

A new Species of *Protoceratops* (Dinosauria, Neoceratopsia) from the Late Cretaceous of Inner Mongolia (P. R. China)¹

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Abstract

The basal neoceratopsian dinosaur *Protoceratops hellenikorhinus* nov. sp. is described on the basis of material discovered by the Sino-Belgian Expeditions in Inner Mongolia, in Campanian (Upper Cretaceous) deposits at Bayan Mandahu (Inner Mongolia, P.R. China). This new species is characterised by its large size and by a series of cranial autapomorphies linked to the important development of the mandibular adductor musculature. The nasal horns and the fronto-parietal depression are better developed in adult males of *Protoceratops hellenikorhinus* than in *P. andrewsi*. Ontogenetic data indicate that development of the nasal horns is delayed after the appearance of sexual discriminant characters in *P. hellenikorhinus*. Two discriminant functions, based on only three measurements, were established: the first one separates the two species of *Protoceratops*, while the second one separates adult males from adult females and juveniles within the genus *Protoceratops*. Phylogenetic analysis indicates that the family Protoceratopsidae, including *Protoceratops* and *Bagaceratops*, is monophyletic. Basal Neoceratopsia appeared in Asia, then migrated to North America. The following migrations (from Asia to North America but also possibly the return to Asia) could have happened at different loci of the Neoceratopsia phylogenetic tree.

Key words: Neoceratopsia, *Protoceratops*, Late Cretaceous, Inner Mongolia, phylogeny.

Résumé

Protoceratops hellenikorhinus nov. sp., un néocératopsien primitif, est décrit sur base d'ossements découverts par les Expéditions Sino-Belges en Mongolie intérieure, dans les dépôts du Campanien (Crétacé Supérieur) de Bayan Mandahu (Mongolie intérieure, R. P. de Chine). Cette nouvelle espèce est caractérisée par sa grande taille et une série d'apomorphies liées au développement important des muscles adducteurs de la mandibule. Les cornes nasales et la dépression fronto-pariétale sont plus développés chez les mâles adultes de *Protoceratops hellenikorhinus* par rapport à *P. andrewsi*. Des données ontogénétiques montrent que les cornes nasales ne s'individualisent chez *Protoceratops hellenikorhinus* qu'après l'apparition des caractères sexuellement discriminants. Deux fonctions discriminantes, basées sur seulement trois mesures crâniennes, ont été établies, l'une pour séparer les deux espèces du genre *Protoceratops*, et l'autre pour séparer les mâles adultes des femelles adultes et juvéniles au sein du genre *Protoceratops*. Une analyse phylogénétique permet de montrer le caractère monophylétique de la famille Protoceratopsidae, incluant les genres *Protoceratops* et *Bagaceratops*. Les néocératopsiens primitifs sont apparus en Asie avant de migrer vers l'Amérique du Nord. Les migrations successives (d'Asie vers l'Amérique du Nord mais également un possible retour en Asie) ont pu se produire à différents endroits de l'arbre phylogénétique des néocératopsiens.

Mots-clefs: Neoceratopsia, *Protoceratops*, Crétacé supérieur, Mongolie intérieure, phylogénie.

Introduction

Protoceratops is probably the most emblematic dinosaur from the Gobi Desert. The first specimen was discovered in the Djadokhta Formation (Campanian) at the legendary Flaming Cliffs (Bayn Dzak, P. R. Mongolia) by the Third Central Asiatic Expedition of the AMNH on September 2, 1922 (ANDREWS, 1932). This skull (AMNH 6251) of a juvenile individual, lacking the front of the face and the frill, was described as *Protoceratops andrewsi* GRANGER & GREGORY, 1923. Numerous well-preserved specimens were subsequently unearthed during field seasons 1923 and 1925. DASHZEVEG (1963) discovered a new locality with *P. andrewsi* at Toogreeg, in the same area and in the same formation as the type locality Bayn Dzak. In 1971, the Polish-Mongolian expeditions collected three specimens of *P. andrewsi* at Toogreeg (MARYANSKA & OSMOLSKA, 1975). Besides *P. andrewsi*, the Djadokhta Formation has also yielded the larger basal Neoceratopsia *Udanoceratops tshizhovi* KURZANOV, 1992. Other basal Neoceratopsia were discovered in Late Cretaceous formations of P.R. Mongolia: *Microceratops gobiensis* BOHLIN, 1953 (Bayn Shiren Fm: Turonian – Lower Campanian), *Bagaceratops rozhdestvenskyi* MARYANSKA & OSMOLSKA, 1975 and *Breviceratops kozlowskii* (MARYANSKA & OSMOLSKA, 1975; KURZANOV, 1990) (Barun Goyot Fm: Campanian). SERENO (2000) considered *Breviceratops* as a junior synonym of *Bagaceratops*. NESSOV also described new Neoceratopsia taxa from Central Asia: *Asiaceratops salsopaludalis* NESSOV & KAZNYSHKINA, 1989 (Lower Cenomanian of Karakalpakstan Autonomous Republic, Uzbekistan), *Turanoceratops tardabilis* NESSOV & KAZNYSHKINA, 1989 (Upper Turonian of Uzbekistan) and *Kulceratops kulensis* NESSOV, 1995 (Upper Albian of Karakalpakstan Autonomous Republic, Uzbekistan).

Basal Neoceratopsia are also known from northern China. From winter 1929 to May 1931, Sino-Swedish Expeditions investigated Cretaceous localities in Inner

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Mongolia and western Kansu provinces. From the material collected in Kansu, BOHLIN (1953) established the new genus *Microceratops* with two species: *Microceratops gobiensis*, from Tsondolein Khuduk and ? *M. sulcidens*, from Chia Yü Kuan. DODSON & CURRIE (1990) considered only one species of the genus *Microceratops*, *M. gobiensis*. SERENO (2000) regarded

M. gobiensis and *M. sulcidens* as *nomina dubia* because of the absence of any diagnostic features on the holotype material and the abundance of immature individuals. From one articulated and immature skeleton referred by MARYANSKA & OSMOLSKA (1975) to *M. gobiensis*, he built a new genus and species, *Graciliceratops mongoliensis*. BOHLIN (1953) also described scarce fossils

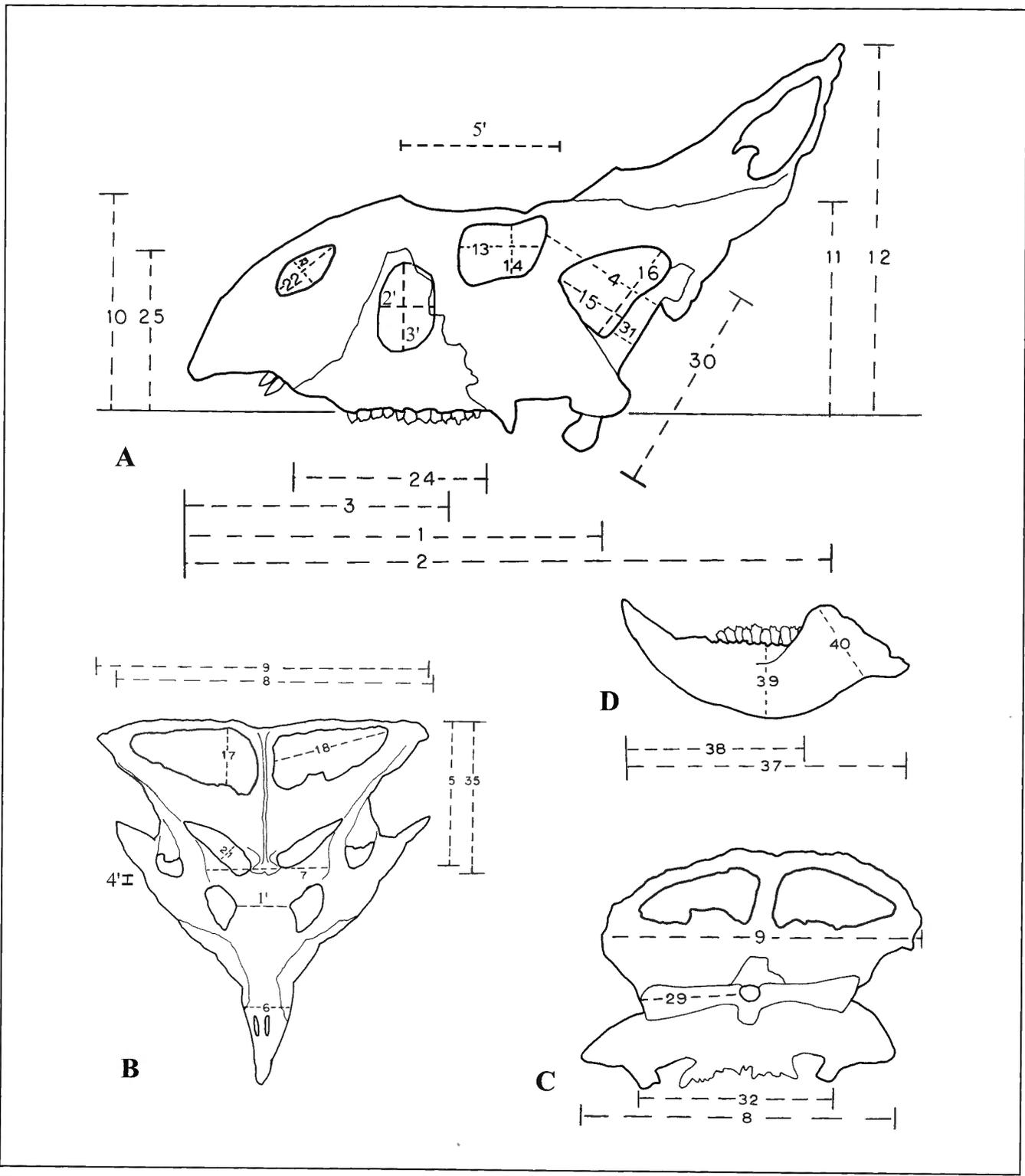


Fig. 1 — Cranial measurements of *Protoceratops*. A. Left lateral view of the skull (schematic drawing of a *P. andrewsi* from AMNH). B. Dorsal view. C. Occipital view. D. Lateral view of the jaw. (DODSON, 1976, mod.).

discovered at Ulan-Tsonch in Inner Mongolia as *Protoceratops andrewsi*. However, this material is too fragmentary to be identified at a specific or even at a generic level. Other Chinese Neoceratopsia include *Archaeoceratops oshimai* DONG & AZUMA, 1997, from the Lower Cretaceous of the Mazongshan area Gansu Province. SERENO (1997) also regarded *Chaoyangsaurus youngi* ZHAO, CHENG & XU, 1999, from the Middle or Upper Jurassic of Liaoning Province, as a Neoceratopsia. However, ZHAO *et al.* (1999) preferred the hypothesis that *Chaoyangsaurus* is the sister group to *Psittacosaurus* + Neoceratopsia, but indicated that more material is needed to determine its phylogenetic position more precisely.

The Bayan Mandahu Formation of Inner Mongolia lies about 50 km northwest of the Lang Shan mountains that separate the southern part of the Mongolia plateau and Gobi Basin from the Yellow River alluvial plain (see location map in SMITH *et al.*, this volume). The fossiliferous deposits are exposed along the Ni Qi Daba Gorge that cuts the badlands of Bayan Mandahu. This gorge is approximately 45 km long, 1 to 5 wide and 24 to 32 m deep (DONG & CHENG, 1996). The Bayan Mandahu formation is located about 25 km west of Ulan-Tsonch locality previously investigated by Sino-Swedish expeditions. The Bayan Mandahu Formation was explored in 1988 and 1990 by Sino-Canadian expeditions (see e.g. DONG, 1993) and subsequently by Sino-Belgian expeditions in 1995, 1996 and 1999. Sedimentary, geological and palaeontological data indicate that the Bayan Mandahu Formation and the Djadokhta Formation in P.R. Mongolia are stratigraphic correlatives (JERZYKIEWICZ *et al.*, 1993). The vertebrate fauna of Bayan Mandahu includes a variety of squamates (WU *et al.*, 1996; GAO & HOU, 1996), the turtle *Zangerlia neimongolensis* (see BRINKMAN & PENG, 1996), multituberculate mammals (SMITH *et al.*, this volume), the theropod dinosaurs *Oviraptor philoceratops* (see DONG & CURRIE, 1996), *Velociraptor mongoliensis* (JERZYKIEWICZ *et al.*, 1993) and *Saurornithoides mongoliensis* (see CURRIE & PENG, 1993), and the ankylosaur *Pinacosaurus mephistocephalus* (see GODEFROIT *et al.*, 1999). However, the Bayan Mandahu fauna is largely dominated by protoceratopsian dinosaurs. DONG & CURRIE (1993) referred embryonic remains to both *Protoceratops andrewsi* and cf. *Bagaceratops* sp. JERZYKIEWICZ *et al.* (1993) also suggested the presence of the larger form *Udanoceratops*.

