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CRANIAL ANATOMY OF *SAUROLOPHUS ANGUSTIROSTRIS* WITH COMMENTS ON THE ASIAN HADROSAURIDAE (DINOSAURIA)

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A complementary description of the skull of the Upper Cretaceous hadrosaurine dinosaur *Saurolophus angustirostris* is given with some remarks on growth changes. It is suggested that the nasal crest in *Saurolophus* provided the additional, enlarged respiratory surface to the nasal cavity and served as the thermoregulatory device. The relatively weak, or loose, junctions between many skull bones in the hadrosaurid dinosaurs are explained as being related to the amortization demands of their delicate narial structures. All hadrosaurid taxa described from Asia are critically reviewed.

Key words: Dinosauria, Hadrosauridae, skull anatomy, nasal crest, intracranial mobility, Upper Cretaceous, Asia.

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Streszczenie. — Uzupełniono opis czaszki dinozaura z rodziny Hadrosauridae *Saurolophus angustirostris* (górna kreda Mongolii) i zwrócono uwagę na jej zmiany wzrostowe. Przedstawiono hipotezę, że grzebień nosowy występujący na czaszkach przedstawicieli rodzaju *Saurolophus* zwiększał dodatkowo powierzchnię jamy nosowej i służył procesom termoregulacyjnym. Uznano, że przyczyną występowania wielu luźnych połączeń między kośćmi czaszki dinozaurów z rodziny Hadrosauridae była konieczność zabezpieczenia ich delikatnych i skomplikowanych struktur nosowych przed wstrząsami powstającymi podczas intensywnych ruchów żujących szczęk. Dokonano krytycznego przeglądu wszystkich taksonów Hadrosauridae opisanych dotychczas z Azji. Praca niniejsza była finansowana przez Polską Akademię Nauk, w ramach problemu międzyresortowego MR II-6.

CONTENTS

INTRODUCTION

The most complete and abundant hadrosaurid material recorded so far from the Upper Cretaceous of Asia is that of *Saurolophus angustirostris* ROZHDESTVENSKY from the Nemegt Formation, Nemegt Basin, Mongolian People's Republic. The species was preliminarily described by ROZHDESTVENSKY (1957) who later added (1965) some comments on its allometric changes. The original material of *S. angustirostris* collected by the Mongolian Paleontological Expedition of the USSR Academy of Sciences in 1947–1949 includes several complete skeletons derived from the Altan Ula, Tsagan Khushu and Nemegt localities. It is housed in the Paleontological Museum of the USSR Academy of Sciences in Moscow. During the Polish-Mongolian Paleontological Expeditions several other specimens of this species were collected from the Nemegt Formation. One complete skeleton of a young individual was found at the locality Altan Ula IV. The skull of this specimen provided some new data on the circumorbital and crestal regions, which we published earlier (MARYAŃSKA and OSMÓLSKA 1979). This skull also allows us to supplement herein ROZHDESTVENSKY's original description. Until recently *S. angustirostris* was the only known representative of the Hadrosauridae in the Nemegt Formation. However, new material collected by the Polish-Mongolian Paleontological Expeditions (1963–1971: KIELAN-JAWOROWSKA and DOVCHIN 1969, KIELAN-JAWOROWSKA and BARSBOLD 1972) indicates that in addition to *S. angustirostris* which was the dominant herbivore in the Nemegt Formation (OSMÓLSKA 1980), other hadrosaurids occurred in this formation. The description of this new material, as well as the supplementary description of the postcranial skeleton of *S. angustirostris* will be published at a later date (MARYAŃSKA and OSMÓLSKA in preparation).

The results of recent studies on the North American Hadrosauridae (DODSON 1975, HOPSON 1975, BRETT-SURMAN MS, 1979) indicate that sexual dimorphism and allometric changes are distinctly pronounced in these dinosaurs. These studies resulted in the significant reduction of the number of taxa within the North American hadrosaurids. The number of the Asian hadrosaurid taxa is comparatively large (table 1). Some of these should be considered invalid because they were based on insufficient or nondiagnostic material. A majority of the remaining taxa were based on fragmentary specimens which may be synonimized in the future. In this paper we have tried, to revaluate the previously described Asian hadrosaurid taxa.

During our studies on *S. angustirostris* we profited immensely from the experience and the friendly help of Dr. A. K. ROZHDESTVENSKY (Paleontological Museum of the USSR Academy of Sciences, Moscow), who made available to us his unpublished data and drawings. Thanks to the permission of the authorities of the Paleontological Museum of the USSR Academy of Sciences in Moscow, and of the Geological Institute of the Mongolian Academy of Sciences in Ulan Bator, we were able to study all the hadrosaurid materials stored there, including those still undescribed. Dr. S. M. KURZANOV (Paleontological Museum, USSR Academy of Sciences, Moscow) and Dr. R. BARSBOLD (Geological Institute, Mongolian Academy of Sciences, Ulan Bator) were very helpful and generous with information. Dr. M. K. BRETT-SURMAN (Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore) kindly provided a copy of his unpublished MS; Dr. D. A. RUSSELL (Palaeobiology Division, National Museum of Canada, Ottawa) and Dr. W. P. COOMBS (Pratt Museum, Amherst College, Amherst) provided valuable data on *Saurolophus* specimens from the North America. The help and kindness of all these persons is acknowledged and our thanks are expressed.

Abbreviations used:

AMNH — American Museum of Natural History, New York;
GSC — Geological Survey of Canada, Ottawa;
GSP — Geological Institute, Academy of Sciences of the Mongolian People's Republic, Ulan Bator;
IVP — Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Museum of Natural History, Peking;
PIN — Paleontological Museum, USSR Academy of Sciences, Moscow;
ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

THE HADROSAURIDAE IN ASIA

The Hadrosauridae described thus far from the Upper Cretaceous deposits of Asia come from: the South Sakhalin (NAGAO 1936), Shantung (WIMAN 1929, YOUNG 1958, HU 1973, ZHEN 1976), Neimengguzizhiqu (= Inner Mongolia; GILMORE 1933*a*, ROZHDESTVENSKY 1966), Gobi Desert (ROZHDESTVENSKY 1952, 1957), Laos (HOFFET 1943), Asiatic part of the USSR (RIABININ 1925, 1930, 1931, 1939, ROZHDESTVENSKY 1968). Although it is believed that the hadrosaurids in Asia range stratigraphically from the Cenomanian to the Maastrichtian, the age of the hadrosaurid bearing deposits cannot be determined precisely. The same is true for the mutual time relations of the majority of the described hadrosaurid taxa in Asia. The most primitive species are a hadrosaurine *Gilmoreosaurus*[1] *mongoliensis* (GILMORE, 1933) and a lambeosaurine *Bactrosaurus johnsoni* GILMORE, 1933, both from the Iren Dabasu Formation (GILMORE 1933*a*). A Cenomanian age was suggested for this formation by ROZHDESTVENSKY (1966, 1974, 1977*a*). Whatever the stratigraphic age of these two species is, so far there is no evidence that they are Cenomanian forms, although they may be indeed the oldest described Asian hadrosaurids. Similarly, *Saurolophus angustirostris* ROZHDESTVENSKY, 1952, may be the stratigraphically youngest Asian duck-billed dinosaur, probably not older than the late Campanian.

Another deficiency of the Asian hadrosaurid material is that except for *S. angustirostris* none of the previously described species is known from a complete skull; many of these species are based upon a single specimen (if not on singular postcranial bones). Very often there is also no assurance whether the associated postcranial bones and the fragmentary skull belong to the same taxon. In several instances, two or more species were found in the same formation, horizon and locality, e.g. as was the case with *Tanius chingkankouensis* YOUNG, 1958 and *Tsintaosaurus spinorhinus* YOUNG, 1958 (Young 1958) or with *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis* (GILMORE 1933*a*). Postcranially, the hadrosaurids are rather conservative and it is difficult to determine them, even generically, basing on the postcranial bones. A few postcranial elements are possible exceptions (BRETT-SURMAN MS). The same is true for most of the separate cranial bones, which do not display enough features of taxonomic value. For these reasons even the subfamilial assignment of taxa has often been questioned.

In WIMAN'S paper (1929) *Tanius sinensis* was first described from the Chiangchunting locality in Shantung, which has been based upon a fragmentary specimen comprising a skull lacking the snout and a portion of the postcranial skeleton. The flat skull roof and the postcranial skeleton of this holotype specimen expose the characters typical of the Hadrosaurinae (LULL and WRIGHT 1942). The only dorsal vertebra associated with the holotype and assigned by WIMAN (1929: pl. 7: 2) to the same species, may however belong to a lambeosaurine dinosaur. Its neural spine is comparatively high as is typical of the dorsal vertebrae in representatives of this subfamily and distinctly thickened distally. YOUNG (1958) described two new species from the Wangshih series at Hsikou (Chingkankou) in Shantung. These are: *Tanius chingkankouensis*

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[1] Considering *Mandschurosaurus* RIABININ a *nomen dubium*, BRETT-SURMAN (MS, 1979) introduced the new generic name *Gilmoreosaurus* BRETT-SURMAN, 1979 to include „*Mandschurosaurus*" *mongoliensis* GILMORE, 1933.

