TERESA MARYAŃSKA & HALSZKA OSMÓLSKA

PROTOCERATOPSIDAE (DINOSAURIA) OF ASIA

(Plates XXXVI-L)

Abstract. — The paper describes a new protoceratopsid material from the Gobi Desert, Mongolia. One new genus and species *Bagaceratops rozhdestvenskyi* and one new species ?*Protoceratops kozlowskii* are described from the supposed Middle Campanian. Additional osteological data are given concerning *Microceratops gobiensis* BOHLIN, which are based on new material from the deposits probably older than the Campanian. Individual variability of *B. rozhdestvenskyi* was studied, as well as some aspects of post-embryonic ontogeny of the Protoceratopsidae. The supposed relationship of genera within the Protoceratopsidae is discussed. The Psittacosauridae are considered here as an early and highly specialized family of the suborder Ceratopsia. They could not be, however, ancestral either to the Protoceratopsidae or Ceratopsidae. None of the known protoceratopsid genera can be considered ancestral to the Ceratopsidae.

Contents

INTRODUCTION

The first known representative of the family Protoceratopsidae in Asia — *Protoceratops andrewsi* GRANGER & GREGORY, 1923 — was discovered by the Third Asiatic Expedition of the American Museum of Natural History in Mongolia and was preliminarily described by GRANGER & GREGORY (1923). The species was later described in detail by BROWN & SCHLAIKJER (1940*a*, 1940*b*, 1940*c*) and discussed or mentioned by many subsequent authors (HAAS 1955; OSTROM 1964, 1966; ROZHDESTVENSKYI 1965; KURZANOV 1972). A new locality for *P. andrewsi* — Toogreeg (Toogreegeen Shire, Toogreegeen Us) (Тугрикин — Ус), situated in the same region as the type locality Bayn Dzak, was discovered by DASHZEVEG (1963). NIKOLOFF & HUENE (1966) reported the discovery of a new occurrence of *Protoceratops* sp. in the locality spelled by them as Tugruk. It is, however, clear that it was the same locality mentioned earlier by DASHZEVEG (*l. c.*). The age of the deposits was incorrectly determined by NIKOLOFF (*l. c.*,

Table 1

Distribution of the Protoceratopsidae in Asia

Species	Locality	Formation	Supposed stratigraphic age	Asocisated vertebrate fauna *
Bagaceratops rozhdestvenskyi gen.n. sp.n.	Khermeen Tsav I and II (SW of Nemegt Basin, MPR)	Khermeen Tsav formation **	?Middle Campanian (according to KIELAN-JAWOROWSKA 1974, 1975*a*, 1975*b*)	*Djadochtatherium catapsaloides*, *Nemegtbaatar gobiensis* and other multituberculates, *Barunlestes butleri*, *Asioryctes nemegtensis*, *Deltatheridium pretrituberculare tardum*, *Macrocephalosaurus gilmorei*, *Cherminsaurus kozlowskii*, *Erdenetesaurus robinsonae*, *Darchansaurus estesi* and other lizards, *Velociraptor* sp., *Oviraptor* sp., ankylosaurs
?*Protoceratops kozlowskii* sp.n.	Khulsan (Nemegt Basin, MPR)	Barun Goyot Formation	?Middle Campanian (KIELAN-JAWOROWSKA 1974, 1975*a*, 1975*b*)	*Djadochtatherium catapsaloides*, *Nemegtbaatar gobiensis* and other multituberculates, *Barunlestes butleri*, *Asioryctes nemegtensis*, *Deltatheridium pretriturberculare tardum*, *Naransaurus chulsanensis*, *Macrocephalosaurus gilmorei* (?) and other lizards, *Zangerlia testudinimorpha*, *Gobipteryx minuta*, *Velociraptor* sp., *Tylocephale gilmorei*, sauropod indet. (teeth), carnosaur indet. (tooth)
Protoceratops andrewsi GRANGER & GREGORY, 1923	Bayn Dzak (Shabarakh Usu, MPR)	Djadokhta Formation	Santonian (KIELAN-JAWOROWSKA 1974)	*Djadochtatherium matthewi*, *Kryptobaatar dashzevegi* and other multituberculates, *Deltatheridium pretrituberculare pretrituberculare*, *Zalambdalestes lechei*, *Kennalestes gobiensis*, *Deltatheroides cretacicus*, *Hyotheridium dobsoni*, *Adamisaurus magnidentatus*, *Macrocephalosaurus ferrugenous* and other lizards, *Shamosuchus djadochtaensis*, *Gobiosuchus kielanae*, *Velociraptor mongoliensis*, *Saurornithoides mongoliensis*, *Oviraptor philoceratops*, *Pinacosaurus grangeri*, hadrosaur indet. (teeth)
	Toogreeg (Bayn Dzak region, MPR)	Toogreeg formation **	Santonian (contemporaneous with Djadokhta Formation: MARTINSON, 1966, KURZANOW 1972)	*Velociraptor mongoliensis*

cont.

Species	Locality	Formation	Supposed stratigraphic age	Associated fauna *
Protoceratops andrewsi GRANGER & GREGORY, 1923	Ulan Tsonch (Kansu, China)	Ulan Tsonch formation **	?Santonian (possibly contemporaneous with Djadokhta Formation on basis of dinosaurs)	*Shamosuchus* sp., cf. *Velociraptor mongoliensis*,
Microceratops sulcidens BOHLIN, 1953	Chia Yü Kuan (Kansu, China)	Chia Yü Kuan formation **	possibly older than Djadokhta Formation on basis of dinosaurs	*Heishansaurus pachycephalus*, *Chiayüsuchus cingulatus*, *Chiayüsaurus lacustris*, carnosaur indet. (tooth), tortoises,
Microceratops cf. *gobiensis* BOHLIN, 1953	Tanankou, S of Tzoyun (N. Shansi, China)	Tanankou formation **	older than Djadokhta Formation on basis of dinosaurs	cf. *Velociraptor mongoliensis*, *Bactrosaurus johnsoni*,
Microceratops gobiensis BOHLIN, 1953	Tsondolain Khuduk (Kansu, China)	Tsondolain Khuduk formation **	older than Djadokhta Formation on basis of dinosaurs	"*Stegoceras*" *bexelli*,
	Sheeregeen Gashoon (N of Nemegt Basin, MPR)	Sheeregeen Gashoon formation **	older than Djadokhta Formation on basis of dinosaurs	"*Syrmosaurus*" *disparoserratus*, ornithomimid indet., primitive hadrosaur indet., theropod indet. *Paralligator gradilifrons*,

* Quoted after: BOHLIN 1953, ELŻANOWSKI 1974, GILMORE 1943, KIELAN-JAWOROWSKA 1969, 1970, 1974, 1975*a* 1975*b*, KONZHUKOVA 1954, MALEYEV 1954, MARYAŃSKA 1971, MŁYNARSKI 1972, MOOK 1924, OSBORN 1924, OSMÓLSKA 1972, SULIMSKI 1972, 1975, YOUNG 1958*a*.

** Informal lithostratigraphical unit, see discussion in KIELAN-JAWOROWSKA 1975*a*.

Fig. 3) to be Lower Cretaceous. HUENE, in the same paper, suggested that the protoceratopsid from this site may represent *Leptoceratops* rather than *Protoceratops*. Judging from the teeth illustrated by these authors, the form mentioned by them represents, in fact, *P. andrewsi*. This was also demonstrated by KURZANOV (*l. c.*), who studied material from the same locality.

The white sand and sandstone in Toogreeg (Toogreeg formation) are lithologically different from the deposits in Bayn Dzak, but they yielded the same dinosaurian species. The Polish-Mongolian Expeditions collected in Toogreeg, in 1971, three specimens of *P. andrewsi* as well as a skeleton of *Velociraptor mongoliensis* OSBORN. The lizards and mammals were not found in this locality. Judging from the dinosaurian remains, the deposits in Toogreeg are contemporaneous with the sediments of the Djadokhta Formation in Bayn Dzak. Another occurrence site of *P. andrewsi* — Ulan Tsonch in Kansu (China) was reported by BOHLIN (1953). This author (*l. c.*) established also a new genus *Microceratops* with two species: *M. gobiensis* BOHLIN, 1953 from Tsondolein Khuduk (Kansu) and ? *M. sulcidens* BOHLIN, 1953 from Chia Yü Kuan (Kansu). The exact age of these deposits was not determined. The material of *Microceratops*, although very incomplete (consisting mainly of teeth and fragments of the postcranial bones), exhibits very distinct differences from *Protoceratops*.

Subsequently YOUNG (1958*a*) reported the presence of a protoceratopsid cf. *Microceratops gobiensis*, represented by jaws and fragments of the limb bones, in Tzoyun, North Shansi (China). In the course of the Polish-Mongolian Palaeontological Expedition, between 1964 and 1971 (KIELAN-JAWOROWSKA & DOVCHIN 1969, KIELAN-JAWOROWSKA & BARSBOLD 1972), new material of *P. andrewsi*, including six very immature skulls, was collected from the Djadokhta Formation in Bayn Dzak.

A specimen of *Microceratops gobiensis* BOHLIN (referred to as "small unidentified reptile" by KIELAN-JAWOROWSKA & BARSBOLD 1972) was found in Sheeregeen Gashoon locality (Sheeregeen Gashoon formation) by the Polish-Mongolian Palaeontological Expedition, in 1971. The age of these deposits is believed to be older than that of the deposits with *P. andrewsi*[1].

Two immature skulls and other skeletal elements of ?*Protoceratops kozlowskii* sp. n. were discovered in Khulsan (Nemegt Basin, Barun Goyot Formation; GRADZIŃSKI & JERZYKIEWICZ 1972, Fig. 4, nos.: 1, 4, 5). Many skulls, some of which are very immature, of *Bagaceratops rozhdestvenskyi* gen. n., sp. n. were collected in the red beds of Khermeen Tsav (GRADZIŃSKI & JERZYKIEWICZ 1974) situated some 40 km south-west from the westernmost part of the Nemegt Basin. For the purposes of simplicity the informal lithostratigraphical unit "Khermeen Tsav formation" is used in this paper (see KIELAN-JAWOROWSKA 1975*a*) for the red beds above mentioned. Similarly, the informal lithostratigraphical units are introduced in this paper for the deposits in other localities, which yielded the protoceratopsid remains and which so far were not determined stratigraphically (Table 1). The deposits in Khulsan (Barun Goyot Formation) and the red beds in Khermeen Tsav (Khermeen Tsav formation) are most probably contemporaneous, being according to KIELAN-JAWOROWSKA (1974) definitely younger than the Djadokhta Formation and possibly of the Middle Campanian age. These two localities yielded, however, different protoceratopsid species, although the most of other reptilian fauna and the mammals are the same in both of them (Table 1).

The protoceratopsid material described in this paper is quite abundant and comparatively well preserved. It consists mainly of skulls and occasionally of some fragmentary postcranial skeletons; it was obtained not by means of the excavations but found on the eroded surfaces of the strata. Most of this material is represented by small, young skulls, some of which are much smaller than the smallest "immature individual" of *P. andrewsi* described by BROWN & SCHLAIKJER (1940*a*). These would appear to be the smallest dinosaurs yet described. The Asian species, as well as the North American representatives of this family, demonstrate that the Protoceratopsidae were well diversified during the Upper Cretaceous, but known forms cannot be arranged in a continuous phyletic sequence (Table 7).

The material here described is housed in the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw.

The photographs were taken by Miss E. MULAWA (Palaeozoological Institute, Polish Academy of Sciences, Warsaw) and Mr L. DWORNIK (Museum of Earth, Polish Academy of Sciences, Warsaw). The drawings were made by Mrs K. BUDZYŃSKA (Palaeozoological Institute, Polish Academy of Sciences, Warsaw).

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Abbreviations used for institutions:

AMNH — American Museum of Natural History (New York).
NMC — National Museum of Canada (Ottawa).
ZPAL — Palaeozoological Institute of the Polish Academy of Sciences (Warsaw).

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[1] When this paper was in page proof, Rozhdestvensky's work appeared (1974) in which he considers the Sheeregeen Gashoon deposits as being stratigraphically younger than the Djadokhta Formation and of the Campanian age. Convincing evidence for this opinion is, however, still lacking.

SYSTEMATIC PART

Suborder CERATOPSIA Marsh, 1890
Family PROTOCERATOPSIDAE Granger & Gregory, 1923
Genus MICROCERATOPS Bohlin, 1953
Microceratops gobiensis Bohlin 1953

(Pls XXXVI-XXXVIII, Text-figs 1-4)

1953. *Microceratops gobiensis* nov.sp.; B. Bohlin, p. 34, text-figs 13, 14*a-c*, 15*c-f*, 16, 19*a-c*, *e-g*; Pl. 2, Figs 4-6, 8-12.

Revised diagnosis. — Lightly built, cursorial protoceratopsid of small size. Parietosquamosal frill short, fenestrated. Jugal shallow. Mandible shallow with straight ventral border. Fore and hind limbs long, slender; length of tibia 116% that of femur; metatarsus long, narrow, compact.

Material. — One individual (ZPAL MgD-I/156) consisting of: damaged skull, including posterior portion of jugals, quadrates, quadratic wings of pterygoids, quadratojugals, fragments of ectopterygoids, fragment of maxilla containing three teeth, basiooccipital, fragment of exoccipital, posterior part of parietosquamosal frill; mandibles lacking predentary and splenial but containing three dentary teeth; postcranial skeleton including 23 vertebrae (nearly all with damaged neural arches) among which are 4 posterior cervicals, 12 dorsals, 7 sacrals; right scapula, proximal part of left scapula, left coracoid, right humerus, radius and fragmentary ulna, proximal and distal extremities of left humerus, proximal parts of both pubes, fragments of both ilia and fragment of right ischium, right femur, tibia and nearly complete pes, distal part of left tibia, fragmentary left pes, tarsals, ribs; from strata considered to be of early Upper Cretaceous age (Sheeregeen Gashoon formation) of the locality Sheergeen Gashoon, Gobi Desert, Mongolian People's Republic.

Description. — *Skull* (Pl. XXXVII, Fig. 2, Text-fig. 1). The basicranium is very incomplete and the sutures are obscure. The frill is well developed, although short, and bears a slightly convex posterior margin. The fenestrae are large. The lateral region of the posterior margin of the frill is formed, to a large extent, from the squamosal. The posterior part of the squamosal is thick, and dorsoventrally flattened in its medial portion. The element remains very thick behind the quadratic cotylus, where its outer margin becomes more elevated. The quadrate seems to curve backwards dorsally. The quadratojugal is drop-shaped and relatively narrow ventrally. It would appear to be devoid of any medial projection. The quadratojugal is attached to the quadrate, but its ventral edge is placed well above the mandibular articulation. The jugal is narrow, with a horizontal ventral profile and a vertical ascending wing. The jugal is very weakly expanded laterally in its posterior extremity. An overlapping contact between the adjacent wings of the quadrate and pterygoid is very loose.

Mandible (Pls XXXVI, XXXVII, Fig. 1). — The mandibular ramii diverge posteriorly at an angle of about 60°. The dentary is shallow and its outer surface is slightly convex. The coronoid process is relatively low and seems to be medially inclined. The dorsolateral edge of the dentary rises anteriorly, and a surangular ridge is present, below which the mandible is slightly concave. The articular is very massive and forms more than a half of the articular surface for the quadrate. Maxillary and dentary teeth are poorly preserved, but both possess a very strong, asymmetrically placed median ridge. The maxillary teeth bear weakly developed posterior carina.

Cranial measurements see Table 3.

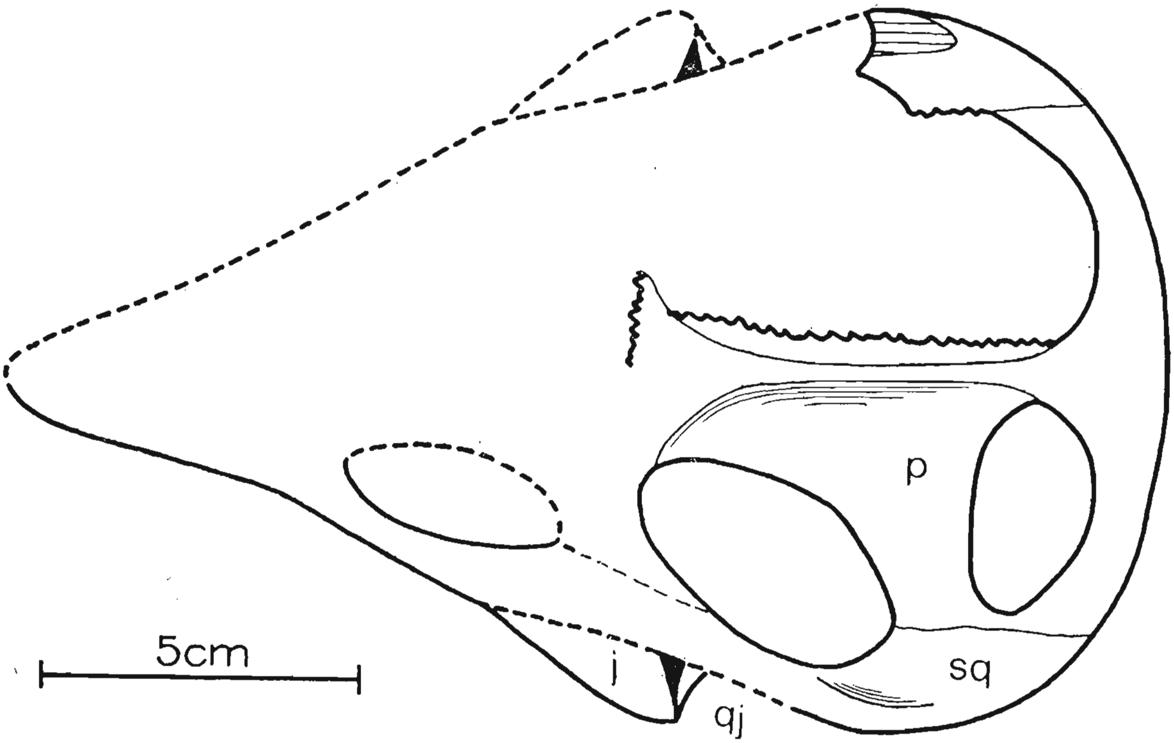


Fig. 1

Microceratops gobiensis Bohlin, diagrammatic reconstruction of the skull in dorsal view. Based on specimen ZPAL MgD-I/156. Abbreviations: *a* — angular, *aaf* — additional antorbital fenestra, *af* — antorbital fossa, *afe* — antorbital fenestra, *ar* — articular, *bo* — basioccipital, *bpt* — basipterygoid process, *bs* — basisphenoid, *c* — coronoid, *ci* — carotid foramen, *d* — dentary, *ec* — ectopterygoid, *eo* — exoccipital, *eu* — Eustachian opening, *f* — frontal, *fd* — frontal depression, *fo* — fenestra ovalis, *fr* — fenestra rotundum, *h* — nasal horn core, *in* — internal nare, *j* — jugal, *l* — lacrimal, *lf* — lacrimal foramen, *m* — maxilla, *n* — nasal, *op* — opisthotic, *or* — orbitosphenoid, *p* — parietal, *par* — prearticular, *pd* — predentary, *pl* — palatine, *pm* — premaxilla, *po* — postorbital, *pr* — prootic, *prs* — presphenoid, *ps* — parasphenoid, *pt* — pterygoid, *q* — quadrate, *qj* — quadratojugal, *qpt* — quadrate wing of the pterygoid, *r* — rostral, *sa* — surangular, *so* — supraoccipital, *sq* — squamosal, *v* — vomer, *ve* — vessel opening, I-XII openings for nerves.

Postcranial skeleton (Pls XXXVI, XXXVII, Fig. 3, XXXVIII, Text-figs 2-4). — The vertebrae are of the same shape as in other protoceratopsids but seem to be slightly more delicate in construction. There are apparently seven vertebrae in the sacrum, but they are not coalesced. This character is rather peculiar, but it cannot surely be attributed to the possible immaturity of the individual. RUSSELL (1970) stated that the posterior sacral vertebrae are not coalesced in adults of *Leptoceratops gracilis*. The scapula is very slender, but strongly thickened at the glenoid. The coracoid is large and markedly convex externally; its anteroventral margin is strongly recurved. The posterolateral projection is long and strongly pointed, and notch separating it from the glenoid is broad and deep. The humerus is very slender and possesses a long shaft. Its proximal extremity is slightly expanded, and the medial border is strongly deflected inwards. The deltoid crest is situated on the proximal half of the shaft. The distal extremity of the bone bears well developed, rounded condyles. The axes of both articular surfaces are parallel. The radius is very slender and has but weakly expanded extremities. Its length is about 70% of that of the humerus. The preserved proximal portion of the pubis (Text-fig. 4C) is massive, although the prepubis is rather rod-like and only slightly flattened dorsoventrally. The postpubis is broken away, but its base suggested that it was slender. The remaining pelvic elements (Text-fig. 4*A*, *B*) are too fragmentary to warrant description. The femur is slender and curved; its anterior surface is convex in lateral profile. The articular head is large, distinctly medially directed and bears a short, massive condylar neck. The moderately large and weakly pendant fourth trochanter is placed slightly above the midlength of the shaft. The distal condyles are well developed. The medial condyle is the smaller of the two and passes dorsally into a sharp crest on the posterior surface of the femur.

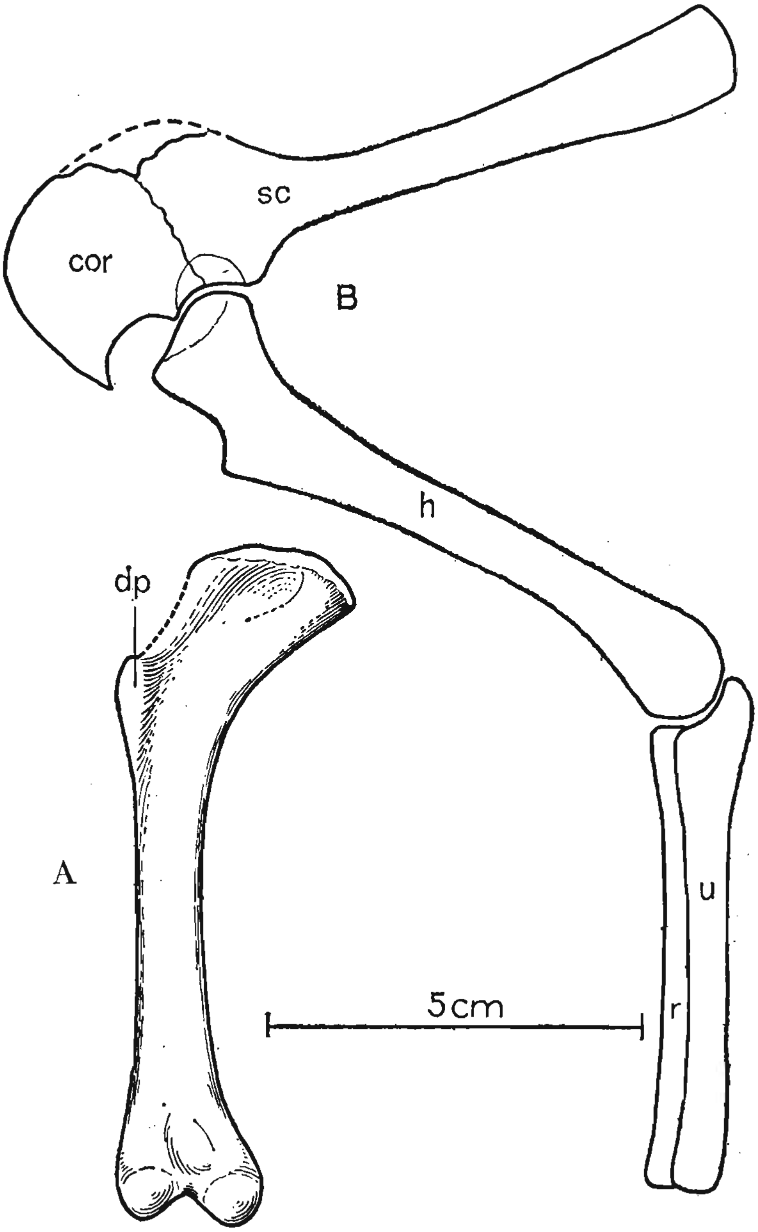


Fig. 2

Microceratops gobiensis Bohlin, *A* — right humerus, anterior view; *B* — reconstruction of the left pectoral girdle with fore limb. Abbreviations: *cor* — coracoid, *dp* — deltopectoral crest, *h* — humerus, *r* — radius, *sc* — scapula, *u* — ulna; ZPAL MgD-I/156.

The intercondylar fossa is deep. The tibia is very long and slender, exceeding the femur in length. The proximal articular end is more expanded than the distal one. The metatarsus is very long (55% of the femur length) and contains four metatarsals, as preserved. It is very narrow, compact and strongly arched. The metatarsals are closely applied to each other along their entire lengths, although metatarsal I diverges somewhat distally from the metatarsal II. Metatarsal I is short and very thin, its length being slightly more than 3/4 that of the metatarsal II. Metatarsal II is slightly shorter than metatarsal III, which is the longest and most robust element in the foot. Metatarsal IV is slightly shorter than metatarsal II, and more slender than the latter element. The phalangeal formula of pes is 2, 3, 4, 5, 0. Phalanx 1 of digit I is distinctly the longest of all the pedal phalanges. The proportions of the phalanges of the remaining digits are generally similar to those in *P. andrewsi*, with the exception that phalanx 5 of the digit IV is the shortest of all phalanges. The unguals are pointed and dorsoventrally flattened.

