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STRUCTURE OF NASAL AND ORAL CAVITIES  
IN THE PROTOCERATOPSID DINOSAURS  
(CERATOPSIA, ORNITHISCHIA)

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Snout is very deep and laterally compressed in the Protoceratopsidae. Oral cavity is highly vaulted longitudinally and transversely. It wedges into the middle of the nasal chamber dorsally causing that ventral portion of the latter parallels oral cavity on both its sides. Fenestra exochoanalis is oriented almost vertically, opening on the side of the oral cavity. Structure of the snout and hard palate results in narrowing and deepening of the nasal passage, thus inhaled air passed close to large surface of the mucosa — covered walls of the nasal cavity. Blood cooling effect of that narrow air passage may have been significant in the Protoceratopsidae. Choana opened well in front of the entrance to larynx: separation of feeding from breathing was not complete, although extensive.

**Key words:** Dinosauria, Protoceratopsidae, nasal cavity, oral cavity, anatomy, thermoregulation.

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## INTRODUCTION

The Protoceratopsidae, an Upper Cretaceous ornithischian dinosaur family of the suborder Ceratopsia, are represented by 5 comparatively primitive genera and 7 species. They are characterized by a very deep and narrow, wedge-shaped snout. The snout is provided anteriorly with a beak-like rostral bone, which is a common character of all horned dinosaurs. The fenestra exochoanalis of protoceratopsids is vertically elongated in most cases and rather highly placed on the side of snout. The antorbital fossa is high rather than long in the protoceratopsids and the antorbital fenestra is very strongly reduced in size, being but a small foramen placed posterodorsally within the antorbital fossa. Nevertheless, this reduced antorbital fenestra communicates with the nasal cavity as does the larger opening in other archosaurs (Osmólska 1985). At least in some protoceratopsids (*Bagaceratops rozhdestvenskyi* and *Protoceratops andrewsi*)

a large slit (*afc*) leads from the bottom of the antorbital fossa to a sinus extending within the main body of the maxilla above the tooth row. Whether the slit connecting the antorbital fossa and the sinus is a distinctive character of all protoceratopsids remains to be proved. Although the sinus cannot be considered as belonging to the nasal or oral cavities it is discussed in this paper, because, being indirectly connected with the nasal cavity through the antorbital fenestra, it may have played a role in ventilation of the lungs.

The snout structure in horned dinosaurs (Ceratopsia) is only superficially known. The most detailed osteological description of that region, provided with excellent, instructive illustrations, was given by Hatcher (*in: Hatcher et al.* 1907) for the most advanced ceratopsian family — the Ceratopsidae. Little is known of the snout structure in the Psittacosauridae, which are in some respects the most primitive ceratopsian family, although otherwise a very specialized one. Brown and Schlaikjer (1940) and Maryańska and Osmólska (1975) provided some data concerning the snout region in the Protoceratopsidae.

The aim of the present study is to describe the nasal and oral cavities in the Protoceratopsidae, and to draw attention to some likely physiological consequences the peculiar anatomy of these cavities might have had for these dinosaurs.

Observations were mainly made on a disarticulated fragmentary skull of *Bagaceratops rozhdestvenskyi* (ZPAL MgD-I/129: comp. Maryańska and Osmólska 1975), as well on the numerous *Protoceratops andrewsi* skulls in ZPAL (Institute of Paleobiology, Polish Academy of Sciences, Warsaw), PIN (Paleontological Institute, USSR Academy of Sciences, Moscow), and GIN (Laboratory of Paleontology and Stratigraphy, Geological Institute, Mongolian Academy of Sciences, Ulan Bator) collections. Some *Psittacosaurus* sp. skulls in the PIN and GIN collections were also studied. The osteologic data which follow concern mainly *B. rozhdestvenskyi*, unless stated otherwise.

I am greatly indebted to Drs. R. L. Carroll (McGill University, Montreal) and P. Dodson (University of Pennsylvania, Philadelphia) for their efforts to improve the English to the present paper.

#### OSTEOLOGIC DESCRIPTION

*Osseous nasal cavity.* This cavity (*nc*) is narrow and deep; it is bounded laterally by the deep premaxillae (*pm*) and maxillae (*mx*) as well as by the lacrimals (*l*) and portions of the nasals (*n*) and prefrontals, close to the top of skull. The dorsoanterior boundary of the cavity is formed of narrow, thick processes of the premaxillae, the dorsal margin by the rather narrow nasals. The floor of the nasal cavity is formed anteriorly by the short secondary palate (pl. 53: B). It consists of long palatal processes

of the premaxillae, the narrow tongues of the maxillae wedged between the premaxillae and of the narrow tip of a vomerine bar, wedged between the maxillae. Posterior to the secondary palate, a central, ascending backwards part of the floor is formed by a thickened vomerine bar (fig. 1). The ascending part of the floor divides the ventral half of the nasal cavity into deep narrow grooves or channels (*ncc*) which parallel the oral cavity on both sides (figs 2, 4). The palatine contributes to the posteromedial and medial walls of each nasal cavity channel.