Table 1

Hadrosaurid taxa described from Asia

Original determination and assignment	Young: 1958	Steel: 1969	Rozhdestvensky: 1964a, 1974, 1977a	This paper
1. *Trachodon amurense* Riabinin, 1925 (= *Mandschurosaurus amurensis* Riabinin, 1930) Hadrosaurinae	*Mandschurosaurus amurensis* Hadrosaurinae	*M. amurensis* Hadrosaurinae	*M. amurensis* incertae subfamiliae	"*M.*" *amurensis* incertae subfamiliae
2. *Tanius sinensis* Wiman, 1929 Hadrosaurinae	*T. sinensis* Hadrosaurinae	*T. sinensis* Hadrosaurinae	*T. sinensis* Lambeosaurinae	*T. sinensis* Hadrosaurinae
3. *Tanius chingkankouensis* Young, 1958 Hadrosaurinae	*T. chingkankouensis* Hadrosaurinae	*T. chingkankouensis* Hadrosaurinae	?*T. sinensis*	*T. chingkankouensis* Hadrosaurinae
4. *Tanius laiyangensis* Zhen, 1976 Hadrosaurinae	—	—	—	*T. laiyangensis* Hadrosaurinae
5. *Saurolophus kryschtofovici* Riabinin, 1930 Saurolophinae	*nomen dubium*	*S. kryschtofovici* Saurolophinae	?*Mandschurosaurus amurensis* incertae subfamiliae	*nomen dubium*
6. *Saurolophus angustirostris* Rozhdestvensky, 1952 Saurolophinae	*S. angustirostris* Saurolophinae	*S. angustirostris* Saurolophinae	*S. angustirostris* Saurolophinae	*S. angustirostris* Hadrosaurinae
7. *Cionodon kysylkumense* Riabinin, 1931 Hadrosauridae	—	*Thespesius kysylkumense* Hadrosaurinae	*nomen dubium*	*nomen dubium*
8. *Mandschurosaurus mongoliensis* Gilmore, 1933 Hadrosaurinae	*M. mongoliensis* Hadrosaurinae	*M. mongoliensis* Hadrosaurinae	*Bactrosaurus johnsoni* Hadrosaurinae	*Gilmoreosaurus mongoliensis* (= *Mandschurosaurus mongoliensis*; Brett-Surman, 1979) Hadrosaurinae
9. *Mandschurosaurus laosensis* Hoffet, 1943 Hadrosaurinae	?*Mandschurosaurus* sp. incertae subfamiliae	*M. laosensis* Hadrosaurinae	—	*nomen dubium*
10. *Bactrosaurus johnsoni* Gilmore, 1933 Lambeosaurinae	A.M.N.H. 6553, type *B. johnsoni* Lambeosaurinae A.M.N.H. 6365 *Tanius* sp. Hadrosaurinae	*B. johnsoni* Lambeosaurinae	*B. johnsoni* Hadrosaurinae	A.M.N.H. 6553 *B. johnsoni* Lambeosaurinae A.M.N.H. 6365 ?*Tanius* sp. ?Hadrosaurinae PIN 2949/1 ?*B. johnsoni* ?Lambeosaurinae (see discussion on p. 10)
11. *Bactrosaurus prynadai* Riabinin, 1939 Lambeosaurinae	*Tanius prynadai* Hadrosaurinae	*Bactrosaurus prynadai* Lambeosaurinae	*Jaxartosaurus aralensis* Lambeosaurinae	*nomen dubium*
12. *Nipponosaurus sachalinensis* Nagao, 1936 Lambeosaurinae	*N. sachalinensis* incertae subfamiliae	*N. sachalinensis* Cheneosaurinae	*N. sachalinensis* Lambeosaurinae	*N. sachalinensis* Lambeosaurinae
13. *Jaxartosaurus aralensis* Riabinin, 1939 Lambeosaurinae	*J. aralensis* ?Lambeosaurinae ?Hadrosaurinae	*J. aralensis* Lambeosaurinae	*J. aralensis* Lambeosaurinae	*J. aralensis* Lambeosaurinae
14. *Tsintaosaurus spinorhinus* Young, 1958 Saurolophinae	*T. spinorhinus* Saurolophinae	*T. spinorhinus* Saurolophinae	*Tanius sinensis* (1964a) *Tanius spinorhinus* (1974) Lambeosaurinae	*Tsintaosaurus spinorhinus* Lambeosaurinae
15. *Aralosaurus tuberiferus* Rozhdestvensky, 1968 Hadrosaurinae	—	—	*A. tuberiferus* Hadrosaurinae	*A. tuberiferus* Hadrosaurinae
16. *Procheneosaurus convincens* Rozhdestvensky, 1968 Cheneosaurinae	—	—	*P. convincens* Cheneosaurinae	"*Procheneosaurus*" *convincens* (the generic name should be replaced: p. 11) Lambeosaurinae
17. *Shantungosaurus giganteus* Hu, 1973 Hadrosaurinae	—	—	—	*S. giganteus* Hadrosaurinae

of the subfamily Hadrosaurinae and *Tsintaosaurus spinorhinus* of the Lambeosaurinae (LULL and WRIGHT 1942). It cannot be doubted that in the Wangshih series representatives of both subfamilies occur, because two different types of sacra were found: one with a groove (the hadrosaurine type) and one with a ridge (the lambeosaurine type) along the ventral surface of the centra. YOUNG (1958) did not designate (in the English text) the holotype for *T. chingkankouensis*. The described and illustrated bones belong to more than one individual. Out of the illustrated postcranial elements, the most valuable diagnostically is a sacrum IVP V724 of the hadrosaurine type. The associated ilium and fragmentary ischium (YOUNG 1958: figs. 26–4, 36) bear the same catalogue number and belong (?) to the same individual. We decided to choose herein this specimen as the lectotype of *T. chingkankouensis*. However, it cannot be excluded that this specific name may appear the junior synonym of *T. sinensis* in the future, as the type specimen of this latter species was found in close proximity. Most of the bones which constitute the type of *T. sinensis* have not been found with the lectotype of *T. chingkankouensis*. Out of the bones not pertaining to the lectotype, but which were referred by YOUNG (1958) to *T. chingkankouensis* and which can be compared with *T. sinensis*, the cervicals are very alike but they have no value for specific determination. The scapulae in both species display some differences in shape, as do the ilia, the latter being markedly distinguished by the form of their antitrochanters. Thus it seems unlikely that these two forms are conspecific. The holotype of *Tsintaosaurus spinorhinus* YOUNG, 1958 (IVP V725) from the same deposits exposes characters typical of lambeosaurines: a hollow nasal crest, ridged sacral centra and high neural spines on the sacrals and caudals. It was considered by YOUNG as representing the subfamily Saurolophinae LULL and WRIGHT and his opinion was largerly accepted, although OSTROM (1961: 80) noticed that *Tsintaosaurus* (displaying "a true narial crest") may represent the Lambeosaurinae. Lately, BRETT-SURMAN (1979: fig. 1) assigned this genus to the Lambeosaurinae, the opinion which we follow here. It may be added, that the maxilla referred to *Tsintaosaurus spinorhinus* by YOUNG (1958: figs. 7, 8) is typical of the Lambeosaurinae in lacking anterior emargination and in having its dorsal apex shifted posteriorly, as well as a groove anterodorsally for accomodation of the lower limb of the premaxilla. ROZHDESTVENSKY (1964*a*, 1974, 1977*a*) considered *Tsintaosaurus* as the synonym of *Tanius*, the latter genus being included by this author in the Lambeosaurinae. ROZHDESTVENSKY'S opinion is not accepted here, since the known characters of the type species of *Tanius* (*T. sinensis*) speak for its assignment within the Hadrosaurinae (see discussion above).

Bactrosaurus was assigned to the Hadrosaurinae by ROZHDESTVENSKY (1966) because of the presence of the frontal bone within the orbital rim of the skull AMNH 6365 from Iren Dabasu. He also considered (1964*a*, 1977*a*) "*Mandschurosaurus*" *mongoliensis* as the synonym of *B. johnsoni*. The skull AMNH 6365, referred by GILMORE (1933*a*) to *B. johnsoni*, does not belong to the same individual as a postcranial skeleton AMNH 6553, which was chosen by GILMORE (1933*a*) as the holotype of *B. johnsoni*. The latter includes a left maxilla, a ridged sacrum, dorsals with clublike high neural spines, a "footed" ischium and an ilium with a highly curved upper outline (this latter character is considered as diagnostically important by BRETT-SURMAN MS). These characters leave no doubt that the holotype of *B. johnsoni* is that of a lambeosaurine and that the original subfamilial assignment of GILMORE (1933*a*) is correct. The skull AMNH 6365 on which ROZHDESTVENSKY based his opinion (1966) may, or may not, belong to *B. johnsoni*. GILMORE himself (1933*a*: 51–52) considered these alternatives, commenting on the close resemblance of the AMNH 6365 skull to that of the holotype of *Tanius sinensis*. He finally referred the skull to *B. johnsoni*, arguing that it was found in the Iren Dabasu quarry No. 141, where all hadrosaurid postcranial bones found were assignable to *B. johnsoni*. This fact gave support, in his opinion, for referring the skull to the lambeosaurine species *(B. johnsoni)* rather than to the hadrosaurines. In our opinion, their occurrence in the same quarry is insufficient evidence as to the conspecifity of these specimens. So the more, since nearby in the Iren Dabasu quarry No. 149 about one km distant, the unquestionable hadrosaurine representative *Gil-*

moreosaurus mongoliensis was found (GILMORE 1933*a*) in the same stratigraphic horizon (BERKEY and MORRIS 1927). Thus, for the time being it seems more reasonable to follow YOUNG (1958) and to determine tentatively the skull AMNH 6365 as ?*Tanius* sp., because its preserved portion does display the anatomical features of a *Tanius* species. Referring this skull to *G. mongoliensis* seems to be similarly inappropriate as its assignment to *B. johnsoni*, although either of these alternatives may prove correct in the future.