Table 2

Dimensions of postcranial skeleton of *Microceratops gobiensis*, ZPAL MgD-I/156 (in mm)

Length of scapula	90
Width of distal end of scapula	13
Width of proximal end of scapula	22
Length of humerus	86
Width of distal end of humerus	18
Length of radius	60 e.
Length of femur	95
Length of tibia	110
Width of proximal end of tibia	28
Width of distal end of tibia	16
Length of metatarsal I	37
Length of metatarsal II	51
Length of metatarsal III	53
Length of metatarsal IV	47
Length of phalanx I^1	22
Length of phalanx I^2	17 e.
Length of phalanx II^1	17
Length of phalanx II^2	15
Length of phalanx II^3	16
Length of phalanx III^1	17
Length of phalanx III^2	12
Length of phalanx III^3	12
Length of phalanx III^4	16
Length of phalanx IV^1	13
Length of phalanx IV^2	9
Length of phalanx IV^3	8
Length of phalanx IV^4	10
Length of phalanx IV^5	8
Total length of 12 dorsal vertebrae	132 e.
Total length of 7 sacral vertebrae	90 e.

Discussion. — *Microceratops gobiensis* BOHLIN is advanced in some of its characteristics, such as in the presence of a fenestrated frill. The frill itself is, however, comparatively short, the jugal is shallow, as is also the mandible, and these latter attributes of the cranial structure may be considered primitive. Additional characters of a primitive aspect are found in the structure of the postcranial skeleton. The hind limb of *M. gobiensis* appears particularly primitive in that it resembles the hind limb of members of the Hypsilophodontidae in its slenderness, and the proportions of the elements of the hind limb (Table 8) compare very closely with those in *Hypsilophodon foxi* HUXLEY (*fide* GALTON, 1971, table 1). The ratio between the length of the entire hind limb (excluding the digits) and the length of the trunk (length of the combined dorsal vertebrae) is 1·92 in *M. gobiensis*, and index which appears to be exceptional among the Ornithischia. This index as well as the length of the tibia, which is nearly 25% longer than the femur, suggests an unusual cursorial ability for *Microceratops*. The long, strongly transversely arched and compact metatarsus, which is nearly half as long as the tibia, the very short metatarsal I and probably a much reduced metatarsal V also underscore the cursorial character of the hind limb in *M. gobiensis*. Judging from the combined length of the humerus and radius, the forelimb was also very long. This is rather surprising in view of the structure of the hind limb, which is of such distinctly bipedal character, as well as in view of the relatively early stratigraphic position of *M. gobiensis*. The forelimb (humerus + radius) to hind limb (femur + tibia) ratio is 0.67 - 0.68 in *Protoceratops andrewsi* and 0.71 in *M. gobiensis*. An index similar to that of *M. gobiensis* occurs in *Leptoceratops gracilis* (0.71 - 0.72), but the limbs in the latter species are massive and of a distinctly quadrupedal character. The hind limb of *M. gobiensis*, which is so strongly reminiscent of the Hypsilophodontidae, which are considered by GALTON (1971) to be highly cursorial animals, indicates that *M. gobiensis* might be a very fast runner, probably one of the best among the post-Triassic ornithischians. Increase in the size and weight of the skull (frill) might have created difficulties in exclusively bipedal locomotion. The lengthening of the forelimb may, then, have been necessary adaptation to make possible a quadrupedal mode of locomotion, which, however, most probably was not very rapid (see below).

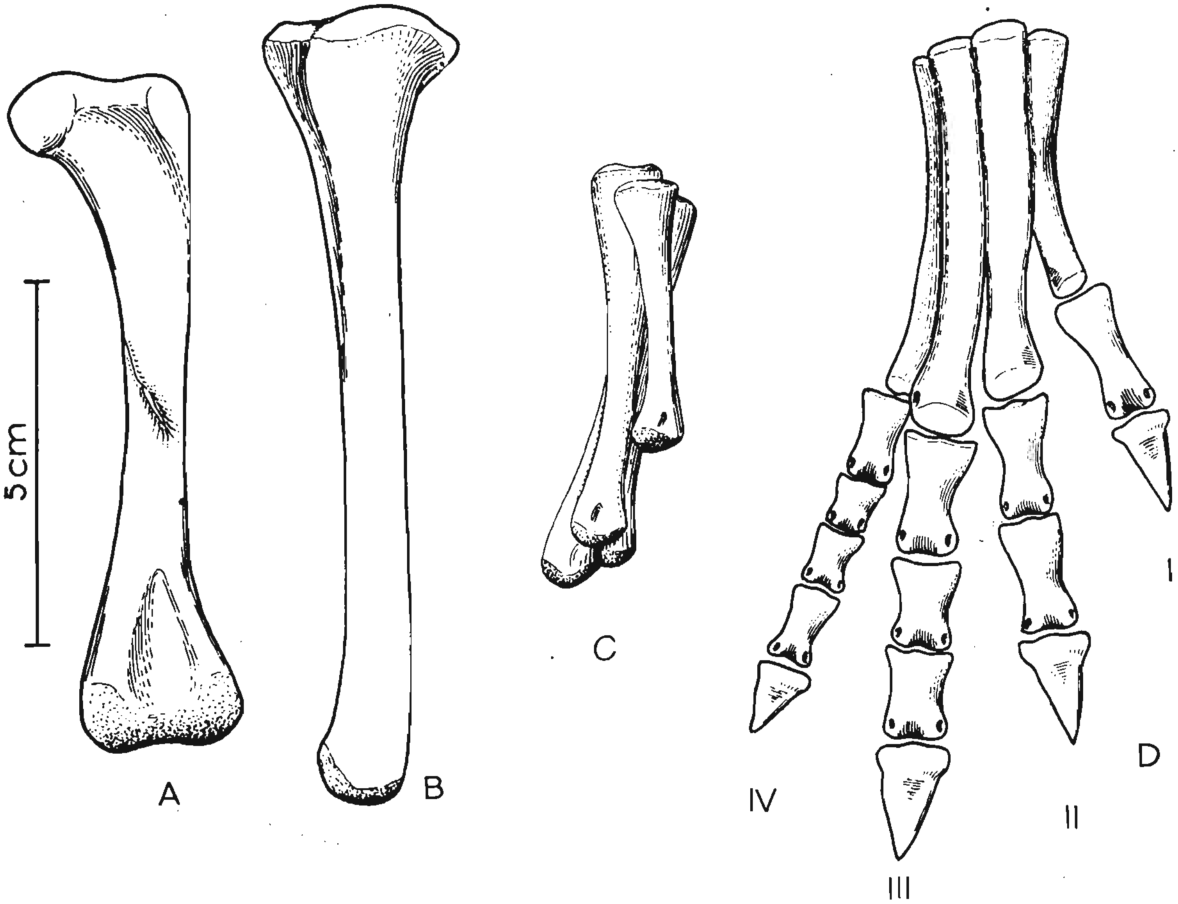
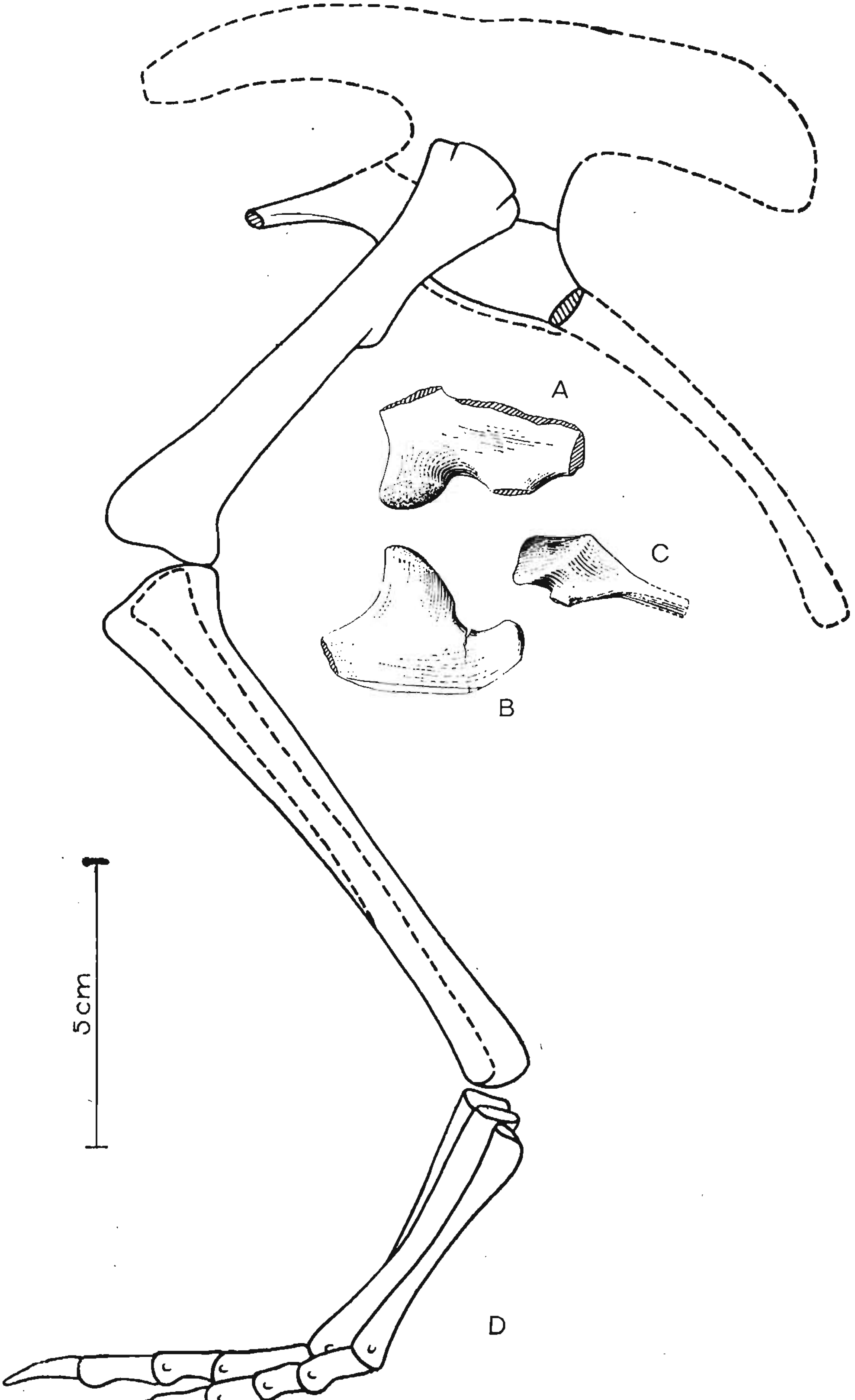


Fig. 3
Microceratops gobiensis Bohlin, *A* — right femur, posterior view; *B* — right tibia, medial view; *C* — right metatarsus, medial view; *D* — right pes, dorsal view; ZPAL MgD-I/156.

A strong medial inflection of the proximal extremity of the humerus seems to reflect the presence of a relatively powerful adductor musculature. Judging from the position of the glenoid, which faces slightly backwards, the humerus was also directed posteriorly, but its distal articulation was generally directed ventrally (Text-fig. 2*B*). The distinct posterior overhanging of the humeral head made possible the posterior rotation of the humerus, to a nearly


A
C
B
5cm
D

horizontal position. However, the amount of forwards movement of the humerus was limited, and even with the maximum possible rotation of the vertebral end of the scapula ventrally (BENNET & DALZELL, 1973) the humerus probably could not assume a vertical orientation. The medial position of the humeral head on the proximal end of the humeral shaft increases the separation between the shaft and the trunk. The slenderness of the forelimb together with the curvature of the humeral shaft seem to imply that it was not well adapted to a locomotory function. Thus, we presume that *Microceratops* was usually bipedal, and that the forelimbs were occasionally used for support during rest and slow locomotion. Unfortunately the manus in *Microceratops* is not known, for its structure would be the best indicator as to what extent the forelimb was adapted to quadrupedal locomotion.

BOHLIN (1953) assumed that the femur and humerus of the *M. gobiensis* material he described could have belonged to the same individual. He suggested that if this were true, the humerus to femur ratio would be 0·84. However, in ZPAL material of this species (which certainly represents one individual) the femoro-humeral index is 0·90. BOHLIN (*l. c.*) also described a foot of ? *M. sulcidens* Bohlin, with fragmentary metatarsals. The pes of our specimen of *M. gobiensis*, in which the natural arrangement of the metatarsals is retained, indicates that the metatarsus was compact in *M. gobiensis.* We think this was also the case in ? *M. sulcidens*, not as it has been reconstructed by BOHLIN (*l. c.*, Pl. 2, Fig. 13). The pes of ? *M. sulcidens* is larger, and the bones are more massive than in *M. gobiensis*, although the general structure is similar. This would imply that BOHLIN was correct in assigning *M. sulcidens* to *Microceratops*, to a species distinct from *M. gobiensis.*

The slenderness and the length of the hind limb with the recurved femur, the long and slender forelimb with the medially deflected humerus and very thin radius, and the slender, rod-like prepubis clearly separate *M. gobiensis* from all other known genera of protoceratopsids. There is no doubt that *Microceratops* is a very well defined form which cannot be placed in synonymy within *Protoceratops*, as has been suggested by some authors.

Genus **PROTOCERATOPS** GRANGER & GREGORY, 1923

?**Protoceratops kozlowskii** sp. n.

(Pls XL, XLI, XLIX, Figs 2, 3, Text-figs 5, 11*B*, *C*)

Holotype: Immature skull with mandible and fragmentary postcranial skeleton (ZPAL MgD-I/117) including poorly preserved vertebrae of the cervical, dorsal and sacral regions, right scapula, left humerus, ulna and radius, left ilium lacking posterior portion and fragment of left ischium, right femur and proximal portion of left femur, fragmentary right tibia and fibula lacking articular extremities, fragments of right metatarsus, fragmentary ribs; Pls XL, XLI, Fig. 1; Text-fig. 5.

Type horizon: Upper Cretaceous, ? Middle Campanian, Barun Goyot Formation.

Type locality: Khulsan, Nemegt Basin, Gobi Desert, Mongolian People's Republic.

Derivation of the name: In honour of Prof. ROMAN KOZŁOWSKI, the eminent Polish palaeontologist.

Diagnosis. — Protoceratopsid with anteriorly sloping cranial profile. Prefrontal very long and narrow, posterior ala extending behind midpoint of orbit. Jugal deep below postorbital

←

Fig. 4

Microceratops gobiensis Bohlin, *A* — fragment of right ilium, lateral view; *B* — fragment of right ischium, lateral view; *C* — proximal part of right pubis, lateral view; *D* — reconstruction of the left pelvic girdle with hind limb; ZPAL MgD-I/156.

bar. Mandible deep with straight lower edge. Nasal — frontal suture located behind anterior margin of orbit. Eight vertebrae coalesced into sacrum in immature specimen. Anterior process of ilium distinctly everted. Humerus short and stout.

Material. — In addition to the holotype the following specimens are housed in ZPAL collection: one very immature, distorted skull with mandible (MgD-I/116); two nearly complete dentaries with fragmentary postcranial elements of young adult individual (MgD-I/118); anterior fragment of dentary and three neural arches of caudal vertebrae (MgD-I/119); anterior parts of two dentaries with teeth and several isolated teeth (MgD-I/120); fragment of maxilla of very immature individual with four teeth (MgD-I/121); several isolated teeth (MgD-I/122); all from the Barun Goyot Formation of Khulsan locality.

Cranial measurements see Table 3.

Description. — *Skull as a whole* (Pl. XL, Text-fig. 5). The following description is based on two immature specimens (ZPAL MgD-I/116, 117) in which the palatal and occipital regions are damaged. The skull is narrow, the width across the quadrates amounting to only about 72% of the basal length. The profile of the skull smoothly descends anteriorly, beginning near the centre of the frontal. The frill is comparatively long, equalling about 67% of the basal length of the skull in this dimension. It becomes more elevated posteriorly. A narrow sagittal crest is developed along the midline of the frill. The posterior margin of the frill has not been well enough preserved to determine the presence or absence of fenestration. The premaxilla bears two teeth, and seven are present in the maxilla. The antorbital fossa is large and deep. The prefrontal is narrow and extremely long, forming at least half of the dorsal margin of the orbit. The frontal is large and contacts the nasal opposite the anterior part of the orbit. The frontals are slightly convex posteriorly, with weakly developed frontal depression, immediately in front of the supratemporal fenestrae. The anterior boundary of the supratemporal fossa is formed entirely from the frontal, and the frontal-postorbital suture is parallel to the long axis of the skull. The postorbital-squamosal arcades are low, and lie nearly parallel to each other and to the midline of the skull. The squamosal projects far above and behind the quadrate. The quadrate is somewhat anteroventrally inclined. The infratemporal fenestra is long, in a vertical direction, and narrow. The jugal is very deep, with a rapidly descending posterodorsal margin; the posterior extremity of the bone curves slightly in a lateral direction. The medial projection of the quadratojugal is long.

Mandible (Pls XL, Figs 1*a*, 1*c*, 2*b*, 2*c*, XLI, Fig. 2). The mandibles in *?P. kozlowskii* are preserved with the two immature skulls mentioned above, as are the two dentaries of the young adult individual (ZPAL MgD-I/118). The mandible is relatively deep and the dentary has a straight ventral margin, the latter feature being apparent in the adult specimen. The anterior edge of the coronoid process curves very steeply upwards, and the symphyseal portion of the dentary is also strongly dorsally recurved. The splenial reaches the symphysis and covers slightly less than a half of the symphyseal border of the dentary. The mandible is slightly concave in the area of contact between the surangular and angular, in the immature specimens, and a surangular ridge is not developed. There are 11 teeth in the dentary of the adult individual (ZPAL MgD-I/118) in a tooth row measuring 5·7 cm in length. The dentary of the smallest specimen (ZPAL MgD-I/116) contains only 7 teeth.

The skull of the smallest, very immature individual of *?P. kozlowskii* (ZPAL MgD-I/116) is high and has a very short snout (Pl. XL, Fig. 2). It is characterized by its very large, convex and broad parietals, and, in conjunction with the extreme breadth of parietals, a very long and straight frontal-parietal suture. The anterior border of the supratemporal fossa is formed from the parietal, the frontal being completely excluded. The frontal is also convex, both transversely

Table 3

Dimensions of skulls (in mm)

Species	ZPAL Cat. No. MgD-	A	B	C	D	E	F	G	H	M	N	O
		length of orbit	center of orbit to front of rostral	center of orbit to posterior end of frill	median length of skull	greatest width of frill	greatest depth of skull (depth of face in brackets)	basal length of skull (condyle to anterior end of maxilla)	width across quadrates	width across jugals	anterior margin of supra-temporal fossa to end of frill	length of mandible
Microceratops gobiensis	I/156	—	—	—	e. 200	e. 110	—	—	e. 100	e. 135	e. 80	e. 110
	I/123	19	21	26	47	24	e. 18 (15)	e. 30	14	28	16	e. 30
Bagaceratops rozhdestvenskyi	I/124	29	53	e. 53	e. 106	?	e. 45 (40)	71	?	?	39	e. 77
	I/125	32	69	89	e. 158	90	60 (58)	92	67	96	64	101
	I/126	37	e. 101	94	e. 195	133	72 (65)	124	95	147	59	137
	I/127	39	101	?	?	?	e. 65 (?)	121	?	e. 146	?	?
Protoceratops andrewsi (immature skulls)	II/7	17	e. 30	32	e. 62	?	29 (19)	e. 36	?	e. 33	17	?
	II/24	22	?	?	?	e. 48	35 (27)	49	46	?	?	e. 60
	II/23	31	e. 58	?	?	e. 58	e. 46 (28)	e. 68	e. 60	e. 70	?	71
?*Protoceratops kozlowskii*	I/116	15	22	?	?	?	18 (?)	29	?	22	?	?
	I/117	22	e. 32	37	e. 70	23	22 (?)	40	e. 29	28	18	?

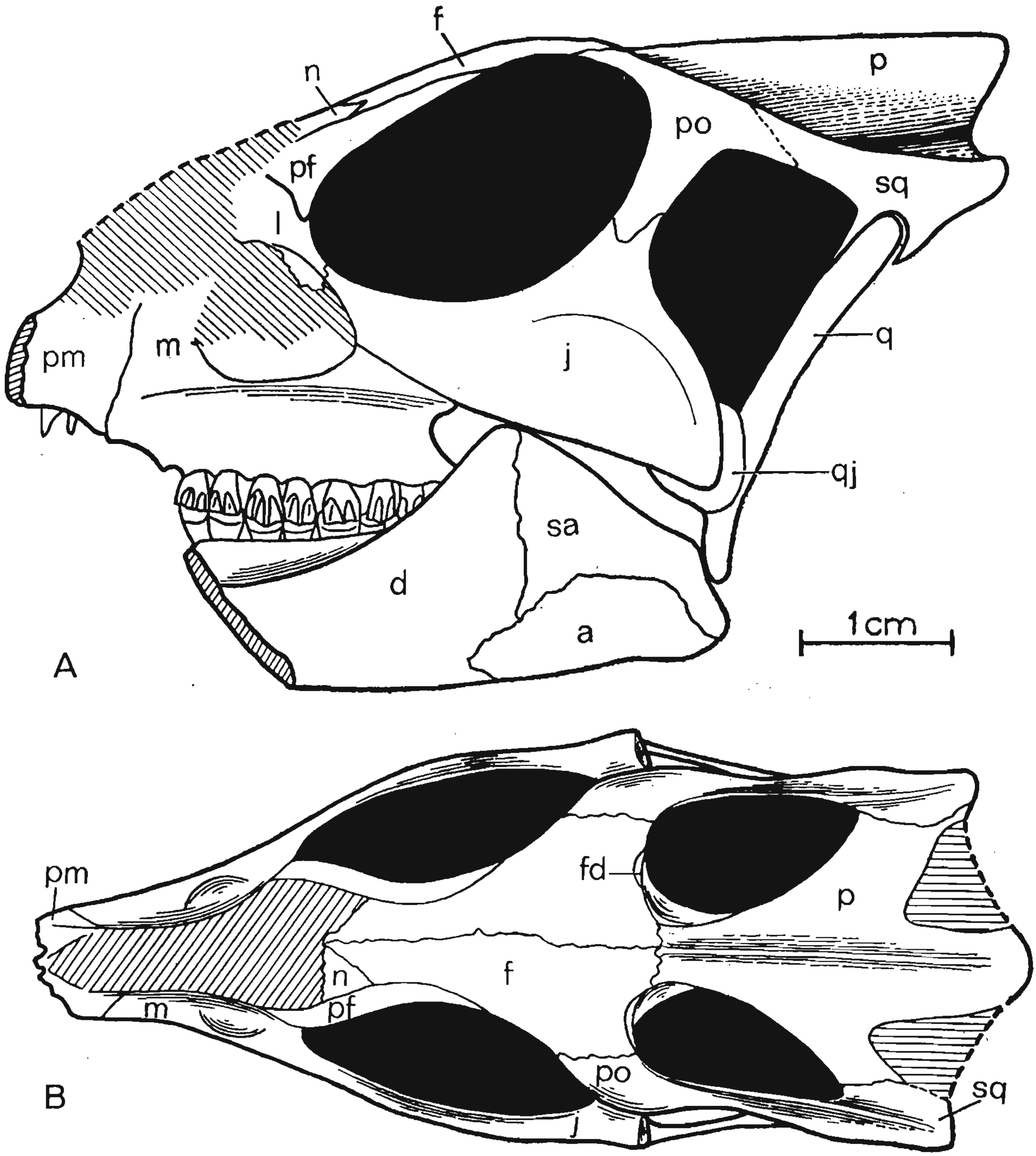


Fig. 5
?*Protoceratops kozlowskii* sp.n., *A* — skull of a holotype specimen, lateral view; *B* — same specimen, dorsal view; ZPAL MgD-I/117. Abbreviations as in Fig. 1.

and longitudinally. It descends steeply anteriorly, as does the nasal, resulting in the very abbreviated anterior profile for the skull. The premaxilla of this very immature individual bears alveolae for two teeth.

Postcranial skeleton (Pls XL, Fig. 1*a*, XLI, Fig. 1). The cervical and dorsal vertebrae are fragmentary in the specimen ZPAL MgD-I/117, their number is unknown. The two posteriormost dorsals are present between the anterior processes of the ilia, and their ribs were in free contact with the ilium. Eight sacral vertebrae, and the basal caudal vertebra articulate with the ilia through their diapophyses and ribs. The neural arches of all vertebrae are badly preserved, and the neural spines have been broken away and lost. Three median dorsal ribs (probably the fifth, sixth and seventh) are preserved, and these are very thin. They were found in articulation with the vertebrae and have a distinct posterior inclination in the ventral part of their arc. The scapula is slender, straight but weakly convex externally. The ventral part of the scapula is slightly expanded anteroposteriorly and robust, and the thin dorsal portion of the scapula is also slightly expanded. No coracoid has been preserved nor have the clavicles and sternalia. The humerus is relatively short and stout, incorporating 53% of the total length of the forelimb (without the manus). The deltopectoral crest is not very strong and is located within the proximal third of the humeral shaft. The shaft is comparatively short, and the proximal and distal extremities are only slightly expanded. The ulna is slender, flattened anteroposteriorly and bears a small olecranon. The radius is relatively long and slender, incorporating 47% of the total length of the limb (without the manus). The ilium has a comparatively long anterior process, with a very shallow ventral shelf which is probably absent at the anterior tip. The eversion of the margin of the anterior process is very distinct. The ischiac peduncle is more massive than the pubic peduncle. The iliac blade is vertical above the acetabulum and there is no trace of an antitrochanter. Only the proximal surface of the postacetabular part of the ilium has been preserved. The ischium is incomplete distally, but seems to have been only slightly curved. The femur is relatively slender. The lesser trochanter is distinctly separated from the shaft by a deep groove, on the external surface of the femur. The fourth trochanter is weak, not pendant, and situated on the upper half of the shaft. The head and the distal articular surface of the femur are poorly preserved. The tibia is circular in cross-section and its distal and proximal extremities are poorly preserved. What is preserved of the fibula is very thin. The bones of the manus and pes are very incompletely preserved.