The anterior process of the palatine is long. It is very steeply inclined lateroventrally at about 20° to the sagittal plane of the skull. The medial

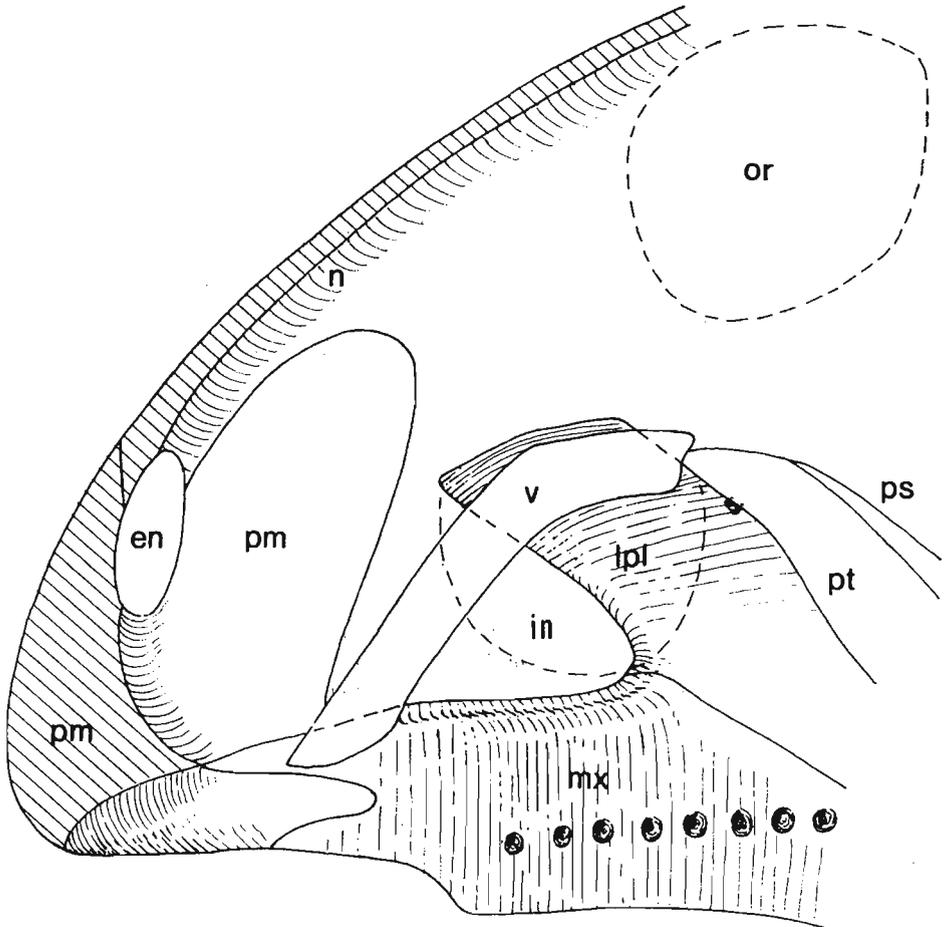


Fig. 1. *B. rozhdestvenskyi*, schemmatic drawing of right half of snout region; medial view. Dashed lines mark positions of orbit and antorbital fossa. Abbreviations: *af* antorbital fenestra, *afc* cleft within antorbital fossa, *en* fenestra exonarina, *ims* sinus within maxilla, *in* fenestra exochoanalis, *l* lacrimal, *lpl* longitudinal palatine wing, *mc* oral cavity, *mx* maxilla, *mxg* groove on maxilla, *mxsf* maxillary shelf, *n* nasal, *nc* nasal cavity, *ncc* ventral channel of nasal cavity, *or* orbit, *pm* premaxilla, *pms* surface for premaxilla, *ps* parasphenoid, *pt* pterygoid, *tpl* transverse palatine wing, *v* vomer, vomerine bar *vpl* ventral tongue of palatine.