The skull PIN 2949/1 illustrated by ROZHDESTVENSKY (1966: fig. 3*v*) and referred by him to *B. johnsoni* also comes from the Iren Dabasu (= Iren Nor) Formation. This fragmentary skull resembles the AMNH 6365 skull above mentioned and at the same time it resembles the *Tanius sinensis* skull (comp. WIMAN 1929: pl. 5). There is a minor difference between the PIN skull as illustrated by ROZHDESTVENSKY *(l. c.)* and those of *T. sinensis* and the AMNH specimen. It concerns the course of the postorbital-squamosal suture within the temporal arcade. Moreover, the maxilla of PIN 2949/1 specimen differs from the maxilla referred by GILMORE (1933*a*: fig. 26) to the type specimen (AMNH 6553) of *B. johnsoni* (fig. 1). For this reason we consider the PIN specimen here discussed as only tentatively referable to *B. johnsoni*.

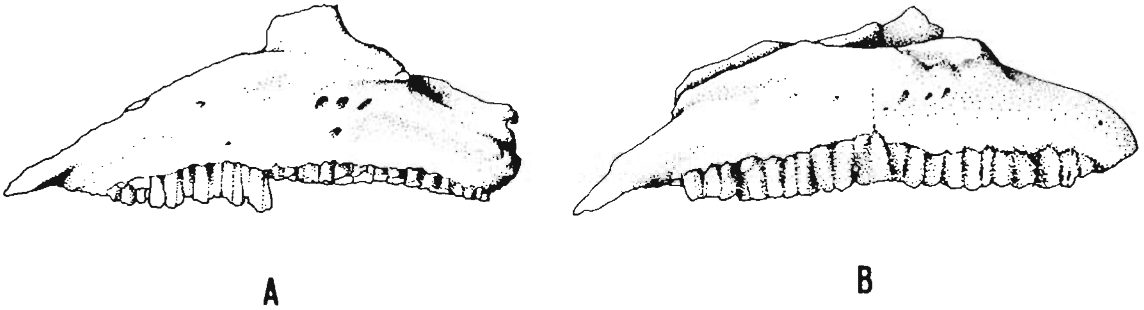

Fig. 1
Lateral view of left maxillae: A *Bactrosaurus johnsoni* GILMORE (AMNH 6553), redrawn from GILMORE 1933: fig. 26; B ?*B. johnsoni* (PIN 2949/1); original. Not to scale.

In conclusion, it may be noticed that there is no doubt that at least two hadrosaurid taxa were represented in the Iren Dabasu Formation: one of the hadrosaurines *(Gilmoreosaurus mongoliensis)* and one of the lambeosaurines *(Bactrosaurus johnsoni)*. Both of these taxa are based upon postcranial skeletons and their skull characters are not certainly known.

So far 17 hadrosaurid taxa have been described from Asia (table 1) 5 of which should be considered as *nomina dubia*. Two undescribed genera and species of lambeosaurines were recently found; one of them at the Baysheen Tsav locality (KRAMARENKO 1974; TSYBIN and KURZANOV 1979: 112), the other in the Nemegt Formation at N Nemegt (MARYAŃSKA and OSMÓLSKA in press). Besides these, several undeterminable hadrosaurids were reported from different sites in Asia, as follows: Baying Bologay (GILMORE 1933*b*), Bayn Shireh (MALEEV 1956), Bugeen Tsav (TROFIMOV and CHUDINOV 1970), Sheeregeen Gashoon (ROZHDESTVENSKY 1974), Bayn Dzak and Khermeen Tsav (GRADZIŃSKI *et al.* 1977) on the Mongolian People's Republic territory, Kansai in the Fergana Valley (ROZHDESTVENSKY 1977*b*), Djara Khuduk in the Kysylkum Desert (ROZHDESTVENSKY 1964*b*) on the USSR Asian territory, and in several sites in the Dzungar and Nanhsiung Basins (DONG 1973, CHENG *et al.* 1973) on China territory.

The mostly uncertain stratigraphic position of the Asian Hadrosauridae and the incompletness of their remains, contrast very strongly with the North American Hadrosauridae, which are the most common element of the Cretaceous herbivore faunas, are often preserved in articulated condition and are well dated stratigraphically. Extensive comparisons between the hadrosaurid faunas on both continents are thus impossible at the moment. The only genus in common is so far *Saurolophus*. *Procheneosaurus*, which until recently was considered another common genus, appears (DODSON 1975) to represent a juvenile stage of the lambeosaurine dinosaurs *Lambeosaurus* and *Corythosaurus*. Thus, the generic name "*Procheneosaurus*" should be now abandoned. Accordingly, a new genus should be erected to include "*Procheneosaurus*" *convincens* ROZHDESTVENSKY, 1968 described from Kazakhstan, as thus far neither *Corythosaurus* nor *Lambeosaurus* are reported from Asia.

SKULL ANATOMY

(pls. 1 and 2)

Material

The description below concerns mainly the skull of the specimen ZPAL MgD-I/159 which is presently the smallest known of the *Saurolophus angustirostris* specimens. This description is supplemented by our observations made on the specimens: PIN 551-359 (young individual), PIN 551-8 (holotype, young adult individual), PIN 551-357, PIN 551-358 (old adult individuals) GSP 100/404 (adult individual). The fragmentary skull ZPAL MgD-I/162 was also taken into consideration. The skull ZPAL MgD-I/159 is complete, although flattened laterally; three of the PIN skulls and the GSP specimen are complete or almost complete, and only the specimen PIN 551-358 is strongly damaged.

Occiput

The occipital region is basically similar to that known in other hadrosaurines (pl. 1: 1*d*): it has the exoccipitals fused above the foramen magnum and a supraoccipital which is slanting anterodorsally. The posterior articular surface of the occipital condyle is distinctly tripartite: its lateral, exoccipital components are well distinguished and rounded. Lateral to the deep, extensive nuchal pit, each exoccipital gives off a dorsal process, which contacts the squamosal in a cotylus-condylus articulations (normal for hadrosaurines). The contact between the paroccipital process and the long postquadratic process of the squamosal is quite free. Two bosses on the supraoccipital for articulation with the squamosals, like those described by GILMORE (1937: 483) and LANGSTON (1960: 348) are also present in *S. angustirostris*. Anterodorsal to the squamosal boss both bones are coossified. The squamosal-parietal contact is distinctly loose medially. The parietal separates the squamosals only in the young skulls; there is an articular surface on the dorsomedial extension of squamosal which laterally overlaps the end of the medial parietal ridge. More laterally, the squamosal and parietal show an unfinished surface where they contact each other, indicating that a cartilage may have been present between these bones.

Skull roof, snout and orbit

The frontal sends anteriorly a narrow, long process, which is directed upward and backward, adhering posteriorly to the nasal along about the lower half of the crest (fig. 2). This process fits into two grooves on the nasal and is separated from its fellow by a pair of ridges formed by the medial edges of the contacting nasals. The prefrontal and nasal are firmly coalesced anteriorly (MARYAŃSKA and OSMÓLSKA 1979) and the suture is visible only on the inside surface of the skull roof. Within the basal region of the crest, the prefrontal develops a short process which props the crest posterolaterally (pl. 2: 1*c*). The prefrontal joins the anterior frontal process at its base along a distinct suture. The contact of the prefrontal with the overlying anterior crestal portion of the nasal is loose along its entire length even in the oldest skulls. The anterior portion of the nasal loosely overlaps the upper limb of the premaxilla. It reaches far forward, extending beyond the anterior border of the external naris. The whole upper edge is formed by the lower margin of this nasal process in the young skulls (p. 18). Posteriorly, the lateral contact of the nasal with the premaxilla is not clear even in the smallest skulls. Along the anterior surface of the nasal, at the orbital region and along the crest, a ridge of variable height is developed (see also MARYAŃSKA and OSMÓLSKA 1979), which runs along the middle of each nasal (fig. 3). The end of each nasal, within the crest, is thickened and roughened (pl. 1: 1*b*, *c*). This thickening is excavated anteriorly, so that the end of each nasal has a candle-extinguisher form (see also ROZHDESTVENSKY 1957). The upper rod-like limbs of the premaxillae loosely attach to each other and to the nasals between which they intervene; they reach backward well behind the posterior boundary of the narial opening. Anterior to the narial opening, each premaxilla contains a canal, which was already mentioned by ROZHDESTVENSKY (1957). This canal is bounded by the lower premaxillary limb medially, ventrally and laterally. It is roofed dorsally by a portion of the upper premaxillary limb, which bounds anteriorly the external narial opening. Two vertical grooves are present on the surface of the premaxillary limb facing the narial opening, above the canal, which may have been connected with the cartilaginous nasal capsule. The paired canals within the premaxillae may have contained the JACOBSON'S organ as suggested by ROZHDESTVENSKY (1957: 135). The maxilla of *S. angustirostris* (fig. 4) seems to be like that in *Edmontosaurus* (LAMBE 1920). As seen dorsally, it develops a thick, horizontal palatal wing which probably joined its fellow along the distance occupied in the adult skull (ZPAL MgD-I/162) by eleven anterior maxillary teeth. Anteriorly to the tooth battery, the main body of maxilla sends a short massive process bearing the oblique, lateral articular surface. An emargination is developed above this process, which separates it from the comparatively long, anterior maxillary process. Both processes of the maxilla abut with their lateral surface against the ventral surface of the broad, externally concave premaxilla. The premaxilla-maxilla contact is quite free and the lateral, somewhat upturned portion of the lower premaxillary limb stands out beyond the vertical wall of the maxilla (pl. 2: 1*a*). Two supraorbitals (fig. 5, 6*a*) are present within the upper rim of the orbit (MARYAŃSKA and OSMÓLSKA 1979). This rim is roughened and highly upturned (pl. 1: 1*a*, *b*; pl. 2). The supraorbitals separate the frontals from the external margin of the orbit. All of the sutures of this region are clearly visible in the young skulls on the ventral surface of the orbital roof. Externally, the contacts of supraorbital II with the postorbital (posteriorly) and supraorbital I (anteriorly) are distinct, while its medial contacts are hardly discernible. Supraorbital I embraces the prefrontal laterally, but the suture is not visible externally.