Table 4

Dimensions of postcranial skeleton of ?*Protoceratops kozlowskii*, ZPAL MgD-I/117 (in mm)

Length of scapula	40 e.
Width of proximal end of scapula	8
Width of distal end of scapula	6
Length of humerus	32 e.
Width of distal end of humerus	8
Length of ulna	31
Length of radius	28
Length of femur	41
Width of proximal end of femur	8
Width of distal end of femur	8
Length of ilium	40 e.

Discussion. — The fact that ?*P. kozlowskii* sp. n. is based largely on very immature individuals renders comparisons with *P. andrewsi* difficult. The smallest skull of the latter species (AMNH 6419) available to Brown & Schlaikjer (1940*a*) and considered by them to be very immature, is still about twice as large as our holotype specimen. However, in our collection of *P. andrewsi* are six skulls which are smaller than AMNH 6419. Four of them are reasonably well preserved and the smallest is only slightly shorter than the holotype skull of *?P. kozlowskii*. The significant differences between these skulls, all of comparable size, are as follows: the prefrontal is long, forming more than a half of the anterodorsal border of the orbit in *?P. kozlowskii* while it occupies only the anterodorsal corner of the orbit in *P. andrewsi;* the anterior tip of the frontal is located slightly behind the anterior limit of the orbit in *?P. kozlowskii*, while in the immature *P. andrewsi* it lies in front of, or opposite the anterior orbital margin; the anterior border of the supratemporal fossa is bounded entirely by the frontal in *?P. kozlowskii*, but mostly by the parietal and postorbital, with the frontal reaching the border over a relative short span in *P. andrewsi;* the jugal is deeper in *?P. kozlowskii* than in *P. andrewsi*, both in the suborbital ramus and in the main body of the bone, and below the postorbital bar; the mandible is deeper in *?P. kozlowskii* than in *P. andrewsi*, and its ventral margin is straight even in the young adult individual. The differences cited above justify, in our opinion, the establishment of a new species for the specimens from Khulsan, which are younger stratigraphically than P. andrewsi. The postcranial skeleton of the young specimen of *?P. kozlowskii* is relatively more massive than that of the young *P. andrewsi* described by BROWN & SCHLAIKJER (1940*a*). In some respects it even resembles the postcranial skeleton of very large individuals of *P. andrewsi* more closely, as, for example, in the presence of eight sacral vertebrae, a number typical of fully adult specimens of *P. andrewsi*, the number in the young individual in this species being seven. The deltopectoral crest in *?P. kozlowskii* is similar in position to that in adult specimens of *P. andrewsi*, while it is more proximally situated in "immature" individuals of the latter species. The structure of the anterior process of the ilium in *?P. kozlowskii* is much more advanced in that it has a distinct eversion of the margin. This feature has so far been considered as a characteristic of the Ceratopsidae, although it is much more strongly pronounced in this family than in *?P. kozlowskii*. This character is only incipiently present in P. andrewsi, and it may indicate, together with some cranial characters, that *?P. kozlowskii* may be descended from *P. andrewsi*. Although the tibia in *?P. kozlowskii* has damaged articular surfaces and its entire length cannot be estimated, what is preserved of it is as long as the femur, indicating that it was surely longer than the latter bone. The differences in the cranial and postcranial characters between *?P. kozlowskii* and *P. andrewsi* are so extensive, that we would assign it to a new genus, if it were not represented by materials which are so scarce and pertain primarily to immature individuals.

Genus **BAGACERATOPS** nov.

Type species: *Bagaceratops rozhdestvenskyi* sp.n.
Derivation of the name: Mong. *baga* — small; probably smaller in size than other protoceratopsids.

Diagnosis. — Genus mototypic; diagnosis, stratigraphic and geographic distribution as for the type species.

Bagaceratops rozhdestvenskyi sp. n.

(Pls XLII-XLVIII, XLIX, Figs 4-6, Text-figs 6-10, 11 D, 12-14)

Holotype: Nearly complete skull with mandible, lacking anterior portion of snout (ZPAL MgD-I/126: Pls XLII, XLIII, Fig. 1, Text-fig. 6).

Type horizon: Upper Cretaceous, red beds (Khermeen Tsav formation) of the same age as Barun Goyot Formation ? Middle Campanian.

Type locality: Khermeen Tsav I, south/west of Nemegt Basin, Gobi Desert, Mongolian People's Republic.

Derivation of the name: in honour of Dr. A. K. ROZHDESTVENSKY, in recognition of his work on dinosaurs.

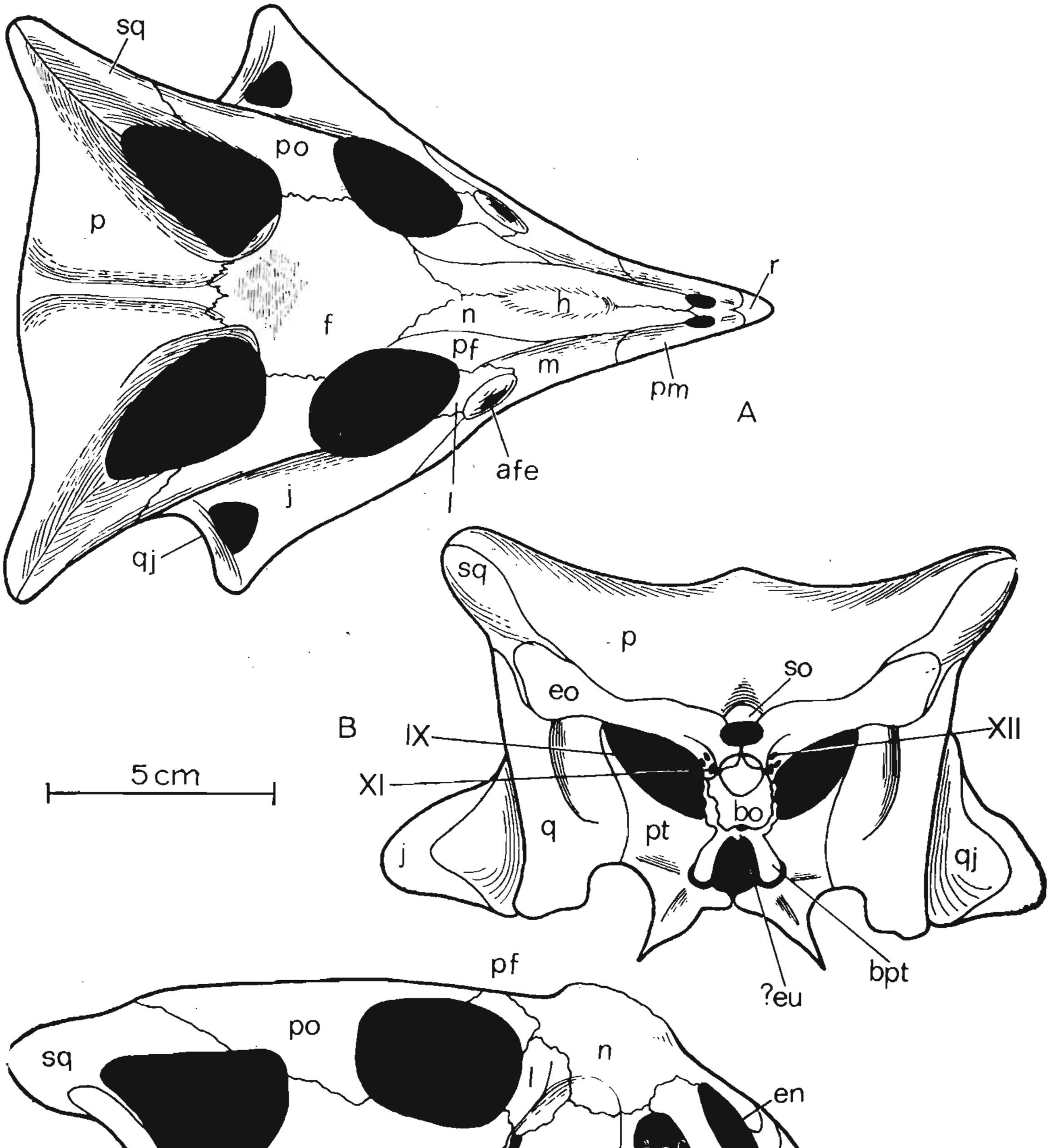
Diagnosis. — Parietosquamosal frill short, most probably without fenestrae. Nasals with prominent horn core. Additional antorbital fenestra present, located in premaxilla-maxilla suture. Preorbital portion of snout short. Premaxillary dentition absent. Ten maxillary teeth. Anterior, edentulous portion of upper jaw very long. Mandible shallow with straight ventral margin.

Material. — In addition to the holotype the following specimens are housed in ZPAL collections: one skull with dentary, of very immature individual (MgD-I/123) lacking palatal as well as basicranial and occipital regions; two nearly complete sub-adult skulls with mandibles (MgD-I/124, 125); nearly complete adult skull lacking nasals and posterior cranial region (MgD-I/129); seventeen fragmentary skulls, some with fragmentary mandibles (MgD-I/127, 128, 130-136, 143-150), eight more or less complete mandibles (MgD-I/137-140, 142, 152-154), several loose teeth (MgD-I/141, 151); some fragmentary postcranial bones (MgD-I/142, 146, 152, 154); all from the Khermeen Tsav formation of locality Khermeen Tsav.

Description. — *Skull as a whole* (Pls XLII, XLIII, Fig. 1, XLIV, Fig. 1, XLV, XLVI, Figs 1, 2, XLVII, XLVIII, XLIX, Fig. 4, Text-figs 6-9). The following description is based on the complete or nearly complete skulls of ZPAL MgD-I/124, 125, 126, 127, 129, which represent adult or sub-adult specimens. The skull is triangular, relatively narrow, the width across the quadrates representing 60-76% of the basal length of the skull (Table 6). The frill is relatively short, the length of the postorbital portion of the skull generally representing 50% of the basal length of the skull (Table 6), and nearly horizontal in position. The fenestrae in the frill seem to be absent on well preserved skulls. The snout is short and contains an additional antorbital fenestra. The dorsal boundary of the antorbital fossa is situated on a level above that of the centre of the orbit. The nasals bear an unpaired horn core of moderate size. In lateral view, the snout is very deep in the region of the external narial opening. A frontal depression is rarely present, and never more than weakly developed. The infratemporal fenestra is large and approximately subquadrangular in outline, with a long, straight upper border (Pl. XLIX, Fig. 4). The palatal region is very narrow and deep. The premaxilla lacks teeth, and the maxilla of the largest specimen is provided with but 10 teeth. The anterior, edentulous region of the upper jaw (excluding the rostral) is long and equals 50% of the total length of the jaw. The axes of the lower articular surfaces of the quadrates converge anteromedially.

Cranial measurements see Table 3.

Bones of the skull. Exoccipital. The exoccipital is strongly elongated laterally but narrow vertically; the main body of the exoccipital is comparatively thin dorsally and more massive ventrally. It bounds the foramen magnum laterally and ventrally and sheaths the basioccipital with a thin blade of bone. Seen in posterior view, the bone contacts the supraoccipital medially and more distally is overlapped by the parietal. It nearly reaches the quadrate laterally but is separated from the latter element by a thin flange of the squamosal. Its share in the formation of the occipital condyle is extremely small. The exoccipital is also visible on the medial wall of the supratemporal fossa, where it is wedged between the parietal and supraoccipital above, and the prootic below. The exoccipital contains three openings, the largest of which is elongated and posteriormost in position, representing the exit of nerve XII; its entrance is visible within the cavity of the *medulla oblonga*. The foramen situated below that for nerve XII probably represents the exit for nerve XI; the entrance for this nerve is also visible within the endocranial cavity, below that for nerve XII. A third foramen pierces the exoccipital laterally and in front of the foramen for nerve XII, but opens on the posterior wall of the middle ear cavity. Most probably, it transmitted nerves IX and X from the foramen rotundum, through the middle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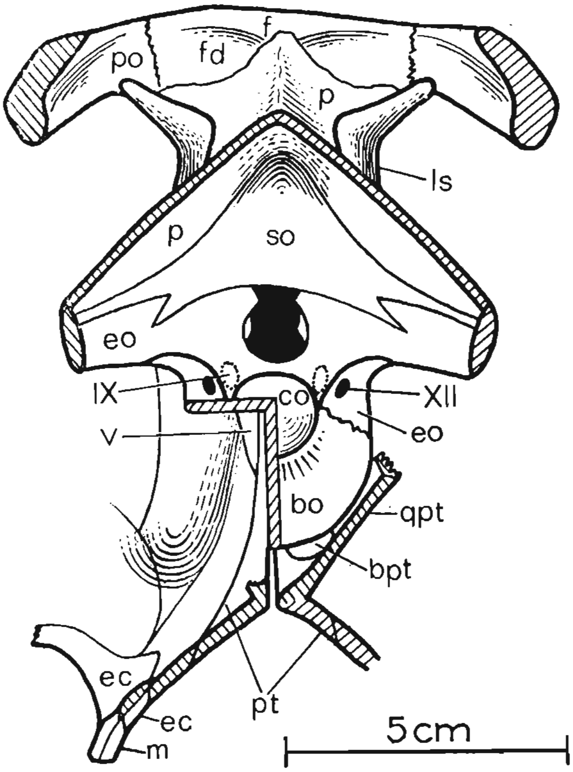

Fig. 7

Bagaceratops rozhdestvenskyi gen. n., sp. n., diagrammatic drawing of the skull, posterior view. Left half of the basioccipital, left exoccipital and left quadrate wing of the pterygoid removed for exposing palatine; ZPAL MgD-I/129. Abbreviations as in Fig. 1.

ear cavity. It is also possible that this foramen could have conveyed the jugular vein away from the head. In *B. rozhdestvenskyi* the exoccipital is very similar to that in other protoceratopsids, where it has been described. *Supraoccipital.* The supraoccipital is very large and laterally expanded. It forms the entire upper boundary of the foramen magnum. The contact of the supraoccipital with the parietal forms a straight line sloping from the cranial midline laterally, in posterior aspect. Medially, this contact is not visible in any specimen at our disposal, the dorsal apex of the supraoccipital having been damaged in each case. The supraoccipital sends a short, narrow tongue ventrolaterally, which is wedged in the exoccipital. Within the endocranial cavity the supraoccipital forms the dorsomedial wall of the inner ear, where it contacts the exoccipital ventrally and the prootic anteriorly. The supraoccipital rises anteriorly along the cranial midline, meeting the parietal at a sharp angle on the occipital surface of the skull. It is also visible on the medial wall of the supratemporal fossa, where it contacts the laterosphenoid anteriorly, the parietal dorsally and the prootic and exoccipital ventrally. The bone is similar in morphology to the element in *P. andrewsi*, althought its contact with the parietal on the occipital surface of the skull is less sharp in the latter species. *Basioccipital.* The basioccipital forms most of the occipital condyle but is excluded from the margin of the foramen

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Fig. 6

Bagaceratops rozhdestvenskyi gen. n., sp. n., *A* — holotype skull, dorsal view; *B* — same specimen, posterior view; *C* — same specimen, lateral view; ZPAL MgD-I/126. Abbreviations as in Fig. 1.

magnum. The ventral portion of the basioccipital is short and plate-like. Its share in formation of the basal tubera is very small. The bone closely resembles the basioccipital in *P. andrewsi*. *Basisphenoid.* The basisphenoid is massive ventrally. It is overlapped posteriorly by the basioccipital. There is an extensive cleft situated on the contact of these bones centrally, which may correspond to the median eustachian opening identified on the ventral surface of the basisphenoid by BROWN & SCHLAIKJER (1940*a*). A deep, vertical groove is present on the lateral surface of the basisphenoid, which is bounded anteriorly by a high otosphenoidal crest formed of the basisphenoid and the prootic. It communicates with the middle ear cavity and may have contained the ramus palatinus of the facial nerve. The entrance for the carotis interna was present within this groove, located in the prootic far below the exit for nerve VII. The basisphenoid-prootic suture is horizontal and also lies below the exit of nerve VII. The basipterygoidal processes are very long. The basisphenoid is underlain by the parasphenoid in front of the basipterygoid processes. There is an extensive contact between the basisphenoid and the exoccipital along the dorsal portion of the crest-like posterior limit of the above mentioned groove. The basisphenoid of *B. rozhdestvenskyi* is essentially similar to that of other protoceratopsids, with the exception that the basipterygoid processes are longer in our new species. BROWN & SCHLAIKJER (*l. c.*, Fig. 15) located the opening for the exit of VI nerve on the lateral surface of the basisphenoid of *P. andrewsi*. In our opinion, this position is improbable, because nerve VI generally emerges from the braincase more anteriorly, after piercing the sella turcica and passing through the pituitary fossa. *Opisthotic.* The proximal portion of the opisthotic is visible in our specimen. It underlies the exoccipital posteriorly and takes part in the formation of the paroccipital process. It contacts the prootic anteriorly, above the middle ear cavity. The bone was not mentioned by BROWN & SCHLAIKJER (*l. c.*) in their description of *P. andrewsi*. However, as it is evident in the material of *P. andrewsi* at our disposal, the opisthotic is also present in this species, where it occupies the same position as it does in *B. rozhdestvenskyi*. *Prootic.* The dorsal part of prootic forms the posterior portion of the crest which bounds the supratemporal fossa medially. The contact of the prootic with the laterosphenoid anteriorly is visible above the large opening for the exit of nerve V. Dorsally, the prootic contacts the supraoccipital, and, more posteriorly, the exoccipital. It meets the opisthotic posteroventrally, along the lower surface of the proximal portion of paroccipital process. The prootic bounds the middle ear cavity anteriorly and, above the horizontal suture between the prootic and basisphenoid, is pierced by the exit of nerve VII. The prootic in *B. rozhdestvenskyi* is generally similar to the element as described by BROWN & SCHLAIKJER (*l. c.*) in *P. andrewsi*. However, in the latter species the exit for nerve VII is bounded ventrally by the basisphenoid, which is not the case in *B. rozhdestvenskyi*. These authors did not describe the contact between the prootic and opisthotic in *P. andrewsi*, because they did not observe the latter bone in their specimens. The contact is visible, however, in our material of *P. andrewsi*.

The *middle ear cavity* is deep, and is bounded posteriorly and ventroposteriorly by the exoccipital, dorsoposteriorly by a thin tongue of the opisthotic, and anteriorly and dorsoanteriorly by the prootic. It would appear that a thin ascending wedge of the basisphenoid also reaches the middle ear cavity ventrally. On the medial wall of the cavity are exposed two foramina, separated from each other by a thin bridge of bone (only the dorsal portion of which is preserved in our specimens); the anterior foramen is the fenestra ovalis, and behind it is the fenestra rotundum. BROWN & SCHLAIKJER (*l. c.*, Fig. 15) illustrated one round opening, the "fenestra ovalis", within the middle ear cavity of *P. andrewsi*. This bridge of bone is present, however, in our specimens of *P. andrewsi*, dividing the concavity into two fenestrae in most specimens.

Parasphenoid. The limits of this bone are quite distinct on one young specimen of *B. rozhdestvenskyi* (ZPAL MgD-I/133). Its posterior contact with the basisphenoid is visible on the ventral surface of the basicranium, in front of the basipterygoid processes. The parasphenoid underlies the centre of the basisphenoid at this point (which is irregularly thickened here) and also descends along at least the basal portions of the basipterygoid processes; it forms two sharp ridges which converge anteriorly, and then continues forwards in form of a single, laterally compressed blade. The suture of the parasphenoid with the basisphenoid is not visible on the lateral surfaces. The parasphenoidal rostrum passess between the pterygoids and its relationship to these bones is the same as in *P. andrewsi.* The contacts with the presphenoid (if it indeed existed) is not preserved. *Presphenoid* and *orbitosphenoid.* On the same specimen, which yielded the foregoing information on the parasphenoid, two paired ossifications are present, which are located in the vicinity of the centrally placed, large opening for the exit of nerve II. They participate in the formation of the anteroventral wall of the braincase and represent, most probably, the lateral wings of the presphenoid and orbitosphenoid. The medial portions of these bones are damaged. The presphenoid seems to be bound suturally to the laterosphenoid laterodorsally, and forms the ventrolateral boundary of the optic foramen. It is pierced on the side of the skull by an opening, which may represent the exit for nerve III and probably also for nerve VI. The dorsal part of the presphenoid contacts the element, here tentatively described as the orbitosphenoid, anteriorly. This bone bounds the optic foramen dorsoanteriorly and forms the lower boundary of the exit for nerve I. It is pierced by two foramina. The lower and the larger of those is located close to the contact between the orbitosphenoid and laterosphenoid, adjacent to the presphenoid. It probably represents the exit for nerve IV. Other openings visible in this region may represent the

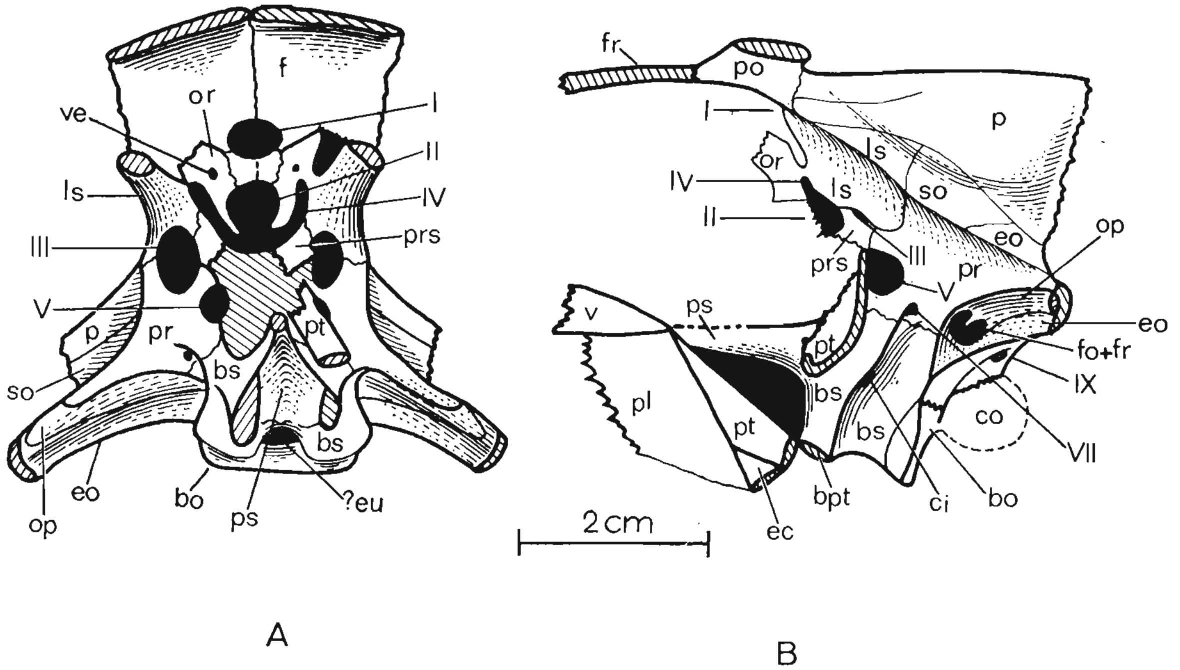


Fig. 8

Bagaceratops rozhdestvenskyi gen.n., sp.n., *A* — brain case, anterior view; ZPAL MgD-I/133; *B* — brain case, lateral view; ZPAL MgD-I/133. Palatal region compiled from the specimen ZPAL MgD-I/129. Abbreviations as in Fig. 1.

openings for blood vessels. These two bones have not been previously described in the protoceratopsids, for their sutures become obscure with individual maturity. *Laterosphenoid.* This element forms the anterior portion of the crest which bounds the supratemporal fossa medially. A thick, laterally ascending ramus of the laterosphenoid contacts the postorbital and an anterolateral tongue of the parietal, on the anteromedial wall of the supratemporal fossa. It also contacts the ventral surface of the frontal anteriorly. The contact between the laterosphenoid and supraoccipital noted by BROWN & SCHLAIKJER in *P. andrewsi* (*l. c.*) was not observed because the skulls of our specimens were damaged in this area. The laterosphenoid meets the supposed presphenoid and orbitosphenoid medially. *Frontal.* The frontal forms a very small portion of the orbital margin. The bone extensively underlies the nasal anteriorly; on the dorsal surface of the skull the frontal-nasal suture is located opposite the middle of the orbit. It lies behind the anterior margin of the orbit, even in young specimens. The suture of the frontal with the prefrontal is very extensive on the ventral surface of the skull roof, but is very short dorsally. The postorbital suture is long and straight. The frontal forms about a half of the anterior margin of the supratemporal fossa. The bone is supported by the lateral tongue of the laterosphenoid ventrally, beneath the anterior boundary of the supratemporal fossa. The contact with the parietal is located behind the shallow frontal depression, when the latter is developed. The frontals are slightly concave transversely between their contacts with the postorbitals, in specimens in which frontal depression is lacking. The ventral surface of the froontal bears a broad and shallow groove for receiving the olfactory tract. The frontal in *B. rozhdestvenskyi* is basically similar to that of *P. andrewsi*, but the anterior terminus of the bone on the dorsal midline of the skull is always behind the anterior margin of the orbit. This is the case not only in large skulls (as in *P. andrewsi*), but also in the smallest specimen, which is much smaller than any known in *P. andrewsi.* The frontal depression (present only in one specimen) is shallower and not so extensive longitudinally as it is in the "male" skulls of *P. andrewsi* (BROWN & SCHLAIKJER, 1940*a*). It is formed exclusively in the frontals and we accordingly call it the "frontal depression" rather than the "frontoparietal depression". One of our specimens which lacks this depression (ZPAL MgD-I/126) clearly shows that the posterior portion of the frontals is concave, beginning more or less behind a line connecting the posterior margins of the orbits. This specimen is similar in this respect to the "female" skull of *P. andrewsi* (BROWN & SCHLAIKJER, *l. c.*). The frontal in *B. rozhdestvenskyi* is similar to that of ?*P. kozlowskii* in that its anterior limit is situated behind a line connecting the anterior margins of the orbits. The posterior region of the frontals in *B. rozhdestvenskyi* is concave as in *P. andrewsi*, but not in ?*P. kozlowskii*, where the frontals are somewhat convex posteriorly, both in a transverse and longitudinal direction. The frontal forms only part of the anterior border of the supratemporal fossa in *B. rozhdestvenskyi*, not the entire border as in ?*P. kozlowskii;* the frontal depression (when present) is also more deep in *B. rozhdestvenskyi* than in the latter species. It is however not known whether these two characters may be considered to have taxonomic value, for the available skull of ?*P. kozlowskii* is of a young individual. The frontal of *L. gracilis* differs from that of *B. rozhdestvenskyi* in more broadly entering into the formation of the orbital margin. The posterior region of the frontal in *L. gracilis* is slightly concave and comparable to this part of the skull in the specimen of our species which lacks the frontal depression (ZPAL MgD-I/126). The frontal of "*Leptoceratops*" sp. (GILMORE, 1939) is much more concave transversely in the posterior region of the bone and the frontal depression is deeper than in *B. rozhdestvenskyi. Parietal.* The parietals are fused even in the youngest specimens. They form a relatively short, probably unfenestrated frill. The contact with the frontals is located slightly behind the anterior boundary of the supratemporal