We describe and discuss herein protoceratopsian specimens collected at the occasion of the Sino-Belgian dinosaur expeditions (SBDE) in 1995 and 1996. These are 7 skulls or partial skulls and some post-cranial bones (see list on Appendix 1). All diagnostic material belongs to a single new species, named *Protoceratops hellenikorhinus* nov. sp.

Abbreviations: AMNH: American Museum of Natural History, New York, U.S.A.; IMM: Inner Mongolia Museum, Hohhot, P. R. China; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, P. R. China; PIN: Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; RBINS: Royal Belgian Institute of Natural Sciences, Brussels

Description of the measurements (see Fig. 1): Most of the measurements (from 1 to 40) used in the present paper are those defined by DODSON (1976, tab.2 and text-fig. 1) in *Protoceratops andrewsi*. Five additional measurements (1' to 5') were taken on *P. hellenikorhinus* studied specimens and on *P. andrewsi* reference material in the AMNH (see Table 1):

- 1'. **Distance between orbits:** minimal distance between dorsal margins of the orbits.
- 2'. **Antorbital fenestra length:** maximal length of the fenestra, taken perpendicularly to the maxilla height.
- 3'. **Antorbital fenestra height:** maximal height of this fenestra.
- 4'. **Distance between orbit and supratemporal fenestra:** minimal distance between caudodorsal margin of the orbit and rostral margin of the supratemporal fenestra.
- 5'. **Distance between nasal 'horns' and supratemporal fenestra:** distance between tip of the nasal 'horn' and rostral margin of supratemporal fenestra, parallel to the bilateral symmetry axis of the skull.

Systematic palaeontology

- Order Ornithischia SEELEY, 1888
 Hypo-order Marginocephalia SERENO, 1986
 Suborder Ceratopsia MARSH, 1890
 Infraorder Neoceratopsia SERENO, 1986
 Family Protoceratopsidae GRANGER & GREGORY, 1923
 Genus *Protoceratops* GRANGER & GREGORY, 1923

Type-species: *Protoceratops andrewsi* GRANGER & GREGORY, 1923

Other referred species: *Protoceratops hellenikorhinus* nov. sp.

Emended generic diagnosis: Protoceratopsidae with the following apomorphic characters: tip of prementary reaching or standing higher than the level of the dorsal edge of the coronoid process; double nasal horn.

The following characters differentiate *Protoceratops* from *Bagaceratops* (sister-group), but they are either plesiomorphic, or their polarity cannot be asserted in the current state of our knowledge: frill inclined in a caudodorsal direction, parietal fenestrae better developed, squamosal-jugal suture visible laterally on the rostradorsal edge of the infratemporal fenestra, absence of additional antorbital fenestra and higher mandible.

Protoceratops hellenikorhinus nov. sp.

Derivatio nominis: *hellenikos* (Greek), relative to ancient Greece; *rhis* (Greek), nose; with its elevated and angular snout, this species has some kind of Greek profile.

Holotype: IMM 95BM1/1, nearly complete skull of a 'male' specimen.

Paratype: IMM 96BM1/4, nearly complete skull of a 'female' specimen.

Locus typicus: Quarry 95BM1/1 (N 41° 44' 485'' - E 106° 44' 703'' - Altitude 1307 m) Bayan Mandahu, Urad Houqi Banner, Bayan Nor League, Inner Mongolia Province, People's Republic of China (see location plan in SMITH *et al.*, this volume).

Stratum typicum: Bayan Mandahu Formation, ? correlated with the Djadokhta Formation in People's Republic of Mongolia, Campanian, Upper Cretaceous.

Diagnosis: Ventral edge of the dentary straight; caudal edge of the angular formed by a caudally facing triangular surface; long projection of the squamosal contacting the quadratojugal; straight and strongly reduced longitudinal ridge on maxilla.

DESCRIPTION OF THE HOLOTYPE IMM 95BM1/1 (see Figs. 2, 3 and 4; Plates 1 and 2)

This very well preserved skull was found isolated, without postcranial elements. It was discovered with its snout pointing upwards: this 'standing' pose is common for *Protoceratops* specimens discovered in both the Djadokhta and the Bayan Mandahu formations (see JERZYKIEWICZ *et al.*, 1993). The only missing pieces of the skull are the rostral bone (and the rostralmost portion

Measurements/Specimens	IMM 95BM1/1	IMM 96BM1/4	IMM 96BM2/1	IMM 96BM1/7	IMM 96BM1/1	IMM 96BM5/5	IMM 96BM5/3
1. basal skull len	430	305	225	365			
2. total skull len	720		389		690		
3. preorbital len	288	260	112	340			
4. postorbital len	170	118	111		185	220	35
5. frill len	320		181				
6. skull wid maxilla	86	38	27	54			
7. skull wid postorb	230	147		148			
8. skull wid jugal	554	425					
9. skull wid frill	624						
10. skull ht nasal	325	154	118	200	318		
11. skull ht postorb	275		148				
12. skull ht frill	441		158				
13. orbit len	103		67				
14. orbit ht	90		38				
15. lat temp. fen len	100	59	51		94	115	20
16. lat temp. fen ht	98	77	74		99	141	18
17. parietal fen len			53				
18. parietal fen wid			37				
21. up temp. fen wid	71	46					
22. ext. nares len	72		27	45			
23. ext. nares wid	27		12	19			
24. maxilla len	215		110				
25. maxilla ht	197		81				
29. exoccipital len	208						
30. quadrate len	256	180	120				
31. quadrate wid	24		16				
32. quadrate sep	392	330					
35. parietal len	340		185				
37. jaw len total	414	306		410	425		
38. jaw len to cor pr	255						
39. ht ramus	106			101	115		
40. ht coronoid proc	133			131			
1'. dist between orbits	87	86					
2'. antorb fen len	71		38			85	
3'. antorb fen ht	126	85	52			132	
4'. dist orb-suprtemp fen	41	38	33				
5'. dist horn-suprtemp fen	161	134	122	163			

Table 1 — Measurements taken on the seven best-preserved skulls of *Protoceratops hellenikorhinus*, following DODSON (1976) for the measurements 1 to 40. The measurements are in millimeters.

of the premaxillae), the caudal part of the basioccipital and the longitudinal median ridge of the frill formed by the parietals. This skull does not show any indication of post-mortem deformation. Some sutures are less clear than others (for example in the area of the nasals, the lacrimals and the prefrontals). This is a large-sized skull, with a basal length and a total length respectively estimated at 430 and 720 mm.

Premaxilla -The rostralmost part of this bone is eroded, because this part of the skull was exposed when this specimen was discovered in the field. The suture with the nasal is partially visible, indicating that the ventral part of the external naris is formed by the premaxilla. The suture with the maxilla slopes rostroventrally. The ventral margin of the premaxilla is straight and continuous with the rostral part of the ventral margin of the maxilla. No evidence of premaxillary teeth has been found: there is no trace of sockets and the ventral edge remains thin along its whole length.

Antorbital fossa -This fossa forms an oval depression extending on the maxilla, the lacrimal and a small part of the jugal. The great axis of the fossa is slightly oblique with the dorsal edge in a more caudal position than the ventral one. Both its ventral and dorsal margins are excavated by pockets that are attenuated rostrally, but well

marked caudally. The dorsal margin of the antorbital fossa reaches the level of the ventral third of the orbit.

Maxilla - The antorbital fossa forms a large depression on the lateral side of this triangular bone. Ventrally to this fossa, the lateral side of the maxilla is wavy: rostral and caudal slight depressions are separated by a convex area. Ventrally, the alveolar part of the maxilla is shifted medially and separated from the rest of the bone by a straight, sub-horizontal and smooth ridge. This ridge forms an angle of about 120° with the ventral border of the jugal. The ventral edge of the maxilla is straight as far as the first alveolus, then it slopes rostradorsally towards the premaxilla - maxillary suture. Only 2 or 3 maxillary teeth are preserved and the alveoli for the other teeth are hardly discernible; anyway, there are at least 11 alveoli for each maxilla.

Lacrimal -The sutures of this bone with the maxilla, nasal, prefrontal and jugal are not easily observable. The lacrimal forms the rostral margin of the orbit and encloses the caudodorsal part of the antorbital fossa.

Nasal - In lateral view, this bone is strongly angular, so that it forms a prominent bowed arch on the rostradorsal part of the skull. The paired nasals form a dorsomedian gutter that progressively deepens backwards where it separates two distinct nasal horns, whose tips are 4 cm dis-

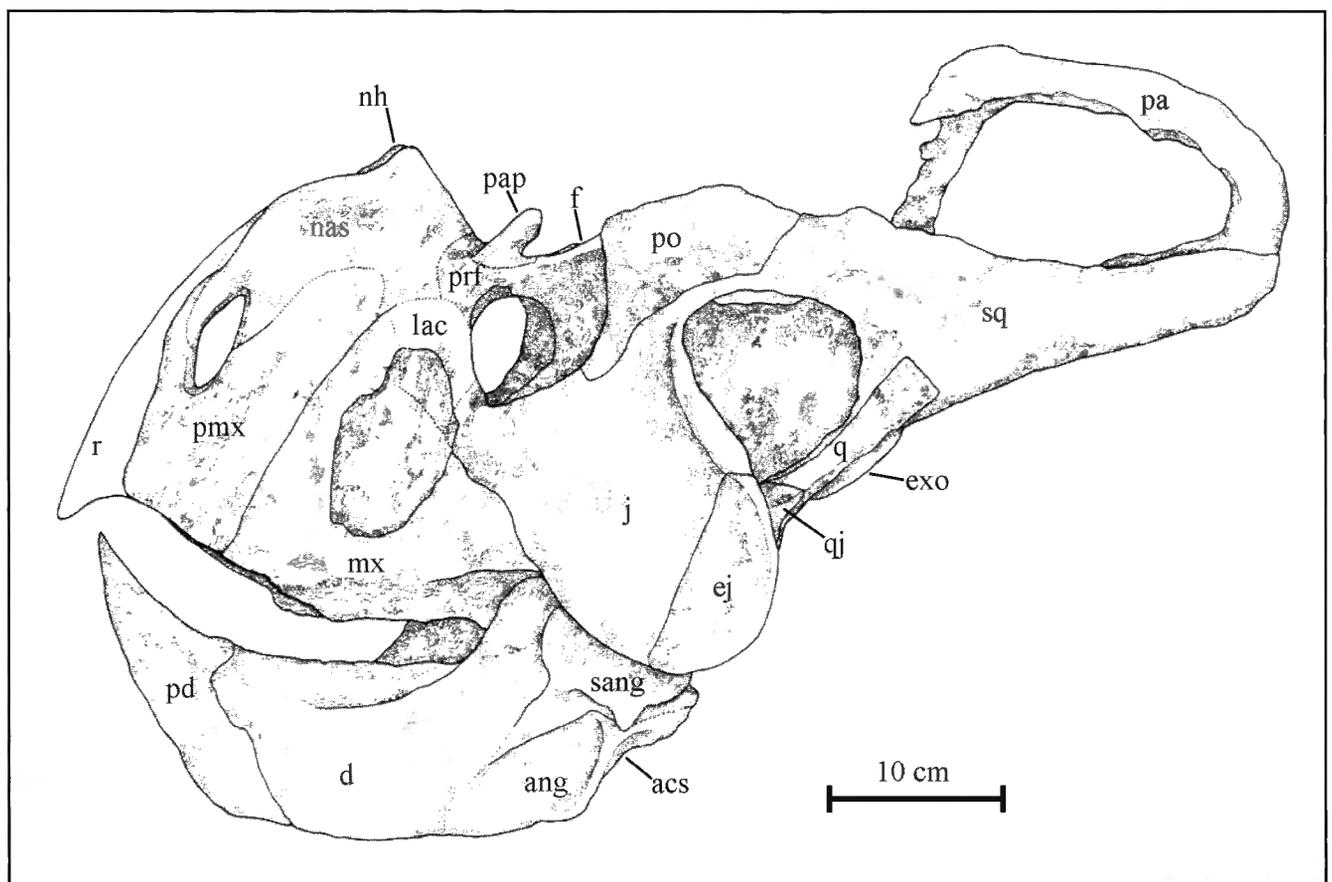


Fig. 2 — Skull of the holotype of *Protoceratops hellenikorhinus* (IMM 95BM1/1) in left lateral view. acs: angular caudal surface; ang: angular; d: dentary; ej: epijugal; exo: exoccipital; f: frontal; j: jugal; lac: lacrimal; mx: maxilla; nas: nasal; nh: nasal horns; pa: parietal; pap: palpebral; pd: prementary; pmx: premaxilla; po: postorbital; prf: prefrontal; q: quadrate; qj: quadratojugal; r: rostral; sang: surangular; sq: squamosal.