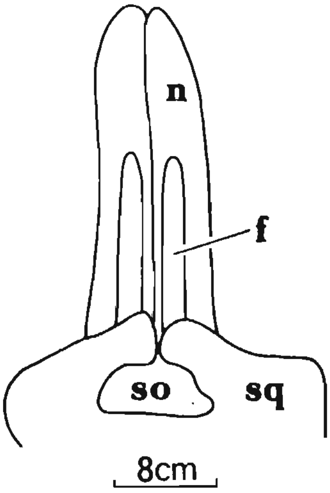

Fig. 2
Diagrammatic drawing of crest in *Saurolophus angustirostris* ROZHDESTVENSKY showing position of anterior frontal processes; after MARYAŃSKA and OSMÓLSKA 1979.

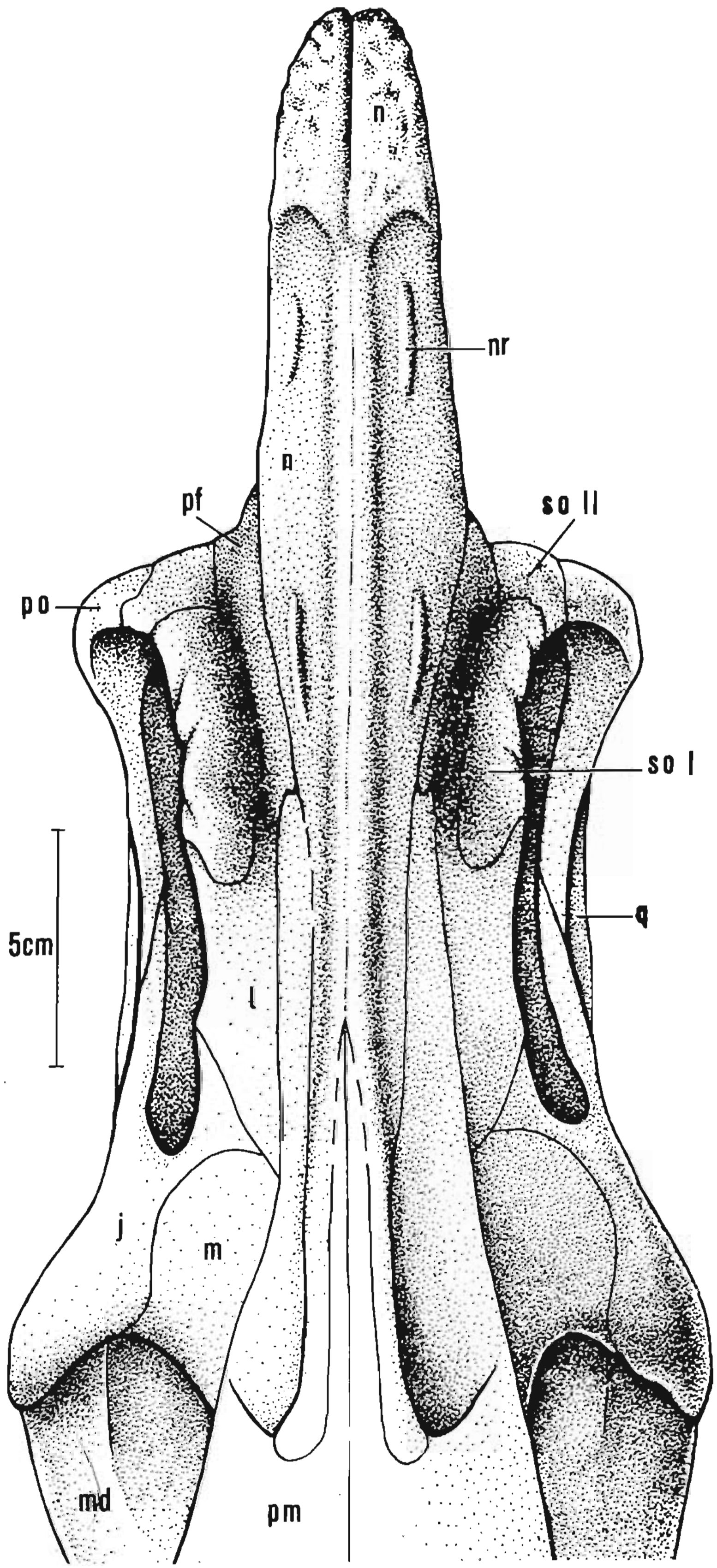

Fig. 3

Saurolophus angustirostris Rozhdestvensky, reconstruction of the skull, anterior view; based upon ZPAL MgD-I/159; after Maryańska and Osmólska 1979.

Abbreviations: *j* jugal, *l* lacrimal, *m* maxilla, *md* mandible, *n* nasal, *nr* nasal ridge, *pf* prefrontal, *pm* premaxilla, *po* postorbital, *q* quadrate, *so I, so II* supraorbitals *I* and *II.*

Table 2

Skull dimensions in *Saurolophus angustirostris* (mm)

Cat. nos.	PIN 551-357	PIN 551-8 holotype	PIN 551-359	ZPAL MgD-I/159
length: ant. end of premaxilla — quadrate (A)	1250	970e	600	430
length: ant. end of premaxilla — exoccipital (B)	1480	1000e	730	490
length: ant. end of premaxilla — anterior end of external nare (C)	380	280	160	123
length: ant. end of premaxilla — post. end of ext. nare (D)	540	—	225e	175
length of skull along crest (E)	—	1360	680	500
length: ant. end of premaxilla — ant. end of orbit (F)	925	640e	390	280
length of crest (G)	—	400	180	150
length of frontal within crest (H)	—	250	120	—
length of skull roof post. to base of crest (I)	210	150	130	120
crest projection on skull roof (—), or beyond skull roof (+) (J)	—	+190	−60	−85
length of maxillary tooth row (K)	—	400	260	160+
max. diameter of orbit (L)	380	270	190	113
min. diameter of orbit (M)	—	100	90	80
max. diameter of infratemporal fenestra (N)	420	300	190	153
min. diameter of infratemporal fenestra (O)	—	100	50	45
height of quadrate (P)	540	380	270	210
width across jugals (Q)	540	320	140e	145e
width across exoccipitals (R)	440	320	190	94+
anterior (ventral) width across maxillae (S)	—	100	60	30
width of crest base (T)	—	140	90	66

Table 3

Mandible dimensions in *Saurolophus angustirostris* (mm)

Cat. nos.	PIN 551-357	PIN 551-8	PIN 551-359	ZPAL MgD-I/159
length of mandible	1240	960	590	425
length of mandible ant. to coronoid process	950	660	380	295
length of edentulous portion	—	370	190	160
max. height of mandible	180	140	100	77
dorsal width across dentaries in front of tooth row	—	50	—	20
height of coronoid process	—	200	—	93
length of predentary	—	240	—	114
max. width of predentary	300	200	—	70

