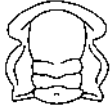


Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance

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Our knowledge of Mesozoic tetrapods is based mainly on osteological evidence. The discussion of the evolution of any homeostatic system is highly speculative because direct non-osteological evidence is uncommon. Here we report an extraordinarily well-preserved cast of a pair of lobulated protuberances in the skull of the marine metriorhynchid crocodyliform *Geosaurus* from the Tithonian (Jurassic) of Patagonia (Argentina). These protuberances are interpreted as representing salt glands. Based on their topology, these glands are identified as the nasals. Optimization of this character on a phylogenetic tree permits us to infer the ancestral condition for archosaurs. The relationship between salt gland and diet is also analysed. The presence of hypertrophied salt glands in the skull of *Geosaurus* suggests that as early as 140 million years ago, some Mesozoic marine reptiles had evolved an extra-renal osmoregulatory system. This achievement was an important clue in the successful colonization of marine environments. Salt glands preclude the risk of lethal dehydration and allow marine reptiles to include an important amount of invertebrates in their diet. □ *Salt glands, metriorhynchids, osmoregulation, diet.*

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Reptiles successfully colonized marine environments during the Mesozoic. Ichthyosaurs, plesiosaurs, crocodylians and mosasaurs were the largest swimming predators of Mesozoic marine communities (Massare 1988). The marine environment imposes strong functional constraints, leading to major modifications of the primitively terrestrial body plan to adapt it to marine life. The morphological modifications of their skeletons dealing with their adaptations to marine life are well known. Hydrodynamic properties of different body forms have been discussed by Massare (1988, 1997), how tetrapods feed in water by Taylor (1987), the evolution of paddle-like limbs by Caldwell (1996a–c), and functional adaptations of the histological features of their bones have been studied in ichthyosaurs, mosasaurs and thalattosuchian crocodylians (e.g. Buffrénil & Mazin 1990; Hua & Buffrénil 1996; Sheldon 1997). Nevertheless, we know almost nothing about the physiological mechanisms accompanying these adaptations, as these mechanisms are difficult to infer unless imprints of skeletal evidences were preserved.

Marine reptiles have been defined as any reptile able to grow and feed in a saltwater environment, and which inhabit the marine environment on an occasional or permanent basis (Hua & Buffetaut 1997). One of the main problems to be resolved for a marine

reptile is maintenance of the quantitative and qualitative salt balance.

The kidneys of reptiles and birds have a lower concentrating ability than the kidneys of mammals (Schmidt-Nielsen & Fänge 1958; Peaker & Linzell 1975), and marine forms resolve the problem of disposing of excess salt by means of an extra-renal excretion mechanism. Schmidt-Nielsen and co-workers (Schmidt-Nielsen & Fänge 1958; Schmidt-Nielsen & Sladen 1958) have demonstrated that in these groups cephalic glands, generically described as salt glands, have acquired an osmoregulatory function excreting hypertonic solutions. In marine reptiles and birds, salt glands are the major excretory route for sodium, potassium and chloride. In marine and estuarine reptiles, different cephalic glands may function as salt glands, nasal (in marine and estuarine lizards), lacrimal (in marine turtles and *Malaclemys*), posterior sublingual (hydrophidae sea snakes), premaxillary (in the homalopsid snake *Ceberus*) and lingual glands (in estuarine crocodylians) (Minnich 1982). In birds, as in lizards, the salt glands are nasal glands (Peaker & Linzell 1975).

