

**EVIDENCE FOR SALT GLANDS IN THE TRIASSIC REPTILE
DIADEMODON (THERAPSIDA; CYNODONTIA)**

by

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ABSTRACT

Fossilised skulls of *Diademodon* exhibit rostral depressions which may have housed salt glands. The possible functions of salt glands in this advanced cynodont are examined. *Diademodon* appears to have been more reptilian than mammalian in its general physiological organisation.

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INTRODUCTION

No extant reptile is able to produce urine which is hyperosmotic to its plasma. Reptiles, especially if herbivorous and resident in an arid environment, encounter problems of water conservation and monovalent ionic balance more severe than those experienced by animals with a mammalian kidney. To cope with these problems reptiles employ extrarenal routes, typically via rectal and/or salt glands, for the excretion of ions. Several terrestrial reptiles exhibit nasal salt secretion (Schmidt-Nielsen *et al.*, 1963; Templeton, 1963, 1964; Norris and Dawson, 1964; Dunson, 1976), and use the secretion both to achieve anion and cation balance (Shoemaker *et al.*, 1972; Peaker and Linzell, 1975) and to eliminate salts with a minimum of fluid loss.

Whilst the structure and function of salt glands in modern reptiles have been studied rather extensively (Schmidt-Nielsen *et al.*, 1963; Templeton, 1963, 1964; Norris and Dawson, 1964; Dunson, 1969, 1970, 1976; Dunson *et al.*, 1971; Shoemaker *et al.*, 1972; Peaker and Linzell, 1975; Minnich, 1968, 1970, 1972; Crowe *et al.*, 1970; Braysher, 1971; Duvdevani, 1972), the evolution of these glands has received relatively little attention. Ewer (1965) has suggested that *Euparkeria capensis*, a member of the archosaurian stock, probably possessed nasal glands. It is interesting to consider whether cranial salt glands were present in the Cynodontia, the

group of Permo-Triassic reptiles from which the mammals are believed to have developed (Barghusen, 1968; Crompton and Jenkins, 1968).

MATERIAL AND DESCRIPTION

A number of cynodont crania from the Permo-Triassic of Southern Africa were examined by three of us (F.E.G., C.E.G. and J.W.K.) in an attempt to define any feature, either on the rostrum or around the orbit, which could be considered to have housed a salt gland. The specimens which were studied represented all of the cynognathoid and tritylodontoid genera which are currently recognised from this geographical region (Hopson and Kitching, 1972).

Of all the material scrutinised, only specimens of *Diademodon*, *Cynognathus* and *Trirachodon* were found to possess any evidence of superficial cranial glands. The evidence is in the form of depressions located on either side of the snout in a dorsolateral position, approximately midway between the front of the orbits and the back of the external nares (fig. 1). Nearly every available specimen of *Diademodon* has been examined by one of us (F.E.G.); the depressions were discernible on every fossil in which the relevant region of the snout was preserved. In the case of *Cynognathus*, however, some specimens show the depressions whilst others do not. The small cynodont *Trirachodon* also shows rostral depressions clearly in at least several specimens.

