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NASAL SALT GLAND IN DINOSAURS

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Large, herbivorous dinosaurs display, as a rule, enlarged external nostrils. It is considered here, that they accommodated large functioning salt gland homologous with the lateral nasal gland of Recent reptiles and birds. All dinosaurs were probably uricotelic animals which had to use the extrarenal way of excreting excess of monovalent ions. It is suggested here that they were able to use the nasal salt gland for this purpose. Its presence may have been especially important for unloading the excess of potassium ions ingested by large herbivores with their vegetarian food, or/and for getting rid of sodium ions—by herbivores living in saline environment. An alternative is also given, that the development of large functioning salt gland may have been exclusively a result of large body size and consequently of large amount of potassium ions ingested, independent of fresh water availability in the environment.

Key words: Dinosaurs, paleoecology, physiology, nasal salt glands.

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INTRODUCTION

The external nostrils are almost always extended in the large herbivorous dinosaurs, and sometimes a deep, distinctly delimited depression is present around them. This modification occurs both in the ornithischians and in the herbivorous saurischians. The widely known examples amongst ornithischians are: the enlarged external nostrils of the iguanodonts and stegosaurids (fig. 1:A—E), multiplied openings in the external narial region of some ankylosaurs (fig.1:F), extended and accompanied by a vast depression nostrils of the hadrosaurines (fig. 1:G) and the nostrils surrounded by an extensive depression in the ceratopsids (fig. 1:H,J).

Amongst saurischians, the sauropods have enormously enlarged external nostrils and some of them have deep, bowl-like depressions in front and below the nares (fig. 2:A,B). The floor of these depressions is very

often uneven (in *Brachiosaurus*) and clearly indicates the presence of some glandular body. In the Triassic *Plateosaurus*, the feeding habits of which are still disputable, but which probably was a herbivore, the external nostrils are also extended and an imprint of the circumnarial depression is well marked (fig. 1:K).

Only few herbivorous dinosaurs have small external nostrils and they all were relatively small animals, by dinosaurian standards. Besides, many of these were either the early representatives of Ornithischia, or considered as primitive within their group. Among them the heterodontosaurids, hypsilophodontids, pachycephalosaurids and psittacosaurids (fig. 2:C—F) may be quoted. It may be also mentioned, that the enlarged external nostrils are also present in some terrestrial thecodonts considered as herbivorous (Walker 1961), that is in the aetosaurids (fig. 1:L).

Contrary to the herbivores, the carnivorous dinosaurs almost invariably have nostrils of "normal" size and the depression around them, if at all marked, is only very faint and small (fig. 2:G,H).