The presence of salt glands as an extrarenal route of salt excretion is not restricted to marine forms. Thus, nasal salt glands are found in some terrestrial lizards including probably all members of the Family Iguani-

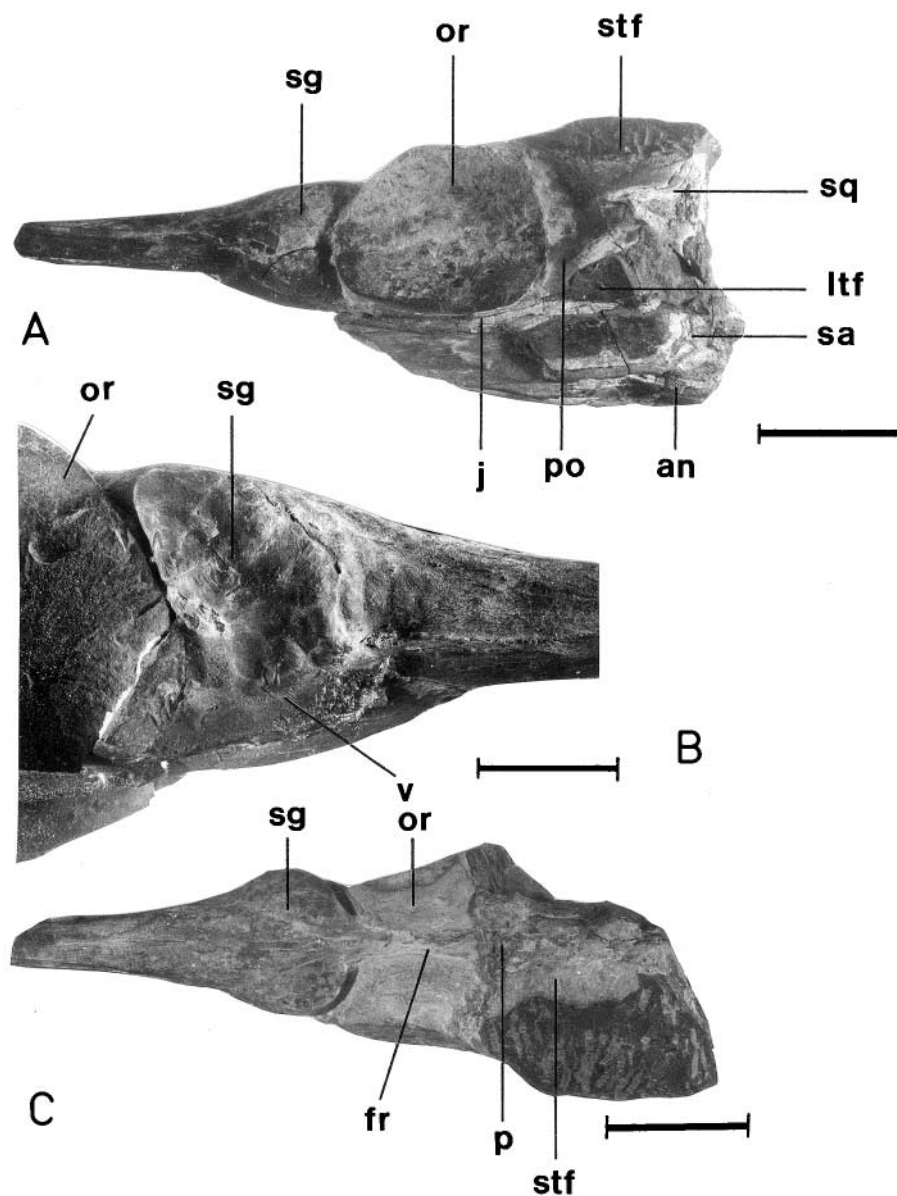


Fig. 1. *Geosaurus araucanensis*. MLP 76-XI-19-1. □A. Left lateral side. □B. Detail of the right lateral side. □C. Dorsal view. Abbreviations: an, angular; fr, frontal; j, jugal; ltf, laterotemporal fenestra; or, orbit; p, parietal; po, postorbital; sa, surangular; sg, salt gland; sq, squamosal; stf, supratemporal fenestra; v, vessels. Scale bar = 5 cm.

dae (Minnich 1982). Dunson (1976) proposed that salt glands evolved in the process of adjustment by reptiles to habitats low in availability of water or high in salt content. Habitats high in salt content include marine habitats and/or herbivorous diet (Peaker & Linzell 1975). Thus, in terrestrial lizards, the relationship between diet and salt gland function has been proposed many years ago (Sokol 1967) and confirmed in later studies (e.g. Dunson 1976; Hazard *et al.* 1998).