tant. These nasal horns exceed the level of the dorsal edge of the postorbitals in height. They are distinctly limited rostrally by a concavity on the dorsal margin of the nasals; their caudodorsal border is straight and very inclined towards the orbits. In dorsal view, the lateral sides of the nasal are steeply inclined ventrally; the nasals consequently form a wide-based dome, giving the snout a massive aspect. The dorsal margin of the small, elongated and nearly vertical external nares is formed by the nasals.

Prefrontal - The prefrontals form the rostradorsal limit of the orbits. They are medially separated from each other by the contact between the nasals and the frontals and they are pushed laterally by the strong development of the nasals.

Palpebral - This triangular bone, which contacts medially the prefrontal, is thick and prominent. It extends backwards, outwards and slightly upwards and roofs the orbit. Indeed, the palpebral partially covers a lateral notch in the frontal, along the dorsomedial side of the orbit.

Postorbital - On the caudodorsal corner of the orbit, the postorbital has the shape of a wing in lateral view. It extends caudally towards the level of the middle of the infratemporal fenestra. Its dorsal edge is convex, forming a dorsal protuberance in lateral view of the skull. Its dorsolateral side bears a longitudinal crest that progressively attenuates backwards. The ventral process of the postorbital, which participates in the caudal margin of the orbit,

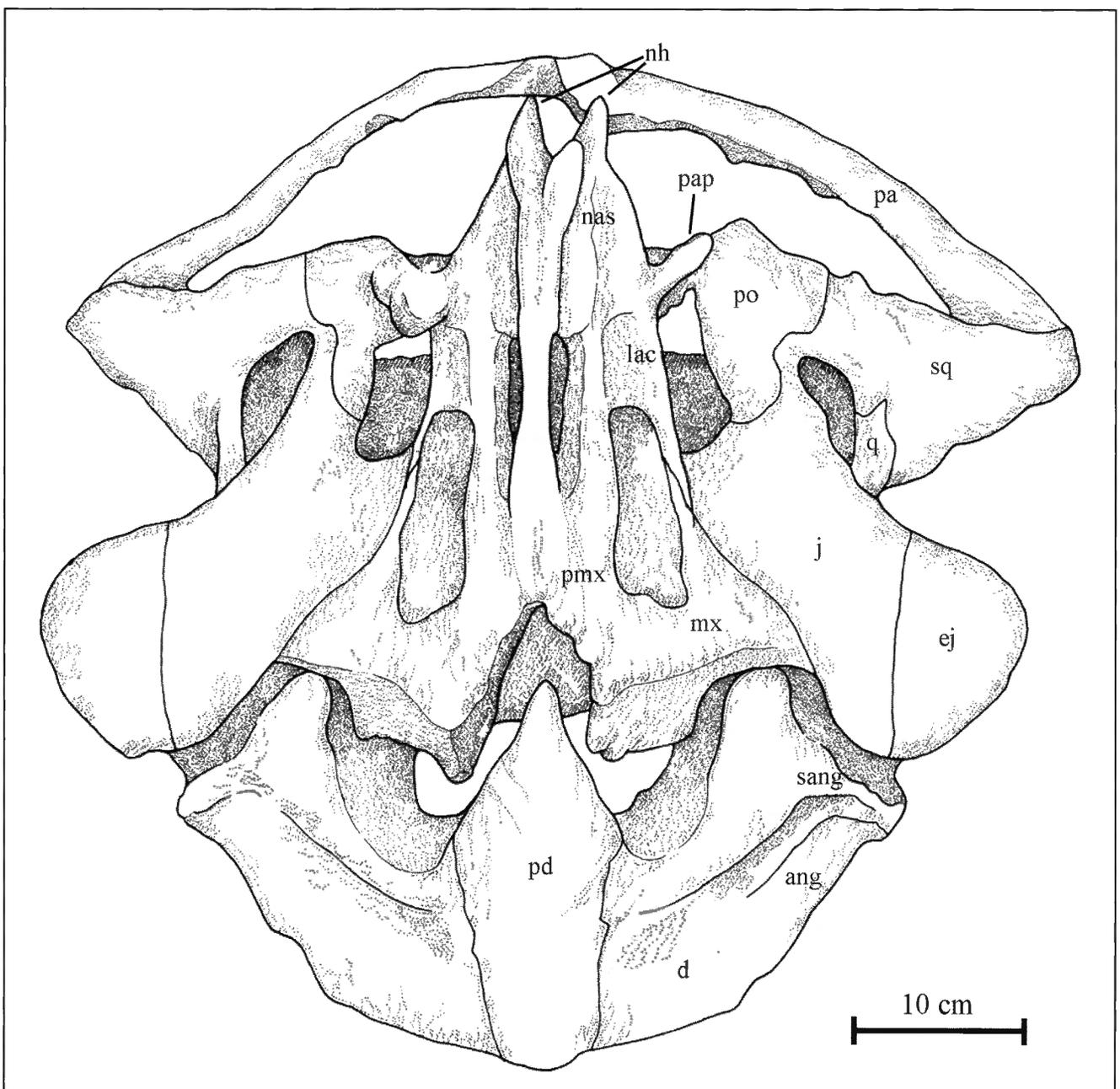


Fig. 3 — Skull of the holotype of *Protoceratops hellenikorhinus* (IMM 95BM1/1) in rostral view. ang: angular; d: dentary; ej: epijugal; j: jugal; lac: lacrimal; mx: maxilla; nas: nasal; nh: nasal horns; pa: parietal; pap: palpebral; pd: predentary; pmx: premaxilla; po: postorbital; q: quadrate; sang: surangular; sq: squamosal.

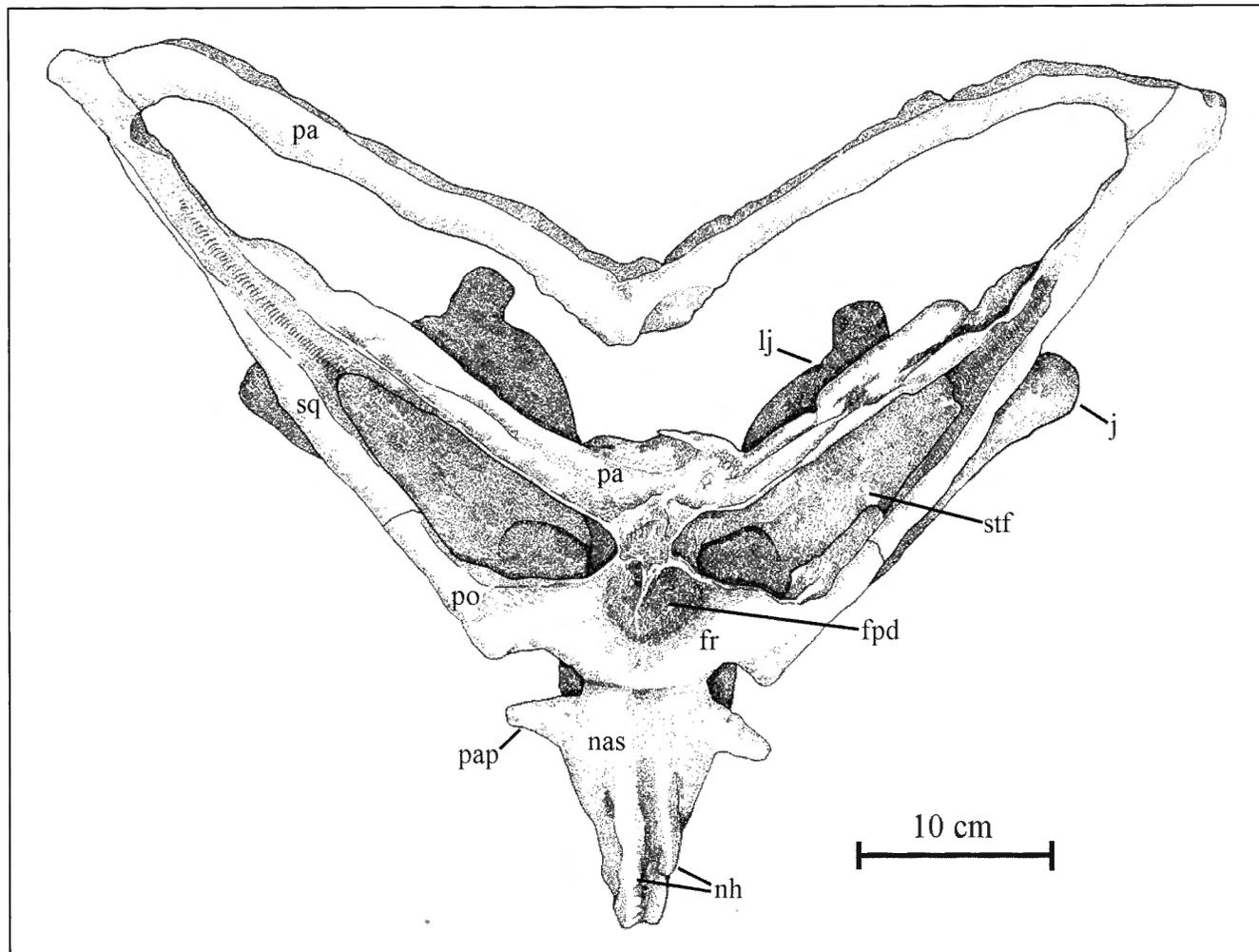


Fig. 4 — Skull of the holotype of *Protoceratops hellenikorhinus* (IMM 95BM1/1) in dorsal view. f: frontal; fpd: fronto-parietal depression; j: jugal; lj: lower jaw; nas: nasal; nh: nasal horns; pa: parietal; pap: palpebral; po: postorbital; sq: squamosal; stf: supratemporal fenestra.

is rather slender; its rounded tip does not reach the level of the ventral border of the orbit.

Frontal - The paired frontals form the roof of the skull between the nasals and the parietals. The strong development of the nasal dome pushes the frontals caudally, so that the nasal-frontal suture has a rounded and caudally concave shape. A strong fronto-parietal depression excavates the caudal part of the frontals and a small rostral portion of the parietals. This depression is deeper rostrally and its rostral wall is very steeply inclined. It extends forwards beyond the level of the middle of the orbits.