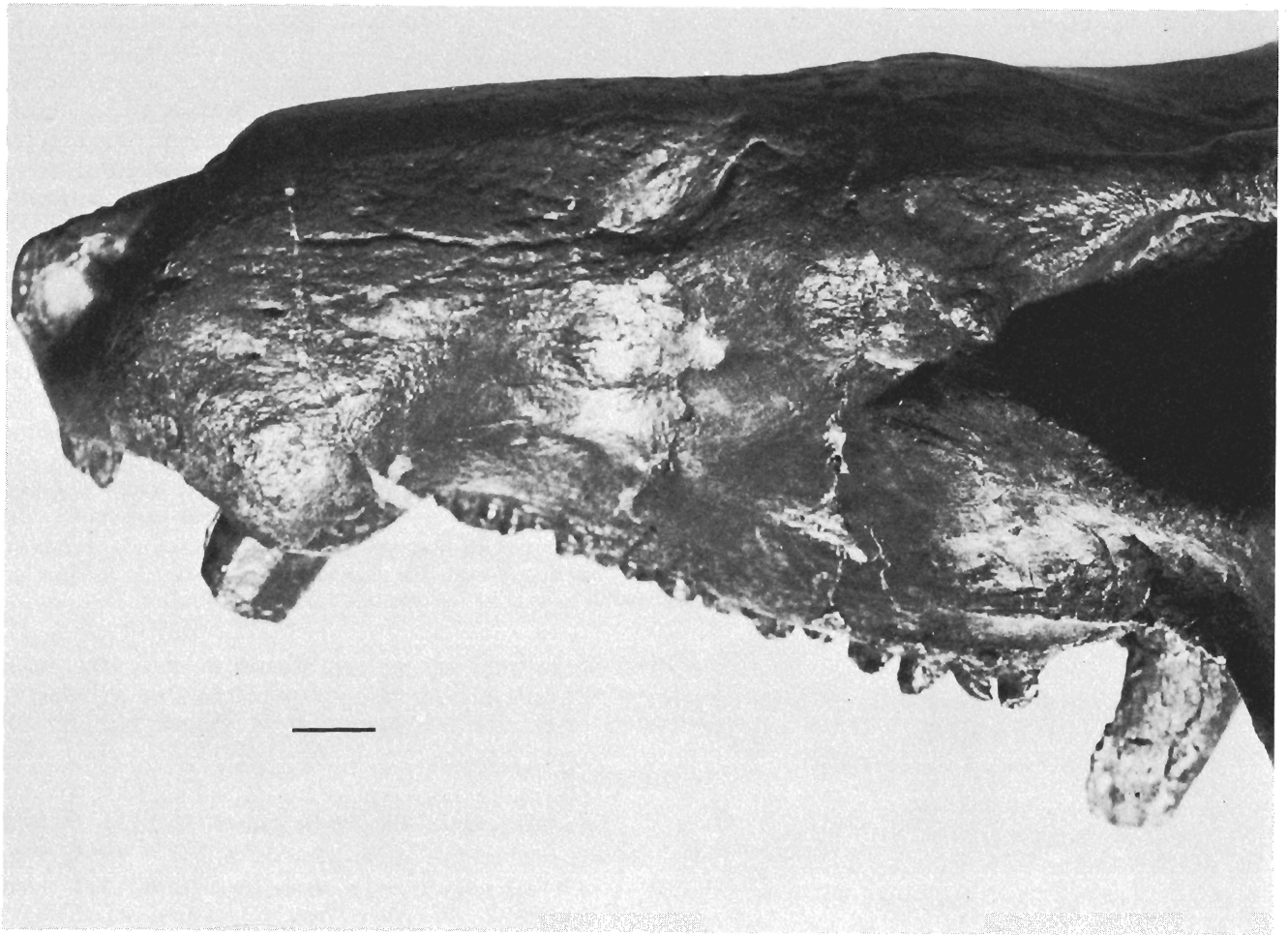


Figure 1. Left side of rostrum of a large *Diademodon* cranium (Bernard Price Institute, Field Number 2522) showing grooves emanating from the glandular depression and several foramina on the side of the maxilla. (Scale mark = 10 mm)

Our purpose is to describe the morphology of the depressions in *Diademodon*, and to attempt to assess both whether these are salt gland cavities, in view of previous claims which have been made for them, and the degree to which this therapsid approached a mammalian type of biological organisation.