Several authors have inferred the presence of salt glands in extinct forms. Thus, in herbivorous dinosaurs the presence of nasal salt glands has been inferred and interpreted as an important mechanism for unloading the excess of potassium ions ingested by these large herbivorous creatures (Osmolska 1979). In crocodylians, the antorbital cavity has been correlated with the

presence of these glands (Nash 1975; Buffetaut 1982). Correlation between the antorbital fenestra and a gland, in particular a salt gland, has also been proposed in many other groups of archosaurs (see Witmer 1997 for review). In birds, depressions in the supra-orbital region of the skull of the Cretaceous *Hesperornis* and *Ichthyornis* (Marples 1932) were interpreted as evidence for the presence of salt glands (Peaker & Linzell 1975). More recently, the presence of salt glands has been inferred based on the large foramen interorbitale of *Santanachelys*, a Cretaceous sea turtle (Hirayama 1998). But, until now, there has been no direct evidence for the presence of such salt glands.

In this paper we report the fine preservation of the cast of lobulated protuberances rostral to the orbits in a Late Jurassic marine crocodile, *Geosaurus*. They

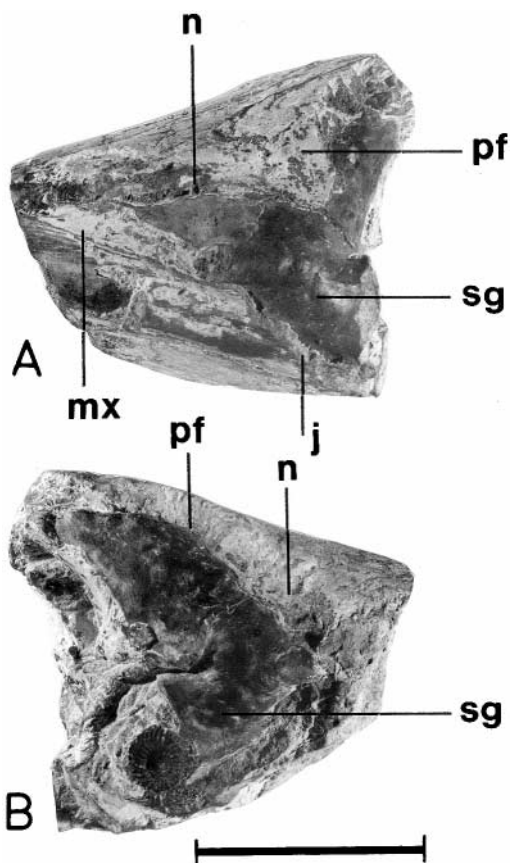


Fig. 2. *Geosaurus araucanensis*. MLP 86-XI-10-6. □A. Left lateral side. □B. Right lateral side. Scale bar = 5 cm. Abbreviations: j, jugal; mx, maxilar; n, nasal; pf, prefrontal; sg, salt gland.

reflect the shape of connective tissue surrounding lobulated organs, which are interpreted as salt glands. We consider the phylogenetic reconstruction of ancestral condition in archosaurs and how physiology may constrain the diet of marine reptiles. As Witmer (1997) points out, inferences about soft tissues form the basis for a cascading suite of palaeobiological inferences. Direct evidence such as that reported here is exceptionally rare, and sheds light on the remarkable evolutionary processes of the tetrapods' adaptation to life in the sea.