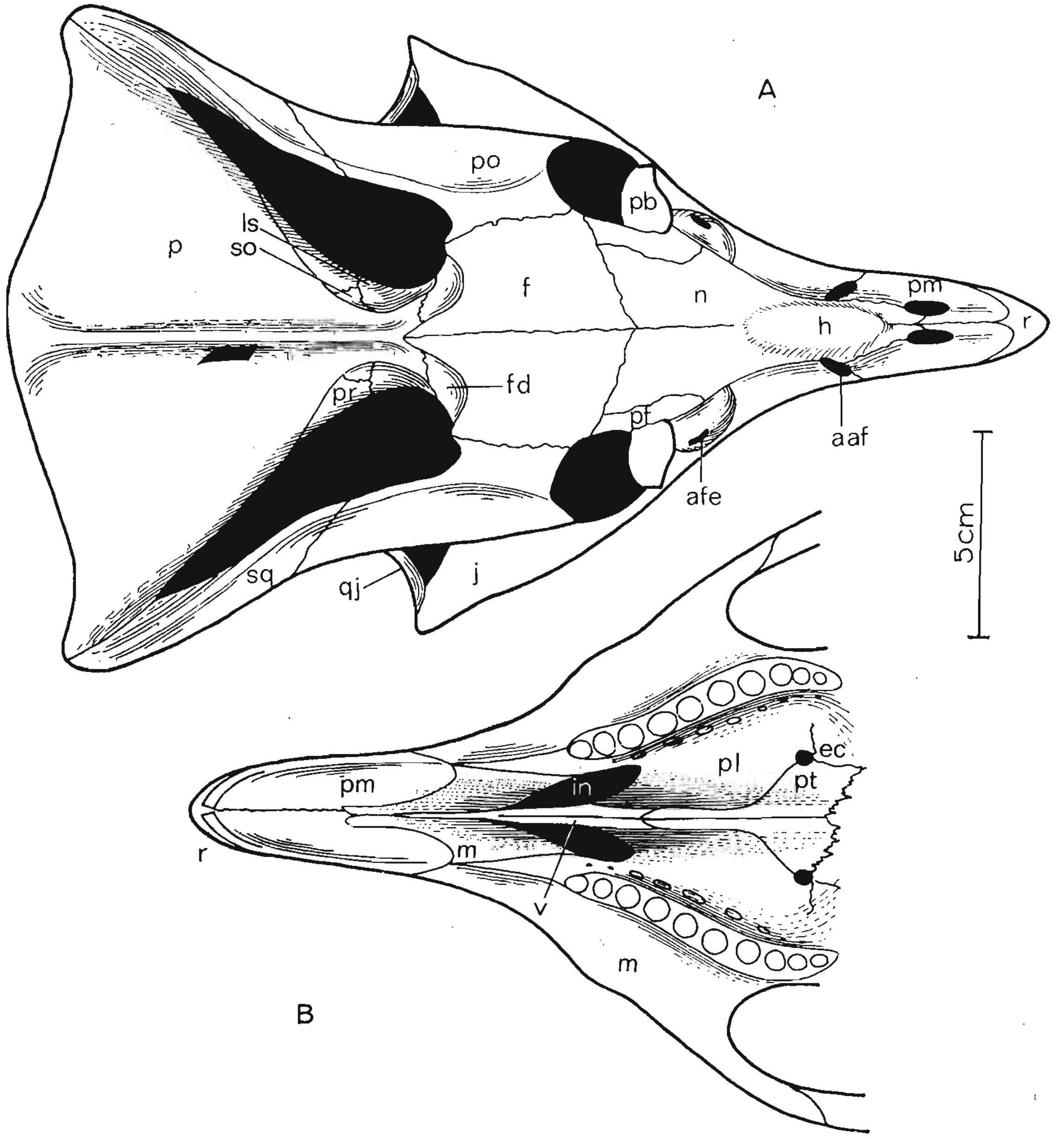


Fig. 9
Bagaceratops rozhdestvenskyi gen. n., sp. n., *A* — reconstruction of the skull of the large individual, dorsal view. Based on specimens: ZPAL MgD-I/127, 129, 133; *B* — anterior portion of the skull, palatal view; ZPAL MgD-I/129. Abbreviations as in Fig. 1.

fossa. The narrow, anterolateral tongue of the parietal is wedged between the frontal and laterosphenoid, its tip reaching the suture between the frontal and postorbital. The contact between the parietal and laterosphenoid is extensive on the medial side of the supratemporal fossa; more posteriorly the parietal contacts the supraoccipital and, ventrally the exoccipital, all within the supratemporal fossa. The suture between the parietal and squamosal is long and extends posterodorsally, reaching the posterior margin of the frill. The contact between the parietals and supraoccipital is not preserved medially, on the occipital surface of the skull; laterally, the contact between these bones is long. More distally, the parietal contacts the underlying exoccipital. The posterior margin of the parietal frill is slightly thickened and straight or slightly concave. The parietals are greatly thickened along the line of their fusion where a high sagittal crest is developed. The parietals form more than a half of the roof of the braincase. The parietals in *B. rozhdestvenskyi* differ from those in *P. andrewsi* in being shorter, never elevated posteriorly and probably unfenestrated. In these characters they resemble the parietals in *L. gracilis*, although in the later species the bones are slightly shorter longitudinally. *Rostral.* The rostral is only fragmentarily preserved on two specimens (ZPAL MgD-I/124, 127). From the impressions preserved on the premaxilla it is possible to state that it overlapped about a half of the ventral edge of the premaxilla. *Premaxilla.* The premaxilla is comparatively large. In lateral view, it is flat and subquadratic. There are two dorsal processes, one of which bounds the anterior half of the narial opening and the other forms the entire posterior border of this structure. The posterior process also forms the anterior margin of an additional antorbital fenestra. The palatal wing of the premaxilla is narrow and steeply inclined. The palatal wings of both premaxillae are separated from each other along their posterior third by narrow, anterior tongues of the maxillae. The ventral edge of premaxilla is straight and moderately sharp. The premaxilla in *B. rozhdestvenskyi* differs from that of *P. andrewsi* in that its ventral edge is straight, while it is concave in the latter species. This edge is convex in *L. gracilis*. The suture premaxilla-maxilla is long in lateral aspect in *P. andrewsi* and *L. gracilis*, but not in *B. rozhdestvenskyi*, where an additional antorbital fenestra is present. The premaxilla in ?*P. kozlowskii* is fragmentary, but it would seem that there was no additional fenestra between the premaxilla and maxilla. The premaxilla in *B. rozhdestvenskyi* is devoid of premaxillary teeth and alveoli, in which respect it resembles *L. gracilis*, and differs from both species of *Protoceratops*. *Maxilla.* The maxilla is deep and contains a large portion of the antorbital fossa (= maxillary sinus of STERNBERG, 1951, = antorbital recess of GALTON, 1970, 1973) on its lateral surface. A small antorbital foramen is present dorsoposteriorly (= preorbital fossa of LULL, 1933, = antorbital fenestra of GALTON, 1970, 1973). The floor of the invaginated portion of the antorbital fossa is pierced by an elongate cleft which communicates with a narrow intramaxillary sinus. The contact of the maxilla with the nasal is very short, but the contact with the jugal is much longer. The maxillary ridge is relatively weakly developed. In ventral aspect, a narrow process can be seen, extending anteriorly from the maxilla. The anterior maxillary processes of both maxillae are separated by the vomer along their anterior extremities. They are wedged between the premaxillae. The posterior wing of the maxilla is vertically oriented and contacts with the palatine through a long, oblique suture. The anterior quarter to third of the ventral edge of the maxilla is edentulous and comparatively sharp. The maxilla in our species is generally similar to that of *P. andrewsi*, but the antorbital fossa appears to be slightly shallower in the latter species; the floor of the investigated region is perforated by a slit-like opening in both species. The absence of an additional antorbital fenestra in *P. andrewsi*, ?*P. kozlowskii* and *L. gracilis* causes the anterior portion of the maxilla to appear slightly longer in these species. The contact of the maxilla with the nasal is short in *B. rozhdestvenskyi*, as it is in *P. andrewsi*, but is longer in *L. gracilis*. The edentulous margin of the maxilla is relatively shorter in *P. andrewsi* and *L. gracilis* than in *B. rozhdestvenskyi*; the latter species also has fewer (10) maxillary teeth in the largest specimen in ZPAL collections. It would appear that the ventral margins of both maxillae are closer to each other in *B. rozhdestvenskyi* than in the other known protoceratopsid forms, with the result that the palatal portion of the snout appears to be broader in *P. andrewsi*, ?*P. kozlowskii* and *L. gracilis*. *Nasal.* A narrow tongue of the nasal overlaps the premaxilla ventrolaterally and forms between one-half and one-third of the posterodorsal border of the external narial opening. Another tongue of the bone forms more than a half of the internarial bridge. The suture between the nasal and the frontal is located posterolaterally, above the centre of the orbit, where the nasal is very close to the orbital margin and is separated from the latter structure by a very narrow, posterior lamina of the prefrontal. The suture with the prefrontal is relatively long dorsally, and nearly parallels the long axis of the skull. On the lateral surface of the snout, the nasal is overlapped posteriorly by the lacrimal. Its contact with the lacrimal is very short. Dorsoanteriorly the nasal forms the internal border of the additional antorbital fenestra, although this region is covered externally by a large ascending tongue of the premaxilla. The nasal supports a more or less developed unpaired horn core in all specimens of *B. rozhdestvenskyi*. It is comparatively narrow at the base, relatively high in one specimen (ZPAL MgD-I/125), and lower and more elongate longitudinally in others. There are also some differences in the position of the horn core. Although its centre is always located in front of the orbit, the posterior slope sometimes lies above the anterior portion of the orbit. The nasal in our species differs markedly from that of *P. andrewsi* in that its posterior end closely approaches the orbital margin and the nasal horn core is more strongly developed. The nasal is devoid of a horn core in *L. gracilis*. The unpaired horn core is larger in *Montanoceratops cerorhynchus* (BROWN & SCHLAIKJER 1940*b*) than in *B. rozhdestvenskyi*. The horn core is located much further anteriorly in *M. cerorhynchus*, similarly to its position in ceratopsids. There is some evidence of fusion of the two halves at the base of the horn core in *M. cerorhynchus*, but the horn core in *B. rozhdestvenskyi* lacks, even in the most immature specimens, any trace of separation. *Lacrimal.* The lacrimal is only fragmentarily preserved in all of the specimens of *B. rozhdestvenskyi* at our disposal. It would appear, however, that the bone forms no more than three quarters of the anterior margin of the orbit, and is distinctly less well exposed on the lateral surface of the snout than is the case in *L. gracilis*, and slightly less so than in *P. andrewsi*. In contrast to conditions in *P. andrewsi*, the lacrimal curves strongly outwards to meet the anterior margin of the orbit in *B. rozhdestvenskyi*. As a result, the posterior wall of the antorbital fossa lies at a high angle to the longitudinal axis of the skull and in some specimens is nearly perpendicular to the cranial midline. *Prefrontal.* The prefrontal in *B. rozhdestvenskyi* is very similar in shape and proportions to that of *P. andrewsi*. The prefrontal of ?*P. kozlowskii* (young specimen) is quite different from that of *B. rozhdestvenskyi* (and of *P. andrewsi* as well) in its great length and in the posterior terminus of the element extending slightly behind the centre of the orbit. The prefrontal of *L. gracilis* is broader than that of *B. rozhdestvenskyi* and the two species of *Protoceratops*. *Palpebral.* The palpebral is triangular and slightly concave medially. The bone is relatively thick, but it thins gradually towards the contact with the prefrontal, as well as in a posterodorsal direction. It forms a loose articulation with the prefrontal. By comparison with the palpebral in *P. andrewsi*, this element seems to be broader but shorter in *B. rozhdestvenskyi*. The postorbital contacts the frontal on the dorsolateral wall of the skull. It overlaps the squamosal posteriorly and jugal ventrally. The postorbital caps the distal end of the laterosphenoid anteriorly and nearly contacts the anterolateral tongue of the parietal, within the supratemporal fossa. The lateral ramus of the postorbital forms a nearly right angle to the dorsal ramus. There is no trace of the horn core, and the dorsal surface of the bone is only weakly rugose. The anterior edge of the postorbital, which forms the posterior margin of the orbit, is vertical and straight. The postorbital forms the external half of the anterior margin of the supratemporal fenestra, where its contact with the frontal is rugose. The postorbital in *B. rozhdestven-*

skyi is generally similar to the element in a juvenile skull of *P. andrewsi.* It differs, however, in that the bone reaches the anterodorsal corner of the infratemporal fenestra covering the jugal completely in the region of the upper part of the postorbital bar. The lateral portion of the postorbital slopes slightly backwards in the young skull of *?P. kozlowskii,* in which character it differs both from that of *B. rozhdestvenskyi* and *P. andrewsi.* The postorbital is less expanded medially within the supratemporal fenestra in *P. andrewsi,* and it forms the external half of the anterior margin of the fenestra only in the very young individuals of this species. The postorbital was not described in *L. gracilis.* The postorbital in *M. cerorhynchus* is incompletely preserved, but it does possess a strong rugosity, which is lacking on the postorbital of our species. *Squamosal.* The squamosal is comparatively low, and parallels the long axis of the skull in lateral view. Its straight lower margin forms nearly the entire upper boundary of the infratemporal fenestra. It is overlapped laterally by the postorbital and contacts the jugal in the vicinity of the dorsoanterior corner of the fenestra. This contact is not visible, for it is covered laterally by the postorbital. A cotylus in the squamosal fits over the dorsal extremity of the quadrate posteriorly. That portion of the squamosal which forms the lateral margin of the frill is abbreviated behind the quadrate. It contacts the parietal within the supratemporal fossa and forms the lateral part of the frill in this area. The squamosal is broadly overlapped by the parietal medially. The postquadratic process of the squamosal separates the dorsal part of the exoccipital from the quadrate. The squamosal of *B. rozhdestvenskyi* is quite different from that of *P. andrewsi* and *?P. kozlowskii,* primarily in that the postquadrate portion is shorter. It is also shallower posteriorly and horizontal in an anteroposterior direction in both species of *Protoceratops.* The upper boundary of the infratemporal fenestra in *P. andrewsi, ?P. kozlowskii* and *L. gracilis* is formed partly from the squamosal and partly of the postorbital, but in *B. rozhdestvenskyi* it is nearly exclusively formed from the squamosal. The bone is not produced behind the quadrate in *L. gracilis,* as it is to a certain extent in our species. The squamosal in *M. cerorhynchus* is much shorter and deeper than in *B. rozhdestvenskyi.* *Jugal.* The jugal is relatively shallow along its entire length and its ventral margin is nearly horizontal, sloping but slightly in a posterior direction. The posterior ala of the jugal is slightly deflected outwards. The jugal forms the entire ventral margin of the orbit which is nearly horizontal. The ascending wing of the jugal is vertical and its posterior edge is straight. The jugal-maxilla suture is nearly horizontal posteriorly. The contact with the ectopterygoid is visible along the anterolateral border of the subtemporal fenestra. The epijugal is fragmentarily preserved on only a few specimens. The jugal of the species herewith described is, as is that of *L. gracilis,* very similar to the element in young specimens of *P. andrewsi,* for it is nearly horizontal even in adult individuals. In *B. rozhdestvenskyi* the jugal is shallower than in the latter species. In the species of *Protoceratops* the posterior margin of the ascending wing of the jugal is also arched, but this region of the element is straight in our species. The jugal in *?P. kozlowskii* is very deep, even in the young individual, and the ascending wing slopes dorsoposteriorly, and is not vertical as in *B. rozhdestvenskyi.* *Quadratojugal.* The quadratojugal is a relatively large, drop-shaped bone. It is broad ventrally and sheaths the quadrate posteriorly and, to some extent, laterally down to the articular surface. The bone embraces the posterior extremity of the jugal posteriorly and medially. The medial projection of the quadratojugal is short, while the posterior projection is relatively longer and more extensive laterally. The quadratojugal is well removed from the squamosal, but a narrow dorsal tongue does reach the posterior boundary of the infratemporal fenestra. The above described quadratojugal differs ventrally from that of *P. andrewsi* for the medial projection is shorter and extends to the articular surface of the quadrate as it does in *L. gracilis.* The posterior projection of the quadratojugal appears to be less well developed in *P. andrewsi* than in *B. rozhdestvenskyi*. *Quadrate*. The posterior edge of the quadratic shaft is straight. The long axis of the articular surface for the mandible is oblique, so that the medial condyle is in front of the lateral condyle. The quadrate is separated dorsally from the exoccipital by a ventral tongue of the squamosal, as in *P. andrewsi*. The contact of the quadrate with the pterygoid seems to be similar to that in *P. andrewsi*, but could not be satisfactorily observed on any specimen. The oblique orientation of the articular surface of the quadrate in *B. rozhdestvenskyi* seems to be a character peculiar to this species. *Pterygoid*. This bone is incomplete in all of our specimens. To the extent to which it is preserved it is basically similar to the pterygoid in *P. andrewsi*. There is no wing of the pterygoid extending posteriorly beneath the basioccipital tuber in *B. rozhdestvenskyi*, as is present in *L. gracilis* (STERNBERG, 1951). In this character the pterygoid in our species resembles that of *P. andrewsi*. *Ectopterygoid*. The ectopterygoid is preserved only laterally and in its anterior palatal portion. It bounds the posterior palatine fenestra, and closely overlaps both sides of the maxilla posteriorly, behind the tooth row. The ectopterygoid forms most of the medial and anterior margin of the subtemporal fenestra. The external tip of the ectopterygoid is thick, narrow and meets the internal surface of the maxilla close to the contact of the latter bone with the jugal. Its contact with the lacrimal is unknown. *Palatine*. The palatal portion of the bone is nearly vertical and forms the posterior as well as posteromedial boundary of a moderately large internal naris. It contacts the maxilla ventrally along a long oblique suture and the pterygoid and ectopterygoid dorsoposteriorly. Medially, the palatine overlaps the posterior part of vomer. The lateral wing of the palatine lies at an angle to the palatal wing. It forms the posterior wall of the ventral portion of the nasal cavity and closes the narrow intramaxillary sinus posteriorly. It has extensive contacts with the jugal, lacrimal and maxilla in the region where these bones meet near the small antorbital foramen, within the antorbital fossa. It cannot be ascertained whether or not this portion of the palatine contacted the prefrontal because the bone is damaged in this region. The internal nares are placed entirely in the parasagittal plane and their posterior boundary is situated opposite the fourth and fifth maxillary tooth (from the front of the jaw). The palatine in *B. rozhdestvenskyi* is generally similar to the bone in *P. andrewsi*, but it is less steeply placed in the latter species, where the palate is broader and less highly arched. In comparison with the palatine in *L. gracilis*, that of *B. rozhdestvenskyi* is shorter and the internal naris is larger. *Vomer*. The vomer is a very long bone in *B. rozhdestvenskyi*. It is thin and unpaired anteriorly, where it is wedged between the anterior tongues of the maxillae. Behind this region the vomer thickens very distinctly, and it is evident that it is fused with its fellow. The vomer is overlapped by the palatine and medially overlaps the pterygoid, as in *P. andrewsi*.

Mandible (Pls XLII, Fig. 1, XLIII, Fig. 1, XLIV, Fig. 2, XLVII, XLVIII, Fig. 1*a*, XLIX, Fig. 6, Text-figs 6*C*, 10). The mandible is long and shallow, with a straight ventral margin. No more than 10 teeth are present. The mandibular shelf is very broad and its external surangular ridge is very strong. The coronoid process is low. *Predentary*. The predentary is long and shallow, and covers the entire symphysis. The anterior portion of the predentary is badly preserved. In the adult individuals the predentary occupies about one-third of the total mandibular length in lateral aspect and meets the dentary posteriorly along a straight suture. The predentary in *L. gracilis*, *P. andrewsi* and probably also ?*P. kozlowskii* is distinctly larger than that in *B. rozhdestvenskyi*. The ratio of its length to that of the entire mandible is similar to the ratio of these structures in *M. cerorhynchus*, as estimated by BROWN & SCHLAIKJER (1942). The posterior region of the contact between the predentary and dentary on the lateral surface of the mandible is not straight in *L. gracilis*, as it is in *B. rozhdestvenskyi* and in both species of *Protoceratops*, and is instead deeply notched dorsally. *Dentary*. The dentary is long and shallow, with a straight ventral margin. The surface of the bone curves inward dorsally, forming a horizontal and very broad mandibular shelf, which extends medially to the tooth row. Ten dentary teeth are present in the largest specimen, although only seven teeth are present in the most immature mandible (ZPAL MgD-I/123). The dentary portion of the processus coronoideus, as well as the contact of this bone with the angular and surangular, corresponds in morphology to that of *P. andrewsi*. The contact of the dentary with splenial is visible on the lateral surface of the posterior part of the mandible. The dentary in *B. rozhdestvenskyi* is similar to that of *M. cerorhynchus* and ?*P. kozlowskii* in its considerable length and straight ventral margin, in which characters it differs from the dentaries of other protoceratopsids. The straight ventral margin was, however, observed in one specimen of *P. andrewsi* (AMNH 6419), considered by BROWN & SCHLAIKJER (1940*a*) as a very immature individual and in our small specimens of this species (Pl. XXXIX, Figs 1-3). The extremely shallow dentary, even in the adult specimens, separates *B. rozhdestvenskyi* from other representatives of the family. The broad mandibular shelf, similar to the structure in the dentary of *B. rozhdestvenskyi*, is also present in ?*P. kozlowskii*. *Splenial*. Only the posterior portion of the splenial was sufficiently preserved to warrant a place in the description of our material. The outline of the anterior part of the splenial was, however, present on the dentaries of some specimens, which makes it possible to state that the bone nearly extends to the symphysis. The dorsal margin of the splenial reaches the row of internal dental foramina posteriorly, and along the last two teeth a surface is developed, which may represent a contact between the splenial and the intercoronoid. This surface is absent on all other available specimens. The splenial does not form the lower internal edge of the mandibular fossa. The splenial separates into two tongues posteriorly, which more ventrally overlap the prearticular and angular. The splenial does not contact the articular. In *B. rozhdestvenskyi* the splenial is similar to this bone in *P. andrewsi*. It is, however, shallower in its posteriormost region, where it does not participate in the lower edge of the mandibular fossa either in young or in adult specimens, contrary to conditions in adult specimens of *P. andrewsi*. According to STERNBERG (1951), the splenial in *L. gracilis* is close to the articular, which is not the case in our species. *Surangular*. A sharp ridge is present on the external surface of this bone. The posterior portion of the surangular, above this ridge, is low and longitudinally elongated. The surangular forms the external cotylus of the articular surface for the quadrate, and this surface is separated from the internal cotylus by a ridge of bone. The surangular in

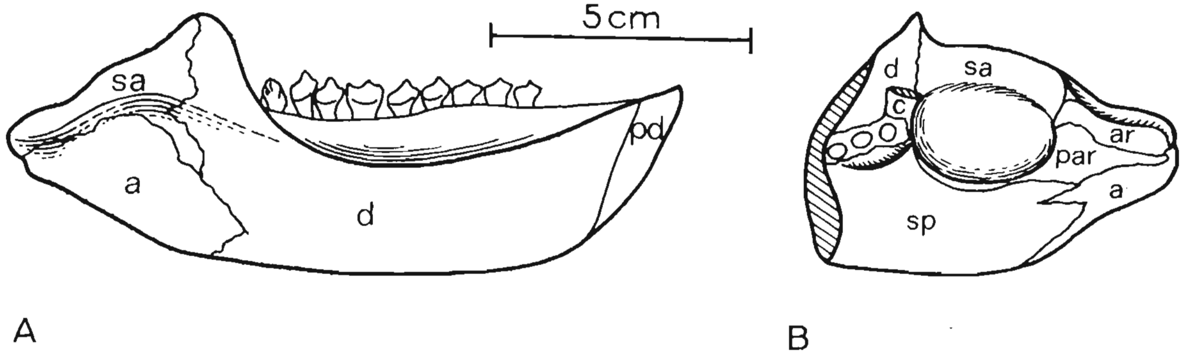


Fig. 10
Bagaceratops rozhdestvenskyi gen.n., sp.n., *A* — mandible lacking symphysal portion, external view; ZPAL MgD-I/137. *B* — posterior portion of mandible, internal view; ZPAL MgD-I/138. Abbreviations as in Fig. 1.

our species is generally similar to that of *P. andrewsi*. There are some differences in the structure of the posterior part of the element; in the latter species the upper margin of the surangular rises steeply anteriorly, while it is parallel to the surangular ridge posteriorly and less steep anteriorly in *B. rozhdestvenskyi*. The entire articular surface for the quadrate is also less massive in *P. andrewsi* than in our species. *Prearticular*. The prearticular is long and narrow. It broadly overlaps the articular posteriorly, and its anterodorsal extremity reaches the contact between the dentary and splenial. The bone forms the entire lower margin of the mandibular fossa. The posterior region of the prearticular contacts the angular ventrally and its anterior ramus underlies the splenial. In *B. rozhdestvenskyi* the bone does not differ greatly from that of *P. andrewsi*, although it does not extend as far forward as the dentary in the latter species. It seems, however, that in the specimen AMNH 6471 of *P. andrewsi*, illustrated by BROWN & SCHLAIKJER (1940*a*, Fig. 20*B*), the bone in question shows to bear a relationship with the surrounding elements similar to that found in our species. *Angular*. The bone lies in a longitudinally horizontal direction and its anterior portion is overlapped by a tongue from the splenial. The angular in our species is similar to the bone in *P. andrewsi*. The angular is more extensive in a vertical direction in *L. gracilis*, what is connected with the strong upward curvature of the posterior part of the mandible. *Articular*. This bone is only fragmentarily preserved in *B. rozhdestvenskyi*. The posteriormost part of the articular is not present. The articular is embraced laterally and anterolaterally by the surangular, ventrally by the angular and medially by the prearticular. It extends anteriorly to the mandibular fossa. The bone is heavy and its articular surface is very slightly concave. It forms the internal articular surface for the quadrate. *Coronoid*. The ventral tongue of the coronoid is preserved in only one specimen of *B. rozhdestvenskyi*, as was also the trace of the contact of the dorsal portion of the coronoid and the dentary. The preserved portion of the coronoid is comparatively massive and lies lateral to and above the tooth row. A thin, ventral spur passes down behind the posterior boundary of the intercoronoid, nearly reaching the splenial. The coronoid in *P. andrewsi* is different from the above described element, in that it lacks the thin downward projection which nearly reaches the splenial in *B. rozhdestvenskyi*. In *P. andrewsi*, the intercoronoid seems to occupy the position of the ventral spur (BROWN & SCHLAIKJER 1940*c*).