Parietal - The parietals of IMM 95BM1/1 are incompletely preserved: a part of the median ridge and the margins of the parietal fenestrae are missing. They are very thin, except along the caudal margin of the frill and on the median ridge. The lateral border of the thin dorsal plate of the parietal is deeply notched by the long and very wide supratemporal fenestra; however, a thin lateral ramus of the parietal still contacts the postorbital and the squamosal. At first sight, the frill of IMM 95BM1/1 appears relatively low, when compared to that of the largest specimens of *Protoceratops andrewsi*. However, DODSON (1976)

showed that the biometrical characteristics of the frill are highly variable in *P. andrewsi*. Moreover, most of the frills of the specimens on display in the AMNH and in the PIN are reconstructed (pers. obs.) and cannot be considered in biometrical analyses. The bilogarithmic diagram presented in Fig. 5 represents the evolution of the height of the skull at the level of the frill (measurement 12 of DODSON, 1976), relatively to the basal length of the skull (measurement 1 of DODSON, 1976). The allometry coefficient between both variables, calculated from *P. andrewsi* specimens, is 1.26 (DODSON, 1976, tab. 2); it means that taller specimens have relatively higher frills than smaller individuals. Fig. 5 also demonstrates that IMM 95BM1/1 is not significantly distant from the calculated line of Bartlett's best fit for *P. andrewsi*. Therefore, it cannot be demonstrated that the frill of IMM 95BM1/1 is lower than that of large *P. andrewsi* individuals. The partial parietal fenestrae preclude a precise comparison with *P. andrewsi* that seems to have less developed fenestrae.

Jugal - This bone is particularly massive and occupies a large surface on the lateral side of the skull. Its ventral border is very rounded, in discontinuity with the longitudinal ridge of the maxilla. The jugal extends far backwards

and downwards, hiding the ventral part of the quadrate, the articulation of the mandible and part of the coronoid process in lateral view. In rostral view, the caudal part of the jugals flares out laterally, giving the skull a particularly wide aspect.

Epijugal – As usual in Neoceratopsia, epijugals are well developed, covering the distal end of the jugals.

Squamosal - The squamosal is a triradiate bone, formed by a main rostro-caudally oriented sub-horizontal blade, a ventral process and a medial wing of this process. The main ramus participates in the lateral border of the frill, supporting the caudal expansion of the parietal. The rostral contact with the jugal is relatively reduced, a thin projection of the squamosal passing between the postorbital and the infratemporal fenestra towards the jugal. In lateral view, the dorsal border of the main blade is slightly convex in its rostral part and concave caudally. The ventral process is long and slender, extending rostrally along the sulcus between the shaft and the lateral wing of the quadrate. This process tapers ventrally and reaches the quadratojugal on the caudoventral corner of the infratemporal fenestra. The ventral process sends a medial wing covering rostrally the medial wing of the quadrate and then, reinforcing it. A second shorter and thinner ventral process of the squamosal extends caudally along the dorsal end of the quadrate.

Quadrate - The quadrate connects the skull with the mandible, contacting both the articular and the surangular. As previously described, the dorsal end of the quadrate is strongly embedded in the ventral part of the squamosal, preventing any mobility: the distal end of the quadrate is wedged between two ventral processes of the squamosal, while its medial wing is coupled with a lateral wing of the squamosal. The distal articular surface of the quadrate is very wide and massive.

Quadratojugal - This bone is not easy to distinguish. It forms the contact point between the caudal surface of the jugal, the ventral projection of the squamosal and the shaft of the quadrate. It contacts the caudoventral corner of the infratemporal fenestra along a short distance.

Exoccipital - This bone forms a sub-horizontal rod extending caudolaterally from the lateral margin of the foramen magnum towards the level of the caudal edge of the quadrate shaft. The exoccipital becomes progressively higher laterally and its lateral margin is rounded. Sutures between squamosal, exoccipital and quadrate on the internal surface of the quadrate are not clear.

Pterygoid - The palate of IMM 95BM1/1 is hidden because the lower jaw is still in connection with the skull. However, the pterygoid appears very short, as observed between the ectopterygoid and the basioccipital.

Prementary - This bone, which forms the rostral margin of the mandible, is very massive, rostrally keeled and rostradorsally pointed. Its dorsal margin is slightly concave; caudally it is subdivided into two branches whose dorsal surface faces laterally. Both the rostral and ventral margins of this bone are nearly straight, forming together an angle of about 125°. A weak constriction on the ventral border of the mandible marks the contact with the dentary.

Dentary - This bone takes an important part in the lateral surface of the mandible. Its dorsal border is very wide, straight, horizontal and pierced by alveoli for more than 10 dentary teeth. The dentary forms the rostral portion of a wide coronoid process. This process is much higher than the alveolar surface of the dentary; its rostral border extends rostrally as an horizontal ridge running along the two thirds of the height of the bone and progressively attenuating. Mainly this ridge is responsible for the very robust aspect of the dentary. The ventral margin of the dentary is much thinner than the dorsal part and nearly perfectly straight, parallel to the alveolar surface of the bone.

Angular - This bone forms the caudoventral corner of the mandible. Its ventral margin is particularly thin and forms an angle of about 130° with its caudal side. The latter progressively widens dorsally, forming a slightly concave triangular surface facing caudally, with the straight dorsal border forming the caudal suture with the surangular.

Surangular - This bone takes an important part in the articulation of the mandible with the quadrate. In lateral view, the surangular also widely participates in the caudal portion of the coronoid process. It forms a prominent lon-

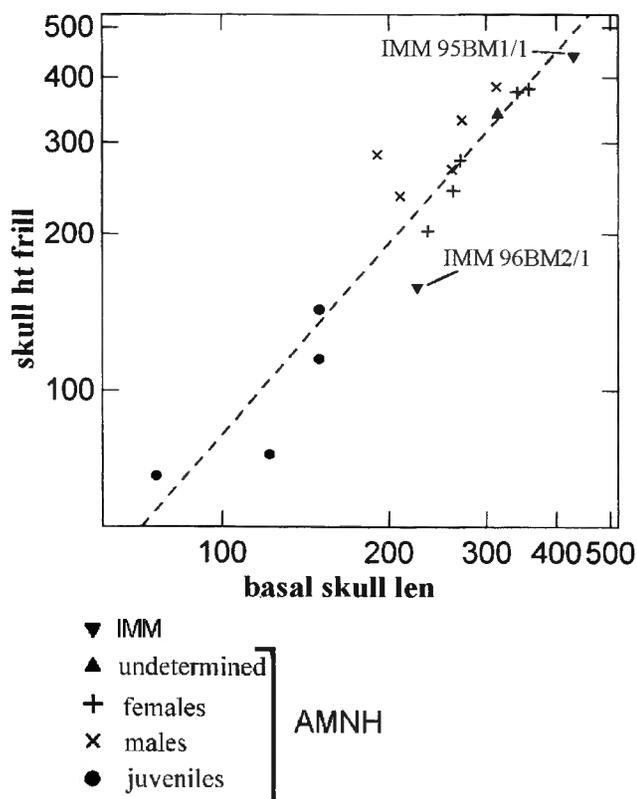


Fig. 5 — Bilogarithmic diagram showing the evolution of the height of the skull at the level of the frill (measurement 12 of DODSON, 1976) relatively to the basal length of the skull (measurement 1 of DODSON, 1976) for individuals of the two species of *Protoceratops*. Measurements are in millimeters.

gitudinal ridge just above its lateral suture with the angular. The ventral margin of this ridge slightly rises caudally.

Articular - The sutures of this bone are not easy to distinguish. Its internal part looks like a prominent hemisphere lying on the caudomedian projection of the angular and the surangular, and wedging the distal end of the quadrate medioventrally.

Splénial - This bone is set on the internal side of the mandibular branches. It is very high caudally, its dorsal border nearly reaching the alveolar surface of the dentary; its dorsal border gradually goes down forwards, so that the tapering rostral end of the splénial contacts the ventral border of the mandible in front of the symphysis. Thus, the two splénials do not come into contact.

Teeth - The teeth present on the holotype are not sufficiently well preserved to be described. So, the following description is mainly based on specimens IMM 96BM1/1, IMM 96BM5/5 and IMM 96BM5/2 (see Plate 3, Fig. 2). The teeth of *Protoceratops hellenikorhinus* are large and robust, more than 50 mm high in the largest specimens. They are single-rooted and their crown is distinctly curved: the concave side is labial on the maxillary teeth and lingual on the dentary teeth. Enamel is only present on the convex side of the crown. The apical half of the enamelled side bears a strong longitudinal ridge that separates two asymmetrical depressed areas ornamented by thinner parallel longitudinal ridges. The concave side of the teeth is worn away, indicating an oblique occlusion. Rostral and caudal sides of the teeth are hollowed by a wide and shallow longitudinal groove.

VARIATION IN *PROTOCERATOPS HELLENIKORHINUS*

Sexual dimorphism

BROWN & SCHLAIKJER (1940) diffidently suggested the existence of sexual dimorphism in *Protoceratops andrewsi*, with male characters thought to include the development of nasal horns and of the fronto-parietal depression and a greater degree of broadening of the frill. Subsequently, KURZANOV (1972) suggested the use of three ratios (measured angles rather than linear dimensions) as sexual discriminators. DODSON (1976) more intensively attempted to define and quantify sexual differences in *P. andrewsi*, using both bivariate plots and multivariate analysis. He demonstrated that measurements of the frill play a great part in the dimorphism, verifying that, in its development, the frill has more significance than simply serving as a site of origin for masticatory muscles.

A similar pattern of morphologic variation is observed in *Protoceratops hellenikorhinus*, indicating that sexual dimorphism is also important in this new species. Individuals IMM95BM1/1 (holotype), IMM 96BM5/5 and IMM 96BM1/1 can be grouped together, as they share the following characters: very high nasals with a pair of individualised horns, relatively short antorbital length and external nares with the long axis relatively close to the vertical. This group of skulls is interpreted as the adult males for this species. On the other hand, spec-

imens IMM 96BM1/4 (paratype) (see Plate 3, Fig. 1) and IMM 96BM1/7 are both characterised by their low nasals devoid of well-marked horn, their relatively longer antorbital length and their external nares with a more oblique long axis. In these individuals, regarded as female specimens of *P. hellenikorhinus*, an important lateral broadening of the dorsal top of the nasals forms two longitudinal, widened and rounded ridges that are not deeply separated. A slight fronto-parietal depression is present on the skull of the females but this is not as expanded as in the males and its rostral margin is not as steeply excavated. Unfortunately, with the exception of IMM 95BM1/1, all the specimens collected at Bayan Mandahu are too incompletely preserved to use DODSON'S (1976) method for sexual scoring. For example, the frill, which shows a great sexual dimorphism in *P. andrewsi*, is either incomplete or distorted in most specimens of *P. hellenikorhinus*.

An attempt has been made to establish a discriminant function, which separates male and female specimens and combines both species of the genus *Protoceratops*. It is based on a few measurements taken on the rostral part of the skull. The purpose of the discriminant analysis is the establishment of linear functions, based on a combination of several measurements separating as far as possible individuals belonging to two or more groups established 'a priori'. The functions maximise the ratio of the among-groups to the within-groups variance and determine the canonical space. For n groups and p measurements, there are $n-1$ discriminant functions (if $n < p$). In a second phase, it is possible to calculate the discriminant score for each individual on each function and, from this score, the probability of being a member of each group. Simple discriminant analysis is based on original descriptors: the measurements are not centred and reduced, as it is the case for the canonical discriminant analysis. Wilk's Lambda quantifies the distance between the centroids of the different groups in the multivariate space. It varies between 0 (maximal dispersion of the centroids) and 1 (no among-groups dispersion). Wilk's Lambda is a multidimensional generalisation of Student's t -test. Wilk's Lambda may be transformed into an 'Approximate F' for comparison with F distribution. (LEGENDRE & LEGENDRE, 1984, mod.)