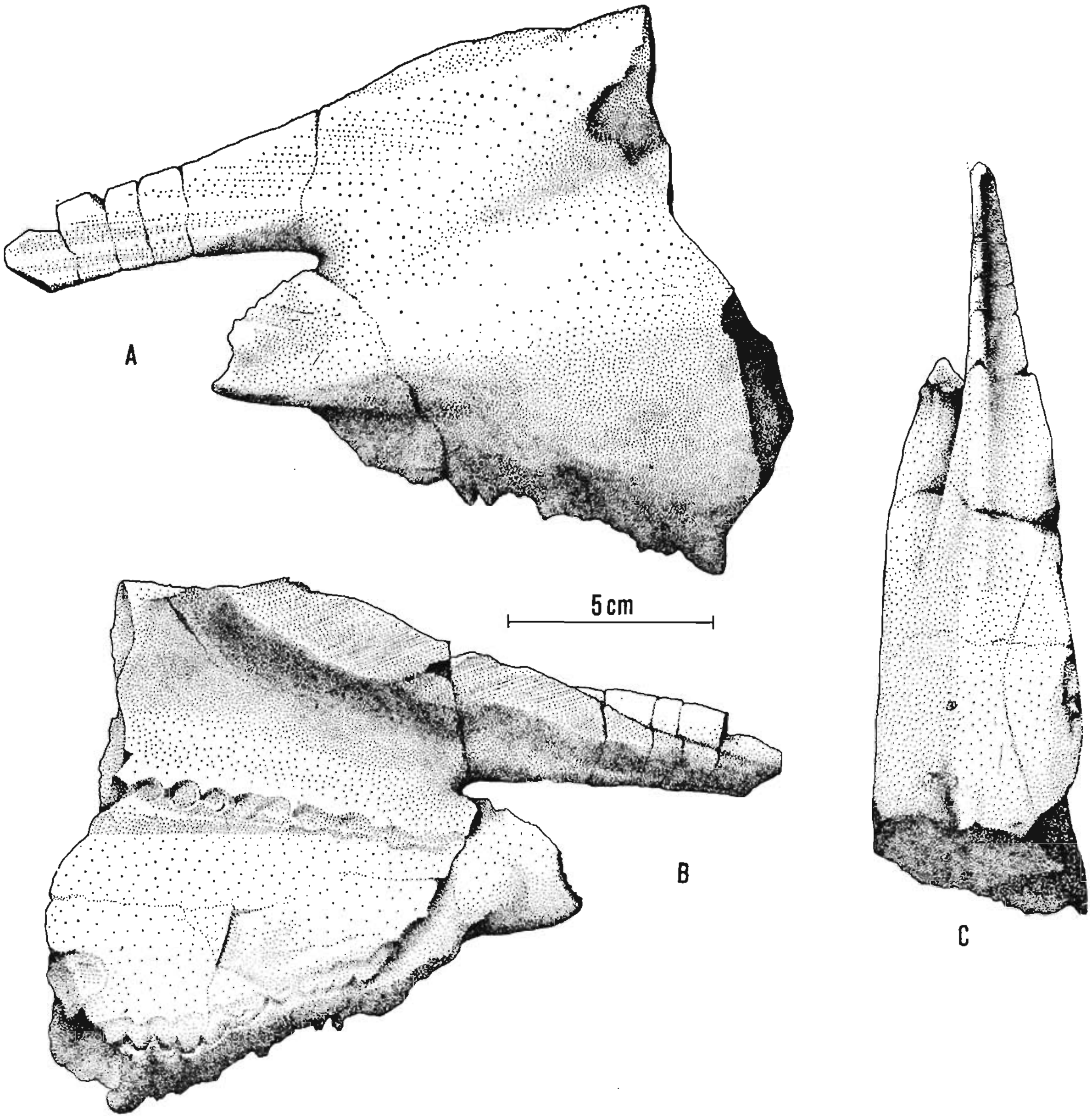

Fig. 4
Saurolophus angustirostris Rozhdestvensky, anterior portion of left maxilla: A external view, B internal view, C dorsal view; (ZPAL MgD-I/162).

Brain case

The sutures between the bones forming the anterolateral wall of the brain case are clearly visible (pl. 2: 1*b*; fig. 5). The laterosphenoid contacts the skull roof rather loosely and its laterodorsal contact with the postorbital is in a form of articulation. The contacts of the parietal with the laterosphenoid, prootic and opisthotic below seem to be loose, at least in the young skull ZPAL MgD-I/159, where it was possible to observe them. The opisthotic is visible below and posterior to the prootic in the posterolateral wall of the brain case, forming the posterior boundary of the foramen ovale. As far as could be observed in our specimen, the opisthotic seems to be present above the prootic (fig. 5). This condition would be rather unique in the hadrosaurids.

Palatal region

The palatal region was seen only through the orbit in all specimens (pl. 2: 1*a*, *b*; fig. 5). Compared to those of other hadrosaurs viewed laterally, the mutual relations of the palatine to pterygoid are like those in *Edmontosaurus*, as illustrated by HEATON (1972: fig. 5). However, the palate is more highly vaulted than in the broad-snouted *Edmontosaurus.*

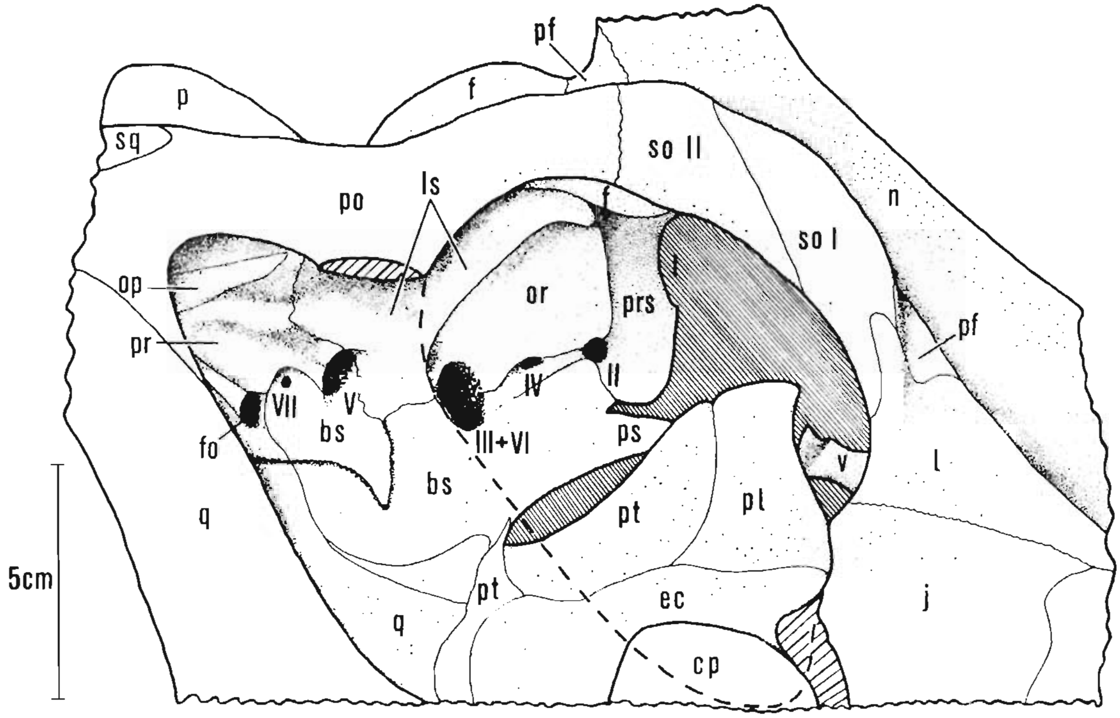

Fig. 5

Saurolophus angustirostris ROZHDESTVENSKY, right lateral view of the brain case wall, as seen through the orbit; based upon ZPAL MgD-I/159.

Abbreviations: *bs* basisphenoid, *cp* coronoid process of mandible, *ec* ectopterygoid, *ls* laterosphenoid, *op* opisthotic, *or* orbitosphenoid, *p* parietal, *pl* palatinum, *pr* prootic, *prs* presphenoid, *ps* parasphenoid, *pt* pterygoid, *sq* squamosal, *v* vomer, others as in fig. 3.

Mandible

As can be judged from the published illustration of *S. osborni* (BROWN 1912: fig. 1*b*) there are no significant differences between the mandibles of *S. angustirostris* and *S. osborni.* Thus, we describe below only the predentary, as it has not been described in *Saurolophus,* and it seems to be somewhat different than in other hadrosaurids. The predentary in the young specimen (pl. 1: 1*a*, *b*) is narrow and U-shaped, with flat, broad upper margins of its lateral branches. Its anterior portion displays a comparatively sharp margin. The predentary reaches posteriorly along more than a half of the edentulous dentary portion. The medial surfaces of the lateral branches are vertical. The anterior margin of the predentary bears some pits and possibly also a weak crenulation. A paired medial, posteriorly directed process is present on the ventral side of the predentary while the dorsal process is unpaired. The predentary is very loosely attached to the dentaries; its posterior extremities do not adhere to the latter bones.