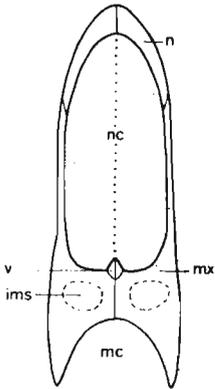


Fig. 3. *B. rozhdestvenskyi*, cross-section of snout in secondary palate region; schematized. Dotted line marks presumed membranous medial nasal septum. Abbreviations as in fig. 1.

the level of the upper boundary of the antorbital fossa, is there no bony wall between the suborbital and the nasal cavities. The internal shelf of the maxilla (*mxsf*) forms the floor of the channel (fig. 4). This shelf roofs a spacious sinus (*ims*) extended above the tooth row within the maxilla. This shelf is narrow and horizontal along the anterior half of the fenestra

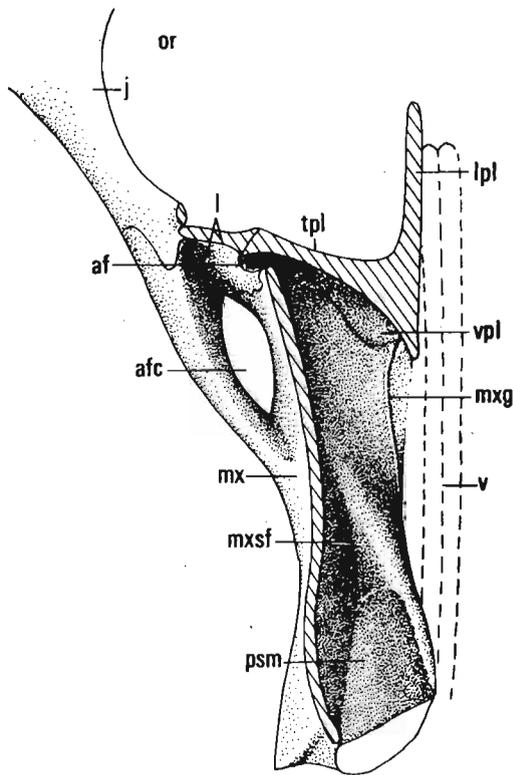


Fig. 4. *B. rozhdestvenskyi*, right ventral channel of nasal cavity in dorsal view. Nasal cavity horizontally sectioned on level of the antorbital fenestra; schematized. Dashed lines mark positions of vomers. Abbreviations as in fig. 1.

exochoanalis (fig. 2, left). More posteriorly the shelf becomes gradually more oblique medially and fades away close to the posteroventral corner of the fenestra exochoanalis (fig. 2, right), at the point where the anteroventral tongue of the palatine overlaps the maxilla. Along the ventral boundary of the fenestra exochoanalis there runs a shallow groove on the internal margin of the shelf; the groove disappears at the suture between the above mentioned palatine tongue and the maxilla (fig. 4). Medially, the ventral channel of the nasal cavity is broadly open to the oral cavity: almost the entire medial side of the channel is occupied by the fenestra exochoanalis; a short bony medial wall of the channel is present only dorsally and it is formed by the anterodorsal tip of the longitudinal palatine wing. Externally, the channel is bounded by the lateral, vertical flange of the maxilla, which forms the medial wall of the antorbital fossa. In the region of the posteroventral corner of the fenestra exochoanalis, the channel extends laterally into a narrow space between the medial wall of the fossa and the lateroposteriorly directed transverse palatine wing; the wall and the wing meet posteriorly at an acute angle.

*Oral cavity.* The oral fissure reached back probably to a short distance in front of the first maxillary tooth, along the sharp ventral edge of the premaxilla. More posteriorly, a cheek might have been present, which prevented chopped food from falling from the mouth (comp. Galton 1973). The upper lip, if present, would have been restricted to a short distance along at most two thirds of the premaxillary edge, between the suture with the rostral bone anteriorly and about the first maxillary tooth. Probably the

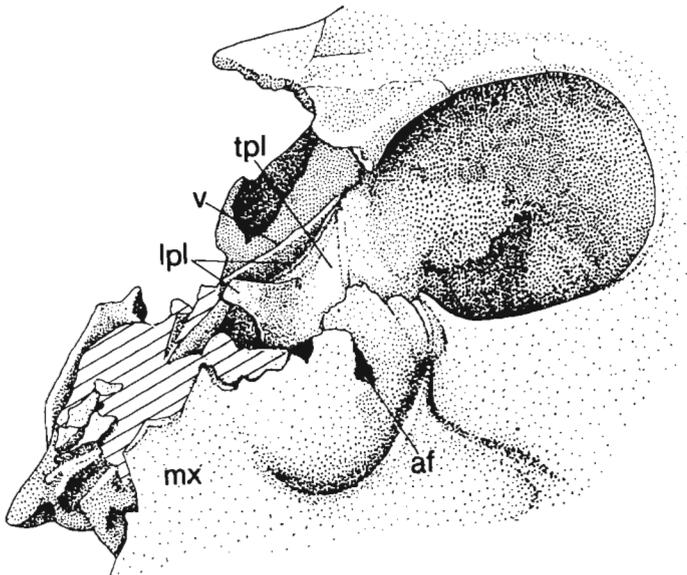


Fig. 5. *P. andrewsi*, GIN 100/512, side view of snout in orbital and antorbital region; see also pl. 54: 1; schematized. Abbreviations as in fig. 1.