The SYSTAT version 8.0 (SPSS Inc., 1998) programme was used to perform the discriminant analyses in the present paper. The studied sample is composed of 19 skulls of *Protoceratops andrewsi*, housed in the AMNH and a-priori classified as adult males, adult females and juveniles by DODSON (1976) (the 'unsexed' skull AMNH 6413 is rejected in the present analysis), and of 3 skulls of *P. hellenikorhinus* classified following the same criteria. Other skulls from Bayan Mandahu available for this work are not sufficiently well preserved to be included in a discriminant analysis.

The discriminant function found here is a linear combination of 3 measurements on the skulls of the genus *Protoceratops*: preorbital length (**preorb. l.**), maxillary width (**max. w.**) and nasal height (**nasal h.**). This function is:

$$Y = 0.033 \text{ preorb. l.} + 0.064 \text{ max. w.} - 0.063 \text{ nasal h.} + 0.229$$

Wilks' lambda = 0.296 Approx. F = 15.084 df = 3
 p = 0.0000 (< 0.0005)

With this function, the separation between the two groups (8 males and 14 females and juveniles) is recovered for 96 % of the sample (see Fig. 6 = canonical scores). Only one male (AMNH 6467) does not fall into the correct group. This function is practical because it is based on only 3 measurements taken on the rostral part of the skull, usually much better preserved than the caudal part.

Ontogeny

The smallest skull of the sample (IMM 96BM5/3, see Plate 4, Fig. 1) has a total length estimated at 120 mm, thus more or less six times smaller than the biggest adult male IMM 96BM5/5. Although very incomplete, IMM 96BM5/3 displays the contact between the squamosal and the quadratojugal on the caudoventral corner of the infratemporal fenestra, an autapomorphy of *Protoceratops hellenikorhinus*.

The second smallest skull, IMM 96BM2/1 (see Fig. 7; Plate 4, Fig. 2), has a total length of 389 mm. DODSON (1976) suggested that, in *P. andrewsi*, sexual maturity may be recognised at the moment when males can be distinguished from females and juveniles by morphometric characters: according to this criterion, the youngest mature male he recognised is AMNH 6409, with a total length of the skull of 304 mm. The skull IMM 96BM2/1 already shows a relatively important nasal height and the long axis of the external nares is sub-vertical; it may thus be regarded as a mature male. However, nasal horns are not individualised in this specimen. Therefore, development of the nasal horns is delayed in relation to the appearance of sex-

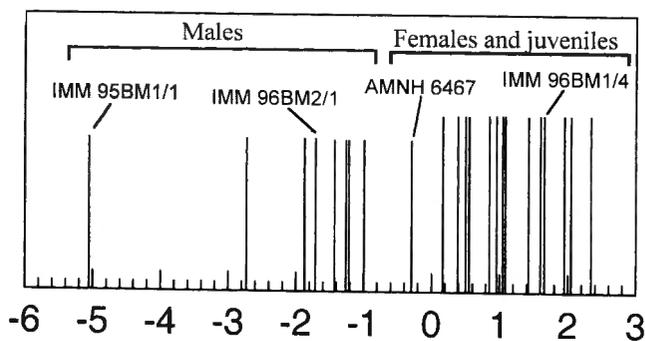


Fig. 6 — Canonical scores for the discriminant function separating adult males from adult females and juveniles of the genus *Protoceratops*. Skulls of *P. hellenikorhinus* are coded IMM.

ual discriminant characters in *P. hellenikorhinus*. The term "sub-adult" is used by SAMPSON *et al.* (1997) on centrosaurine dinosaurs for individuals with complete sexual maturity but lacking several adult characters.

Several very small skulls found at Bayan Mandahu by the Sino - Canadian expeditions in 1988 and 1990 were identified as embryos of *P. andrewsi* by DONG & CURRIE (1993). However, it is not possible to identify these specimens at a specific level from the published descriptions and illustrations, as diagnostic characters are not preserved, or very difficult to distinguish in such very young individuals. In the current state of our knowledge, they must rather be referred to as *Protoceratops* sp. Without further evidence, the presence of *P. andrewsi* at Bayan Mandahu seems very unlikely.

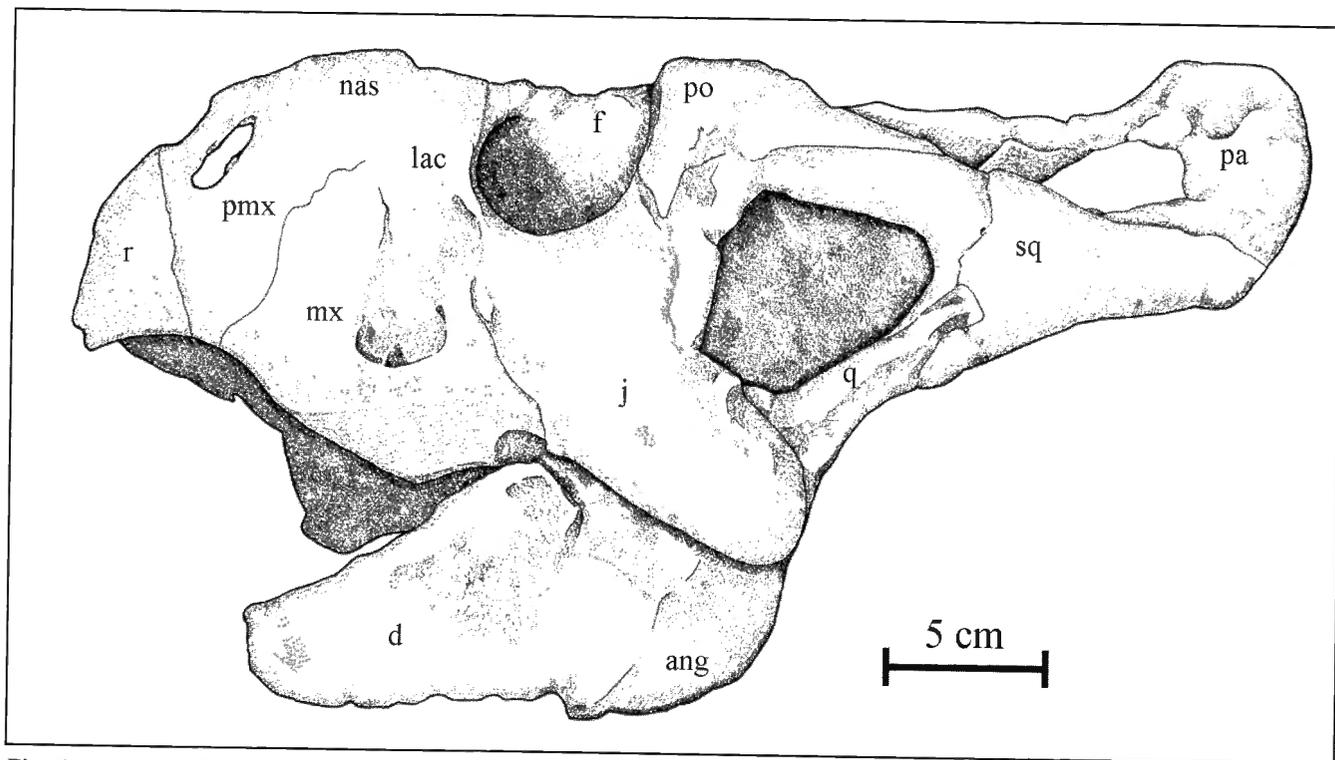


Fig. 7 — Skull of young adult male *Protoceratops hellenikorhinus* IMM 96BM2/1 in left lateral view. ang: angular; d: dentary; exo: exoccipital; f: frontal; j: jugal; lac: lacrimal; mx: maxilla; nas: nasal; pa: parietal; pmx: premaxilla; po: postorbital; q: quadrate; r: rostral; sq: squamosal.

Other sources of variation

Several other characters are variable within the *Protoceratops hellenikorhinus* sample, but this variability can be explained neither by ontogeny nor by sexual dimorphism.

The level of the ventral margin of the orbit, in relation with the rostral and caudal parts of the skull shows some degree of variation. For example, the dorsal margin of the antorbital fossa is lower, in relation to the ventral margin of the orbit, in IMM 96BM5/5 than it is in the holotype IMM 95BM1/1.

The longitudinal ridge on the maxilla, very attenuated on the holotype, is even more reduced on the specimens IMM 96BM1/7 and IMM 96BM2/1. The angle between the attenuated longitudinal ridge on the maxilla and the lower margin of the jugal varies from one skull to the other, because of the easy deformation of the thin ventral margin of the jugal, which then shows different orientations on the different skulls.

The character 'contact between squamosal and quadra-tojugal on the caudoventral corner of the infratemporal fenestra' is also variable. Indeed, some skulls do not display this contact. But this is probably an artefact of preservation due to the slenderness of the distal extremity of the ventral projection of the squamosal, which is easily broken off.

The specimen IMM 96BM6/4, consisting of a left maxilla, a left jugal, a right hindlimb and a series of caudal vertebrae in connection, is still problematic for generic identification. The maxilla lacks the longitudinal well-marked ridge characteristic of *Protoceratops andrewsi* and the neural spines of the caudal vertebrae clearly pro-

ject caudally, whereas these spines are nearly perfectly vertical in *P. andrewsi* (BROWN & SCHLAIKJER, 1940). It may therefore be referred to as *P. hellenikorhinus*. However, no criteria have been found to differentiate this fragmentary specimen from *Bagaceratops rozhdestvenskyi* MARYANSKA & OSMÓLSKA, 1975. This latter taxon has been described from the Barun Goyot Formation in P.R. Mongolia, but JERZYKIEWICZ *et al.* (1993) and DONG & CURRIE (1993) mentioned its presence in the Bayan Mandahu Formation. *Bagaceratops* mainly differs from *Protoceratops* by the presence of a supplementary antorbital fenestra, a shorter and nearly horizontal frill probably devoid of parietal fenestrae, and an odd nasal horn. These diagnostic parts of the skull are unfortunately not preserved in IMM 96BM6/4. However, the shape of the caudodorsal projection of the jugal is rather reminiscent of that of *Protoceratops*.

COMPARISONS WITH *PROTOCERATOPS ANDREWSI*

For the comparison with *Protoceratops andrewsi*, see BROWN & SCHLAIKJER, 1940, Fig. 4 pages 150-151, Fig. 7 pages 160-161, Fig. 14 page 180, Fig. 18 page 198, Fig. 20 page 204 and Plates 5 and 6.

A first important, although not diagnostic, difference between both species of the genus *Protoceratops* is the larger size of the skull in adult males of *P. hellenikorhinus*. In this species, the total length of the skull is up to 800 mm (estimation for the skull IMM 96BM5/5) (see Fig. 8), whereas the skull of *P. andrewsi* specimens studied by DODSON (1976) do not go beyond 491 mm.