GROWTH CHANGES

Some comments on the growth changes of *Saurolophus angustirostris* were already included in ROZHDESTVENSKY's papers (1957, 1965). The specimen ZPAL MgD-I/159 is the smallest known individual (table 2) thus allowing us to complete ROZHDESTVENSKY's data. As he demonstrated (1965: 99, fig. 4), the relative length of the crest increases whereas angle of the inclination of the crest to the skull roof decreases during growth; the crest in the youngest specimens ends well in front of the posterior border of the skull, but it projects markedly behind the skull in mature individuals (table 2). During growth, the base of crest moves backward, occupying most of the horizontal portion of the frontals (table 4). According to ROZHDESTVENSKY (1965: table on p. 132) the length/height ratio of the skull in *S. angustirostris* changes during growth, the index counted by this author being 1·7 for the young skull and 2·0–2·5 for adult skulls. The same index as counted by ROZHDESTVENSKY for *S. osborni* (type skull, adult) is 1·7. It is not clear which measurements were used by ROZHDESTVENSKY (1965) for these calculations. Counting the skull length/height ratio (anterior end of premaxilla — quadrate condyle distance to quadrate heigh) we obtained (table 4) indices 2·0; 2·2; 2·3 respectively for ZPAL MgD-I/159, PIN 551-359 (young skulls), PIN 551-357 (adult skull). The same index counted by us for *S. osborni* is 2·8. Thus, our calculations do not confirm ROZHDESTVENSKY's conclusion that the proportions of young *S. angustirostris* skulls resemble more these in *S. osborni* than the adult skull proportions in *S. angustirostris*.

Table 4

Skull ratios in the species of *Saurolophus*

Species	Cat. nos.	Ratios (comp. Table 2)										
		$\frac{A}{P}$	$\frac{Q}{A}$	$\frac{F}{A}$	$\frac{D}{A}$	$\frac{C}{F}$	$\frac{C}{A}$	$\frac{I}{E}$	$\frac{K}{A}$	$\frac{I}{G}$	$\frac{H}{G}$	$\frac{S}{A}$
S. angustirostris	ZPAL MgD-I/159	2·0	0·33e	0·65	0·40	0·43	0·28	0·24	0·38e	0·80	–	0·07
	PIN 551–359	2·2	–	0·65	0·37	0·41	0·27	0·19	0·43	0·72	0·66	0·10
	8 (holotype)	2·50e	0·33e	0·66e	—	0·43e	0·29e	0·11	0·42e	0·37	0·62	0·10e
	357	2·31	0·43	0·74	0·43	0·41	0·30	—	—	—	–	–
S. osborni	AMNH 5220 (holotype)	2·8	—	0·72	0·58	–	0·27	–	0·38	—	–	–

Additionally, some more obvious successive growth changes manifested in the skulls in *S. angustirostris* may by quoted (comp. table 4):

— the snout becomes relatively longer in adult individuals;

— the long axes of the orbit and of the infratemporal fenestra decline posteriorly, in connection with the backward migration of the crestal base and backward bending of the upper portion of quadrate;

— the frontals on young skulls show a distinct, rounded convexity medially (pl. 2: 1*c*), which later disappears;

— the share of the parietal in the anterior boundary of the upper temporal fenestra increases;

— the separation of the squamosals by the parietals gradually diminishes and finally disappears; on young skulls the end of the medial parietal ridge intervenes dorsally between the squamosals; the latter attach to each other on larger skulls;

- the insertion site for the ligamentum nuchae within the supraoccipital — squamosal region becomes markedly deeper, until at last, the supraoccipital becomes horizontal;
- the longitudinal ridge occurring on the dorsal (anterior) surface of each nasal becomes higher; on small skulls this ridge is low and interrupted (fig. 3), whereas on the very large skulls (e.g. PIN 551-357) the ridge transforms into a high, thin-walled septum in the supraorbital region; externally, between this septum-like structure and the medial ridge of the nasal crest, the nasal develops a system of irregular "chambers" bounded by thin bony laminae;
- the nasal gradually tends to overhang the external naris dorsally; in young individuals, the upper narial border is formed from the very edge of the nasal, while later, the naris is partly roofed by the nasal with the ventral surface of this bone, rather than its edge, bounding the naris;
- the jugal — lacrimal contact thickens toward the orbit, becoming tuber-like and successively narrowing the lower part of the orbit;
- the dental batteries in the young occupy less than half of the length of the mandible, whereas in the adults they occupy more than that;
- the direction of the coronoid process changes during growth, from being almost perpendicular to the mandibular axis, in the young, to being anteriorly inclined, in the adults;
- the predentary becomes gradually more open dorsally, which is caused by a change in the inclination of the medial wall of the lateral branches from almost vertical to oblique; at the same time, the dorsal, ad-oral surfaces of the lateral branches, which are flat in the young, become concave in adults; the very front of the predentary flattens.

The number of skulls of *S. angustirostris* accessible for investigation (5) does not allow precise analysis of allometric growth changes. We were only able to calculate some skull indices, which are given in table 4.

COMPARISONS

As was already noticed by ROZHDESTVENSKY (1957, 1965), the skull of *S. angustirostris* is narrower as a whole than that in *S. osborni* BROWN, 1912, and its crest is most probably longer. However, the length of the crest and the angle of its inclination to the skull roof cannot be considered as significant taxonomically, because both these characters depend on the individual age (tables 2, 4). There is no distinct difference in the relative length of the snout between comparably sized specimens of *S. angustirostris* and *S. osborni*, but the length of the maxillary dental battery is relatively greater in *S. angustirostris*. The frontal takes a significant share in the formation of crest (fig. 2) in the Mongolian species (MARYAŃSKA and OSMÓLSKA 1979); it also takes part in crest formation in *S. osborni* according to BROWN (1912) and LULL and WRIGHT (1942), but according to OSTROM (1961) it does not. However, its share in the crest in the North American species is most probable; the anterior frontal processes which prop the nasals posteriorly within the crest are very narrow in *S. angustirostris* and they are broken off in some specimens. There are always grooves left on the posterior surface of nasals which mark the former position of these frontal processes. The prefrontals prop the base of the crest posterolaterally in *S. angustirostris*; the presence of these bones in the crest of *S. osborni* was mentioned by BROWN (1912), but in the North American species they seem to reach much further along the crest. The longitudinal bony septum (MARYAŃSKA and OSMÓLSKA 1979) and the irregular chambers on the anterior surface of the crest in *S. angustirostris* mentioned herein (see above and p. 20) were not observed so far in *S. osborni*.

A crest superficially similar to the *Saurolophus* crest was described by YOUNG (1958) in *Tsintaosaurus spinorhinus*, which was the reason for assignment of this genus to the Saurolophinae (YOUNG 1958). However, it should be stated here that the structure of the crest is entirely different in both genera, the hollow crest of *Tsintaosaurus* being formed from the nasals exclusively. The postcranial skeleton of *Saurolophus* is of the hadrosaurine type while that of *Tsintaosaurus* is typically lambeosaurine. Thus these two genera cannot be assigned within the same subfamily.

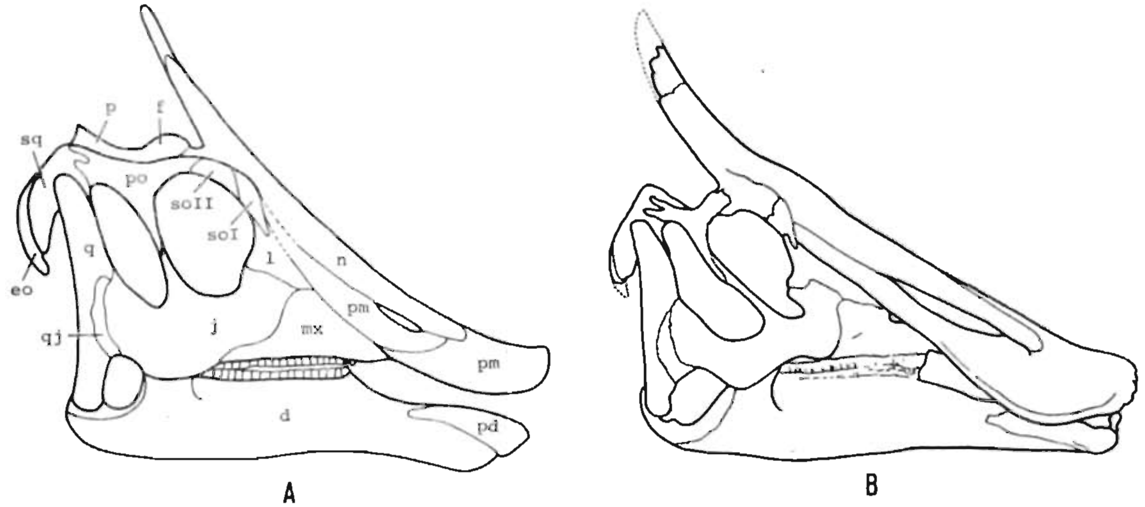

Fig. 6

A *Saurolophus angustirostris* ROZHDESTVENSKY, lateral view of skull; based upon ZPAL MgD-I/159; B *Saurolophus osborni* BROWN; redrawn from BROWN 1912: fig. 1b, simplified. Not to scale. Abbreviations: *d* dental, *eo* exoccipital, *pd* predental, *qj* quadratojugal, others as in figs. 3 and 5.

We have noticed previously (MARYAŃSKA and OSMÓLSKA 1979) that the frontal in the Mongolian representative of *Saurolophus* is completely excluded from the orbital margin by the supraorbitals I and II. It is reasonable to accept that if *S. angustirostris* and *S. osborni* are congeneric, as the gross anatomy of both species seems to indicate, the frontal in the latter species should be also separated from the orbital margin by the supraorbitals. Unfortunately, the upper orbital margin seems to be damaged in all known skulls of *S. osborni* (M. K. BRETT-SURMAN'S, W. P. COOMBS' and D. A. RUSSELL'S personal informations) which may be the reason that the presence of supraorbitals was not noticed in this species.