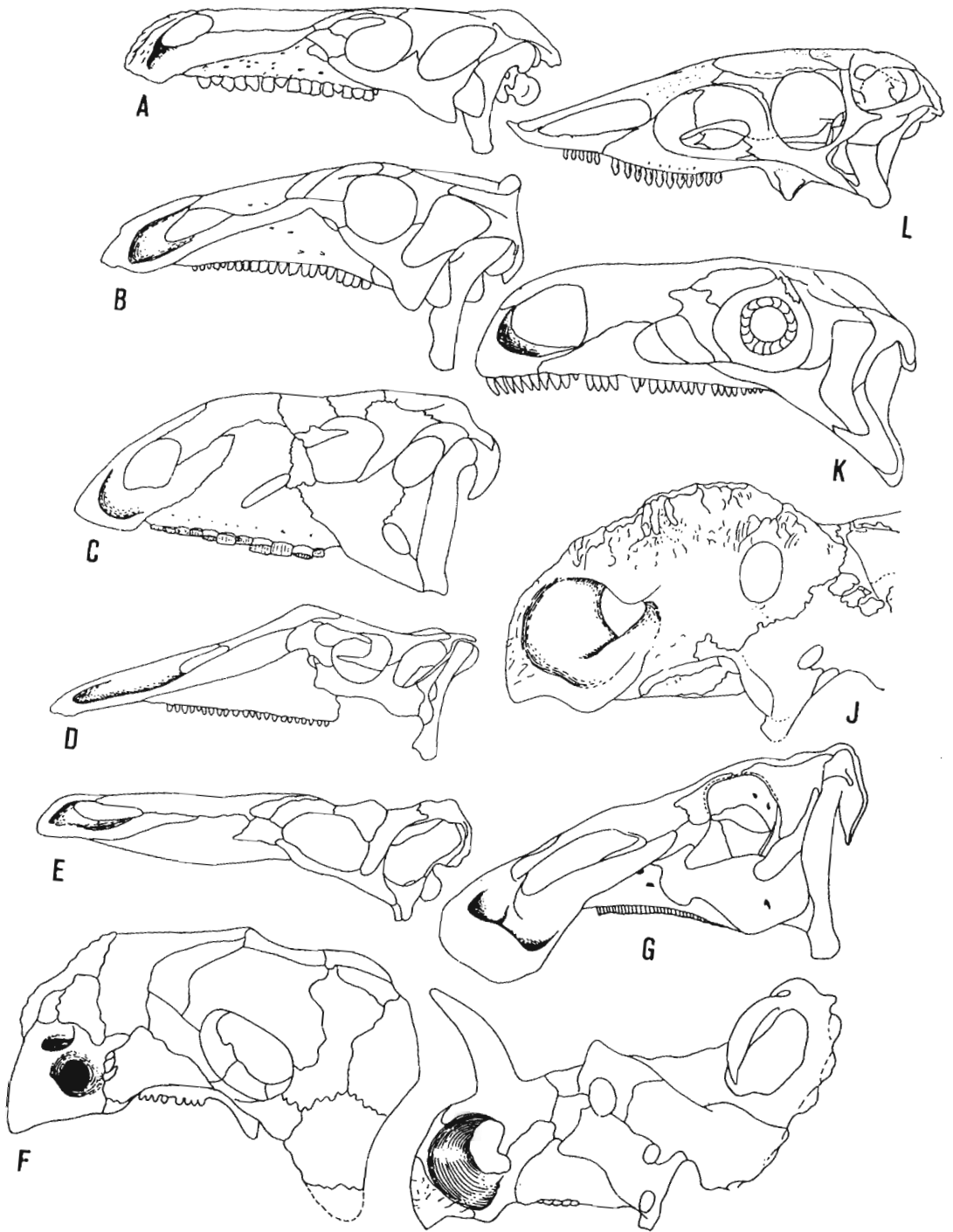
Thus, a correlation seems to occur, at least in dinosaurs, between the diet and the external nostrils' size and form. To my opinion, this correlation is most easy to explain by assuming that the enlarged external nostrils (and maybe also in some instances—the circumnarial depressions) housed the large, functioning salt gland. Recently Wheeler (1978) related the large external nostrils in some dinosaurs to the presence of the enlarged nasal capsule, which played an important role in the brain cooling system of these dinosaurs. His hypothesis, generally, appears sound to me. But, it seems that the very size of the nostrils does not necessarily evidence the elaborate thermoregulatory abilities of the nasal capsule, or its size. More important for the thermoregulation seems to be the size and architecture of the entire nasal cavity, not only of the nasal capsule, which in reptiles occupies the anterior portion of the nasal cavity.