The rostral depressions in *Diademodon* appear as relatively deep, well-delineated excavations. They are lodged entirely within the confines of the maxilla (Brink, 1955, 1956; Grine, 1978). In a number of specimens the surface of the maxilla anteriorly shows numerous foramina, which we interpret as the openings of neurovascular canals. Also, in certain instances, slight grooves are visible in the bone between the maxillary depressions and the external nasal aperture (fig. 1). A number of apparently well-preserved crania, however, show no trace of such grooves. In an attempt to determine whether, in this latter group of fossils, there were tubules connecting the medial walls of the depressions with the interior of the nasal cavity, one specimen was cut in serial coronal sections (Grine, 1978). Examination of the sections revealed no evidence either of tubules piercing the maxilla medial to the depression or of canals running anteriorly through the substance of the

bone. We conclude that in *Diademodon* the glands which were housed in the rostral depressions were drained by a series of ducts which made exit from the cavities and coursed forward across the external surface of the snout to reach the external nasal aperture. In some instances, either through poor preservation or because the ducts simply did not excavate the adjacent bone, the grooves are not apparent on the surface of the rostrum.

Several specimens show a concentration of rather large foramina in the maxilla, superoposteriorly to the glandular depressions (fig. 1). These foramina probably represent the openings of neurovascular canals through which the blood vessels and nerves exited to supply the rostral glands of *Diademodon*.

PALAEOENVIRONMENTAL SETTING

If we are to postulate that *Diademodon* and at least two other therapsids from the same geological horizons (the late Early to early Middle Triassic *Cynognathus* Zone, or *Kannemeyeria* Assemblage Zone sediments) possessed salt glands, it is instructive to consider the environment in which these animals might have functioned.

Calcareous concretions occur throughout the

Beaufort Group sediments, and by comparison with Quaternary calcretes of similar origin (Goudie, 1972) their presence suggests a warm to hot climate (mean annual temperature of 16–20 °C) and a periodically distributed rainfall (mean annual of 100–500 mm). Continental reconstructions (Smith, 1971; King, 1971) suggest that the Southern African region of Gondwanaland lay along the borders of a widespread arid zone. The sediments of the *Cynognathus* Zone consist mainly of mudstones which are interbedded with fine- to medium-grained feldspathic and micaceous sandstone horizons and lenses. The localised lenses appear to be indicative of scour-channel activity within the sequence (Kitching, 1977). It appears that there was intermittent drying and rejuvenation of water courses.

The Beaufort sediments probably accumulated in fairly low latitudes over broad, low-gradient floodplains drained by wide, shallow and impersistent rivers with transient shallow lakes and pools. From both lithological and sedimentological evidence it appears that the *Cynognathus* Zone sediments in particular were deposited in a considerably reduced basin and under relatively hotter and much drier conditions than are envisaged for the preceding *Lystrosaurus* Zone. To judge from the unstratified dark red to maroon mudstones, the abundance of calcareous concretions and the presence of “desert roses”, composed of pseudomorphs of calcite after gypsum, the climate may have been sufficiently dry to warrant the term arid. *Cynognathus* Zone times were probably characterised by what might be called a semi-desert environment.

The dietary habits of *Diademodon*, *Cynognathus*, and *Trirachodon* constitute yet another aspect which must be considered in relation to the possible role of the rostral glands in these animals as functional salt glands. The postcanine dentition of *Cynognathus* is comprised entirely of sectorial teeth, and is undoubtedly suited to a carnivorous diet. *Trirachodon* appears to have been herbivorous and perhaps insectivorous in its habits. The dentition of *Diademodon* indicates that whilst this reptile was probably omnivorous, perhaps the younger individuals were more insectivorous whilst the adults practised more selective herbivory (Hopson, 1971; Grine, 1976a, 1976b, 1977; Grine and Hahn, 1978; Grine *et al.*, 1978).

DISCUSSION

As mentioned previously, terrestrial reptiles which inhabit arid regions and subsist on a largely herbivorous diet face the problem of obtaining and conserving water. Sokol (1967) has suggested that in terrestrial lizards the presence of nasal salt glands is associated primarily with herbivory, and that the role of the glands may be the regulation of ionic balance rather than the conservation of water.