In *P. andrewsi*, the longitudinal ridge on the maxilla is well marked and more dorsal in its medial part than in its

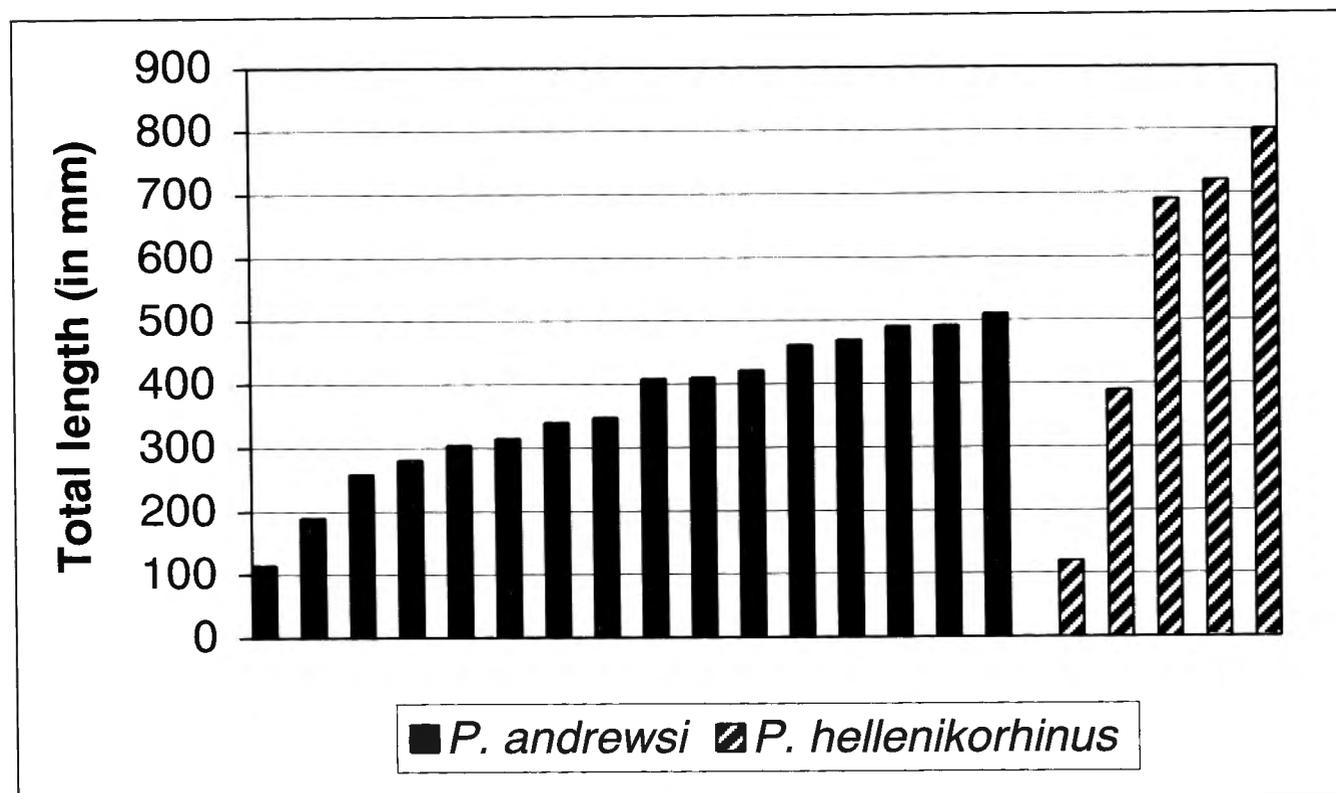


Fig. 8 — Diagram showing the total length of the skull (measurement 2 of DODSON, 1976) for individuals of the two species of *Protoceratops*. The measurements are in millimeters.

rostral and caudal parts, drawing a curve. This ridge is thus continuous with the ventral margin of the jugal. In *P. hellenikorhinus*, on the other hand, this ridge is strongly attenuated, rectilinear and discontinuous with the ventral limit of the jugal.

Nasal horns are not well developed in *P. andrewsi*, but only incipient; the dorsal margin of the nasals forming the horn is regularly convex in this species. In *P. hellenikorhinus*, on the other hand, the rostral border of the nasal horns is distinctly concave in adult males, so that they look better individualised. Sexual dimorphism in the development of the nasal horns is more important in the latter species. The position of these horns, far from the rostral end of the skull and near the orbit, does not seem to be appropriate for fighting. Thus, this structure has more probably a visual recognition function as previously proposed by DODSON (1976).

The contact between the ventral process of the squamosal and the quadratojugal, on the caudoventral corner of the infratemporal fenestra, is diagnostic for *P. hellenikorhinus* and has never been observed in *P. andrewsi* (BROWN & SCHLAIKJER, 1940).

The bilogarithmic diagram presented in Fig. 9 shows that the exoccipital is proportionally much shorter in the holotype of *P. hellenikorhinus* than in *P. andrewsi*. Unfortunately, this bone is never completely preserved in other specimens collected by the SBDE at Bayan Mandahu.

In *P. hellenikorhinus*, the rostral margin of the predentary is straighter than in adults of *P. andrewsi*, in which the rostral and the ventral margins of the predentary are not distinct and form a continuous curve. The condition observed in *P. hellenikorhinus* is closer to that in juveniles of *P. andrewsi*, in which there is also a distinct angle between the rostral and ventral margins of the predentary.

In the same way, the ventral border of the dentary is straight in both *P. hellenikorhinus* and in the juveniles of *P. andrewsi*, whereas it is distinctly curved in adults of *P. andrewsi*. The absence of curvature is apparently not linked to a decrease in height of the mandibular ramus, as shown in Fig 10. On the other hand, the straight ventral border of the dentary gives a more robust aspect to both the rostral and caudal parts of the mandible, forming a straight ventral margin by keeping the juvenile condition of *P. andrewsi*.

The caudal triangular surface of the angular, described above in *P. hellenikorhinus*, is also present in *P. andrewsi*. However, it has a more lateral orientation in the latter species, being exposed on the lateral side of the mandible. According to HAAS (1955), this surface represents the insertion area for *M. depressor mandibulae*; the other end of this muscle inserts on the lateral wing of the squamosal. If this interpretation is correct, OSTROM (1964) showed that *M. depressor mandibulae* is not very efficient in *Protoceratops andrewsi*. Because of the rotation of the triangular surface of the angular, *M. depressor mandibulae* inserts in a more caudoventral position relatively to the articulation area of the lower jaw and is therefore mechanically more efficient in *P. hellenikorhinus*.

In the males of *P. andrewsi*, the fronto-parietal depression does not extend rostrally beyond the level of the caudal margin of the orbit, as observed in the males of *P. hel-*

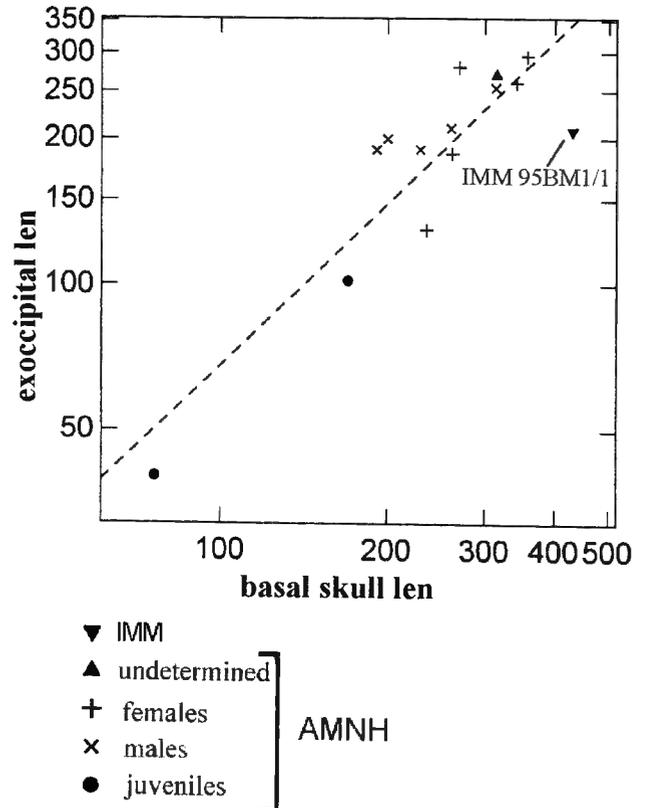


Fig. 9 — Bilogarithmic diagram showing the evolution of the exoccipital length (measurement 29 of DODSON, 1976) relatively to the basal length of the skull (measurement 1 of DODSON, 1976) for individuals of the two species of *Protoceratops*. Measurements are in millimeters.

lenikorhinus, in which it extends rostrally up to the level of the middle of the orbit. According to BROWN & SCHLAIKJER (1940) and DODSON & CURRIE (1990), the development of the fronto-parietal depression in ceratopsians reflects the extension of the insertion areas for the adductor muscles of the lower jaw, because it strengthens the summit of the skull against the increased tension resulting from the action of these muscles. Consequently, the more important extension of this depression in *P. hellenikorhinus*, in comparison with *P. andrewsi*, may be correlated to the more robust lower jaw, the caudally oriented surface on the angular, but also with the quadrate deeply embedded in the squamosal, with a wide ventral end, and with the particularly widened supratemporal fenestrae.

Both splenials do not come into contact in the holotype of *P. hellenikorhinus* IMM 95BM1/1. Unfortunately, this area is not accessible in other skulls available for the present study, so that variation of this character is unknown in *P. hellenikorhinus*. The splenials always come into contact in *P. andrewsi* (BROWN & SCHLAIKJER, 1940).

A discriminant function was found that permits a good separation of both species within the genus *Protoceratops*. This function is a linear combination of the following measurements: postorbital length (**postorb. l.**), maxillary width (**max. w.**) and nasal height (**nasal h.**).

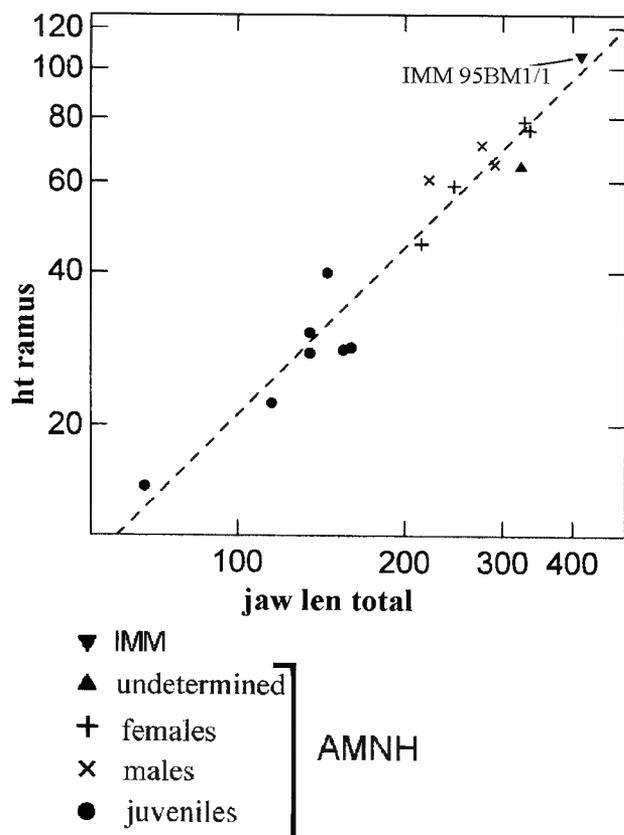


Fig. 10 — Bilogarithmic diagram showing the relation between height of the ramus (measurement 39 of DODSON, 1976) and total length of the jaw (measurement 37 of DODSON, 1976) for individuals of the two species of *Protoceratops*. Measurements are in millimeters.

$$Y = 0.014 \text{ postorb. l.} - 0.110 \text{ max. w.} + 0.33 \text{ nasal h.} - 0.529$$

$$\text{Wilks' lambda} = 0.497 \quad \text{Approx. F} = 5.728 \quad \text{df} = 3$$

$$p = 0.0067$$

Although this function permits the complete separation between the members of the two groups (18 specimens of *P. andrewsi* and only 3 specimens of *P. hellenikorhinus*, see Fig. 11), Wilks' lambda and 'p' remain relatively high, because of the small number of *P. hellenikorhinus* specimens available for this analysis.

PHYLOGENETIC RELATIONSHIPS OF *PROTOCERATOPS*

The phylogeny of basal Neoceratopsia and more particularly the status of the family Protoceratopsidae have recently been discussed by several authors. SERENO (1986) believed that the Protoceratopsidae are not monophyletic, but constitute a group of successively more derived forms, *Montanoceratops* STERNBERG, 1951 being the most derived member of the paraphyletic Protoceratopsidae.