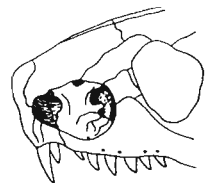
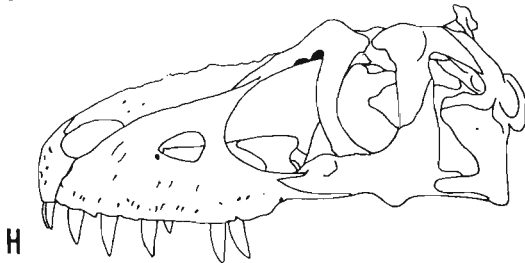
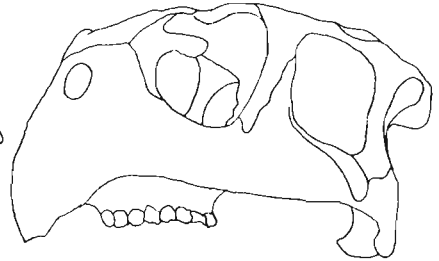
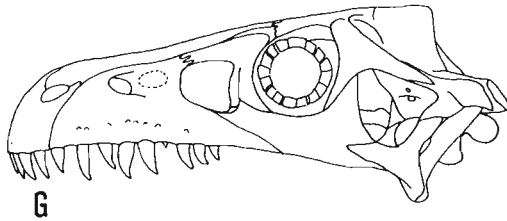
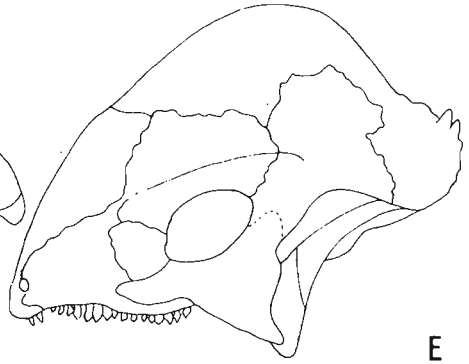
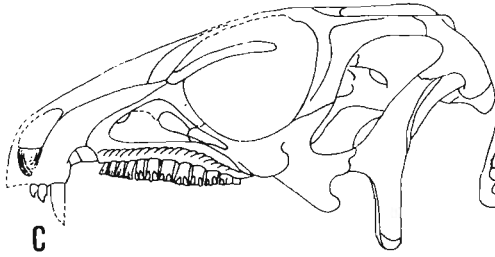
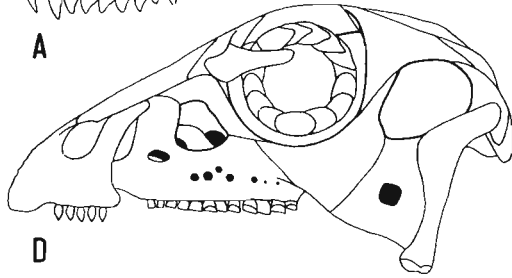
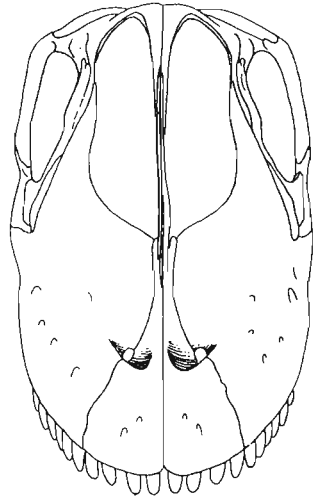
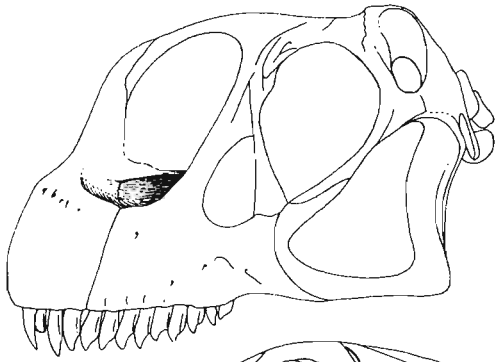
SALT GLAND IN RECENT REPTILES AND BIRDS

The salt gland, or more precisely the lateral (=external) nasal gland performing the salt excretion, is known amongst living reptiles only in the lizards (Parsons 1970), the salt excreting gland in the marine turtles being one of the orbital glands (Abel and Ellis 1966). The modified lateral

Fig. 1. Skulls of: A *Camptosaurus*, after Gilmore, 1909; B *Iguanodon*, after Hooley, 1925; C *Tenontosaurus*, after Ostrom, 1970; D *Ouranosaurus*, after Taquet, 1976; E *Stegosaurus*, after Gilmore, 1914; F *Pinacosaurus*, after Maryńska, 1977; G *Edmontosaurus*, after Lambe, 1920; H *Monoclonius*, after Lull, 1933; J *Pachyrhinosaurus*, after Langston, 1968; K *Plateosaurus*, after Huene, 1926 (nostril modified after specimens housed in the Humboldt Museum, Berlin); L *Stagonolepis*, after Walker, 1961.