Material and methods

The material reported here comprises two partial skulls of *Geosaurus araucanensis* Gasparini & Dellapé, 1976 (Crocodylomorpha: Metriorhynchidae) held in the Museo de La Plata collection: MLP 76-XI-19-1 (Fig. 1) and MLP 86-XI-10-6 (Figs 2, 3B). Both specimens display the cast of lobulated protuberances rostral to the orbit. In MLP 76-XI-19-1 almost all

bones have been removed by natural means but it can be identified as a crocodyliform, based on the long nasal tubes and the position of the cranial fenestrae. The lateral position of the orbits and the lateral expansion of the prefrontal region are key features of the Family Metriorhynchidae. The long, slender rostrum and the relative positions of the cranial elements and cavities show that it is generically and specifically identical with the holotype of *Geosaurus araucanensis* (Fig. 3A). A third skull of *G. araucanensis* (MLP 72-IV-7-3) and the holotype (MLP 72-IV-7-1) have been examined for comparative data. MLP 86-XI-10-6 and MLP 72-IV-7-3 were scanned using computed tomography. The voltage was set at 125 kV. Window widths ranged between 1,900 and 2,661 units. Selected scan is shown in Fig. 4.

Stratigraphy and palaeoenvironment

MLP 76-XI-19-1 and MLP 86-XI-10-6 were collected from the Tithonian levels of the Vaca Muerta Formation at Sierra de Reyes, Mendoza province (36° 40' S; 69° 20' W) and Cerro Lotena, Neuquén province (39° 11' S; 69° 40' W), respectively. Both localities are situated in the Neuquén Basin, north-western Patagonia, Argentina. During the Tithonian, an important event (the Vaca Muerta Formation) followed by a gradually shallowing up cycle (the Picún Leufú Formation) was recorded in the Neuquén Basin. The transgression of the Vaca Muerta Formation (Tithonian) was a rapid event, biostratigraphically well defined, which covered most of the basin (Spalletti *et al.* 2000). These authors have demonstrated a simple pattern distribution of carbonatic and siliciclastic facies, grading transitionally from shallow to deep areas, that defined inner ramp, middle ramp, outer ramp and basinal ramp environments. Most of the Tithonian reptiles of the Neuquén Basin, ichthyosaurs, pliosaurs, marine turtles and metriorhynchid crocodiles (Gasparini & Fernández 1997; Gasparini *et al.* 1999) were found in the middle-outer ramp (Cerro Lotena) and basinal ramp where those of Sierra de Reyes may be included. The excellent preservation of the skeletons may be related to the anoxic bottom conditions, the lack of predators and benthic scavengers, the almost null kinetic energy, and the development of soupy substrate, which would have damped the body impact (Spalletti *et al.* 1999).

Description

MLP 76-XI-19-1 consists mainly of the cast of a skull and mandible, with fragmentary remains of some of