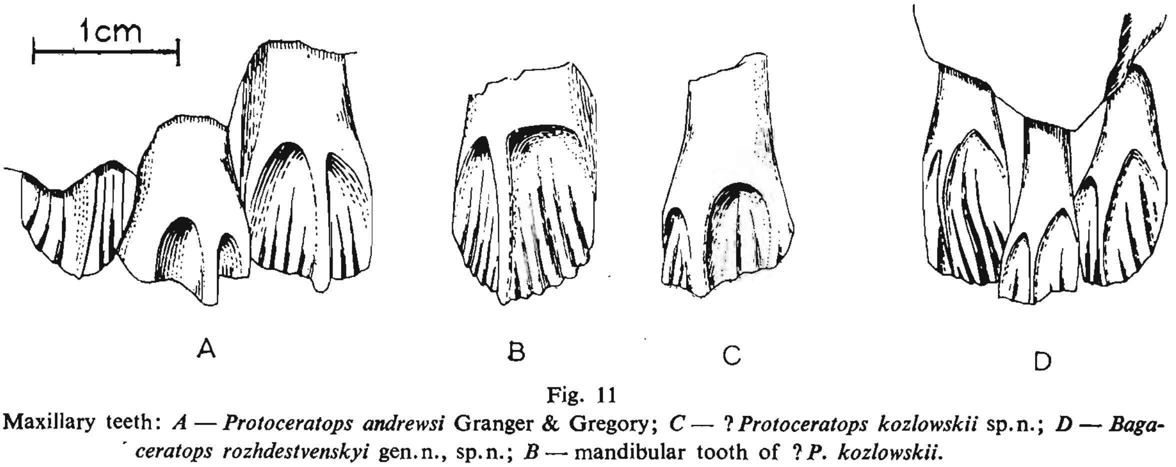


Fig. 11

Maxillary teeth: *A* — *Protoceratops andrewsi* Granger & Gregory; *C* — ? *Protoceratops kozlowskii* sp.n.; *D* — *Bagaceratops rozhdestvenskyi* gen.n., sp.n.; *B* — mandibular tooth of ? *P. kozlowskii*.

Dentition (Pl. XLIII, Figs 2-4, Text-fig. 11 *D*). The teeth in all protoceratopsids do not differ in their general structure. They bear a very strong single longitudinal rib placed slightly excentrically, and several much lower and thinner ridges, located on either side of the median one. The angle of the wear surface, in relation to the longitudinal plane of the tooth, is quite different on the maxillary and mandibular teeth in all protoceratopsids, although it varies slightly along the tooth series, within the same maxilla or mandible. The wear surfaces are oblique in both upper and lower teeth, but the angle, which the wear surfaces form with the enameled sides of the crowns, is much larger on the maxillary than on the mandibular teeth. In consequence, the occlusal surface is almost vertical and more extensive on the mandibular teeth (this does not apply to *Leptoceratops*, in which the mode of occlusion differs from that of other protoceratopsids). For the purposes of taxonomic determination, the maxillary teeth are more important within the Protoceratopsidae, because the teeth in the lower jaws are very similar in all species. The number of teeth differs not only in the various species, but it also changes with maturity and teeth are still being added comparatively late during individual growth. The shape of the protoceratopsid tooth and the number and the character of the smaller, lateral ribs are variable even in the adult individuals and vary accordingly to the place which the tooth occupies in the jaw. For these reasons, we recommend that isolated protoceratopsid teeth should not be used as a basis for the erection of new taxa. Comparisons can best be made between the teeth of the middle part of the maxilla, where the teeth are most typically developed. In *B. rozhdestvenskyi* the maxillary teeth are basically similar to those in *P. andrewsi* (Pl. XLIX, Fig. 1, Text-fig. 11*A*). A difference may be seen, however, in the side portions of the enameled surface of the crown. These are shallow and rise gradually towards the root in *B. rozhdestvenskyi.* They are deep on both sides of the central ridge along the entire height of the crown in *P. andrewsi*, and deep "pockets" are developed, in this species, on the uppermost part of the crown, at the boundary with the root. These pockets are generally U-shaped in *P. andrewsi,* while the corresponding portions of the crown are generally V-shaped in *B. rozhdestvenskyi.* A comparison cannot be made with the teeth in *?P. kozlowskii,* because only a series of the maxillary teeth of a very immature specimen of this species is available in ZPAL collection. The teeth of the adult individual were derived from the mandible (Pl. XLIX, Fig. 3, Text-fig. 11*B*) and are therefore not useful in specific determinations. There is only one isolated maxillary tooth of *?P. kozlowskii* (Pl. XLIX, Fig. 2, Text-fig. 11*C*) in ZPAL collection and it seems to be very similar to the teeth in *P. andrewsi.*

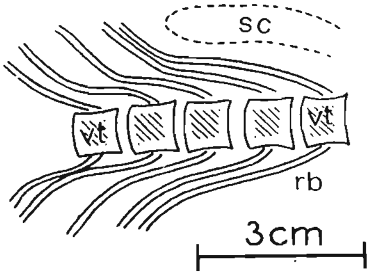


Fig. 12

Bagaceratops rozhdestvenskyi gen.n., sp.n., diagrammatic drawing of the natural arrangement of the ribs on anterior dorsals (see also Pl. XLIX, Fig. 5). Based on specimen ZPAL MgD-I/154. Abbreviations: *rb* — ribs, *sc* — imprint of the posterior extremity of scapula, *vt* — vertebrae.

Postcranial skeleton. The preserved portions of the postcranial skeleton (ZPAL MgD-I/142) contains fragmentary sacrum with at least 6 coossified centra, the right ischium (Text-fig. 13*A*), which is almost complete but lacks its posterior, distal portion, the fragment of left ischium as well as a proximal part of the left pubis with fragmentary postpubis. The proximal half of the left femur (Pls XLVI, Fig. 3, Text-fig. 13*B*) was found in articulation with the fragmentary sacropelvic region above mentioned. The fragments of the tibia and fibula were also found in the same piece of matrix. The ischium is generally similar to this bone in *P. andrewsi* but its anterior process is more slender and relatively longer in *B. rozhdestvenskyi* sp. n. The femoral head is more massive in our species and not so well differentiated from the shaft as it is in *P. andrewsi*. The neck of the femur is also thicker and the head is placed only slightly above the greater trochanter in *B. rozhdestvenskyi*, while it is located considerably higher in *P. andrewsi*. The lesser trochanter is well developed and blade-like in our species.

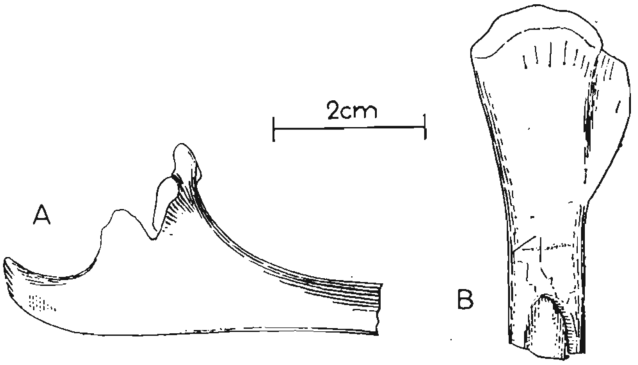


Fig. 13
Bagaceratops rozhdestvenskyi gen. n., sp. n., *A* — proximal portion of the right ischium, medial view; *B* — proximal end of the right femur, lateral view; ZPAL MgD-I/142.

Another specimen is present in ZPAL collection (MgD-I/154), which contains several anterior dorsal vertebrae with the ribs in the natural arrangement, preserved partly in form of imprints (Pl. XLIX, Fig. 5, Text-fig. 12). There are also preserved the imprints of the scapular blades on both sides of the vertebral column. The specimen shows that the ribs on the several first anterior dorsals (supposedly 1-3) are placed differently than it was usually reconstructed in *P. andrewsi*. They seem to be close to the vertebral column so far backwards as they are covered by the scapula. Their proximal portions nearly parallel the axial line and direct backwards. The ribs behind the distal ends of scapula distinctly deviate from the axial line, already in their proximal portions.

Discussion. — *Bagaceratops rozhdestvenskyi* gen. n., sp. n. differs from all previously described Protoceratopsidae in the presence of an additional antorbital fenestra, which, most probably, communicates with the nasal cavity. The frill is not completely preserved in any of the skulls in ZPAL collection, but in two skulls, which have it most complete (ZPAL MgD-I/125, 126) the fenestration appears to be absent. The relatively short snout and frill, the toothless premaxilla, the well developed, unpaired nasal horn core and the shallow mandibles separate this species from both species of *Protoceratops*. *B. rozhdestvenskyi* resembles *Leptoceratops gracilis* BROWN in its probably unfenestrated frill and in the absence of the premaxillary dentition, but it differs from this species in having a slightly longer frill and a nasal horn core developed. The occlusal surfaces of the mandibular teeth in our species also differ from those of *L. gracilis*, and they are more similar to those of *P. andrewsi* and ?*P. kozlowskii*. The nasal horn core is only slightly less pronounced in *B. rozhdestvenskyi* than in *Montanoceratops cerorhynchus* BROWN & SCHLAIKJER, but in the latter species the horn core is placed more anteriorly and bears a distinct trace of the groove dividing it into two halves, which is not the case in *B. rozhdestvenskyi*. Our species resembles *Microceratops gobiensis* Bohlin in the relative length of the frill, but in *M. gobiensis* this structure is fenestrated, probably unlike that of *B. rozhdestvenskyi*. The jugals in both of these species are similar in their shallowness, which is a primitive character. The mandible, which is shallow in our species, also resembles that of *M. gobiensis*. More detailed comparisons of the individual bones of the skull are noted under the descriptions of these bones.

GENERAL REMARKS

VARIABILITY OF THE SKULLS IN *BAGACERATOPS ROZHDESTVENSKYI*

Variations in the cranial morphology and proportions of *P. andrewsi* were described by Brown & Schlaikjer (1940*a*). Some of differences were interpreted by these authors as probably being derived from sexual dimorphism. Recently Kurzanov (1972) discussed sexual dimorphism in *P. andrewsi*. According to this author, some of the characters considered by Brown & Schlaikjer (*l. c.*) to be linked to sexual dimorphism, such as the parietofrontal depression, are due, in fact, to individual variation. Kurzanov states (*l. c.*) that in his opinion true sexual characters include: 1. the nasal horn core, present in males and absent in females; 2. the angle of inclination of the frill, not less than 40° in males, and not more than 20° in females; 3. the angle of widening of the frill, not less than 70° in males and not more than 30° in females; 4. the angle of widening of the face, not less than 40° in males and not more than 15° in females. Our collection contains skulls of individuals of *B. rozhdestvenskyi* in different stages of growth; some of these were certainly very young and possibly sexually immature. Thus, we are not able to indicate which features are sexual characters in their skulls. However, five skulls in our collection may belong to mature individuals. They do not differ greatly in size, and all exhibit a very limited inclination of the frill, a widening of the frill equal to about 23°, a widening of the face between 34-40°, and a horn core present in every case where the

Table 5

Variability of skulls in *Bagaceratops rozhdestvenskyi*

ZPAL Cat. No. MgD-I/	124	125	133	127	126	130	129	128
Basal length in mm	71	92	?	121	124	?	?	?
Horn core	elongate	short, high	?	?	elongate	elongate	?	?
Frontal depression	?	absent	absent	?	absent, frontals slightly concave	?	present	absent, frontals slightly concave
Inclination of frill	nearly horizontal	nearly horizontal	?	?	nearly horizontal	?	?	weakly steep
Angle of widening of frill	?	18°	?	20°	23°	?	?	23°
Facial angle	?	24°	?	34°	40°	?	34°	?

nasals are preserved. A frontoparietal depression, comparable to that in "males" of *P. andrewsi* (according to BROWN & SCHLAIKJER, *l. c.*) is developed only in one of the above mentioned mature skulls, and in other skulls the frontal is only slightly concave. The only specimen (ZPAL MgD-I/125) which departs from this pattern, exhibiting a widening of the frill of only 16°, a widening of the face of 24° and a comparatively strongly developed horn core, may represent a gender opposite to that of the others. However, it is much smaller, and can at most represent a young adult, if not an immature specimen. In our opinion, the sexual characters indicated by BROWN & SCHLAIKJER (*l. c.*) and KURZANOV (*l. c.*) cannot be applied as such to our species because they do not separate our material into two distinct groups. It is more probable, that in our species the characters cited above are linked either with the individual or ontogenetic variability. The table above (Table 5) illustrates cranial variability in *B. rozhdestvenskyi*. The characters listed therein have been interpreted to be of a sexual character by BROWN & SCHLAIKJER (1940*a*) and KURZANOV (1972). The specimens are arranged from the smallest to the largest.

ONTOGENY OF THE PROTOCERATOPSIDAE

The smallest skull of *P. andrewsi* described by BROWN & SCHLAIKJER (1940*a*) and considered by them as pertaining to a very immature individual (AMNH 6419) is 130 mm long (medial length). The smallest dentary (AMNH 6499), 23 mm long and containing 6 alveoli, was considered by these authors as of an unhatched individual. In our collection of *P. andrewsi*, derived from the same locality, there are 6 skulls (Pl. XXXIX) smaller than AMNH 6419, the smallest of which measures about 62 mm (ZPAL MgD-I/7) in medial length. The mandible articulated with this skull contains a dentary about 25 mm in length. Judging from the wear on the teeth, this specimen represents the skull of an hatched individual. There are eight teeth in the maxilla. We can confirm that the growth changes observed in our material are in the agreement with BROWN'S & SCHLAIKJER'S earlier observations (*l. c.*). ZPAL collection also includes the skulls of immature individuals of other species of protoceratopsids, including ?*P. kozlowskii* sp. n. (Pl. XL, Fig. 2) and *Bagaceratops rozhdestvenskyi* gen. n., sp. n., some of which are ontogenetically less mature than the smallest specimens of *P. andrewsi*. An immature skull (47 mm long) of *B. rozhdestvenskyi* (ZPAL MgD-I/123) is well preserved and represents the youngest and the smallest individual of a dinosaur so far reported (Pl. L, Figs 1-3, Text-fig. 14). For this reason we include the following detailed description.

The skull in question of *B. rozhdestvenskyi* exhibits features which could be expected in any immature reptile (Table 6). In keeping with its immaturity, the orbits are very large (nearly 2/3 of the basal length of the skull) and the snout is very short (less than a half of the basal length). This skull already bears a distinct, unpaired swelling on the nasals, which does not exhibit any trace of an internasal suture. The suture between the nasal and the frontal is placed well in front of the centre of the orbit. The frontal forms a large part of the dorsal orbital margin. That portion of the parietals which roofs the braincase is slightly convex, broad in dorsal view, without a trace of an interparietal suture and possesses a very weakly developed medial crest. A shallow, obliquely situated depression is present on each of the parietals; these depressions converge posteriorly. The frill is short, does not project behind the quadrate and is not elevated posteriorly. It is also devoid of the fenestration. A well developed longitudinal crest is present medially, on either side of which the frill slopes slightly toward the supratemporal fossa. The squamosals parallel each other in dorsal aspect. The additional antorbital fenestra is already present in this very immature skull. The maxillary wing of the jugal is long, shallow and horizontal in position. The ascending wing of the jugal is vertical. The infratemporal fossa is subquadrangular in shape, and the postorbital reaches to its posterodorsal corner. The squamosal is horizontal in lateral view and its ventral edge is straight, forming most of the dorsal boundary of the infratemporal fossa. The quadrate is only partly preserved, yet its dorsal portion is only slightly inclined posteriorly. Six teeth are present in the maxilla. The posteriormost tooth is not worn, or is but little worn, in the left maxilla, although the fifth tooth is already distinctly worn. The labial, enameled sides of the crowns of both these teeth differ greatly from the same surfaces of the teeth in older individuals of this species, in being less specialized. The ridges are few in number, more equal in development; the thick, central ridge is only very slightly higher than the lateral ones and divides the crown nearly symmetrically. The fourth tooth is nearly completely worn and a large replacement tooth is present and was about to become functional. The third tooth is worn, but its crown is large and the morphology of the enameled side more closely resembles that of the tooth in older individuals. The second tooth is already present, but is not as fully erupted as the replacement tooth in position 4. The first tooth is also small, but too poorly preserved to merit description. The right maxilla exhibits the same characters and arrangement of teeth,

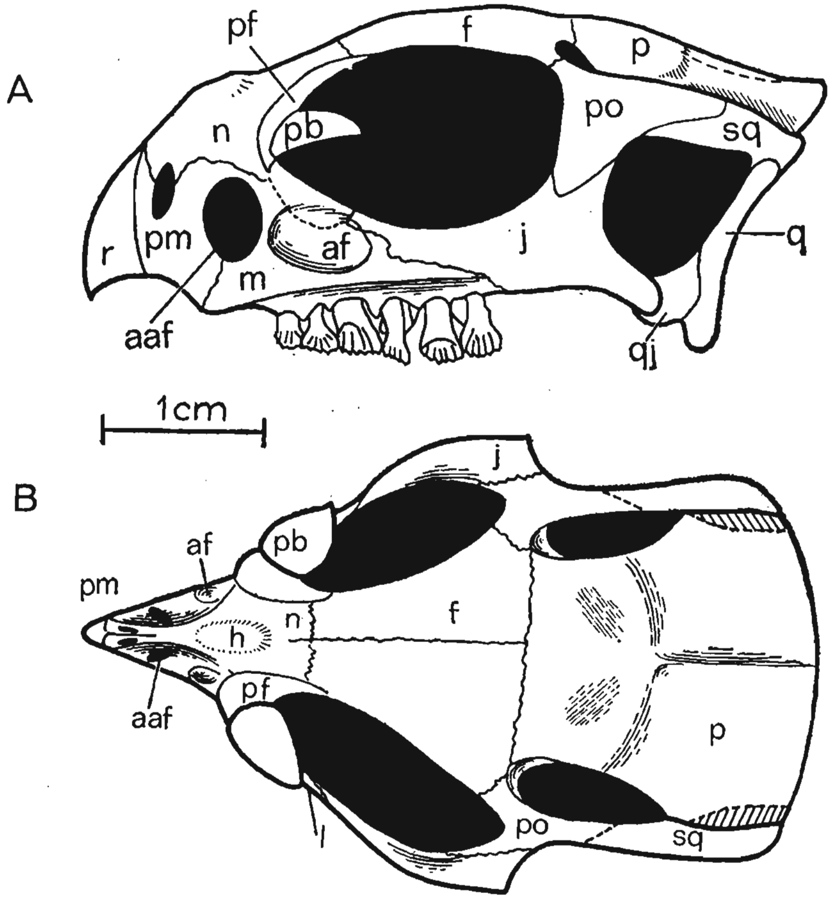


Fig. 14
Bagaceratops rozhdestvenskyi gen.n., sp.n., immature skull: *A* — lateral view; *B* — dorsal view; ZPAL MgD-I/123. Abbreviations as in Fig. 1.

but with the difference that the old fourth tooth has already been worn away. The right mandible is preserved, although its posterior portion is lacking. The mandible is very shallow and possesses a distinct horizontal shelf lateral to the tooth row. There are seven teeth in the mandible, but the first and the last have been broken away. As in the case in the maxilla, replacement teeth are present in positions 2 and 4, the latter being more nearly functional than the former. The second, fifth and sixth teeth are smaller and unspecialized.

A small, slightly eroded skull with a mandible (ZPAL MgD-I/116) and the fragments of the lower and upper jaws of two other specimens (ZPAL MgD-I/120, 121) of *?P. kozlowskii* are present in ZPAL collection from the Barun Goyot Formation of Khulsan, all of which are about the same size as the immature skull of *B. rozhdestvenskyi* described above. The skull of the immature specimen of *?P. kozlowskii* is similar to that of *B. rozhdestvenskyi* in that the anterior portion of the parietals is broad and convex and the teeth are similarly unspecialized (although there would appear to be seven in the maxilla). Both of these attributes are evidently due to the extremely immature stage of ontogenetic development of the individual. The skull of the immature individual of *?P. kozlowskii* differs from the juvenile specimen of *B. rozhdestvenskyi* in all characters which we consider to have taxonomic value. It is evident from an examination of these immature skulls of *B. rozhdestvenskyi* (ZPAL MgD-I/123) and *?P. kozlowskii* (ZPAL MgD-I/116), that the broad, straight suture between the frontals and parietals extends across the centre of the convex cranial roof. In these skulls the parietal forms the entire anterior and medial boundary of the supratemporal fossa, which is externally bounded by the postorbital. In a slightly older individual of *?P. kozlowskii* (ZPAL MgD-I/117) the anterior boundary of the supratemporal fossa is nearly entirely formed from the frontal, as is also the case in adult, much larger individuals of *P. andrewsi.*

In the succession of skulls of *P. andrewsi,* which are smaller than AMNH 6419, we observe that the frontoparietal suture migrates gradually backwards and, in the specimen ZPAL MgD-II/23, it reaches the position which it occupies in AMNH 6419. The latter specimen, from the collections of the American Museum of Natural History, is only slightly larger than ours. However, it differs from smaller as well as larger skulls of this species in the position of the postorbital, which enters into the formation of the anterolateral boundary of the supratemporal fossa. This difference is most probably a manifestation of intraspecific variation. In contrast, the supratemporal fossa is formed about equally from the parietal and postorbital in immature skulls of *B. rozhdestvenskyi,* with the exception of the smallest skull (ZPAL MgD-I/123) of this species. The frontal reaches the anterior boundary of the fossa for the first time in much larger, presumably adult skulls of *B. rozhdestvenskyi.* The smallest skull of *P. andrewsi* (Table 3) in our collection (ZPAL MgD-II/7) has an incipiently developed horn core on the nasals, which is divided into two parts by a suture. The nasal horn core is more prominent and entirely unpaired already in the smallest skull of *B. rozhdestvenskyi.*

We calculated some indices (Table 6), which illustrate the growth changes and may be useful in the identification of particular growth stages of specimens of different species within the family Protoceratopsidae. As these indices demonstrate, the skull in *B. rozhdestvenskyi* exhibits the following changes during its early ontogenetic development:

1. the relative length of the orbit decreases;
2. the length of the snout increases slightly;
3. the length of the frill at first increases, than appears to stop growing and its length becomes relatively shorter during the successive stages;
4. the width of the frill increases;
5. the width across the quadrates and jugals increases.

Table 6

Skull ratios in the Protoceratopsidae

Species	Cat. Nos.	$\frac{E}{D}$	$\frac{G}{D}$	$\frac{C}{G}$	$\frac{A}{G}$	$\frac{M}{G}$	$\frac{B}{G}$	$\frac{N}{G}$	$\frac{H}{G}$	$\frac{A}{D}$
Bagaceratops rozhdestvenskyi	ZPAL MgD-I/123	0.51	0.64	0.87	0.63	0.93	0.70	0.53	0.46	0.40
	,, I/124	?	0.68	0.75	0.40	?	0.74	0.54	?	0.27
	,, I/125	0.60	0.58	0.97	0.35	1.03	0.75	0.70	0.60	0.20
	,, I/126	0.68	0.63	0.76	0.29	?	0.81	0.50	0.76	0.19
	,, I/127	?	?	?	0.32	1.20	0.83	?	?	?
Protoceratops andrewsi	ZPAL MgD-II/7	?	0·56	0.88	0.47	0.91	0.83	0.47	?	0.27
	,, II/24	?	?	?	0.45	?	?	?	0.90	?
	,, II/23	?	?	?	0.45	1.02	0.85	?	0.88	?
	AMNH 6419	0.59	0.56	0.90	0.45	?	0.86	?	0.96	0.25
	,, 6408	0.69	0.55	1.00	0.28	?	0.89	?	0.91	0.16
	,, 6439	0.93	0.50	1.10	0.27	?	1.20	?	1.00	0.13
	,, 6414	0.88	0.53	1.08	0.27	?	0.98	?	1.04	0.14
	,, 6466	0.77	0.49	1.09	0.30	?	1.08	?	0.98	0.15
?P. kozlowskii	ZPAL MgD-I/116	?	?	?	0.53	0.75	0.75	?	?	?
	,, I/117	0.33	0.57	0.92	0.55	0.70	0.80	0.67	0.72	0.31
Leptoceratops gracilis	NMC 8887	?	0.72	?	?	?	?	0.45	?	?
	,, 8889	?	0.71	?	?	?	?	0.46	?	?