Note size and structure of the nostrils.





nasal gland also serves in some birds as the extrarenal pathway for discharging large salt loads (Fänge, Schidt-Nielsen and Osaki 1958; Schmidt-Nielsen 1975). As a rule, the problem of eliminating salt excess is encountered by birds and lizards living in some peculiar habitats, for example by the marine species, the salt-marsh species and the desert species. The need for using the extrarenal way of salt excretion is a consequence of the incapability of the reptilian kidney to produce the urine hyperosmotic to the blood and of the avian kidney to produce urine of more than twice the osmotic concentration of the blood (Gordon 1968). The use of the nasal gland for discharging the excess of salt is, therefore, often met with when the water economy is vital, as it is in the desert lizards and birds, including the ostrich (Gordon 1968: 278). The reptilian and avian kidney is unable to handle large amounts of the monovalent ions (K^+ , Na^+ , Cl^-). These are discharged mostly by means of the salt gland. In the marine birds (e.g. sea gull: Schmidt-Nielsen 1963) and in the marine lizards (e.g. Galapagos iguana: Schmidt-Nielsen and Fänge 1958), which ingest great quantities of sodium and chloride with their food, the main product of the salt gland excretion is Na^+Cl^- . This is however not so in the terrestrial lizards which have a vegetarian diet and live in dry habitats. The gross product of the salt gland secretion is then potassium (Templeton 1967, 1972) abundantly occurring in plant tissues. The important characteristic of the salt gland is that it may function periodically (differently than the kidney which functions continuously) and it can easily be switched from the sodium excretion to potassium excretion and vice versa, according to need.

REASONS FOR THE SALT GLAND PRESENCE IN DINOSAURS

Similarly as Recent reptiles and most of Recent birds, probably all dinosaurs had the lateral nasal gland, which was capable of producing a fluid moistening the nasal respiratory surfaces, but which very often could augment the renal excretion of monovalent ions, when necessary. There was probably no reason to engage this gland into monovalent ions excretion in the carnivorous species, unless they took the saline-water-dwelling prey. The herbivorous species may have encountered a necessity to use their lateral nasal gland for unloading potassium excess which was ingested with great masses of potassium rich plant tissue (and ad-

Fig. 2. Skulls of: A *Camarasaurus*, after Gilmore, 1925; B *Brachiosaurus*, after Janensch, 1935—1936; C *Heterodontosaurus*, after Charig and Crompton, 1974; D *Hypsilophodon*, after Galton, 1974; E *Stegoceras*, after Gilmore, 1924; F *Psittacosaurus*, after Chao, 1962; G *Dromaeosaurus*, after Colbert and Russell, 1969; H *Daspletosaurus*, after Russell, 1970; J *Ennatosaurus*, after Tatarinov and Eremina, 1975. Note size and structure of the nostrils.

ditionally also Na^+ if they fed on the saline water weed). The excretion of electrolytes via kidney, with urine, is related to the water availability (Cloudsley-Thompson 1971). Therefore, it is highly probable that the salt gland (= lateral nasal gland) was functioning and thus greatly enlarged, especially in these habitats where some drinking water deficiencies existed (maybe only seasonally) or where the saline conditions prevailed.

There is neither evidence that the herbivorous dinosaurs were marine animals, nor it is reasonable to assume that they all lived in the salt-marshes, nor at the brakish-water aquens. Obviously, not many of them, if any, were desert dwelling forms. What seems to be proved is, that they lived under warm to subtropical climates throughout the entire Mesozoic and that the vegetation quantities they processed were very large, even assuming that they were ectotherms.

During the Late Cretaceous, when the nostril enlargement in herbivores seems to be most common, many of these dinosaurs inhabited coastal plains, including the estuarine regions, salt lakes shores and brakish-water bayous (Dodson 1971; Russell 1971) or regions influenced by seasonal climates with dry and rainy seasons alternating (Gradziński 1970; Lefeld 1971; Osmólska in press). In fact, it seems that many more dinosaurs, than it is realised, may have inhabited the regions with seasonal climate in which the dry period was accentuated. Direct evidence for the dry periods occurrence may only be rarely registered by fossil record. The primary productivity of many Recent tropical and subtropical habitats in Africa (or in South America during the Neogen), especially these of the savannah, savannah-forest or gallery-forest types, is sufficiently abundant during the rainy seasons to leave eventually enough palaeobotanical evidence, which may give an impression of the all-year-around prosperity of the flora. These types of open habitats support recently herds of large herbivorous mammals (and they also probably did so during the Neogen in South America), despite of the periodical water deficiencies during the drought seasons (understood as limitations of the drinking water reservoirs and of the water content in the dried plants).