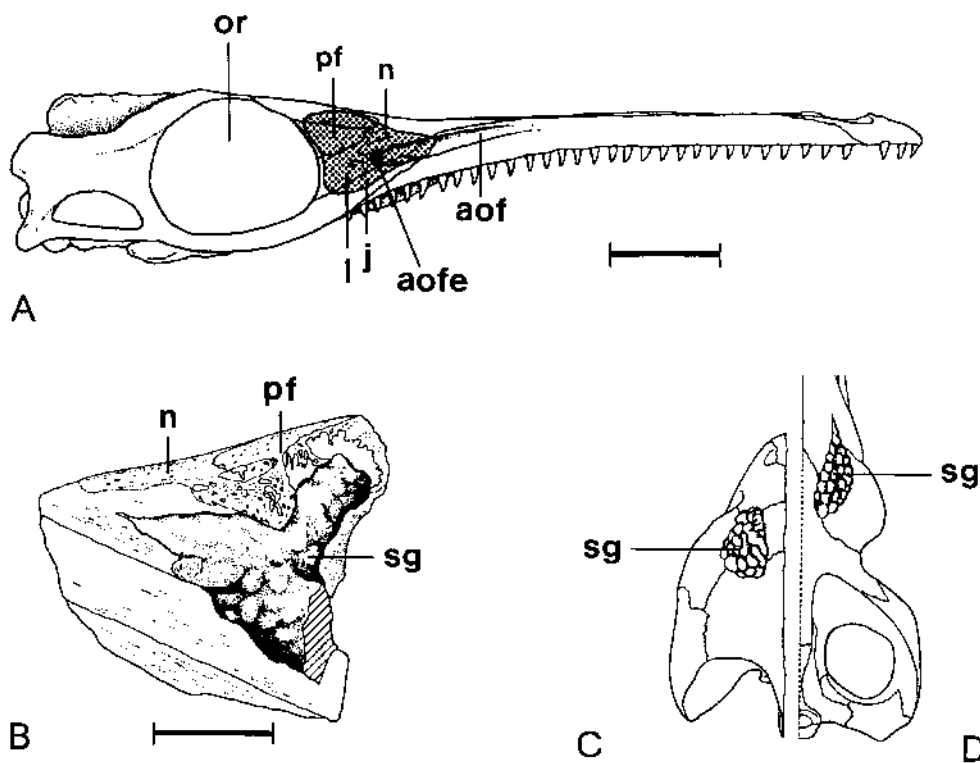


Fig. 3. *Geosaurus araucanensis*. □A. Line drawing of the holotype (MLP 72-IV-7-1) with the salt gland superimposed, scale bar = 5 cm. □B. Line drawing of MLP 86-XI-10-6, scale bar = 3 cm. □C. Salt gland in *Caretta caretta* (modified from Schumacher, 1976); □D. Inferred position of salt gland in *Geosaurus araucanensis*. Abbreviations: aof, antorbital fossa; aofe, antorbital fenestra; j, jugal; l, lacrimal; n, nasal; or, orbit; pf, prefrontal; sg, salt gland.

the bony elements. In left lateral view are visible fragments of the jugal, postorbital and squamosal, surrounding the superior and lateral temporal fenestrae (Fig. 1A). As in other metriorhynchids, the orbits are placed laterally, and the postorbital has a posterior expansion and a broad contact with the squamosal. From the mandible, there remain fragments of the surangular and angular (Fig. 1A). In dorsal view (Fig. 1C) can be seen fragments of the frontal and parietal, which form the dorsal border of the orbits and supratemporal fenestrae. In ventral view, the frag-

ments of the long vomer are interposed between the two ductus nasopharyngei, which are filled with sediment. The positions of the vomer and ductus are the same as observed in the tomography of MLP 72-IV-7-3 (Fig. 4).

In MLP 76-XI-19-1 are preserved fine details on the cast, such as the sutures between nasal and frontal, and between the nasal and maxillary. In this cast (Fig. 1), just in front of the orbits, occur extraordinarily well-preserved paired protuberant structures. These protuberances are symmetrically placed and both have the same structure. Based on these, the protuberances cannot be considered as teratological structures and/or results of an irregular taphogenesis.

In dorsal view, the protuberances have the form of teardrops. In lateral view they are subtriangular and their posterior borders are concave, as they are supported by the anterior wall of the orbit. The body of each protuberance is globular and its anterior part is much more depressed and sharp. The surface of each protuberance is formed by several small lobules and the imprints of blood vessels can be seen on them (Fig. 1B). The position of some of these vessels is symmetrical on the left and right sides. The lobules on the lateral surface are larger (approximately 0.7×0.5 cm) than in the dorsal surface (0.4×0.5 cm). The lobules are more diffused on the anterior part of the protuberances.

