure of salt gland of the loggerhead turtle

function as a reservoir for the secretion. A ridge prevents the secretion from flowing back into the posterior part of the nasal cavity, from where it would drain into the oesophagus. On the other hand, a sudden expiration of air would force the liquid out through the nostril.

Secretion from salt glands. Marine turtles, when given an injection of hypertonic sodium chloride, secrete a highly concentrated salt solution from the orbital salt gland. This we could demonstrate in the diamond-back terrapin (*Malacolemys terrapin*), a brackish water turtle from Florida, which, when given 10 ml. of 10 per cent sodium chloride per kgm. body-weight, secreted a fluid which appeared as 'tears' in the eye. The sodium concentration of this fluid was 616-784 m.equiv. sodium/l. This salt concentration is well above that of sea water (about 500 m.equiv. sodium/l.).

In a large specimen of the completely marine loggerhead turtle, the duct of the salt gland was easily cannulated, and it could be established with certainty that the secretion came from this particular gland. Samples of secretion obtained after salt load and stimulation with methacholine contained 732-878 m.equiv. sodium/l., 810-992 m.equiv. chlorine/l. and 18-31 m.equiv. potassium/l. These concentrations are similar to those produced by the salt gland of marine birds.

The fact that turtles cry tears when they go on shore to lay their eggs has received much attention. The anthropomorphic interpretation that the tears are induced by the pain of egg-laying has been rejected by naturalists, who instead have speculated that they may serve to keep the eyes from drying out, or to keep the sand out. The latter obviously is not compatible with the descriptions such as that given by Carr¹³: "The curious 'crying' by nesting females (apparently a device to keep the eyes washed free of sand) has been noted in other species. The present turtle began secreting copious tears shortly after she left the water, and these continued to flow as the nest was dug. By the time she began to lay, her eyes were closed and plastered over with tear-soaked sand and the effect was doleful in the extreme".

It may instead be suggested that the turtle tears are produced in response to the osmotic load of living and feeding in the sea, and that their major role may be osmo-regulatory.

We had no opportunity to work with living specimens of the salt-water crocodile, nor with living sea-snakes. One water snake, the Mangrove water snake (*Natrix sipedon compressicauda*), which is a sub-species of the common water snake, showed no secretion from head glands when given a salt load. Stimulation with methacholine gave only slight secretion from mucous glands. We did not find any glands in the head of *N. s. compressicauda* that could be interpreted anatomically as salt glands.

The marine iguana has repeatedly been observed to blow out "a thin shower of water vapour" from the nostrils¹⁴. We induced secretion in two animals that had been kept in captivity for three months, by the injection of sodium chloride (10 ml. of 10 per cent solution per kgm. body-weight) and methacholine. The secreted fluid was ejected from the nostrils as fine drops.

When picking up a lizard one of us was hit in the face and eyes with a jet of droplets that had a salty taste. This rather subjective observation of a high salt content was followed by a more accurate

determination with a flame photometer, which showed a concentration of 840 m.equiv. sodium/l. in the secreted fluid.

Since the Galapagos lizard eats only seaweed which has a salt concentration similar to that of sea water, it is not only useful, but also a necessity, for it to have a mechanism for excretion of the salts in a high concentration.

In summary, we can conclude from observations described in this article that the combination of circumstantial (histological) and direct evidence (secretion of salt) indicates that an extrarenal mechanism for salt excretion is present probably in all four orders of marine reptiles, turtles, crocodiles, snakes and lizards. The secretion derives from head glands which resemble the salt glands of marine birds, both in structure and function. The kidney of birds and reptiles cannot produce a urine with high salt concentrations, and one can assume that the extrarenal mechanism for salt excretion is a necessity for successful adaptation to a marine habitat in all sauropsidians.

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