It was suggested by several authors (Farlow 1976: for the Oldman F-tion habitat; Srivastava 1970, 1972: for the Edmonton F-tion habitat), that during the Late Cretaceous on the North American continent there existed some open woodland, savannah-like habitats which were inhabited by various dinosaurs.

The water problem during the seasons of drought is especially acute for the large vegetarian animals, as a carnivore may get enough water with the fluid content of its prey. Therefore, in the first place one would expect that some water-saving mechanisms must have been invented by the large herbivores. These mechanisms include the strategies limiting the water loss with urine. The supposed dinosaurian uricotelic might have

been the perfect preadaptation to this purpose. However, the large quantity of potassium ingested had to be discharged; it was almost certainly too large to be handled by the kidney alone, especially during the dry season (or in habitats where the fresh water was scanty or not available). Accepting, that many large herbivorous dinosaurs were forced to use their lateral nasal glands for monovalent ions excretion, seems to be inescapable.

A less plausible alternative may also be suggested, that developing of the large, more or less continuously functioning salt gland in these dinosaurs may have been independent of the climatic conditions and drinking water supply. It may have as well been dependent only on the amount of potassium ingested, thus indirectly — a function of the size of the animal. In other words, there may exist an upper limit beyond which the urine volume cannot be increased, and, regardless of the water supply to the organism, only a certain quantum of potassium ingested by the large dinosaur could be excreted with urine. To my knowledge, little is known about the body size/renal salt excretion relation in the Recent vertebrates, especially in the largest living forms, thus the assumption above may be only a guess.

Some dinosaurs mentioned as those probably having salt glands — the sauropods and hadrosaurs — were considered earlier as amphibious animals. Lately, many authors argue that they were essentially terrestrial (Ostrom 1964; Bakker 1971; Coombs 1975) and in my opinion evidence presented by these authors in favor of their terrestrial habits are convincing and acceptable.

POSSIBLE POSITION OF THE SALT GLAND IN DINOSAURS

The idea that dinosaurs and terrestrial thecodonts may have had the salt glands is not new. The presence of such a gland in these animals was suggested among others by Broom (1913), Ewer (1965), Reig (1970). These authors connected the salt gland with the antorbital fossa. Such a location for the salt gland does not seem likely to me, for the following reasons:

— The salt excreting function is almost invariably performed by the modified lateral (= external) nasal gland in Recent vertebrates: reptiles (some turtles excluding) and birds (Schmidt-Nielsen 1975 among others). The position of this gland is generally close to the external nare (see Templeton 1972: fig. 2 for *Dipsosaurus*), at the vestibulum, outside the cartilaginous nasal capsule.

— In birds, many of which still preserve the antorbital fossa, the lateral nasal gland secretes the excess of salt and it is not housed by the antorbital fossa.

— If the gland were housed in the antorbital fossa, the secretion must have been carried by the glandular duct very far forward in order to empty anteriorly and to be expelled; this is not impossible but rather unlikely. Emptying the gland posteriorly, into the nasal cavity, within the region of the antorbital fossa does not seem likely also, because of the position of the latter close to choana (Osmólska, in preparation) and therefore the danger of interfering with the respiratory passageway, as well as an eventual possibility of swallowing the secretion and the obvious consequence of this.

— In a significant number of ornithischians, which all had reasons to develop salt glands (as they were herbivorous and large) what was formerly the antorbital fossa became later the intramaxillary sinus (Maryńska and Osmólska 1974, 1975) and was finally separated from direct connection with the nasal cavity, as was the case in ceratopsians and hadrosaurians.