A second specimen, MLP 86-XI-10-6 (Figs 2, 3B), consists of a fragment from the last third of the rostrum

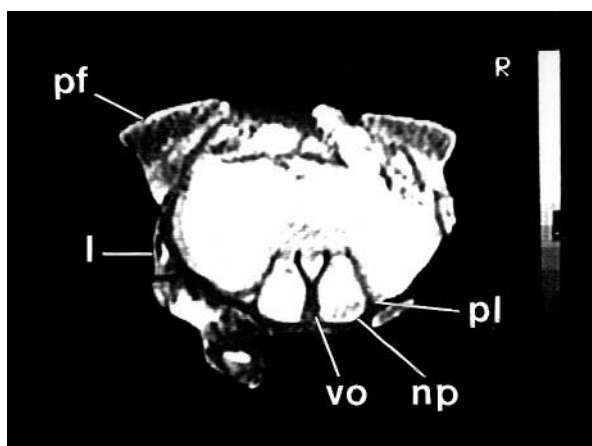


Fig. 4. Computed tomography scans of MLP 72-IV-7-3, transverse section at the level of the lateral expansions of the prefrontals. Abbreviations: l, lacrimal; np, ductus nasopharyngeus; pl, palatine; pf, prefrontal; vo, vomer.

back to the front walls of the orbits. The prefrontals were removed manually, leaving exposed a pair of protuberances with the features of those described above. In lateral and posterior views can be seen a groove on the body of each protuberance which runs downward on the anterior wall of the orbit along the suture between the prefrontal and lacrimal (Fig. 2B). Externally, each protuberance is surrounded by the nasal, lacrimal, prefrontal, jugal and maxilla (Figs 2, 3B).

The topology and morphology of these protuberances preclude the possibility that they are the part of an endocast representing the brain. Endocranial casts generally reflect the shape of the dural envelope which surrounds the brain (Hopson 1979). In the peculiar case of MLP 76-XI-19-1 and MLP 86-XI-10-6 the protuberances described reflect the shape of connective tissue surrounding a pair of organs formed by lobules, the blood supply of which is partially documented by the symmetrical vessels described on their surface (Fig. 1B). This morphology is consistent with that of exocrine glands. In particular, the lobulated protuberances described here, clearly hypertrophied, have the same morphology of the salt glands of some extant birds and reptiles such as *Caretta* (Fig. 3C) figured by Schmidt-Nielsen & Fänge (1958, fig. 1) and Schumacher (1976, figs 2A, 3). In these glands, each lobule is surrounded by connective tissue. It is worthy of remark that in extant reptiles and birds the only glands described with such an enlargement in the posterior part of the rostrum and/or orbital region are the salt glands. These elements permit us to hypothesize that the protuberances preserved in the skull of *G. araucanensis* reflect the shape of salt glands. The secretory capacity of the salt gland depends on many factors, including its size (Withers 1992). Its large size suggests that the salt gland of *Geosaurus* had an increased secretory capacity.

Discussion

Homology of the gland

The homology of the glands reported in this paper is not easy to define, as the main ducts leaving the glands have not been preserved. Topographic position (Fig. 1C) suggests that they are not oral glands, as in extant crocodylians and snakes, or orbital glands, as in turtles. Instead, the glands, although displaced backward, have the same general location as the nasal gland of other sauropsids described by Witmer (1995, 1997). Thus, the glands of *Geosaurus* are outside the nasal capsule, their anterior portion runs along nasomaxillary suture, and they are protected externally by the nasal and maxilla, and, because of their backward displace-

ment, also by the lacrimal and prefrontal. Therefore we identify the glands in *Geosaurus* as nasal salt glands.