entire ventral margin of the upper jaw anterior to the cheeks was covered by a horny sheet. The gape of the mouth would not have been large, considering that the rostrum was curved downwards and the opposite mandibular element—the pretendary, was curved upwards. The tip of the prementary bit posteriorly to that of the rostrum when the mandible was adducted.

The oral cavity (*mc*) of the protoceratopsids is distinctive in being highly vaulted, both longitudinally and transversely. The high longitudinal vault of the roof of the oral cavity results from the steep posterodorsal incline of the vomerine bar posterior to the secondary palate (fig. 1) and, further posteriorly, from the similarly steep posteroventral slope of the palatal processes of the pterygoids (*pt*). The angle between the two roofing portions is about 90°. The high transverse vault of the roof is due to the steep orientation of the anterior processes of the palatines and the corresponding orientation of the fenestrae exochoanales. The transverse profile of the oral cavity roof changes along the length of the cavity. It is comparatively low and broadly arched anterior to the fenestrae exochoanales, acutely angled at the top along the entire exochoanal region (the angle equals 35°—40°) and is arched and significantly broader behind that region. On the disarticulated ZPAL MgD-I/129 *Bagaceratops rozhdestvenskyi* skull (the basal length of which is estimated as 200 mm), the oral cavity has its deepest region just behind the posteroventral corner of the fenestra exochoanalis, where the depth equals about 75 mm, counting from the ventral maxillary edge. The exochoanal region of the oral cavity is wedged dorsally between sides of the nasal cavity, as described above. The side walls of the cavity are very steep along the exochoanal portion, and, for about the ventral half of its height, each one consists of the medial, nearly vertical, sheet of the maxilla. Posterodorsal to the fenestra exochoanalis, the hard palate is formed of the longitudinal palatine wing. Behind the fenestra exochoanalis, most of the lateral wall of the cavity consists of the posterior pterygoid process of the palatine. The palatine-maxilla suture runs obliquely in the ventroposterior direction. The pterygoidal part of the palatine arches gently medially towards its contact with the wedge-like palatal process of the pterygoid. The steep inclination of the palatal process of the pterygoid causes the posterior portion of the hard palate to slope obliquely downward towards the end of the oral cavity, somewhere shortly in front of the tooth row.

#### DISCUSSION

The hard palate of this described type is found, with small differences, in *Bagaceratops* (*B. rozhdestvenskyi*) and in *Protoceratops* (*P. andrewsi*, ?*P. kozlowskii*). Another protoceratopsid in which palate is known is

*Leptoceratops* (*L. gracilis*). The palate was only briefly described by Sternberg (1951: 236—237; pl. 50) and the illustration of that region does not provide enough information on the special structure of the respective bones. However, it seems that the palatine, which in the other two genera is mainly responsible for the peculiar structure of the palate, is much more primitive, and the vertical transverse wing of the palatine has not yet been developed in *Leptoceratops*. Instead of the vertically extended transverse wing, which is ventrally in contact with the maxilla along its entire width in *Bagaceratops* and *Protoceratops*, there is only a short, transverse process anteriorly in *Leptoceratops* which contacts the maxilla laterally; the process is developed in the same oblique plane as the remaining portion of the palatine. This process bounds the fenestra exochoanalis posteriorly. Posterior to the short portion of the palatine-maxilla contact there is an extensive opening ("excavation" or "fossa" in Sternberg's paper) between these two bones. A similar, though less extensive opening seems to be present between the maxilla and palatine in *Psittacosaurus* (Dr. P. Sereno's personal information), placed ventrally and slightly posterior to the fenestra exochoanalis. Judging from Sternberg's description and illustration the fenestra lies in a plane strongly inclined to the sagittal plane of the skull: thus the oral cavity is also deep in *Leptoceratops*. It is also deep in *Psittacosaurus*. Although the fenestra exochoanalis is well visible in palatal view on the illustration of the *Leptoceratops* skull in Sternberg's 1951 paper as well as on these of *Protoceratops* in Brown and Schlaikjer's 1940 paper, figs 11a, 16b) this is only due to a slight lateral tilt to the side of the illustrated skulls.