Among other important differences between the skulls of compared *Saurolophus* species, the size and position of the external narial openings should be mentioned (table 4). These are shorter, reaching posteriorly to a point above the first maxillary tooth in *S. angustirostris*, while they are much further backward in *S. osborni*. The lacrimal in *S. angustirostris* is shorter than this in *S. osborni* and most probably also deeper. The anterior portion of the jugal elongates into a long process which wedges for some distance between the maxilla and lacrimal; this process is short and blunt in *S. osborni*. The quadrate is also somewhat more bowed posteriorly in the Mongolian species.

Comparing the anterolateral wall of the brain case in *S. angustirostris* with that of *S. osborni* as illustrated by BROWN (1912: fig. 3), it may be concluded that the bone named by this author as the presphenoid should be considered as the orbitosphenoid, the presphenoid not being preserved in the paratype skull AMNH 5221 illustrated by BROWN *(l. c.)*. Generally, the mutual relations of the bones within the brain case wall are in *S. angustirostris* (fig. 5) like those in other hadrosaurids (e.g. in *Jaxartosaurus aralensis*; ROZHDESTVENSKY 1968: figs 4, 5).

THE SUGGESTED NATURE OF THE CREST IN *SAUROLOPHUS*

The presence of the system of thin walled chambers on the upper surface of the crest in *S. angustirostris* seems to support our earlier suggestions that the anterior (dorsal) surface of the crest constituted a base for some rigid internal structures (*diverticulum nasi*; MARYAŃSKA and OSMÓLSKA 1979). Certainly, the similar crest of *S. osborni* might carry a similar structure. As the rigid support of these supposed internal crestal structures are found in the form of longitudinal septa and chambers in the large adult skulls, it seems probable that they may have ossified late during the animal life. The free upturned lateral margin of each premaxilla may have been, in fact, extended upward and then medially by a non-ossified membrane in *Saurolophus*, forming a kind of dorsally closed tube (comparable to that of lambeosaurines). Similarly, the candle-extinguisher-like end of each nasal strongly suggests that a membranous sheet may have been present anterior and downward, closing the crest dorsally. The internal, longitudinal subdivision of such a structure on each half of the crest by a bony (or non-ossified) septum was responsible for formation of two parallel channels. The lateral of these channels may have conducted air from the external opening, located at the end of the premaxillary tube, upward. From here, the air may have passed downward, along the medial channel, towards the "primary" external naris (located in its usual position, between the lower limb of premaxilla and the anterior process of the nasal) and further on, to the true nasal passage and to the choana. The suggested structure might only function, providing that both channels were completely separated along their lengths, except at the top, and that there was a sufficiently strong suction of the inhaled air. Thus, if so constructed, the crest in *Saurolophus* was also a hollow structure in the living animal, quite different as a whole, from the solid posteroventral prong in *Lambeosaurus* and *Corythosaurus* (HOPSON 1975). In fact, only the thickened end of the *Saurolophus* crest was solid, in which it resembles the prong in both lambeosaurines mentioned.

The first and main purpose of developing this complicated structure in *Saurolophus* would be the enlargement of the anteriormost, respiratory surface of the nasal passage. In other words, the crest of *Saurolophus* may have been a thermoregulatory device (see also WHEELER 1978). The possibility that this hollow crest may have been, at least partly, homologous to the hollow crests of the lambeosaurines cannot be excluded, although the problem still requires further investigation. If this is the case, the lambeosaurine "premaxilla 2" may be considered as the separate ossification within the initially membranous cover corresponding to the here suggested membranous cover of the premaxilla in *Saurolophus.*

INTRACRANIAL MOBILITY IN HADROSAURIDS AND ITS SIGNIFICANCE

Whether hadrosaurid skulls display the intracranial mobility has already been discussed by some authors (VERSLUYS 1923, WIMAN 1929, GILMORE 1937, OSTROM 1961). To our knowledge, no special attention has been drawn to the peculiar loose junction which occurs between the lower limb of the premaxilla and maxilla, which seems to be characteristic of most, if not all, the Hadrosauridae. In the majority of dinosaurs known to us, the premaxilla-maxilla contact is rather a strong one. Contrary to this, many known hadrosaurid specimens (e. g. *Lambeosaurus lambei* GSC 2869, *Hypacrosaurus altispinus* GSC 8501) show the premaxilla "slid off" of the maxilla. This contact is definitly very loose also in *S. angustirostris.* This species also displays loose contacts between most of the bones within the anterior portion of the snout, as well as within other regions of the skull. A list is given below, of all the loose contacts observed on the juvenile and/or adult skulls of *S. angustirostris*:

1. anterodorsal margin of maxilla — premaxilla (juvenile and adult),
2. upper limb of premaxilla — nasal (juvenile and adult),
3. nasal — nasal (juvenile and adult),

4. prefrontal — posterior surface of nasal within the crestal base (juvenile),
5. frontal — nasal within the crest (juvenile and adult),
6. vomer — palatinum (juvenile, ?adult),
7. lacrimal — premaxilla (juvenile and adult),
8. lacrimal — maxilla (adult, ?juvenile),
9. jugal — maxilla (adult, ?juvenile),
10. jugal — quadratojugal — quadrate (adult, ?juvenile),
11. postorbital — jugal (juvenile and adult),
12. squamosal — quadrate (juvenile and adult),
13. squamosal — exoccipital along the entire contact (juvenile and adult),
14. squamosal boss of supraoccipital — squamosal (juvenile, ?adult),
15. parietal — dorsomedial extension of squamosal (juvenile),
16. lateral wall of brain case — skull roof (juvenile, ?adult),
17. laterosphenoid — postorbital (juvenile and adult),
18. quadrate wing of pterygoid — pterygoid wing of quadrate (juvenile and adult),
19. basipterygoid process — pterygoid (juvenile and adult),
20. dentary — dentary (juvenile and adult),
21. predentary — dentary (juvenile and adult).

Some of these contacts were already discussed by OSTROM (1961) who however considered them as the immovable ones. The loose contacts between these skull bones do not necessarily imply that there were mobile junctions between them, but many of them were certainly bound by means of resilient, connective tissues or a cartilage. Some of these loose contacts are characteristic of juvenile skulls only (4,17) while others were impossible to investigate in adult skulls (6, 18), or in juvenile skulls (8, 9, 10) because of damages or deformations. All of the remaining ones were observed on both juvenile and adult skulls and thus they cannot be considered as due to the age of the individual or as accidental ones.

In fact, only few of the skull bone contacts are rigid in *S. angustirostris*, and these were already firm in the youngest skull. Here should be mentioned: coossification between the supraoccipital and squamosal lateromedially to the squamosal boss, strong sutural union between the parietal and frontal, the frontal and postorbital, and the extremely strong fusion of the bones within the anterior and anterodorsal orbital margin and between the prefrontal and nasal in front of the crest. Thus, all three main types of kinesis (meta-, meso- and prokinesis) were definitely suppressed in *S. angustirostris* as they were probably in other hadrosaurids (OSTROM 1961). Nevertheless, their rudiments are still preserved (comp. nos. 13, 14, 16, 17, 18, 19, 11, 5, 6, on the list above).

The presence of so many loose junctions between skull bones of *S. angustirostris*, and in other hadrosaurids as well (both those which may be considered as rudiments of earlier kineticism and those which are newly acquired), certainly had some functional meaning. Other herbivorous dinosaurs with akinetic skulls (Ceratopsia, Pachycephalosauria, Ankylosauria) display almost complete lost of any mobility between the skull bones. This may indicate, that for explaining the hadrosaurid condition one should look among the characters peculiar exclusively to this group of dinosaurs and absent in others. This lack of rigid contacts between so many skull bones does not seem to be directly connected with the development of powerful dental batteries in the Hadrosauridae; the Ceratopsidae, the skull of which is completely akinetic, display a comparable masticatory apparatus. The most abvious hadrosaurid feature is the development of bony crests and hoods and of extensive narial depressions, which may have served for thermoregulation and/or acclimatization of the inhaled air (WHEELER 1978, MARYAŃSKA and OSMÓLSKA 1979). One would suppose that acquiring a certain degree of akineticism of the skull may have been necessary for the effective functioning of the powerful dental apparatus in the hadrosaurids (OSTROM 1961). On the other side, it may have been purposeful, to separate the important and probably fragile narial and intranarial structures from the possible, undesirable effects of the strong masticatory action of the maxilla by a kind of an "amortization zone". The hadrosaurid premaxillae as well as the crestal structures are usually formed from thin bone, so that the increase in size of these structures did not cause a significant weight increase. Contrary to it, the bones contacting these structures directly are very massive. The rigid contacts between these thin, flexible to some extent, bony premaxilla-nasal framework and the massive maxillary unit, would cause the direct transmission of the masticatory action on the adjoining structures. This in turn, would affect the internal narial structures. The loose junction between the lower limb of premaxilla and the maxilla, which is typical of hadrosaurids as mentioned in the beginning of this chapter, indicates that there may have been developed an elastic binding serving as a "pad" of resilient connective tissue. It may have played here the role of "shock absorber". Independently, the elastic connection between the premaxilla and maxilla may have allowed, as well, for some limited lateral movements of the maxilla anteriorly. Such a movement may have caused some flexion of the jugal. This latter was relatively very thin and possibly flexible to some extent, what was already suggested by Versluys (1923).