On the other hand, DODSON & CURRIE (1990) considered that the Neoceratopsia may be subdivided into two monophyletic families, the Protoceratopsidae, including *Protoceratops*, *Montanoceratops*, *Leptoceratops* BROWN, 1914, *Bagaceratops*, *Microceratops* and the

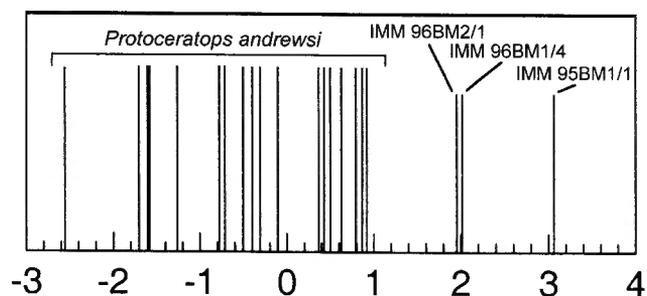


Fig. 11 — Canonical scores for the discriminant function separating the two species of the genus *Protoceratops*.

Ceratopsidae. Characters that may ultimately establish the monophyly of Protoceratopsidae include a shallow, circular antorbital fossa, inclined parasagittal process of the palatine, and a maxillary sinus. Within Protoceratopsidae, *Montanoceratops* would be the sister-group of *Protoceratops*. Ceratopsidae form a better defined monophyletic group, as they would share more than 50 synapomorphies.

The cladogram proposed by CHINNERY & WEISHAMPEL (1998) is based on a revision of *Montanoceratops* and includes recent, but fragmentary, discoveries from Asia: *Asiaceratops*, *Breviceratops* and *Udanoceratops*. Protoceratopsidae are here regarded as a monophyletic group formed by *Protoceratops*, *Leptoceratops* and *Udanoceratops*. Protoceratopsidae form the sister-group of a monophyletic node formed by *Breviceratops*, *Bagaceratops*, *Montanoceratops* and Ceratopsidae. The position of *Breviceratops* and *Bagaceratops* within this clade remains unsolved. *Montanoceratops* is positioned as the sister-group of Ceratopsidae.

As no consensus exists to date concerning the existence, the composition and phylogenetic relationships of the family Protoceratopsidae, we have decided to conduct our own cladistic analysis, using Hennig 86 programme (FARRIS, 1988) and in the light of the anatomical observations on *Protoceratops hellenikorhinus*. This analysis includes the following taxa: *Protoceratops*, *Leptoceratops*, *Archaeoceratops*, *Bagaceratops* (including *Breviceratops*; SERENO, 2000), *Montanoceratops*, and the family Ceratopsidae (unanimously regarded as monophyletic). *Psittacosaurus* OSBORN, 1923 and the Pachycephalosauria were respectively chosen as the first and second outgroups. Several genera of primitive neoceratopsians have not been taken into account because they are known from too fragmentary material, or they clearly require revision. This is the case for *Graciliceratops* (SERENO, 2000), *Asiaceratops*, *Udanoceratops*, *Kulceratops*, *Chaoyangsaurus* and the possible Asian early ceratopsid *Turanoceratops*. We have only retained 31 cranial characters that can be directly observed on the studied *Protoceratops hellenikorhinus* material. All are equally weighted. Characters were coded from direct observations on specimens from the IMM, IVPP, PIN and AMNH, but additional information was collected from literature. The characters and their polarity are briefly described in Appendix 2. Several characters, culled from literature about neoceratopsian phylogeny not retained in the present analysis are also

briefly discussed in Appendix 3. The character-taxon matrix is presented in Table 2.

The cladistic analysis resulted in one more-parsimonious tree shown in Fig. 12, with a tree length of 41 steps, a consistency index (C.I.) of 0.87 and a retention index (R.I.) of 0.87. The distribution of synapomorphies among the recognised nodes is summarised below, in reference to character list in Appendix 2. For multistate characters, the number between brackets refers to the character polarity.

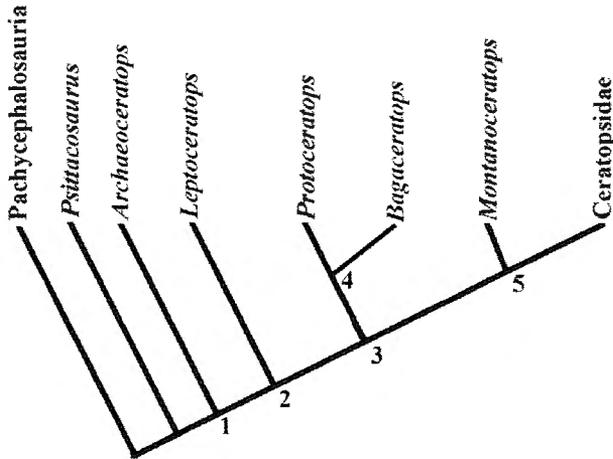


Fig. 12 — Tree generated by HENNIG 86, showing relationships between groups of neoceratopsians (C.I. = 0.87, R.I. = 0.87, tree length = 41 steps).

Node 1 represents the Neoceratopsia (SERENO, 1986), characterised by:

- Basal skull length 20 – 30 % of body length (character 1).
- Frill extending far beyond the occiput (character 20).
- Maxillary teeth with a prominent primary ridge on their labial side (character 30).

Node 2 (*Leptoceratops* and more derived Neoceratopsia) is supported by:

- Keeled rostral (character 2).
- Presence of epijugals (character 14).

- Triturating surface inclined laterally along at least the caudal part of prementary (character 24(1)).
- Enamel only on the labial side of maxillary teeth and on the lingual side of dentary teeth (character 27).

Node 3 (Protoceratopsidae, *Montanoceratops* and Ceratopsidae) is supported by:

- Triturating surface of prementary inclined laterally along its entire length (character 24 (2)).
- Contact point between maxilla, lacrimal and jugal included within the antorbital fenestra (character 7).
- Development of a fronto-parietal depression (character 13 (1)).
- Straight squamosal – parietal suture: medial flange of squamosal absent (character 18).

Node 4 represents the monophyletic family Protoceratopsidae, with the genera *Protoceratops* and *Bagaceratops*, herein characterised by the following synapomorphies:

- Small elliptical external nares (character 4(1))
- Nasal horn caudal to premaxilla – maxilla suture (character 6(2)).
- Antorbital fenestra of comparable size or larger than orbit in adult specimens (character 8).
- Tip of the prementary distinctly higher than the caudal part of this bone in lateral view (character 23).

As previously postulated by SERENO (1986) and CHINNERY & WEISHAMPEL (1998), *Montanoceratops* may be regarded as the sister-group for Ceratopsidae. These taxa form the superfamily Ceratopsioidea (*sensu* SERENO, 1986), characterised by:

- Nasal horn rostral to premaxilla – maxilla suture (character 6 (1)).
- Length of infratemporal fenestra representing less than 10% of the basal length of the skull (character 15).
- Supraoccipital excluded from the foramen magnum (character 22).
- External nares greater than 10% of basal skull length (character 4 (2)).

It must be noted that the character ‘vertical-notch shear tooth occlusion pattern’ (character 27 (1)) is convergently acquired by *Montanoceratops* and *Leptoceratops*. The

Taxa	Characters											
	5		10		15		20		25		30	
<i>Pachycephalosauria</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Psittacosaurus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Archaeoceratops</i>	1	0	0	1	0	0	0	0	0	0	0	1
<i>Leptoceratops</i>	1	1	0	0	0	0	0	0	0	1	0	1
<i>Bagaceratops</i>	?	1	0	1	0	2	1	1	0	0	0	1
<i>Protoceratops</i>	1	1	0	1	0	2	1	1	0	0	1	1
<i>Montanoceratops</i>	1	?	?	2	?	1	1	0	?	1	?	1
<i>Ceratopsidae</i>	1	1	1	2	1	1	1	0	1	1	1	1

Table 2 — Character-taxon matrix of 31 characters for cladistic analysis of 6 ingroup and 2 outgroup taxa. Character state ‘0’ is the primitive state; character states ‘1’ and ‘2’ are the derived states. Unknown character states are designated with ‘?’.

polarity of the following characters is unknown in *Montanoceratops*, so it cannot be asserted whether they characterise Ceratopsoidae or Ceratopsidae:

- . Tip of rostral oriented caudoventrally (character 3).
- . External nares subdivided by a median septum formed by paired premaxillae and nasals (character 5).
- . Contact between paired prefrontals (character 10).
- . Palpebral fused to prefrontal (character 11).
- . Development of orbital horns (character 12).
- . Development of secondary skull roof (character 13 (2)).
- . Squamosal shorter than parietal (character 17).
- . In occipital view, squamosal extending ventromedially with paroccipital process consequently shortened (character 19).
- . Epoccipital bones present (character 21).
- . Coronoid process hook-like in shape (character 25).
- . Lower dental row extending caudally beyond the level of the coronoid process (character 31).

The family Ceratopsidae is unanimously regarded as a well supported monophyletic node. In the present analysis, they share the following cranial and dental synapomorphies:

- . Squamosal - quadratojugal contact on the ventral margin of the infratemporal fenestra (convergently acquired by *Protoceratops hellenikorhinus*) (character 16).
- . More than two teeth in vertical series (character 26).
- . Vertical sheer tooth occlusion pattern (character 28 (2)).
- . Cheek teeth with two roots (character 29).

PALAEOBIOGEOGRAPHY

Neoceratopsian dinosaurs are currently known from Asia

and North America. Consequently, members of this taxon migrated between both areas by Late Cretaceous times. The results of the cladistic analysis are interesting not only from a phylogenetic point of view, but also from a palaeobiogeographic perspective. Whereas more or less precise information is available about the age and discovery spots of taxa taken into consideration in a phylogenetic analysis, these data must always be deduced by several ways for the common ancestor - or node - of sister taxa. Because sister taxa have the same time of origin, it is possible to establish the minimal age of origin for clades. This is the method of 'ghost lineages', developed by NORELL (1992). The estimation of ghost lineage duration in the cladogram presented in Fig. 12, has not been attempted, because of the absence of data about the age of the basal Neoceratopsian *Archaeoceratops*, that strongly affects the interpretation of ghost lineage duration for the whole Neoceratopsia group. However, phylogenetic relationships also constrain palaeobiogeographic inferences (WEISHAMPEL & JIANU, 1997). If the phylogenetic topology of a clade is *a priori* regarded as correct, the parsimony principle may also be applied to the palaeobiogeographic history of the clade. The best palaeobiogeographic scenario will therefore be that implying a minimal number of migratory shifts. Two equally parsimonious palaeobiogeographic scenarios have been deduced from the cladogram presented in Fig. 12. These scenarios are presented in Fig. 13. *Archaeoceratops*, the most basal taxon of the group has been found in Asia, as the out-group *Psittacosaurus*. Therefore, it may be confidently asserted that neoceratopsians have an Asian origin. In the first scenario (see Fig. 13 A), the clade formed by *Leptoceratops* and more derived neoceratopsians also have an Asian origin. This hypothesis implies two migratory shifts from Asia to North America: one migration, leading to *Leptoceratops*, occurred before the Late

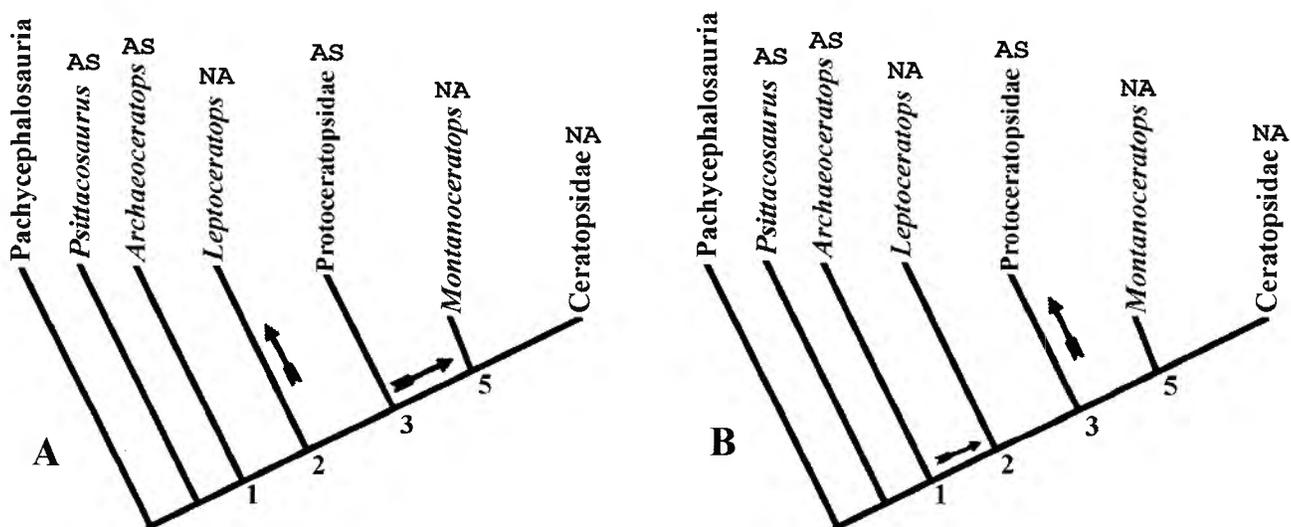


Fig. 13 — Two more parsimonious palaeobiogeographic scenarios deduced from the tree in Fig. 12. AS: Asia; NA: North America. Arrows indicate the minimal migratory shifts. A: first scenario with a migration towards *Leptoceratops* before Late Maastrichtian and another migration leading to Ceratopsoidae before Late Campanian. B: second scenario with a migration leading to common ancestor of *Leptoceratops* and higher neoceratopsians, before, or at the beginning of the Campanian and another migratory shift of the Protoceratopsidae common ancestry, before, or at the beginning of Campanian.