One can thus conclude that a significant deepening of the oral cavity and related transformation of the ventral portion of the nasal cavity posterior to the secondary palate are common characters of protoceratopsids and psittacosaurids. Development of the transverse palatine wing and the corresponding complete bony separation of the nasal cavity ventrally and posteriorly from the suborbital space is a common character of the Protoceratopsidae, *Leptoceratops* probably excluded, and the Ceratopsidae.

Little can be added here regarding Brown and Schlaikjer's (1940) extensive comparison of the snout and palate bones in *P. andrewsi* and the advanced representatives of the suborder Ceratopsia — the Ceratopsidae; their conclusions are still mostly valid. A few comments are made below.

There is no information given by Hatcher (*in*: Hatcher *et al.* 1907) nor Lull (1933) as to the inclination of vomers in the Ceratopsidae, which is so significant in the Protoceratopsidae. As can be judged from Hatcher's illustration of the skull in lateral view with a posterior portion of vomers preserved (Hatcher *et al.*, 1907: fig. 24), they might also have been oblique in *Triceratops horridus* (and most probably in other ceratopsids), although

not so steeply rising backwards as in the protoceratopsids. The characteristic palatine structure was first noticed by Hatcher (Hatcher *et al.* 1907) in the Ceratopsidae and later confirmed for the Protoceratopsidae by Brown and Schlaikjer (1940). These latter authors remarked that the longitudinal wing of the palatine was much longer anteroposteriorly and that respectively the fenestra exchoanalis was much shorter and more anterior in protoceratopsids. Shortening of the longitudinal wing in the ceratopsids was associated and probably related to the change in the angle of the inclination of the transverse palatine wing, which from slightly oblique forward orientation in the protoceratopsids became almost vertical in the ceratopsids. At the same time, the transverse wing, which in the protoceratopsids runs oblique to the sagittal skull plane, became perpendicular to the latter in the ceratopsids. The result of these changes in inclination was a change in the posterior border of the fenestra exchoanalis, which from the inclined, posterodorsal one became vertical. Nevertheless, the fenestra in both groups lies in a plane almost parallel to the sagittal plane of the skull. Thus, in ceratopsids, the ventral channels of the nasal cavity which run parallel to the highly vaulted oral cavity have been also elaborated. The ceratopsid oral cavity is, however, different from that in the protoceratopsids in being wider, which seems secondary, considering the advanced position of the palatine wings.

It should be noted that a similar development of the palatine is observed in the Hadrosauridae. As was clearly shown by Heaton (1972) the entire bone is vertical. The anterior extent of the palatine is strongly shortened and there is a short transverse palatine wing at a right angle to the longitudinal one, which adheres to the jugal laterally. In the Ceratopsia the jugal principally contacts the external flange of maxilla and the lacrimal. There is remarkable similarity in the structure of the palatine between the Ceratopsidae and the Hadrosaurinae; both groups have evidently reached the same grade of the morphological change. The palatine development in the Protoceratopsidae represents a less advanced grade, while that in the Lambeosaurinae (Hadrosauridae) a more advanced one. Parallelism in the development of the palatine observed in the Ceratopsia and Hadrosauridae results in my opinion from a parallel trend towards high vaulting of the oral cavity related, in turn, to adaptation to processing large quantities of plant food.

Within the maxilla of *Bagaceratops rozhdestvenskyi* and *Protoceratops andrewsi* a spacious sinus extends above the tooth row, which communicates dorsally with the antorbital fossa through the cleft (*afc*) in the bottom of the latter. This sinus is clearly visible in bones which have been broken. The maxilla is solid in the ceratopsids judging from Hatcher's illustration of *Triceratops horridus* (1907: fig. 27). The sinus was once considered by me (Maryańska and Osmólska 1975) as homologous with the intramaxillary sinus of Pachycephalosauria. Having disarticulated material

I am now able to state that the protoceratopsid sinus does not communicate with the nasal cavity as does the pachycephalosaurian sinus. Moreover, in the latter group, as well as in some other ornithischians (e.g. hypsilophodontids and ?heterodontosaurids), the intramaxillary sinus is derivative of the antorbital fossa, while that in the protoceratopsids evidently is not. It follows that the protoceratopsid sinus is a new structure and cannot be called "intramaxillary sinus." The function of the protoceratopsid sinus remains unclear. As it communicates with the antorbital fossa, the role of which is considered by me (Osmólska 1985) as possibly associated with breathing and CNS cooling, one can also consider the idea that the sinus might have had a thermoregulatory function. If that is the case, the lack of the sinus in the advanced ceratopsids may be explained by: 1. development of other thermoregulatory devices — horns, frill, double roofing of brain cavity (comp. Wheeler 1978; Osmólska 1985); 2. development of vertically extensive teeth batteries.