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Saurolophus angustirostris Rozhdestvensky, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV
Gobi Desert, Mongolia; ZPAL MgD-I/159

1a. Skull of a young individual, lateral view.
1b. Same specimen, anterior view, stereopair.
1c. Same specimen, top view, stereopair.
1d. Same specimen, posterior view, stereopair.

All × ca 0·26

Photo: ***W Skarżyński***

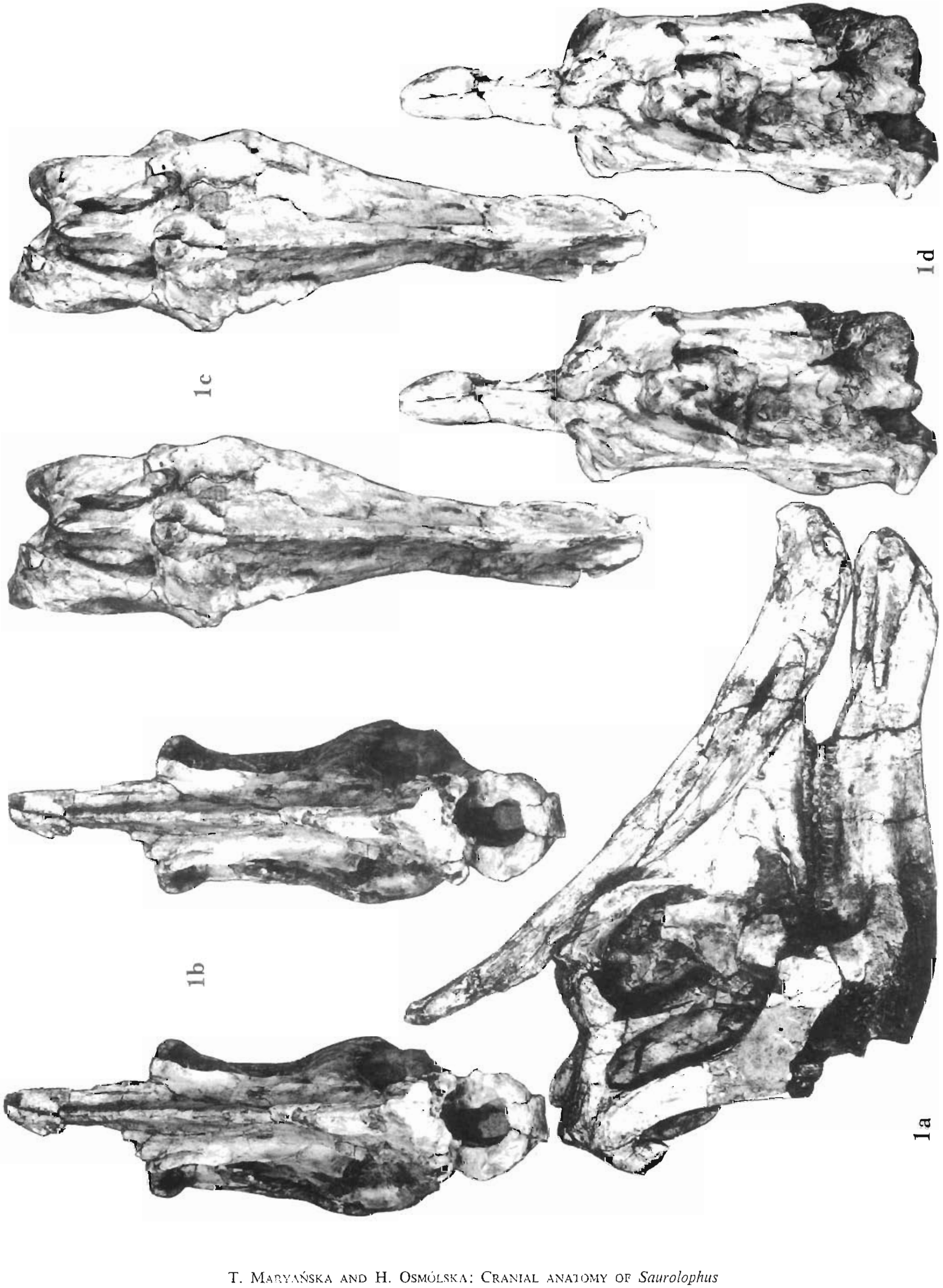
PLATE 2

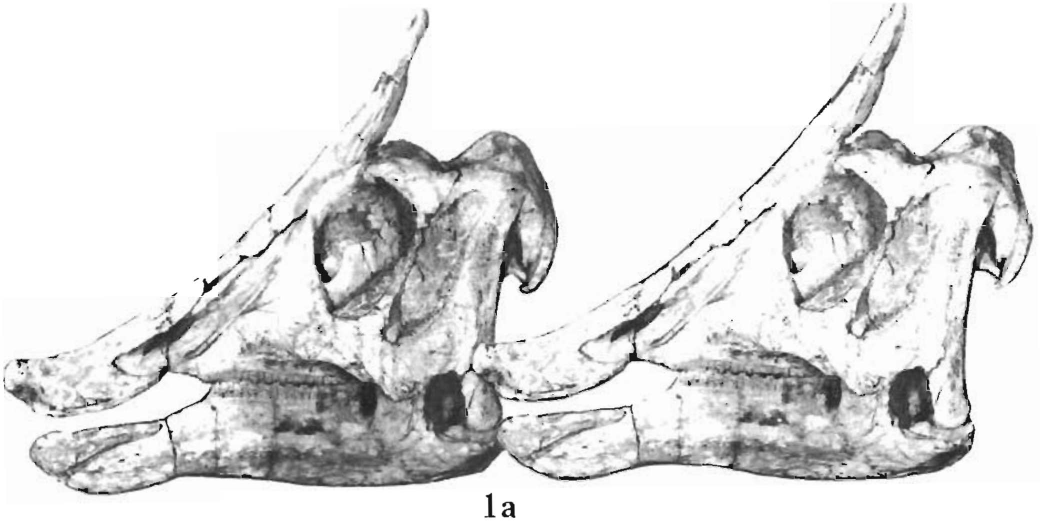
Saurolophus angustirostris Rozhdestvensky, 1952

Upper Cretaceous, Nemegt Formation, Altan Ula IV
Gobi Desert, Mongolia; ZPAL MgD-I/159

1a. Skull of a young individual, lateral view, stereopair; × ca 0·15.
1b. Same specimen, lateral view of the brain case as seen through the orbit; × ca 0·26.
1c. Same specimen, dorsal view of skull roof, slightly inclined anteriorly, end of crest removed, stereopair; × ca 0·5.

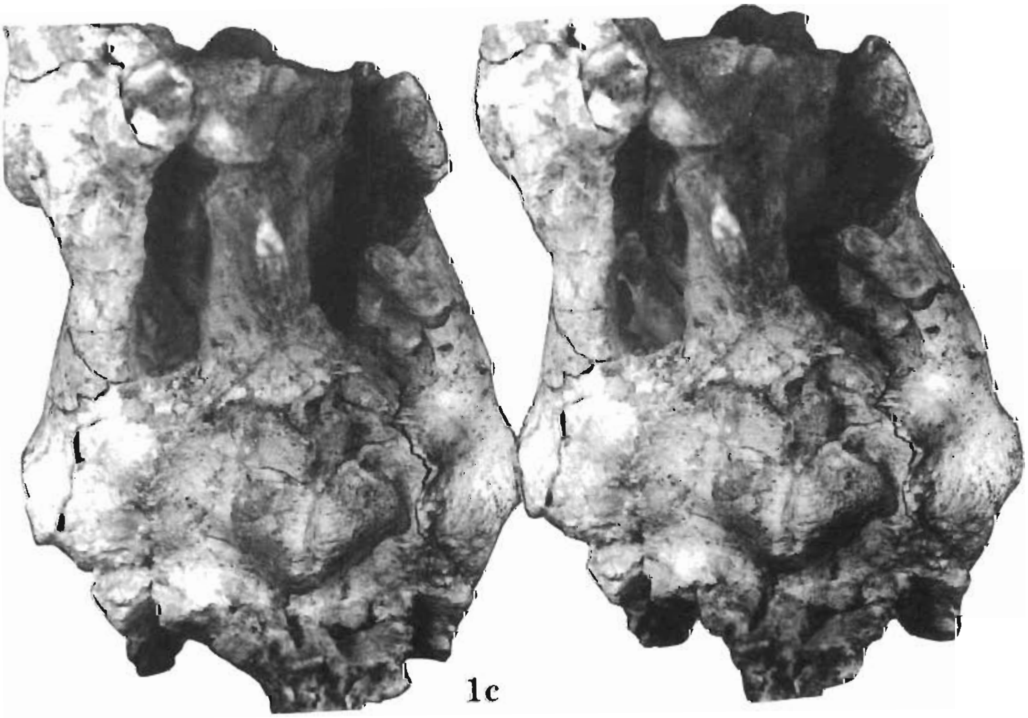
Photo: ***W. Skarżyński***


1d
1c
1b
1a



1a

1b



1c