Mapping character states of living organisms onto phylogenetic trees, in an attempt to reconstruct ancestral character states and test evolutionary hypotheses, has become a popular method (Cunningham *et al.* 1998). In this particular case many interesting questions arise when mapping 'salt gland character states' of extant groups onto phylogeny. One of them is the ancestral condition for salt glands in Archosauria, as well as in Diapsida. Recently, Witmer (1995, 1997) developed an interesting phylogenetic method for the reconstruction of soft tissues in fossils. We simplified this method as we have the particular case of having direct information about soft tissue. We used a phylogeny of Archosauria with Squamata as the sister group, and including those taxa in which salt glands are present ('Extant Phylogenetic Bracket') (Fig. 5). On this hypothesis we performed two-pass systems of a character optimization in an attempt to infer ancestral condition for Archosauria. Three conditions were coded as follows: nasal glands modified as salt glands (a), posterior sublingual glands modified as salt glands (b), lingual glands modified as salt glands (c). As shown in Fig. 5, the condition of the Crocodyliformes and Archosauria nodes is 'nasal glands modified as salt glands'. It is worthy of remark that the addition of the Cretaceous birds *Ichthyornis* and *Hesperornis*, in which nasal salt glands have been inferred, did not modify node assignments. Consistent with this optimization, nasal salt glands are also the most parsimonious assignment to the Diapsid node.

Given this ancestral state reconstruction, we propose a scenario that the common ancestor of diapsids had a nasal gland with the ability to secrete hypertonic solutions, probably acquired at the end of the Palaeozoic. This represents an adaptation for the maintenance of ionic balance in terrestrial forms, especially those that live in arid regions and/or with a restricted diet rich in potassium such as herbivores, and for osmoregulation in salt water in marine diapsids. The 'functional nasal salt gland' was retained in marine forms and terrestrial groups with restricted diets (i.e. herbivorous), but in those groups with no constraints on their ionic balance this function was lost. Later on, during Cretaceous and/or Cenozoic times, other groups of diapsids were secondarily adapted to life in the sea, and salt glands could have been developed independently of other cephalic glands.

Hypertrophied nasal glands in Metriorhynchidae

There is an important point to be discussed about the

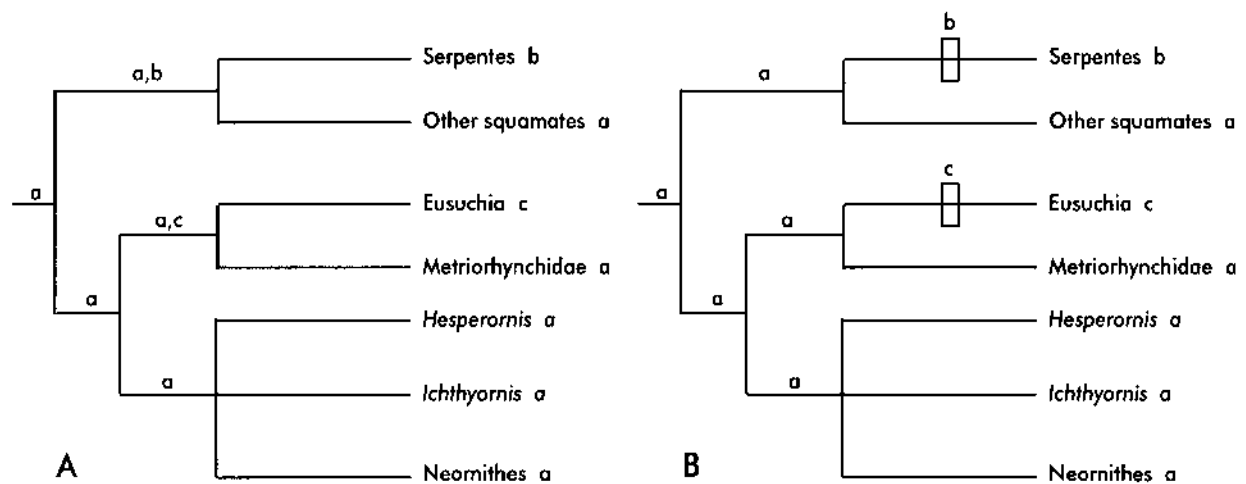


Fig. 5. Optimization of salt gland character. □A. Downpass optimization. □B. Upass optimization. (a) Nasal glands modified as salt glands, (b) posterior sublingual as salt glands, (c) lingual glands modified as salt glands.