A — length of orbit, B — center of orbit to front of rostral, C — center of orbit to posterior end of frill, D — median length of skull, E — greatest width of frill, G — basal length of skull (condyle to anterior end of maxilla), H — width across quadrates, M — width across jugals, N — anterior margin of supratemporal fossa to end of skull. For dimensions comp. Table 3.

As can be seen from the above list, *B. rozhdestvenskyi* follows the same growth pattern as does *P. andrewsi*, although some differences are, however, apparent. Although the snout also increases in relative length in *P. andrewsi*, it is already proportionally longer in the smallest specimen of this species than it is in *B. rozhdestvenskyi*. In the latter species it never reaches 100% of the basal skull length as it does in *P. andrewsi*. The lenght of the frill increases continuously in *P. andrewsi*, in contrast to conditions in *B. rozhdestvenskyi*, and the width of the skull across the quadrates is also relatively larger in the smallest specimen of *P. andrewsi*. The ontogenetic development of *?P. kozlowskii* could not be investigated to the same extent as in *B. rozhdestvenskyi* and *P. andrewsi*, because of the lack of sufficient material. Generally, *?P. kozlowskii* underwent growth changes similar to those of *P. andrewsi*, although differences can be seen in the relative length of the frill. In an immature specimen of *?P. kozlowskii* this structure is already longer than in specimens of *P. andrewsi* of comparable size. This, together with the already noted changes in the position of the frontoparietal suture in *?P. kozlowskii* may indicate that the growth of the frill was more rapid in young individuals of *?P. kozlowskii* than in those of *P. andrewsi*. The ventral outline of the mandible, in young specimens of all of the known species of protoceratopsids, seen in lateral aspect, is straight. The teeth of immature individuals of *B. rozhdestvenskyi* and *?P. kozlowskii* differ from those of adults in lacking any morphologic specialization; this was probably true for all protoceratopsids. The number of the teeth in newly hatched specimens was probably less than eight, the number which has been suggested by BROWN & SCHLAIKJER (1940*a*), and was probably even less than seven, according to the material in ZPAL collections.

DISTRIBUTION AND RELATIONSHIPS OF GENERA WITHIN THE PROTOCERATOPSIDAE.

According to present information, the Protoceratopsidae are restricted to the Upper Cretaceous deposits of the Asian and North American continents.

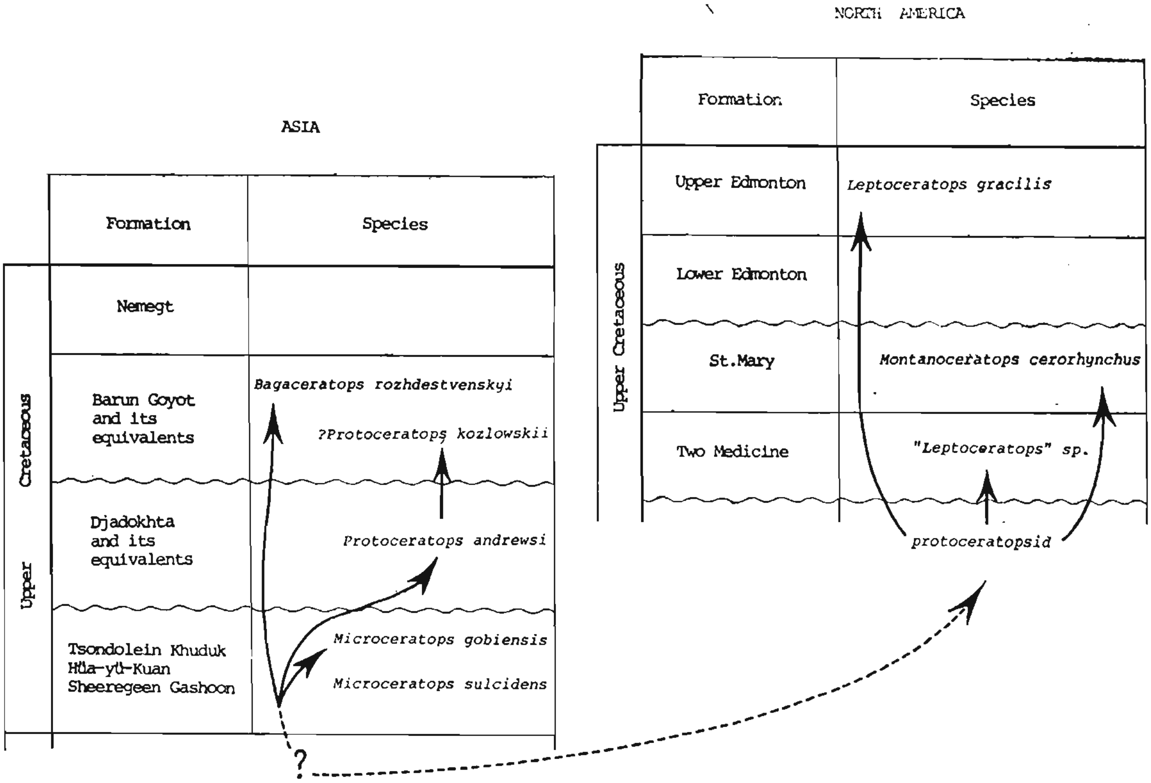
So far the Protoceratopsidae were known from four genera representing a total of five to six species, but only two of these, *Protoceratops andrewsi* GRANGER & GREGORY and *Leptoceratops gracilis* BROWN, contain sufficient material for fully define their skeletal morphology. The new material collected in Mongolia by the Polish-Mongolian Expeditions, which among other forms, also includes diagnostic elements of *Bagaceratops rozhdestvenskyi* gen. n., sp. n. and ?*Protoceratops kozlowskii* sp. n., demonstrates that this family was more differentiated than has been thought and that *P. andrewsi* was not its youngest Asian representative, as it has been considered up to the present. An excellently preserved, although somewhat incomplete specimen of *Microceratops gobiensis* BOHLIN, is also present in our collection. The type of this species, described by BOHLIN in 1953 from the locality Tsondolein Khuduk in China, was found together with a pachycephalosaurid ("*Stegoceras*" *bexelli* BOHLIN). The deposits which yielded these forms were considered by BOHLIN to be older than those of Bayn Dzak (Djadokhta Formation). ROZHDESTVENSKY (1971) expressed the opinion, that *M. gobiensis* might be a junior synonym of *P. andrewsi* and consequently considered the deposits in the two above mentioned localities to be generally contemporaneous. We (MARYAŃSKA & OSMÓLSKA, 1974) followed ROZHDESTVENSKY'S interpretation concerning the age of the deposits in Tsondolein Khuduk in our earlier paper. However, after concluding our study of the new material of *M. gobiensis* from the Sheeregeen Gashoon locality, we no longer doubt that *M. gobiensis* is in many respects much more primitive than *P. andrewsi.* It may, therefore, also be stratigraphically older than the latter species, possibly representing the oldest protoceratopsid known. Additional evidence for an early stratigraphic age for the Sheeregeen Gashoon formation and, consequently, of *M. gobiensis*, is the presence in the same strata of fragmentary jaws of a primitive hadrosaur and of a primitive ankylosaur. A review of the morphology of Asian protoceratopsids permits us to define which characters can be regarded as primitive or as advanced within this family. The following characters are considered by us to be among the most important and meaningful of all characters in determining the relative position of a form within the phylogeny of the Protoceratopsidae:

1. the frill: short — primitive, long — advanced;
2. the horn core: lacking or incipient — primitive, well developed — advanced;
3. the snout: long — primitive, shortened — advanced;
4. the premaxillary teeth: present — primitive, absent — advanced;
5. the frontoparietal depression: absent — primitive, present — advanced;
6. the mandible: shallow with straight ventral border — primitive, deep with curved ventral border — advanced;
7. the long bones of limbs: slender — primitive, massive — advanced; the bones of hind limb long — primitive, short — advanced, the bones of forelimb short — primitive, long — advanced;
8. the ungual phalanges: pointed, claw-like — primitive, blunt, hoof-like — advanced.

These characters enabled us to arrive at a method for establishing the mutual affinities of protoceratopsid genera, which we illustrate on Table 7. The evaluation of the characters enumerated above is generally in agreement with those presented by BROWN & SCHLAIKJER (1940*a*) with one exception: these authors considered that the deep and ventrally bowed dentary in *P. andrewsi* represents a primitive character. This view was a consequence of the opinion that *Protoceratops* was a direct ancestor of the Ceratopsidae, in which the lower jaw has a straight ventral border. Contrary to BROWN'S & SCHLAIKJER'S opinion, we consider that a deep and curved mandible is an advanced structure, taking into account that: *a.* the stratigraphically oldest protoceratopsid, *M. gobiensis*, has a shallow and straight dentary; *b.* the mandible changes during the ontogenetic development in *P. andrewsi* from shallow and straight to deep and curved ventrally; and *c.* the mandible is shallow and straight in the primitive ornithischians.

Table 7

Distribution of the Protoceratopsidae



ASIA

	Formation	Species
Upper Cretaceous	Nemegt	
	Barun Goyot and its equivalents	*Bagaceratops rozhdestvenskyi* *?Protoceratops kozlowskii*
	Djadokhta and its equivalents	*Protoceratops andrewsi*
	Tsondolein Khuduk Hüa-yü-Kuan Sheeregeen Gashoon	*Microceratops gobiensis* *Microceratops sulcidens*

NORTH AMERICA

	Formation	Species
Upper Cretaceous	Upper Edmonton	*Leptoceratops gracilis*
	Lower Edmonton	
	St.Mary	*Montanoceratops cerorhynchus*
	Two Medicine	*"Leptoceratops" sp.*

Microceratops, which is the most ancient genus in the family, and is in some respects very primitive, cannot be considered to be ancestral to any of the later known protoceratopsids, because it already has very long forelimbs (a humerus + radius to femur + tibia ratio of 0.71). A comparable degree of elongation of the forelimbs was achieved in *L. gracilis*, but this species cannot, in our opinion, be derived from *M. gobiensis*, which is specialized in possessing a fenestrated and somewhat longer frill. Our new genus *Bagaceratops* can by no means be derived from the stratigraphically antecedant *Protoceratops*, although it exhibits some more advanced characteristics, such as the loss of the premaxillary dentition, the comparatively well developed horn, and a shortened snout. It has, however, a distinctly shorter frill which lacks probably any fenestration, and the mandible is shallow and its ventral border is straight. In these characters it is therefore more primitive than is *Protoceratops*. ?*P. kozlowskii*, which is stratigraphically younger than *P. andrewsi*, may be regarded as occupying a more advanced level in the evolution of this genus. The frill is proportionally longer in this species, the frontoparietal suture has migrated further posteriorly, and the sacrum is longer, containing eight sacral vertebrae even in immature individuals. The North American protoceratopsids were not available to us, but the most completely know species, *L. gracilis*, could not be derived either from *Protoceratops*, or from any North American genus so far known. In many respects its skeletal morphology is quite primitive. The oldest American protoceratopsid remains were collected in strata of the Early Campanian, implying that the migration of this family from Asia to North America may have occurred prior to Campanian time.

PHYLOGENY OF THE PROTOCERATOPSIDAE AND THEIR RELATIONSHIPS

It is generally believed that the Protoceratopsidae may have been derived from the Psittacosauridae. However, ROZHDESTVENSKY (1955, 1960) suggested it cannot be true. STEEL (1969) expressed the view, that the genus *Psittacosaurus* cannot be a direct ancestor of the horned dinosaurs, because of the absence of a premaxillary dentition in this form. Nevertheless, he assumed that the protoceratopsids "were derived from a more generalized psittacosaurid stock". STEEL's view seems reasonable but we would look for a possible ancestor of protoceratopsids outside this family, for none of the six species constituting the family Psittacosauridae could have given rise to the Protoceratopsidae. To the evidence cited by STEEL (*l. c.*) we can add the following: the most primitive and stratigraphically the oldest protoceratopsid, *Microceratops*, has slender hind limbs, which are more similar to those of primitive bipedal ornithopods than those of any known psittacosaurid (Table 8); the widening of the skull across the jugals is greatest in the psittacosaurids, exceeding that found in any known protoceratopsid and the psittacosaurids lack the antorbital fossa, a primitive character which is present in all protoceratopsids. The most convincing line of evidence against the derivation of protoceratopsids from the psittacosaurids is the strong reduction of the fourth and fifth digits in the manus of the latter group. This reduction is much more extreme than it is in the protoceratopsids, where the fourth digit still retains three phalanges and the fifth two. In the typically cursorial structure of its hind limbs and its fundamentally bipedal posture, *Microceratops* closely resembles the primitive Triassic hypsilophodontids (*sensu* THULBORN 1971, 1972). This indicates, in our view, that the Protoceratopsidae can be derived directly from this group. There is no evidence for the presence of a "psittacosaurid phase" in their evolution. RUSSELL (1970) suggested that "Psittacosaurids, protoceratopsids and ceratopsids represent distinct lineages of the same general group of ornithischian dinosaurs". We find this opinion acceptable.

The Psittacosauridae are generally classified within the suborder Ornithopoda, mainly on the basis of their supposed bipedality. We have elsewhere expressed the view (MARYAŃSKA & OSMÓLSKA, 1974), that bipedality alone cannot be considered as a character of great taxonomic value. The skull of the psittacosaurids exhibits some attributes which are not present

Table 8

Limb ratios in the Psittacosauridae and Protoceratopsidae

Species, Cat. Nos.	tibia / femur	mts III / femur	mts III / tibia	humerus / femur	humerus + radius / femur + tibia	humerus / scapula
Psittacosaurus mongoliensis 1) AMNH 6254	1.06	0.57	0.54	0.73	0.62	?
Psittacosaurus sinensis 2) V. 738 and V. 749	1.06	0.54	0.51	0.85	0.75 (est.)	0.88 (est.)
Protiguanodon mongoliensis 1) AMNH 6253	1.05	0.56	0.53	0.77	0.68	?
Protoceratops andrewsi 3) AMNH 6471	1.06	0.52	0.49	0.81	0.67	0.77
Protoceratops andrewsi 3) AMNH 6424	1.10	0.50	0.45	0.89 (est.)	0.68 (est.)	0.95 (est.)
Leptoceratops gracilis 4) NMC 8888	1.05	0.47	0.44	0.95	0.72	0.98
?*Protoceratops kozlowskii* ZPAL MgD-I/117	?	?	?	0.75	?	0.80
Microceratops gobiensis ZPAL MgD-I/156	1.16	0.55	0.49	0.90	0.71	0.95

Indices calculated basing on measurements given by: 1) OSBORN 1924, 2) YOUNG 1958, 3) BROWN & SCHLAIKJER 1940*a*, 4) STERNBERG 1951.

within any other group of ornithopods but are common to both the Protoceratopsidae and Ceratopsidae. The most obvious of these attributes can be listed as follows:

1. the development of the nasal horn core, which is present in *Psittacosaurus youngi* Chao;
2. the development of the frill, which is at an incipient stage in all psittacosaurids;
3. the widening of the skull across the jugals, a character which is maximally developed in the psittacosaurids;
4. The beak-like character of the anterior portion of the snout; it should be noted that the snout of the psittacosaurids is peculiar according to existing descriptions (OSBORN, 1923, 1924, YOUNG 1958*b*, CHAO 1962) in the mutual relations of the bones and in the absence of a rostral. The bone identified as the "premaxilla" is very small and it is far from the external nares. This relation is so unique among the reptiles that it is difficult to believe such a structure could be found on a reptilian snout. More probably, the "premaxilla" represents in fact the rostral, so the more than this bone is unpaired, and the unusually dorsally expanded "maxilla" includes the premaxilla as well as the maxilla, although the suture between these bones has been obliterated; if our suggestion is correct, the structure of the snout in the psittacosaurids is essentially identical to that in the Protoceratopsidae, except that the antorbital fossa is lacking in the psittacosaurids;
5. the similar structure of teeth.

With so many characters in the skull of the Psittacosauridae occuring also within the

Protoceratopsidae on the one hand and within the Ceratopsidae on the other, we believe that it is more convenient and reasonable to place the family Psittacosauridae within the suborder Ceratopsia, than to leave them within the Ornithopoda, from which they so obviously differ. The idea is not completely new, because many authors have emphasized either the aberrancy of the psittacosaurids (STEEL 1969, ROMER 1956) or their relationship to the Protoceratopsidae (ROMER 1956, YOUNG 1958*b*, GREGORY 1957). ROZHDESTVENSKY (1960, 1964) even suggested that the Psittacosauridae should be placed in a separate suborder. More recently COOMBS (unpublished doctor's thesis) expressed also the opinion that the Psittacosauridae should be assigned to the suborder Ceratopsia. We are not able, at present, to discuss in detail the question of the possible protoceratopsid origin of the Ceratopsidae, as the representatives of the latter family are not available to us. However, we do not think that *Protoceratops*, which is a specialized form (see for example the structure of the mandible) could have given rise to any known ceratopsid. In our opinion it is more probable that the ancestor of the Ceratopsidae can be found among the earlier protoceratopsids, perhaps near the adaptive level of *Microceratops*, rather than among the late Cretaceous representatives of the family. The high degree of differentiation and the specializations of the earliest known ceratopsids suggest a long previous history.

So far no undoubted remains of the ceratopsids have been found in Asia. However, the supposed remains of ceratopsids were described several times from Asian Cretaceous deposits of pre-Campanian age (RIABININ 1931, 1939, GILMORE 1933, ROZHDESTVENSKY 1964*b*, ROZHDESTVENSKY & KHOSATZKY 1967). This material is very fragmentary, and only one specimen, a fragment of a possible horn core in the collections of the Palaeontological Museum in Moscow, was probably derived from a ceratopsid (a similar specimen, assigned to "*Crataeomus pawlowitschii*", was described by SEELEY, 1881, p. 650, Pl. 28, Fig. 4, from the Gosau Formation). If this is true, it is possible that the Ceratopsidae were present in Asia before *Microceratops* appeared. Their absence in higher Cretaceous horizons, as well as the absence of the Protoceratopsidae in the uppermost Cretaceous of Asia, may be taken as evidence that suitable environmental conditions for these reptiles no longer existed. Such conditions were evidently present on the North American continent, where both the Protoceratopsidae and Ceratopsidae lived to the end of the Cretaceous and constituted a significant element of the dinosaurian fauna. The territory of the present-day Mongolia, which has yielded most of the remains of Upper Cretaceous dinosaurs in Asia, was probably far from the sea shore and dominated at that time by rather harsh, xeric environments (except, may be, during the time of deposition of the Nemegt Formation). Milder, more humid environments were probably present to the east and to the west of central Asia. Thus, only more extensive exploration of terrestrial deposits of Cretaceous age in these regions can provide a resolution of the problem of a possible origin or evolution of the Ceratopsidae in Asia.

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EXPLANATION OF PLATES

PLATE XXXVI

Page

Microceratops gobiensis Bohlin, 1953 137
(see also Pls XXXVII and XXXVIII)

? Early Upper Cretaceous, Sheeregeen Gashoon formation, Sheeregeen Gashoon, Gobi Desert, Mongolia

Fig. 1. Entire specimen as found, ventral view. *r* — radius, *h* — humerus, *sc* — scapula, *rp* — right pes, *t* — tibia *f* — femur, *lp* — left pes; ZPAL MgD-I/156, × 0.5.

Photo: E. Mulawa

PLATE XXXVII

Page

Microceratops gobiensis Bohlin, 1953 137
(see also Pls XXXVI and XXXVIII)

? Early Upper Cretaceous, Sheeregeen Gashoon formation, Sheeregeen Gashoon, Gobi Desert, Mongolia

Fig. 1*a*. Left mandible lacking symphyseal portion with fragmentary quadrate visible, lateral view.
Fig. 1*b*. Left and right mandible, dorsal view. Note strong inward flexion of the coronoid process.
Fig. 2. Right half of the frill with medial, parietal crest visible to the left, dorsal view.
Fig. 3*a*. Stereo-photograph of the coracoid with proximal part of the scapula, lateral view. Both elements were found separated and are here glued together.
Fig. 3*b*. Stereo-photograph of the same specimen, medial view; ZPAL MgD-I/156.

All × 1

Photo: E. Mulawa

PLATE XXXVIII

Page

Microceratops gobiensis Bohlin, 1953 137
(see also Pls XXXVI and XXXVII)

? Early Upper Cretaceous, Sheeregeen Gashoon formation, Sheeregeen Gashoon, Gobi Desert, Mongolia

Fig. 1. Right femur in posterior view with right tibia in medial view. Visible: to the left bottom, dorsal vertebrae in ventral view; to the left top, digits IV-II (from left to right) of the left pes, ventral view.
Fig. 2*a*. Right metatarsus, ventral view.
Fig. 2*b*. Same specimen, dorsal view.
Fig. 3. Visible from left to right: right fragmentary ulna and radius, right humerus in anterior view, right scapula in external view; ZPAL MgD-I/156.

All × 1

Photo: E. Mulawa & L. Dwornik

PLATE XXXIX

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Protoceratops andrewsi GRANGER & GREGORY, 1923 165
(see also Pl. XLIX, Fig. 1)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

Fig. 1*a*. Skull with lower jaw of a very young individual, dorsal view; ZPAL MgD-II/7.
Fig. 1*b*. Same specimen, lateral view.
Fig. 2. Fragmentary skull with lower jaw of a young individual, lateral view; ZPAL MgD-II/24.
Fig. 3*a*. Badly eroded skull with lower jaw of a young specimen, dorsal view; ZPAL MgD-II/23.
Fig. 3*a*. Same specimen, right lateral view; quadrate exposed to the left.
Fig. 3*c*. Same specimen, left lateral view.

All × 1

Photo: E. Mulawa

PLATE XL

Page

?*Protoceratops kozlowskii* sp. n. 143
(see also Pls XLI and XLIX, Figs 2, 3)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia

Fig. 1*a*. Skull with fragmentary postcranial skeleton of a young individual, lateral view. Visible: skull, fragmentary bones of the right fore limb, cervical vertebrae, nearly complete right hind limb, lacking pes and a fragment of the ischium. Holotype, ZPAL MgD-I/117, × 0.64.
Fig. 1*b*. Stereo-photograph of the skull of the same individual, dorsal view.
Fig. 1*c*. Stereo-photograph of the same specimen, lateral view.
Fig. 2*a*. Stereo-photograph of the skull of a very immature individual, dorsal view; ZPAL MgD-I/116.
Fig. 2*b*. Same specimen, right lateral view.
Fig. 2*c*. Same specimen, left lateral view.

All × 1, except Fig. 1*a*

Photo: E. Mulawa

PLATE XLI

Page

?*Protoceratops kozlowskii* sp. n. 143
(see also Pls XL and XLIX, Figs 2, 3)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia

Fig. 1*a*. Fragment of the postcranial skeleton (anterior to the right) oblique, laterodorsal view. Visible: dorsal vertebrae, pelvic region, right femur. Holotype, ZPAL MgD-I/117.
Fig. 1*b*. Same specimen, left lateral view. Visible: dorsal vertebrae, left ilium, fragment of the left femur.
Fig. 1*c*. Same specimen (anterior to the right), ventral view. Visible: posterior face of the right femur and a fragment of the ischium, above; proximal portion of the scapula, left humerus, ulna and radius, below.
Fig. 2*a*. Left dentary, medial view; ZPAL MgD-I/118.
Fig. 2*b*. Same specimen, dorsal view.
Fig. 2*c*. Same specimen, lateral view.

All × 1

Photo: E. Mulawa & L. Dwornik

PLATE XLII

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLIII-XLVIII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the skull with lower jaw, lateral view. Holotype; ZPAL MgD-I/126.
Fig. 1*b*. Stereo-photograph of the same specimen, dorsal view.
Fig. 1*c*. Stereo-photograph of the same specimen, occipital view.

All × 0.38

Photo: E. Mulawa

PLATE XLIII

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII, XLIV-XLVIII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the skull with lower jaw, lateral view. Holotype, ZPAL MgD-I/126, × 0.38.
Fig. 1*b*. Same specimen, anterior view, × 0.38.
Fig. 1*c*. Stereo-photograph of the same specimen, oblique postero-ventral view, × 0.38.
Fig. 2. Fragmentary, badly eroded right maxilla with teeth, lateral view; ZPAL MgD-I/136, × 1.
Fig. 3. Loose, slightly worn mandibular tooth, lingual surface; ZPAL MgD-I/151, × 1.
Fig. 4. Loose, not used mandibular tooth, lingual surface; ZPAL MgD-I/151, × 1.

Photo: E. Mulawa

PLATE XLIV

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII, XLIII, XLV-XLVIII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the brain case, oblique posteroventral view; ZPAL MgD-I/133.
Fig. 1*b*. Same specimen, anterior view of the brain case.
Fig. 1*c*. Same specimen, dorsal view.
Fig. 1*d*. Stereo-photograph of the same specimen, lateral view.
Fig. 2*a*. Posterior portion of the left mandible, lateral view; ZPAL MgD-I/138.
Fig. 2*b*. Same specimen, medial view.

All × 1

Photo: E. Mulawa

PLATE XLV

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLIV, XLVI-XLVIII, XLIX, Figs 4-6, and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav, Gobi Desert, Mongolia

Fig. 1*a*. Anterior portion of the skull, left lateral view; ZPAL MgD-I/129.
Fig. 1*b*. Same specimen, right lateral view.
Fig. 1*c*. Same specimen, palatal view.
Fig. 1*d*. Same specimen, dorsal view.
Fig. 1*e*. Same specimen, posterior view.