Therefore, the most probable location site of the salt gland in dinosaurs is the region of the external nostrils, which is in accordance with the data obtained from the Recent vertebrates. It could be questioned whether nostril enlargement alone may be evidence for a gland presence within the anterior narial region. A similar case was already convincingly argued by Bolt (1974: 27) for the supposedly terrestrial amphibians — trematopsids. According to him (*l.c.*) "...enlargement of the gland was blocked in all directions but laterally. Medial enlargement... might have adversely affected nasal functioning... Lateral expansion could occur by enlarging the external naris". Enlargement of the nostrils was also thought by Tatarinov and Eremina (1975) to be caused by the presence of the lateral nasal gland in some pelycosaurs, although these authors refer rather to the moistening function of this gland (fig. 2: *J*). It should be noted here, that a superficial similarity between the nostrils in these pelycosaurs and in the ceratopsids is striking indeed. The moistening function of the gland which was probably housed in one of the narial openings in the ankylosaurs (fig. 1: *F*) was also suggested by Maryńska (1971: 51). I would rather think of its functioning also as the salt gland both in ankylosaurs and in other herbivorous dinosaurs, because of the above discussed obvious correlation between the vegetarian diet and naris enlargement.

CONCLUDING REMARKS

Direct evidence for a certain physiological function in the entirely extinct animals can only exceptionally be provided by fossils. However, it may be often possible to test whether a given preserved anatomical frame would allow the development of a soft structure which performs

in the Recent animals a certain physiological function. Such a frame seems to be provided by the extensive external nares for the enlarged lateral nasal gland in the majority of large herbivorous dinosaurs. It was inferred here, that this gland might function as the salt gland, mainly for excreting the excess of potassium ions ingested with masses of plant tissues. This seems to be also true for some other terrestrial herbivorous archosaurs such as aetosaurid thecodonts. It appears that development of the salt glands was connected with attaining large body size by some herbivores, because the naris enlargement is generally found in these dinosaurs. This rarely characterizes the early, or primitive representatives of the herbivorous groups.

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HALSZKA OSMÓLSKA

NOSOWE GRUCZOŁY SOLNE U DINOZAUROW

Streszczenie

W pracy zwrócono uwagę na fakt, że zewnętrzny otwór nosowy u wielkich dinozaurów roślinożernych jest z reguły bardzo powiększony. Przedstawiono hipotezę, że powodem powiększenia tego otworu była obecność gruczołu solnego, homologicznego bocznemu (= zewnętrznemu) gruczołowi nosowemu, występującemu u współczesnych gadów i ptaków. Tak jak i większość gadów oraz ptaki, dinozaury były zapewne także zwierzętami urikotelicznymi, to znaczy wydalającymi kwas moczowy jako główny produkt rozpadu związków azotowych, w odróżnieniu od ssaków, u których głównym produktem rozpadu jest mocznik, czy płazów i większości ryb, u których wydalany jest amoniak, bądź mocznik i amoniak. Urikotelia umożliwia zwierzętom lądowym oszczędne gospodarowanie wodą, stwarza jednak trudności związane z wydalaniem poprzez nerki większych ilości monowalentnych jonów, takich jak: Na^+ , K^+ , Cl^- . W związku z tym, niektóre ptaki i gady usuwają nadmiar tych jonów poprzez boczny gruczoł nosowy, który w takich przypadkach działa jako tzw. gruczoł solny, ulegając przy tym znacznemu powiększeniu. Morskie iguany (jaszczurki) odżywiają się morskimi roślinami, a także ptaki morskie, które wraz z pokarmem pobierają znaczne ilości sodu w postaci NaCl , usuwają jego nadmiar poprzez gruczoł solny. Tkanki roślinne zawierają bardzo dużo potasu, którego nadmiar u współczesnych roślinożernych jaszczurek usuwany jest przez powiększony gruczoł solny. Podobnie, wielkie roślinożerne dinozaury musiały pobierać bardzo znaczne ilości potasu wraz z pokarmem. Zakładając, że były również urikoteliczne, nie mogły usuwać nadmiaru jonów K^+ inaczej jak poprzez gruczoły solne, które w związku z tym mogły być bardzo znacznie powiększone. Powiększanie bocznego gruczołu nosowego, funkcjonującego jako gruczoł solny, w kierunku medialnym mogłoby utrudniać przepływ powietrza poprzez jamę nosową do płuc. A zatem, powiększanie to mogło odbywać się wyłącznie w kierunku bocznym i ewentualnie tylnym. Rezultatem tego musiało być powiększanie się zewnętrznego otworu nosowego, obserwowane u wszystkich wielkich dinozaurów roślinożernych.