#### CONCLUSIONS

Three anatomical phenomena, dependent on each other, are considered above. One is the conspicuous narrowing and deepening of the snout, the second — related deepening and narrowing of the oral cavity, the third — separation of the nasal cavity ventrally into two channels, opening to the oral cavity on the sides of the latter, caused by wedging of the hard palate and the oral cavity into the middle of the nasal chamber.

Two hypotheses may be considered concerning the primary reason for the changes in the snout and the related transformations. The first would be a feeding adaptation manifested by an almost bladelike narrowing of the snout, significant deepening of the oral cavity, and closer approach of the opposite tooth rows; changes in the nasal cavity are then an unavoidable consequence.

The second hypothesis, to the contrary, would postulate that a refinement of the functions of the nasal cavity: breathing, thermoregulation, olfaction, might have been the reason of its remodelling at the expense of the oral cavity.

There is more anatomical evidence which speaks in favor of the first hypothesis. The beak-like rostral element of the upper jaws, and the usually edentulous premaxillae are present in all Ceratopsia. These anatomical structures, obviously connected with feeding, appeared presumably in the ancestry of ceratopsids prior to snout transformations.

Although remodelling of the narial passage might have been the result of changes in the oral cavity, it was not without effect on its functions. Because the dorsal portion of the nasal chamber changed the least, olfaction should not have been essentially affected. On the other hand, a stream

of inhaled air passed through much narrower and deeper channels in the protoceratopsids than it did in the broad-snouted dinosaurs, what may have influenced thermoregulation. The blood cooling effect of the narrow, deep air passage may have been significant, as it brought the air stream close to the deep, large surface of the mucosa covering the walls of the nasal cavity.

Although there is little evidence allowing reconstruction of the soft palate, I assume that it was attached along the ventral edge of the vomerine bar medially, rising steeply posteriorly together with the rise of vomers. The lateral attachment of the soft palate was probably ventral, somewhere along the medial margin of the internal maxillary shelf. How far the soft palate reached posteriorly can be only speculated. It is probable that it partly obscured the fenestra exochoanalis, ending shortly in front of the posterolateral corner of the fenestra, where there is marked decrease in the width of the maxillary shelf. The choanae probably opened well in front of the entrance of the larynx. It follows that the separation of feeding from breathing may have been extensive but not complete.

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BUDOWA JAMY NOSOWEJ I GĘBOWEJ DINOZAUROW PROTOCERATOPSIDAE  
(CERATOPSIA, ORNITHISCHIA)*Streszczenie*

Protoceratopsidae są prymitywną rodziną roślinożernych dinozaurów rogatych (Ceratopsia), żyjących w okresie kredowym na kontynencie azjatyckim i północno-amerykańskim. Charakteryzują się m.in. głębokim, bardzo silnie bocznie spłaszczonym pyskiem. Ten kształt pyska warunkuje szczególną budowę anatomiczną jamy nosowej i gębowej, na co dotychczas nie zwracano uwagi. Jama gębowa jest wąska i bardzo wysoko sklepiąca podłużnie oraz poprzecznie. Jej centralna część jest wklonowana w jamę nosową (pls. 53, 54; figs 1—5). Spowodowało to przebudowę jamy nosowej, a szczególnie jej brzusznej części, w której wyodrębniła się para głębokich bruzd przebiegających równolegle i bocznie do jamy gębowej. Przedni wyrostek kości podniebiennej stał się niemal całkowicie pionowy, w odróżnieniu od większości innych dinozaurów ptasiomiedniczych (Ornithischia) i innych gadów, gdzie jest on poziomy lub tylko lekko nachylony w stosunku do płaszczyzny strzałkowej czaszki. Wyrostek ten tworzy dwa skrzydła: podłużne, kontaktujące przyśrodkowo z lemieszem, oraz poprzeczne, kontaktujące bocznie z kością szczękową i łzową. Poprzeczne skrzydło zamyka z tyłu brzuszłą bruzdę jamy nosowej i oddziela ją całkowicie od przestrzeni podoczodołowej. Kostna przegroda między jamą nosową i oczodołem nie występuje u innych Ornithischia. Okno nozdrzy tylnych jest położone w płaszczyźnie niemal równoległej do płaszczyzny strzałkowej czaszki, otwierając się do jamy gębowej nie od góry, jak u większości Ornithischia (i innych gadów), lecz z boku.