All × 0.44

Photo: E. Mulawa

PLATE XLVI

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLV, XLVII, XLVIII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1. Damaged skull with lower jaw, of a young individual, lateral view; ZPAL MgD-I/124.
Fig. 2*a*. Skull of a young adult individual, anterior view; ZPAL MgD-I/125.
Fig. 2*b*. Same specimen, preserved portion of the frill removed, posterior view.
Fig. 3*a*. Proximal portion of the femur, anterior view; ZPAL MgD-I/142.
Fig. 3*b*. Same specimen. Visible: proximal articular surface of the femur in dorsal view, above; three sacral centra in ventral view, below.

All × 1

Photo: E. Mulawa

PLATE XLVII

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLVI, XLVIII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Skull with lower jaw of a young adult individual, frill not preserved, left lateral view; ZPAL MgD-I/125.
Fig. 1*b*. Same specimen with preserved posterior portion of the frill, right lateral view.

All × 1

Photo: E. Mulawa

PLATE XLVIII

Page

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLVII, XLIX, Figs 4-6 and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav, Gobi Desert, Mongolia

Fig. 1*a*. Lower jaw with skull of a young adult individual, ventral view; ZPAL MgD-I/125.
Fig. 1*b*. Same specimen, skull in dorsal view. Visible right lateral portion of the frill preserved to the very posterior margin.

All × 1

Photo: E. Mulawa

PLATE XLIX

Page

Protoceratops andrewsi GRANGER & GREGORY, 1923 161
(see also Pl. XXXIX)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

Fig. 1. Fragment of the left maxilla with mostly well worn teeth, lateral view; ZPAL MgD-II/, × 1.

?*Protoceratops kozlowskii* sp. n. 143
(see also Pls XL and XLI)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia

Fig. 2. Loose, worn maxillary tooth, labial surface; ZPAL MgD-I/122a, × 1.
Fig. 3. Loose, not used mandibular tooth, lingual surface; ZPAL MgD-I/122, × 1.

Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLVIII and L)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav, Gobi Desert, Mongolia

Fig. 4. Damaged skull of an adult individual, lateral view; ZPAL MgD-I/127, × 0·5.
Fig. 5. Anterior dorsal region of the vertebral column, dorsal view. Visible: damaged anterior dorsals with ribs (preserved mostly as impressions) in natural arrangement; ZPAL MgD-I/154, × 1.
Fig. 6*a*. Eroded right mandible of a large individual, lacking symphysal portion, lateral view. Visible to the left a fragment of the quadrate placed in glenoid; ZPAL MgD-I/153, × 0.46.
Fig. 6*b*. Same specimen, dorsal view, × 0.46.
Fig. 6*c*. Same specimen, medial view, × 0.46.

Photo: E. Mulawa

PLATE L

Page

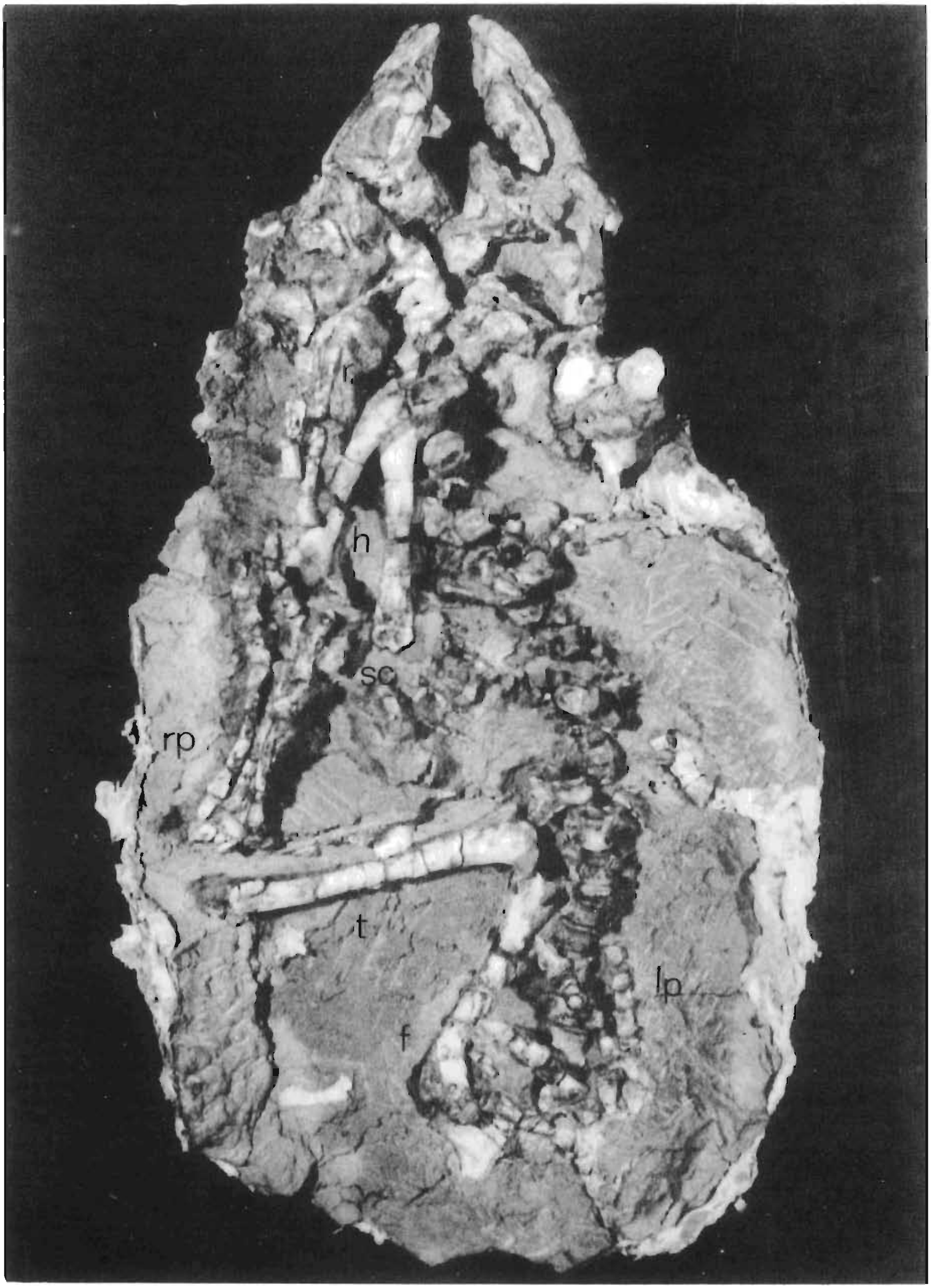
Bagaceratops rozhdestvenskyi gen. n., sp. n. 148
(see also Pls XLII-XLVIII and XLIX, Figs 4-6)

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of a very immature skull, dorsal view; ZPAL MgD-I/123.
Fig. 1*b*. Stereo-photograph of the same specimen, left lateral view.
Fig. 1*c*. Same specimen, right lateral view.
Fig. 1*d*. Same specimen, palatal view.
Fig. 2*a*. Right dentary of the same individual, medial view.
Fig. 2*b*. Same specimen, lateral view.
Fig. 3. Maxillary teeth of the same individual, labial side, × 3.
Fig. 4*a*. Slightly damaged nasals with high, unpaired horn core of a large individual, lacking any trace of the separation, dorsal view; ZPAL MgD-I/135.
Fig. 4*b*. Same specimen, lateral view.

All × 1, except Fig. 3

Photo: E. Mulawa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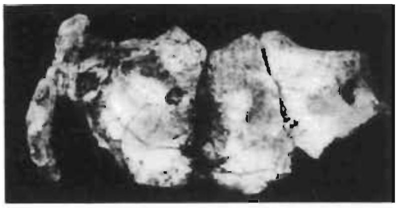

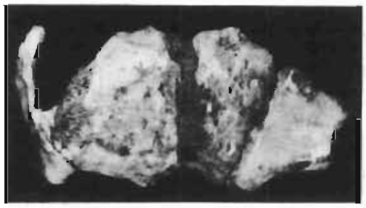

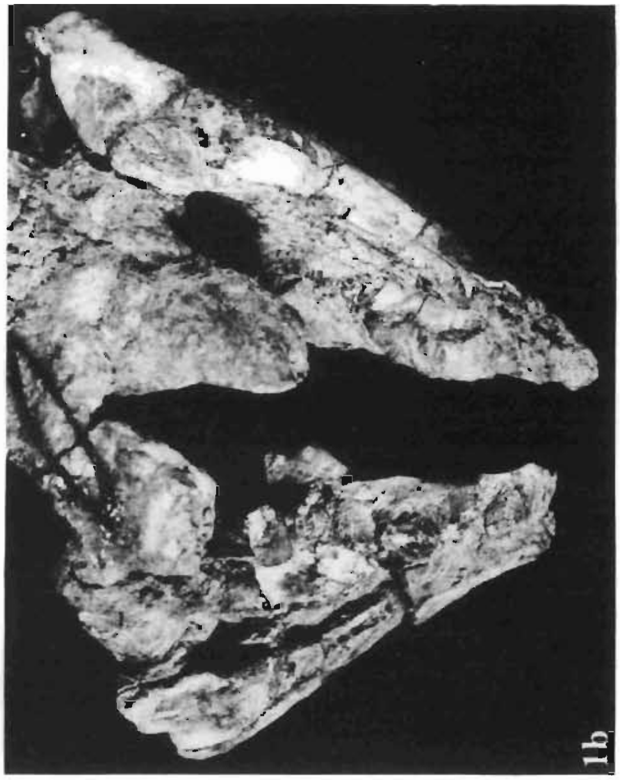

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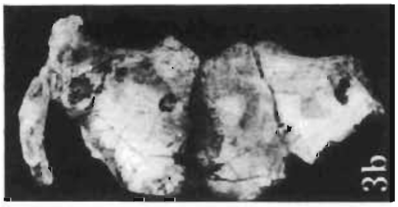

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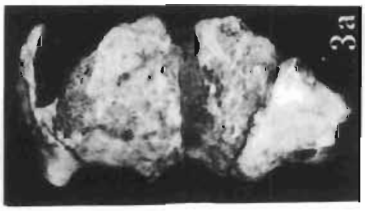

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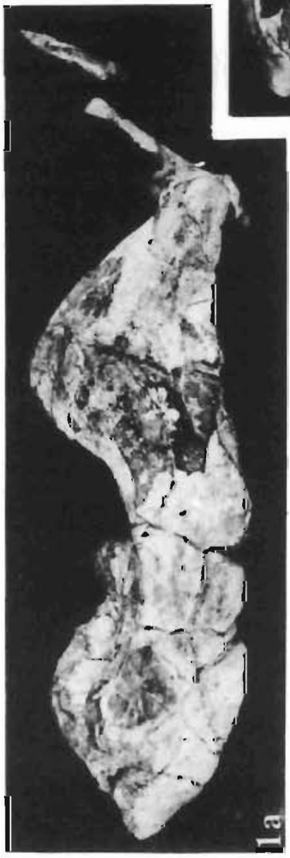

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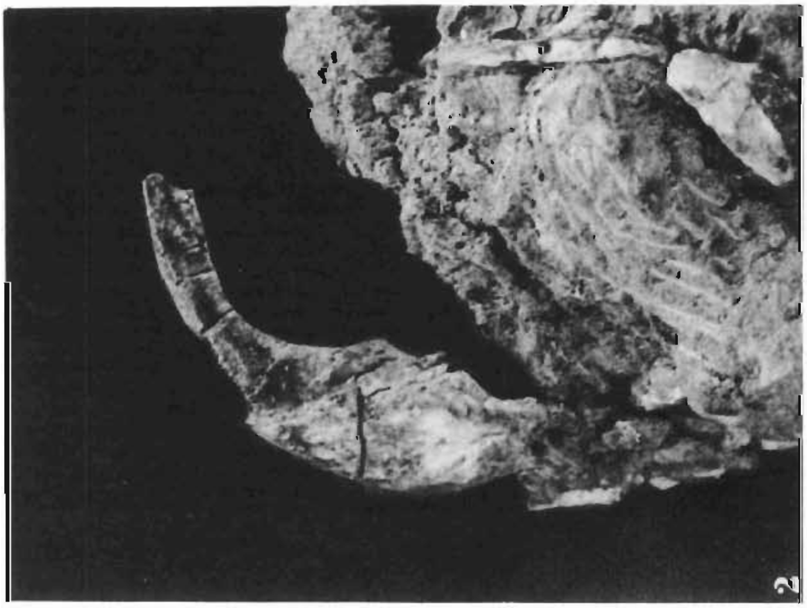

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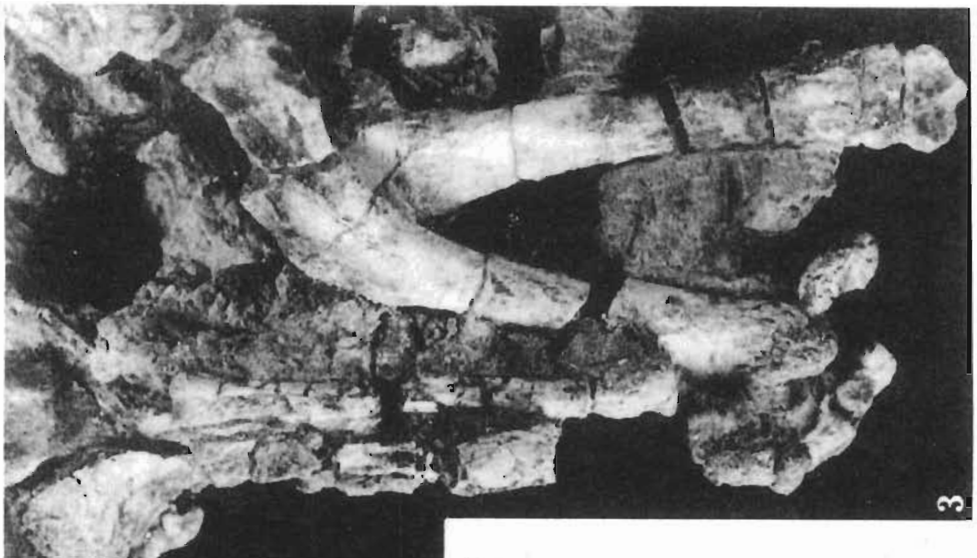

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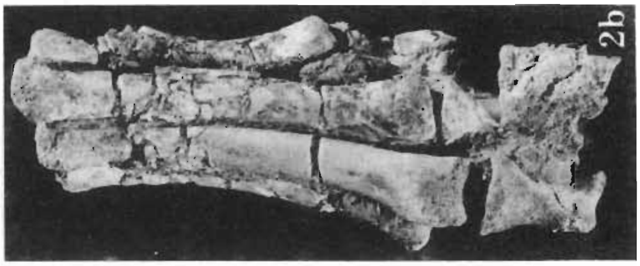

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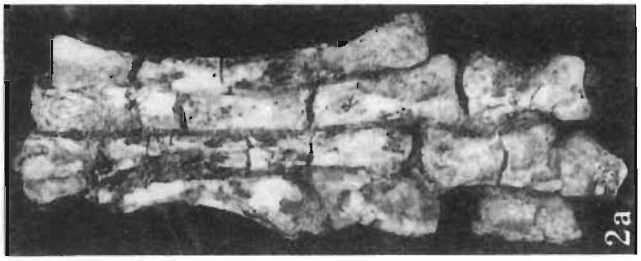

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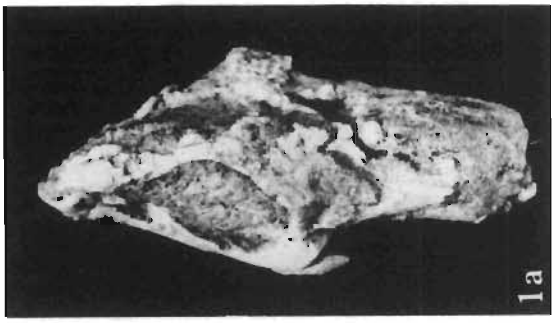
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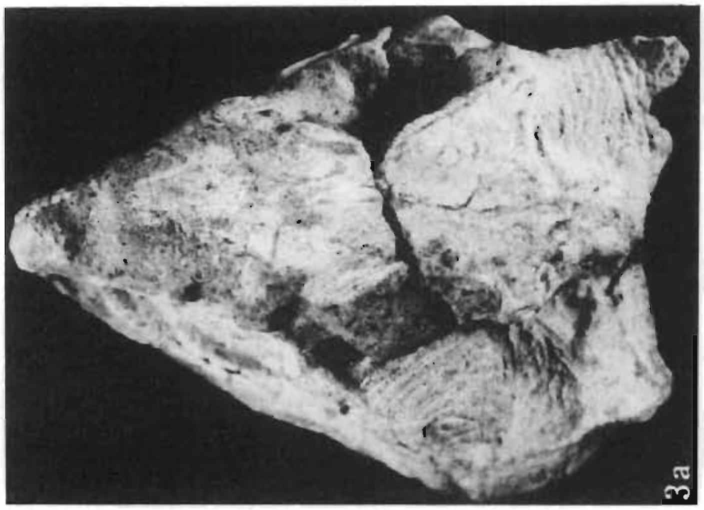
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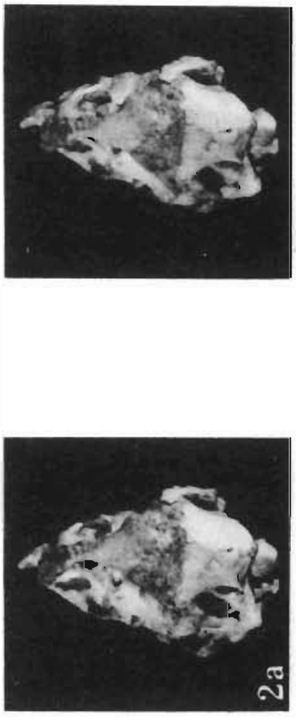

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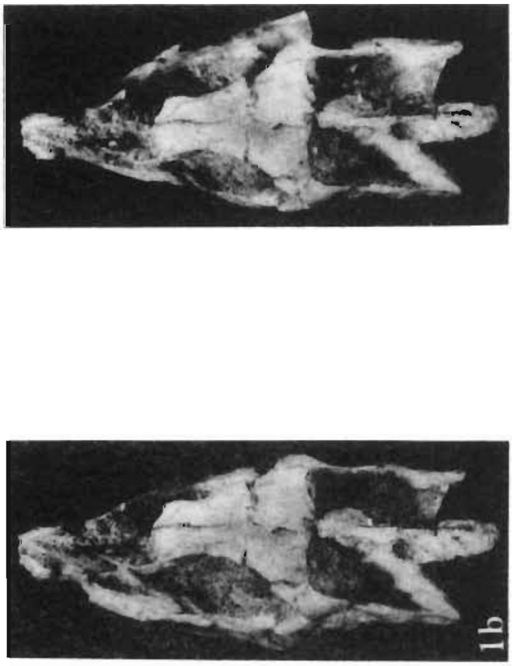

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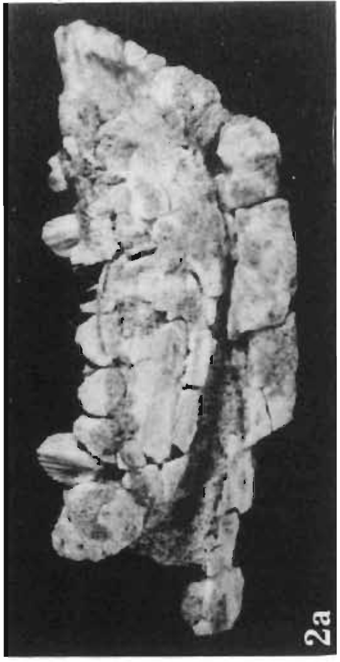

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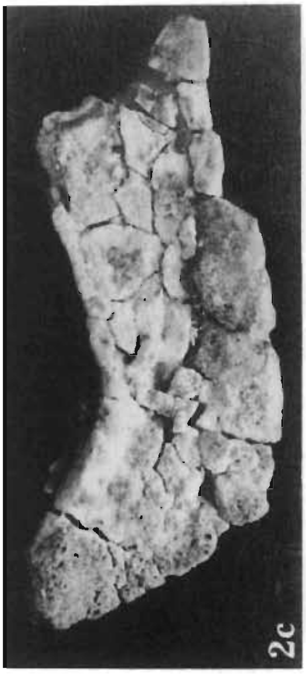