The depressions on the snout of *Diademodon* may have housed salt glands which acted both as ion balancers and osmoregulators; they also may have

played a role in the fluid conservation processes of this animal. The fluid secreted by the glands could have drained through the ducts along the surface of the rostrum where it would have been exuded at the external nares. It is possible that the bilateral pit-like excavations formed by the ventral surfaces and the ventromedially projecting processes of the septomaxillae at the distal end of the nasal aperture (fig. 1), could have acted as receptacles for the accumulation of the secreted fluid. A similar chamber is located just below the nostril and serves the same function in modern terrestrial reptiles (Templeton, 1964; Crowe *et al.*, 1970; Braysher, 1971).

A similar situation to that which was described by Murrish and Schmidt-Nielsen (1970) for the desert iguana, *Dipsosaurus dorsalis*, may be envisaged for *Diademodon*. Obligatory water, excreted with the electrolytes by the nasal salt glands, which otherwise simply would be lost, accumulates in depressions just inside the external nares and is evaporated into inspired air. This partial prehumidification reduces water loss from the respiratory tract. The overall effect on the water balance of the body is the same as if the glands could excrete electrolytes in the crystalline state.

The rostral depressions and grooves have been described by Brink (1955, 1956, 1978) who postulated that the depressions lodged glands which secreted a fluid released around the external nares for the specific purpose of moistening the air before it was inhaled. He also maintained that the glands were “specialised skin glands of sweat gland nature”, and that the existence of such glands implied that, ultimately, mammary glands were present also in *Diademodon*! Brink concluded that cynodonts were, by “zoological” rather than “palaeontological” definition, “mammals in the general sense of the term” (1955).

In several respects Brink’s hypotheses are untenable. Firstly, animals living in environmental conditions like those envisaged for *Diademodon* need to conserve water. Inhaled air is efficiently humidified by the wet linings of the passages of the upper respiratory tract (Schmidt-Nielsen, 1972). No additional water is necessary, and to secrete fluid at the external nares solely to humidify the inhaled air would be counteradaptive. Rather than serving to humidify inspired air, as Brink (1955) proposed, the narial excavations may have served to improve the efficiency of the salt glands in the sense of minimising water loss. Brink’s second assumption, that the presence of nasal glands implies the presence of mammary glands, is totally without foundation.

We believe that the most parsimonious interpretation of the rostral depressions in *Diademodon* is that they housed salt glands of a similar nature to those found in extant terrestrial reptiles.

Taken together, the evidence for polyphyodont tooth replacement in *Diademodon* (Hopson, 1971), prolonged and considerable ontogenetic growth (Grine and Hahn, 1978; Grine *et al.*, 1978) and the

probable presence of salt glands in this therapsid appears to corroborate Hopson's (1971) belief that *Diademodon* was "more reptilian than mammalian in reproductive biology and ontogenetic development"; to this we would add also the physiological organisation of its kidneys.

SUMMARY AND CONCLUSIONS

Some modern terrestrial reptiles which inhabit arid regions and are herbivorous employ nasal salt glands in the regulation of electrolyte balance. We have advanced evidence that the cynodont *Diademodon* may have existed in just such conditions. Fossilised skulls of *Diademodon* exhibit depressions which we believe could have housed salt glands.

These rostral depressions and grooves were originally interpreted by Brink (1955; 1956) as having housed glands and excretory ducts. He postulated further that the glands were sebaceous, and that the existence of such sebaceous glands rendered it possible that "other skin glands could have been specialised to a level where nourishing secretions were made available to the young" (1955).

We accept the first part of Brink's interpretation of the rostral depressions and grooves having housed glands and ducts through which a fluid was released around the external nares. It seems, however, that the most parsimonious interpretation of the nature of these structures is that they were salt glands, and thus it is not necessary to postulate that milk glands were present also in *Diademodon*. Furthermore, it appears that *Diademodon* was more reptilian than mammalian in its ontogenetic development and general physiological organisation.

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