Budowa kości podniebiennej i położenie okna nozdrzy tylnych są bardzo zbliżone u przedstawicieli Ceratopsidae, innej, bardziej zaawansowanej rodziny dinozaurów rogatych. Cechy te zostały zapewne odziedziczone po wspólnym przodku z Protoceratopsidae.

Podobne wykształcenie przedniego wyrostka kości podniebiennej jest znane także u dinozaurów kaczodziobych (Hadrosauridae, Ornithischia). Grupa ta jest bardzo odlegle spokrewniona z Ceratopsia i podobieństwo to jest homoplazją.

Jama nosowa Protoceratopsidae, a szczególnie jej oddechowa, brzuszna część, jest bardzo wąska i głęboka. W związku z tym, strumień wdychanego powietrza przepływał blisko jej ścian, które mają dużą powierzchnię i pokryte były za życia unaczynioną śluzówką. Mogło to mieć duże znaczenie termoregulacyjne, obniżając, poprzez parowanie, temperaturę krwi dochodzącej do mózgu.

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## EXPLANATION OF THE PLATES 53 AND 54

## Plate 53

Schematic drawing of the protoceratopsid snout region;  
based largely on *B. rozhdestvenskyi* ZPAL MgD-I/129

- A. Palatal view.  
B. Dorsal view, skull roof removed.

Abbreviations as in fig. 1.

Drawing by E. Leszak

## Plate 54

*Protoceratops andrewsi* Granger et Gregory, 1923  
Upper Cretaceous, Toogreeg formation, Toogreeg,  
Gobi Desert, Mongolia, GIN 100/512

- 1a. Stereo-photograph of damaged skull, dorsoanterior view of nasal cavity, approx.  $\times 0.2$ .  
1b. Same specimen, side view, approx.  $\times 0.2$ .