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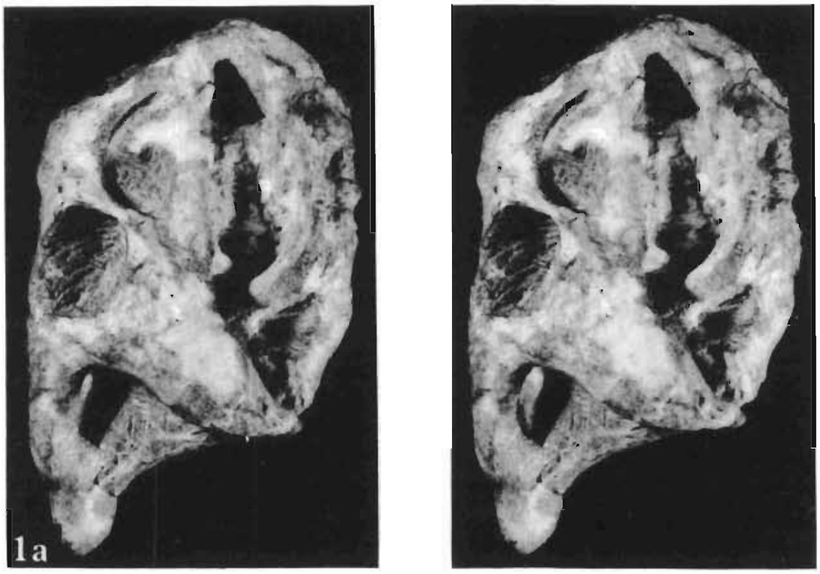
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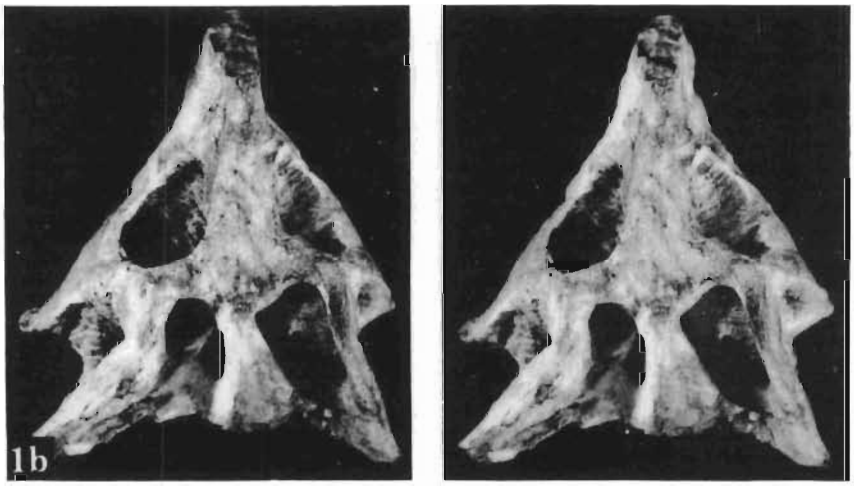
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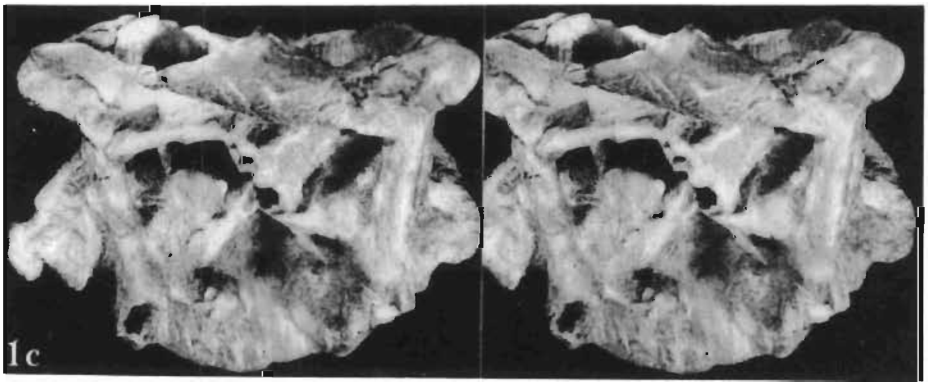
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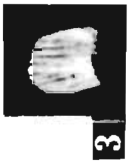
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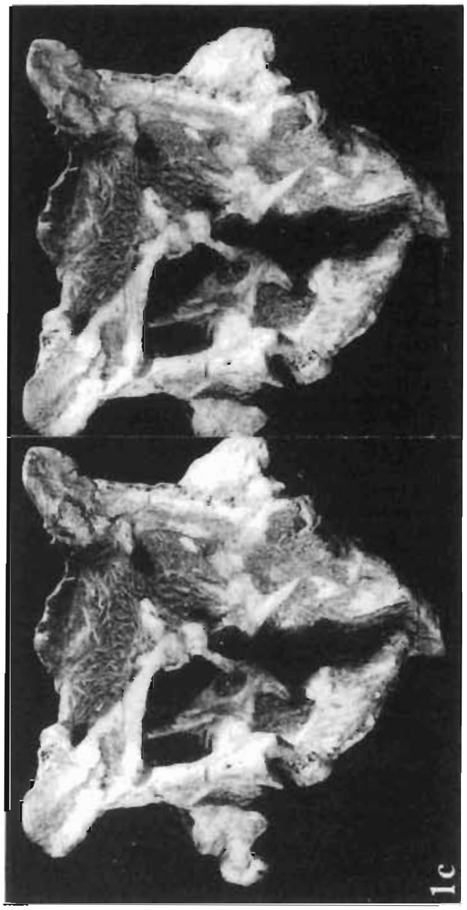
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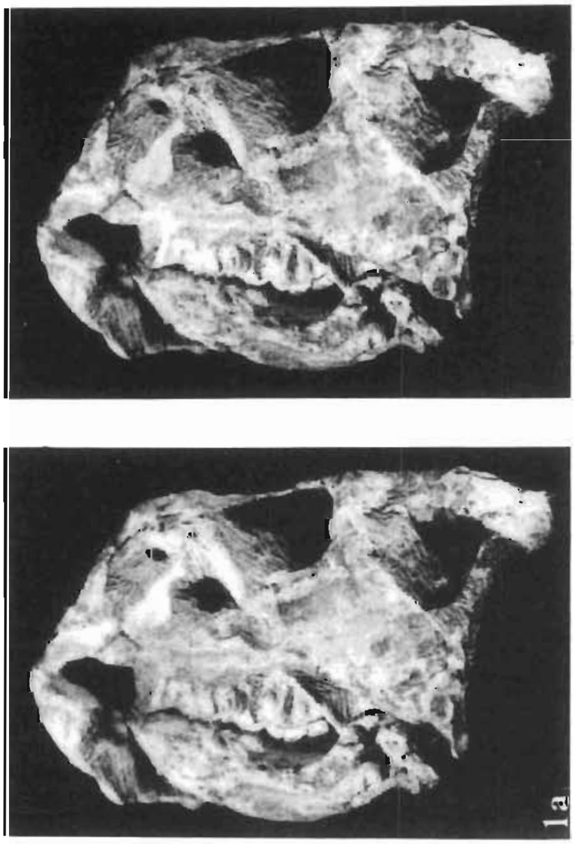
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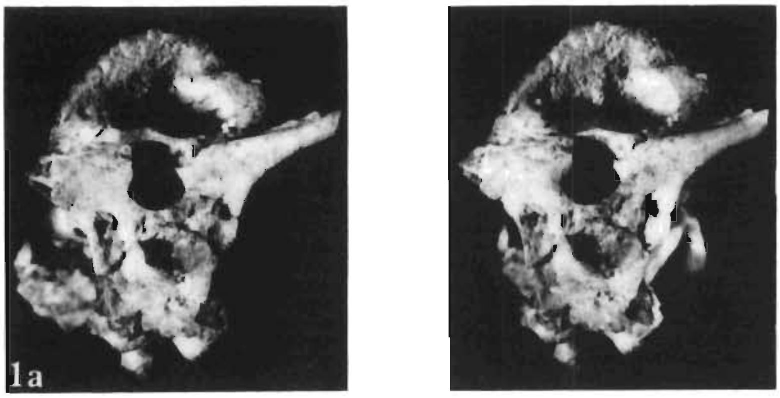
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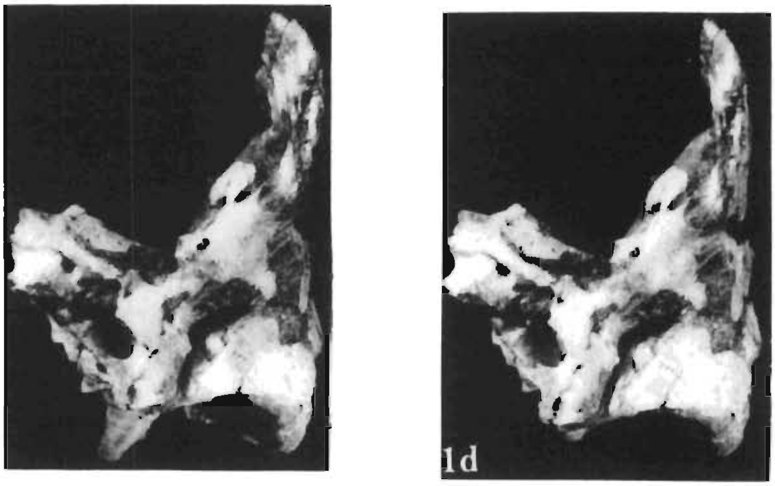
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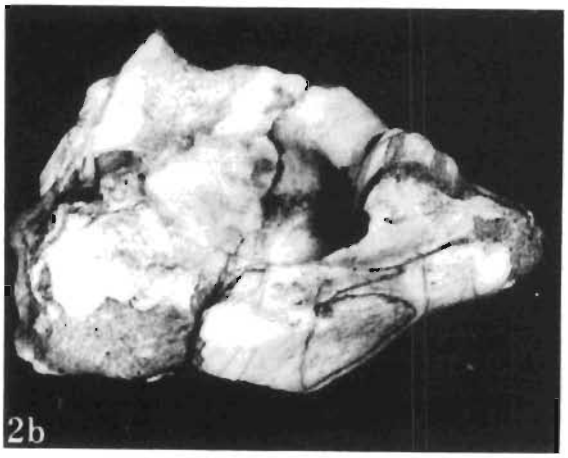
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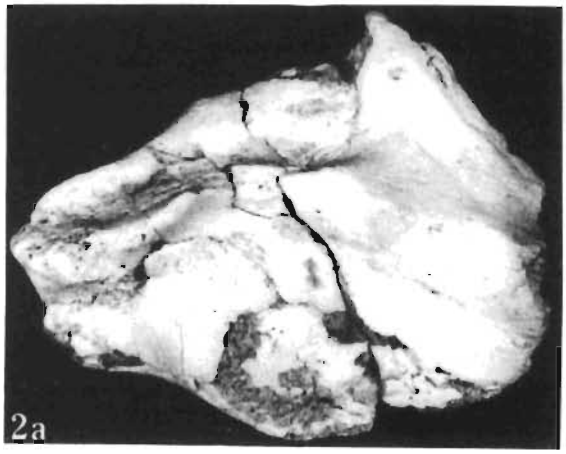
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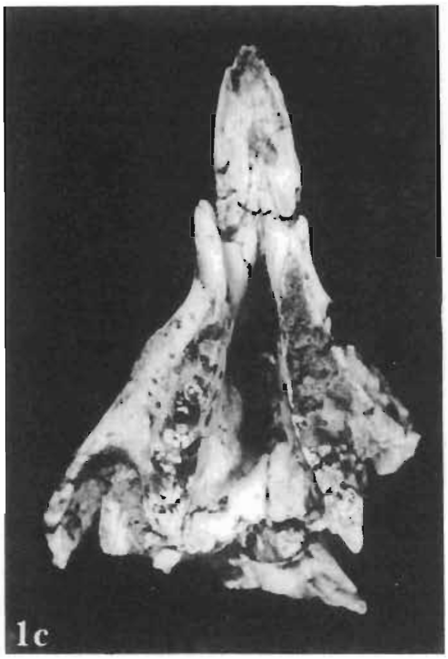
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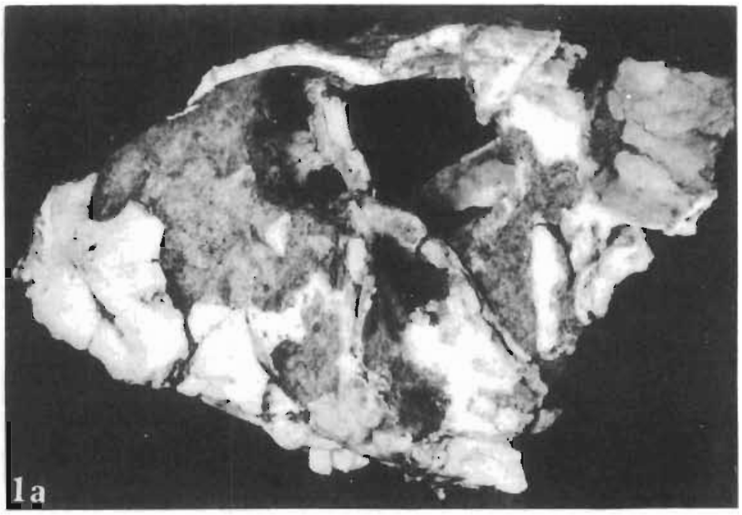
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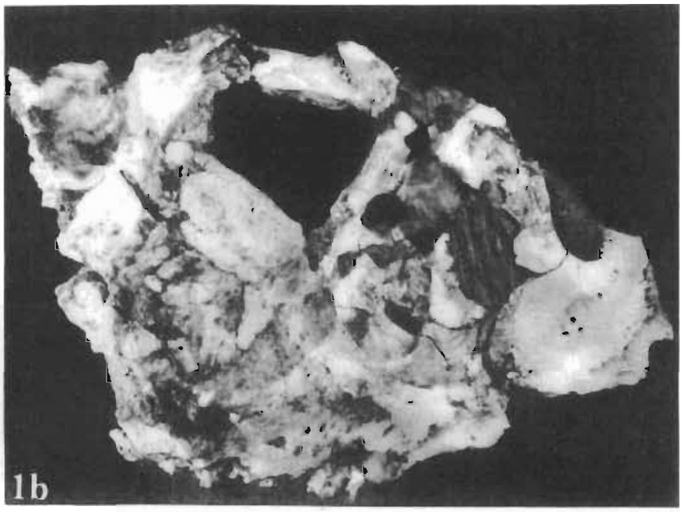
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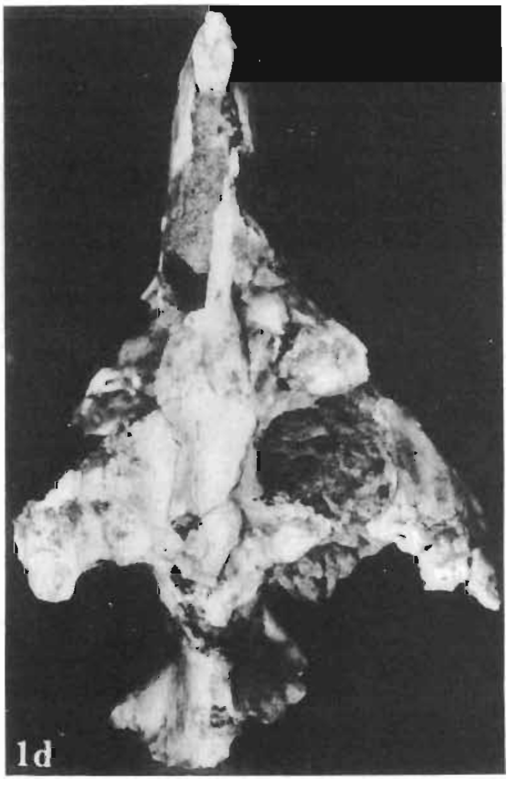
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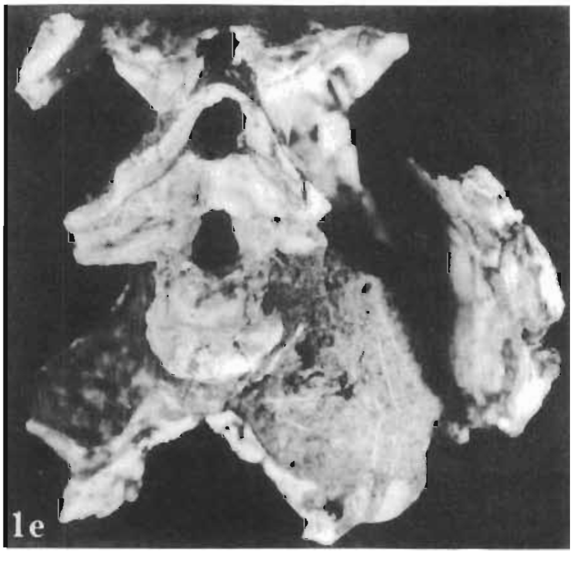
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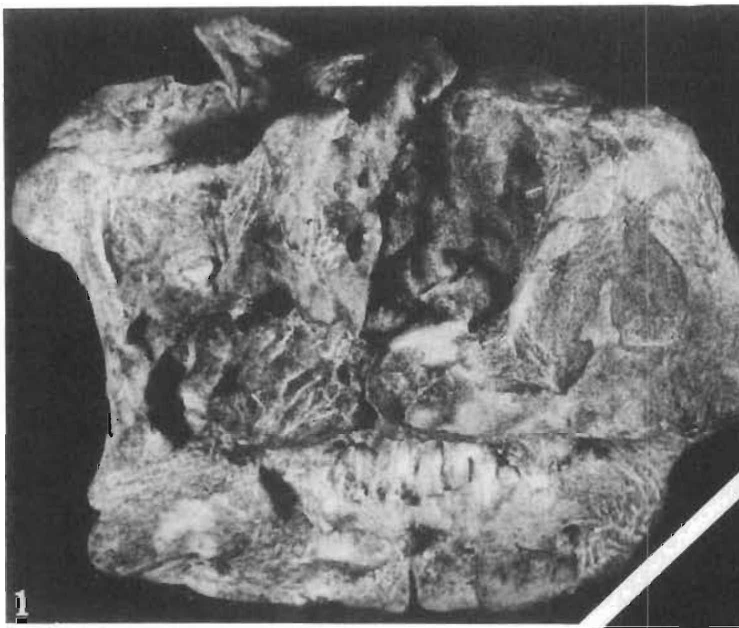
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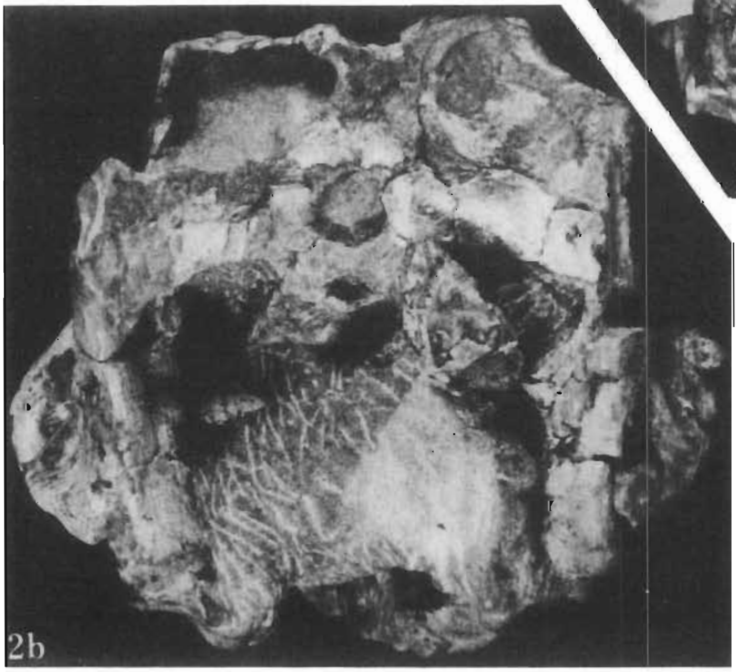
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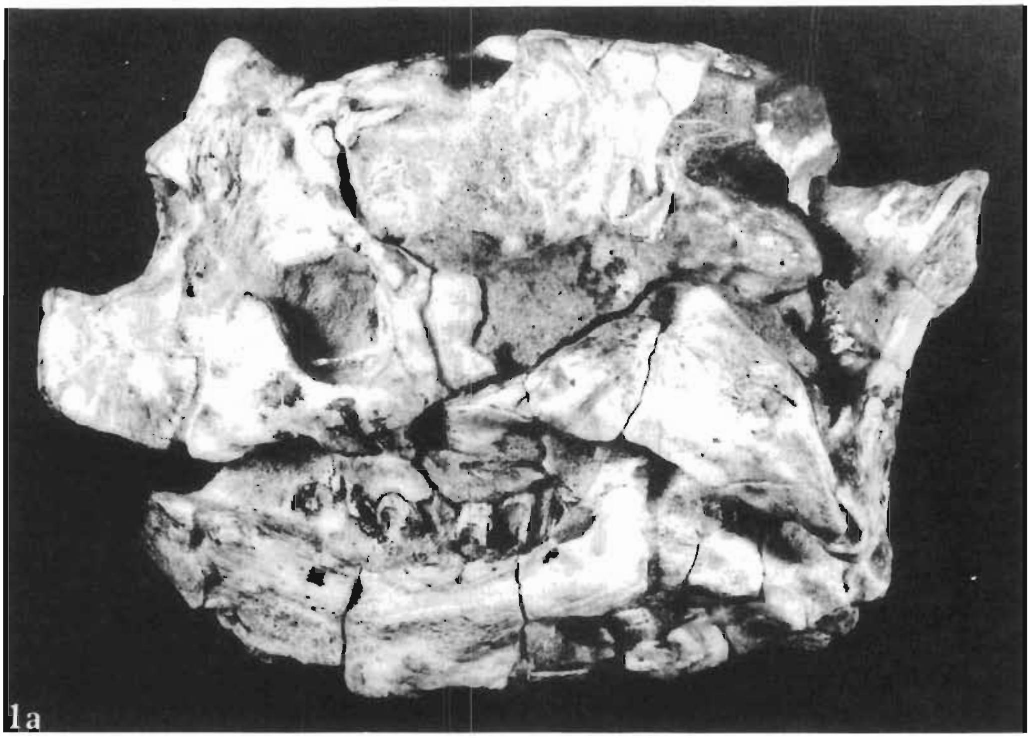

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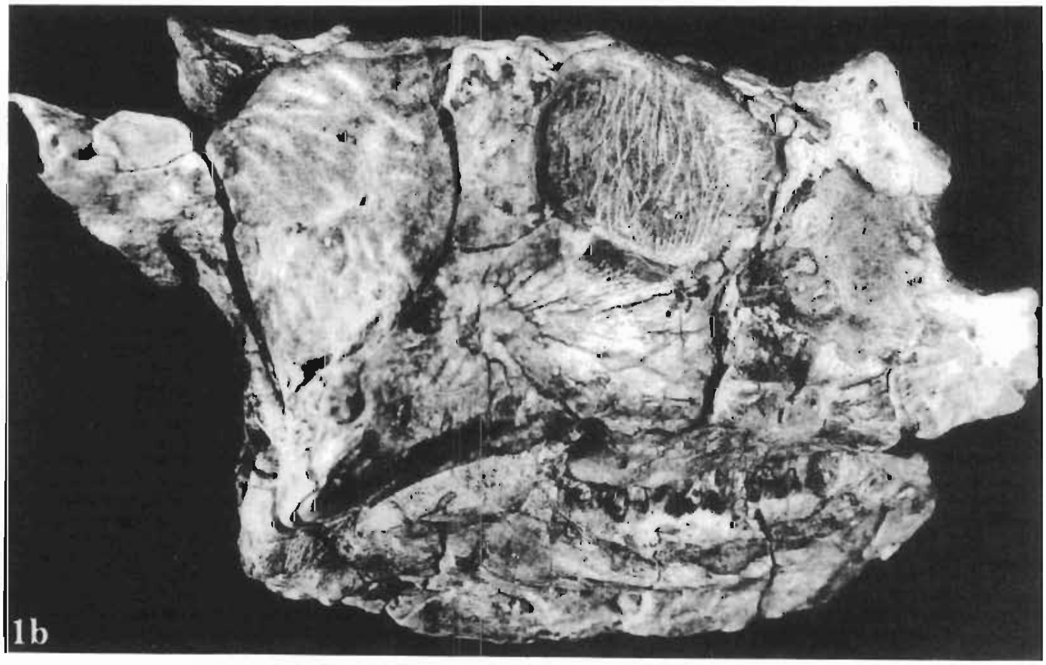

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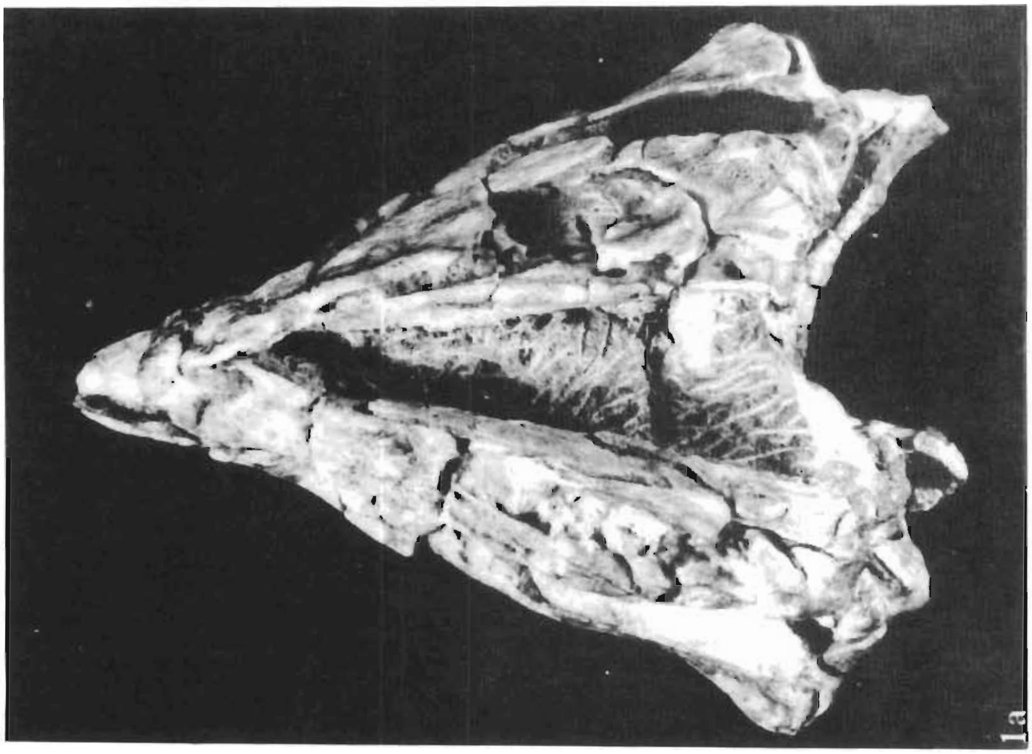
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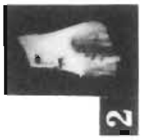
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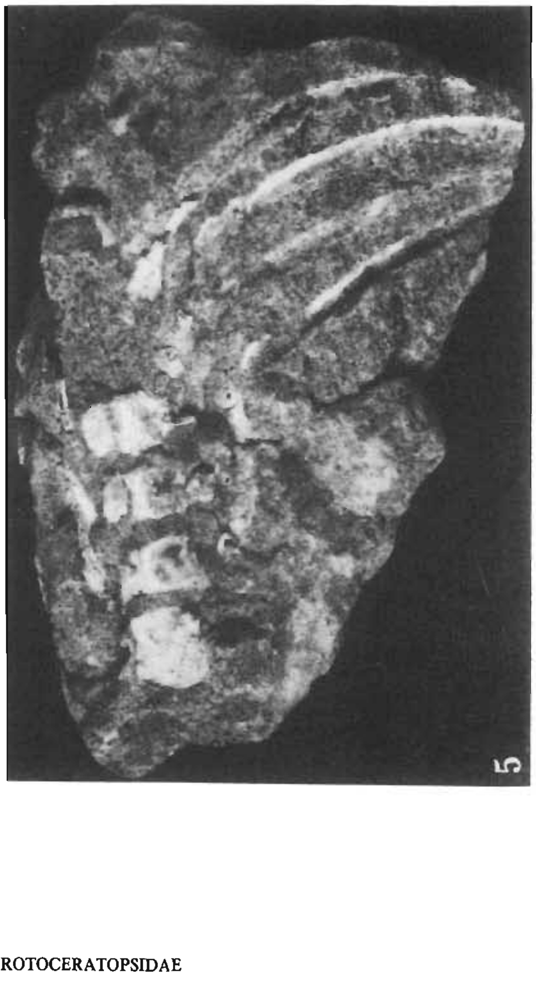
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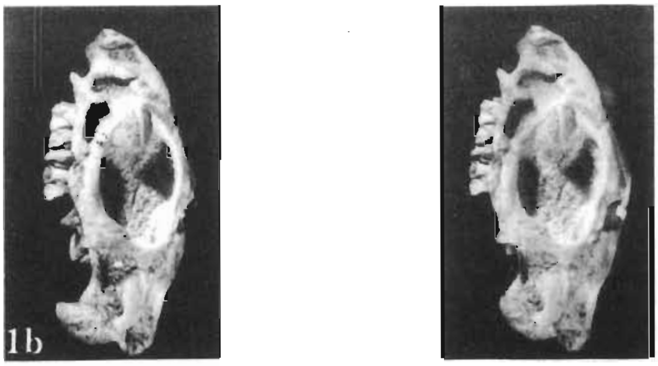
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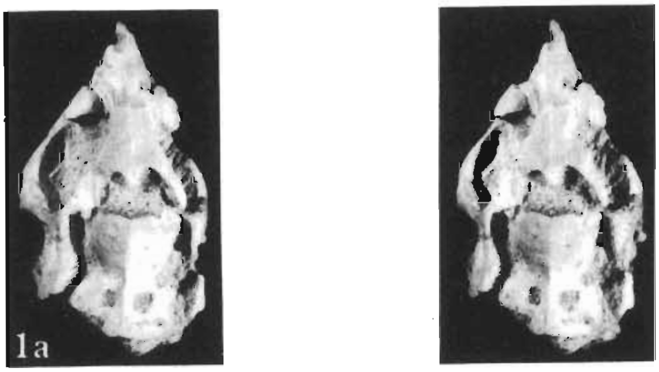
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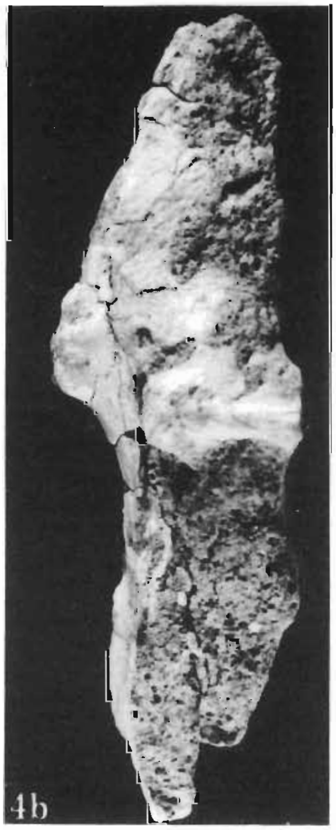
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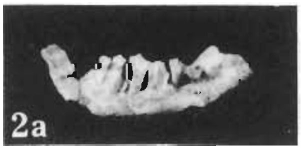
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