hypertrophied nasal glands in Metriorhynchidae: the osteological correlate of the hypertrophied nasal glands. As Witmer (1997, p. 7) pointed out, the morphogenetic primacy of non-skeletal tissues leads us to expect soft tissues often to produce certain bony signatures. One of the most striking features of the skull of metriorhynchids is the lateral expansion of the prefrontals. These expansions were interpreted as a protection of the orbits (Buffetaut 1982) or as having a hydrodynamical function (Hua & Buffetaut 1997). Though the association of the lateral expansion of the prefrontals with a hydrodynamic advantage is not dismissed, another point has to be considered. Metriorhynchid prefrontals, along with lacrimals, are expanded, causing the enlargement of the antorbital region. This enlargement opens an 'additional' place which might house a hypertrophied organ such as the salt gland (Figs 3A, 4). A similar case occurs in extant intertidal lizards of the genus *Uta*. The species of this genus that have salt glands have an enlarged rostral region containing nasal salt glands. These modified nasal glands are nearly five times larger than the nasal glands of the other species of the genus (Hazard *et al.* 1998).

Another point to be discussed is how the salt gland secretion was eliminated. In extant diapsids with nasal salt glands, such as lizards and birds, these glands have one or two ducts that enter the nasal cavity, and secretion flows out of the nostrils. If we assume that the hypertrophied salt glands of *Geosaurus* are nasals, it is probable that the secretion of these glands was eliminated through the nares. Nevertheless, there is an alternative hypothesis that cannot be dismissed. Metriorhynchids are characterized by a peculiar antorbital fossa. In this group the internal antorbital

fenestra is small, bounded by the lacrimal and the nasals, and have a concave and long antorbital fossa excavated into the side of the snout forming a groove directed forward and upward. Several authors (Wenz 1968; Vignaud 1995; Witmer 1997) have remarked on this striking pattern. Based on the topology of the nasal glands of *Geosaurus* and the peculiar form of the antorbital fossa, the possibility that in this distinctive group the antorbital fenestra was used to allow drainage of the salt glands through it into the antorbital fossa and then flowed out cannot be discarded.

Salt glands and diet

It is remarkable that the relationship between salt glands and diet was proposed in iguanids many years ago. Sokol (1967) suggested that the presence of salt glands might be regarded as an adaptation for herbivory. Hazard *et al.* (1998) studied the salt gland secretion of intertidal lizard *Uta tumidarostra* and compared rates of secretion by the salt glands of this species with that of a closely related insectivorous mainland species *U. stansburiana*. They found a close relationship between the diet and salt gland function. Thus, *U. tumidarostra*, which feeds on salty intertidal isopods, has a high salt gland secretion rate compared with *U. stansburiana*, which feeds on terrestrial insects.

The possession of glands with the ability to excrete hypertonic solution from body has an additional advantage for marine reptiles. Salt glands not only prevent lethal dehydration, but also allow them to include a significant proportion of invertebrates in the diet.

It has been previously proposed that the major constraints on the kind of prey consumed were the size of the reptile's gullet and the kind of prey the teeth could handle (Taylor 1987; Massare 1997). But a third constraint is physiological: what kind of prey the reptile could process. An animal capable of excreting ions could eat a significant number of invertebrates, such as cephalopods, which have the same ionic concentration as sea water. This hypothesis is congruent with the diet proposed for metriorhynchids based on dental and osteological characters of their skulls (Hua 1994). This kind of diet is also corroborated by the abundant cephalopod hooklets found in the body cavity of *Metriorhynchus* of the Oxford Clay (Martill 1985).

The discussion of the evolution of any homeostatic system is highly speculative because direct non-osteological evidence is uncommon. Nevertheless, we can improve our knowledge on the soft tissues of extinct forms with a reconstruction, such as the one carried out by Witmer (1997), and by the clues provided by specimens such as the one described here.

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