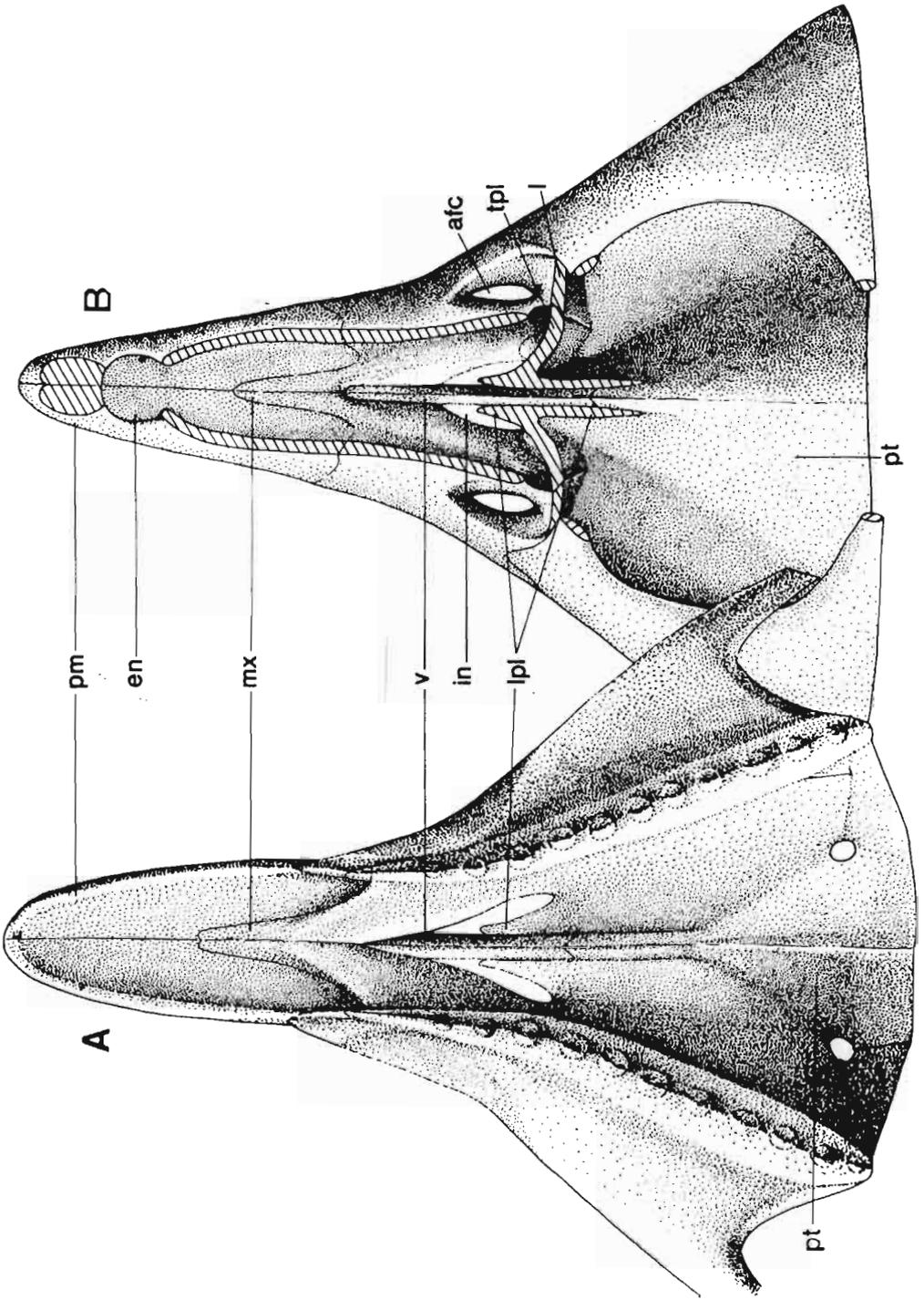
Courtesy of Dr. R. Barsbold

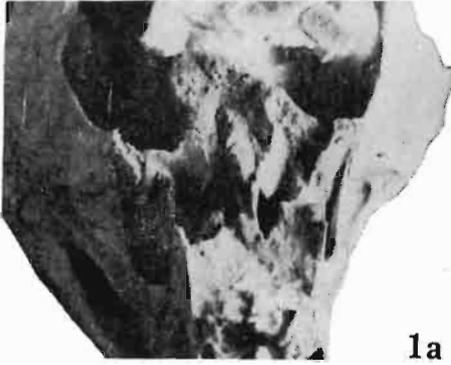
*Bagaceratops rozhdestvenskyi* Maryańska et Osmólska, 1975  
Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav,  
Gobi Desert, Mongolia, ZPAL MgD-I/129

- 2a. Damaged skull, ventral view, approx.  $\times 0.4$ .  
After Maryańska and Osmólska (1975: pl. 45: 1c)  
2b. Same specimen, stereophotograph, ventroanterior view, approx.  $\times 0.4$ .

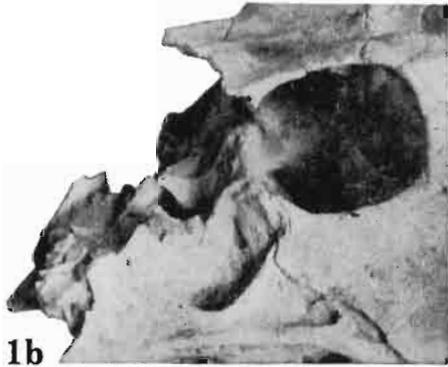
Fig. 1 photo: T. Maryańska  
Fig. 2a photo: E. Mulawa  
Fig. 2b photo: W. Skarżyński

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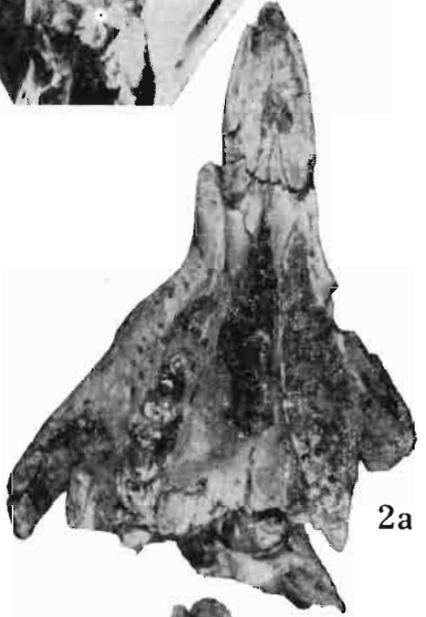




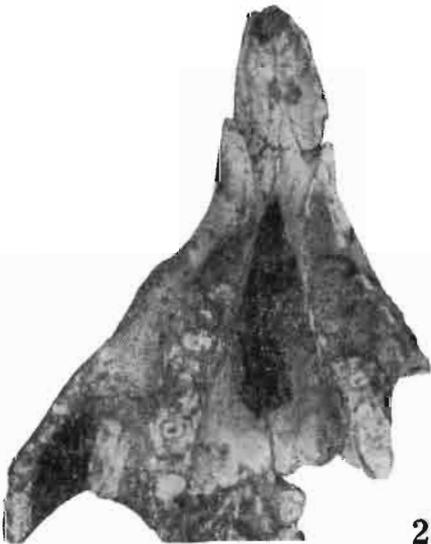
1a



1b



2a



2b