Maastrichtian, while the other one, leading to the North-American Ceratopsioidea, occurred before the Late Campanian. In the second scenario (see Fig. 13 B), the common ancestor for *Leptoceratops* and higher neoceratopsians originates from North America. It therefore implies an earlier dispersal of neoceratopsians from Asia towards North America, before, or at the beginning of the Campanian. It also implies a second migratory shift of the Protoceratopsidae common ancestor from North America back to Asia before or at the beginning of the Campanian. Other palaeobiogeographic scenarios based on the same cladogram imply more migratory shifts between Asia and North America and are therefore less parsimonious. If the Asian genus *Turanoceratops* is really a Ceratopsidae, as postulated by NESOV (1995), or even a Ceratopsioidea, it will in any case imply another migratory shift from Asia to North America. However, *Turanoceratops* clearly requires revision and more material is needed before taking it into consideration from a palaeobiogeographic point of view.

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ABBREVIATIONS OF TABLE 1

antorb fen: antorbital fenestra; cor pr: coronoid process; dist: distance; ext: external; ht: height; len: length; orb: orbit; sep: separation; suprtmp fen: supratemporal fenestra; wid: width.

APPENDIX 1

List of the specimens used in this study

- IMM 95BM1/1: **holotype** of *Protoceratops hellenikorhinus*: well preserved large skull.
IMM 96BM1/1: large skull.
IMM 96BM5/5: large skull.
IMM 96BM5/2: right dentary, 4 teeth, right squamosal and quadrate.
IMM 96BM1/4: **paratype** of *P. hellenikorhinus*: moderate size skull.
IMM 96BM1/7: large skull.
IMM 96BM2/1: small skull.
IMM 96BM5/3: partial very small skull.
IMM 96BM6/4: left maxilla and jugal, right hindlimb and series of caudal vertebrae.

APPENDIX 2

Characters and character states for determining the phylogenetic position of the genus *Protoceratops*.

- Relative size of the skull:** basal skull length less than 15% of total body length (0), or between 20 and 30% (1). (modified from SERENO, 1986). The low aspect of the dentary in lateral view is correlated to the important elongation of the skull in ceratopsids.
- Shape of the rostral:** transversely widened (0), or keeled (1). (SERENO, 1986).
- Orientation of the tip of the rostral:** ventral (0), or caudoventral (1).
- External nares width:** small (less than 10 % of basal skull length) and rounded (0), small and very elongated (1), or increased in size (more than 10 % of basal skull length) and complexity in shape (2). Character treated as unordered (modified from GREGORY & MOOK, 1925 and CHINNERY & WEISHAMPEL, 1998).
- Nasal septum formed by nasals and premaxillae:** absent (0), or present (1). (LULL, 1933).
- Nasal horn in adults:** absent (0), rostral to premaxilla – maxilla suture (1), or caudal to premaxilla – maxilla suture (2). Character treated as unordered.
- Position of antorbital fenestra:** rostral to maxilla – lacrimal – jugal contact point (0), or including this point (1).
- Relative size of antorbital fenestra:** smaller than orbit (0), or similar in size or larger than orbit for adult specimens (1).
- Relative size of orbit:** large orbit, width 20% or more of basal skull length (0), or reduced to less than 20% of basal skull length (1). (CHINNERY & WEISHAMPEL, 1998).
- Middle prefrontal suture:** absent (0), or present (1). (SERENO, 1984).
- Palpebral:** free (0), or fused to prefrontal (1). (CHINNERY & WEISHAMPEL, 1998).
- Orbital horns:** absent (0), or incipient to well-developed (1). (GRANGER & GREGORY, 1923).
- Fronto-parietal depression:** absent (0), present (1), formation of secondary skull roof (2). Character treated as ordered. (modified from SERENO, 1986 and CHINNERY & WEISHAMPEL, 1998).
- Epijugal:** absent (0), or present (1). (SERENO, 1986).
- Relative size of infratemporal fenestra:** large infratemporal fenestra, length 10% or more of basal skull length (0), or reduced to less than 10% of basal skull length (1). (SERENO, 1984; CHINNERY & WEISHAMPEL, 1998).
- Squamosal – quadratojugal contact on the ventral margin of the infratemporal fenestra:** absent or located in a different area (0), or present (1). (SERENO, 1984).
- Squamosal length:** extending to the caudal border of the parietals (0), or shorter than parietal (1). (OSTROM, 1966).
- Squamosal – parietal suture:** caudal part of squamosal forming a medial flange towards the parietal (0), or straight suture, without medial flange of squamosal (1). (SERENO, 1986).
- Squamosal – exoccipital relation:** in occipital view, squamosal limited to dorso-lateral border of paroccipital process (0), or extending ventro-medially, with paroccipital process being consequently shortened (1) (*contra* SERENO, 2000, who regards short paroccipital process as plesiomorphic for Ceratopsidae).
- Relative length of the frill:** reaching the level of the occiput (0), or extending far beyond the occiput (1).
- Epoccipital bones:** absent (0), or present (1). (LULL, 1933).
- Position of supraoccipital:** bordering the foramen magnum (0), or excluded from the margin of the foramen magnum (1). (PENKALSKI & DODSON, 1999).
- Dorsal border of prementary:** in lateral view, tip of the prementary nearly at the same level than caudal part of this bone (0), or distinctly higher (1).
- Triturating surface of the prementary:** horizontal (0), inclined laterally along at least its caudal part (1), inclined laterally along its entire length (2). Character treated as ordered. (SERENO, 1986).
- Shape of coronoid process:** with gently curved, convex summit (0), or attaining a rostral hook on the summit (1). (LULL, 1933).
- Number of teeth in vertical series:** two (0), or more than two (dental batteries) (1). (SERENO, 1986).
- Enamel:** on both sides of the teeth (0), or on the labial side of the maxillary teeth and on the lingual side of the dentary teeth (1). (SERENO, 1986).
- Tooth occlusion direction:** oblique sheer (0), vertical-notch sheer (1), or vertical sheer (2). Character treated as unordered. (OSTROM, 1966; CHINNERY & WEISHAMPEL, 1998).
- Root of cheek teeth:** simple (0), or double (1). (GREGORY & MOOK, 1925).
- Maxillary teeth:** devoid of prominent primary ridge on their labial side (0), or with a prominent primary ridge (1). (SERENO, 1986).
- Lower dental row:** do not extend past the rostral border of the coronoid process (0), or extending caudally to the level of the rostral border of the coronoid process (1). (GRANGER & GREGORY, 1923; CHINNERY & WEISHAMPEL, 1998).

APPENDIX 3

Examples of characters, culled from literature about neoceratopsian phylogeny, that are not retained in the present analysis.

Basioccipital contribution to the occipital condyle – SERENO (1986) considers that exclusion of the basioccipital from the foramen magnum is a synapomorphy for Neoceratopsia. In *Protoceratops*, this character is highly ontogenetic: the basioccipital contributes in the foramen magnum margin in juveniles,

while exclusion is better marked in larger specimens (BROWN & SCHLAIKJER, 1940).

Shape of rostradorsal orbit (HATCHER *et al.*, 1907; CHINNERY & WEISHAMPEL, 1998) – This character is not taken herein into consideration, because it is very difficult to quantify and it is highly variable, mainly depending on the state of preservation of the fossil. It also depends on the presence of the palpebral, whose preservation is seldom in non-ceratopsid Neoceratopsia.

Lacrimal contribution to orbit (SERENO, 1984) – The intraspecific variability of this character is very high, so that it has been decided to reject it in the present phylogenetic analysis. CHINNERY & WEISHAMPEL (1998) assess that the lacrimal is reduced in size in Psittacosauridae, which contradicts SERENO's (1987, 1990) illustrations.

Downwards curve of maxilla – CHINNERY & WEISHAMPEL (1998) consider that this character is present in *Leptoceratops* and *Udanoceratops*, but not in other ceratopsians. However, this character is variable in *Protoceratops* and, in some specimens, it is equally well developed as in *Leptoceratops*.

Presence of premaxillary teeth (GREGORY & MOOK, 1925) – Premaxillary teeth are present in pachycephalosaurs (MARYANSKA, 1990) and occur in some basal Neoceratopsia, including *Archaeoceratops* (DONG & AZUMA, 1997), *Leptoceratops* (BROWN & SCHLAIKJER, 1940) and *Protoceratops andrewsi* (BROWN & SCHLAIKJER, 1940). However, this character must be regarded very cautiously, as absence of these teeth may be an artefact of preservation in non-ceratopsid Neoceratopsia since premaxillary teeth are very fragile. Moreover, as the ventral border of the premaxillae is very thin, it is very difficult to discern alveoli when the teeth are broken off and this border is easily eroded.

Fusion of nasals – According to CHINNERY & WEISHAMPEL (1998), fusion of paired nasals would be synapomorphic for advanced ceratopsids, while these bones remain distinct in the majority of basal neoceratopsians. It has been observed that fusion of the skull bones is very variable in *Protoceratops*

(BROWN & SCHLAIKJER, 1940) and thus may rather be regarded as an ontogenetic character in this genus, as probably in other non-ceratopsid Neoceratopsia.

Sagittal crest of the frill – The shape of this crest is used by SERENO (2000) for his cladistic analysis but the character 'rounded' seems highly variable on crest of Ceratopsidae, for which the shape and robustness of the crest have to be correlated with the more or less developed frill and size of parietal fenestrae.

Shape of mandible ventral border – This character, as defined by CHINNERY & WEISHAMPEL (1998), has not been taken in consideration in the present phylogenetic analysis, as the straight ventral border, observed in several taxa, apparently reflects different phenomena. In *Protoceratops hellenikorhinus*, it reflects the robust aspects of both the rostral and caudal parts of the mandible (see above). In Ceratopsidae, on the other hand, it is clearly correlated to the important elongation of the rostral part of the skull. The mandible of *Bagaceratops*, also characterised by a straight ventral border, very closely resembles that of *Protoceratops andrewsi* juveniles. As currently described specimens of *Bagaceratops* are very small (see MARYANSKA & OSMOLSKA, 1975, tab. 5), they are either juvenile, or neotenic forms; in any case, the straight border of the mandible may rather reflect an ontogenetic phenomenon.

Relative length of prementary – According to CHINNERY & WEISHAMPEL (1998), long prementary (more than 67% of the length of the dentary) is synapomorphic for their family Protoceratopsidae (*Protoceratops*, *Leptoceratops* and *Udanoceratops*; see matrix in their appendix 3, but character not considered in the text). However, this character is clearly ontogenetic in *Protoceratops*, the prementary being proportionally shorter (less than 67%) in larger specimens. In *Psittacosaurus*, the small value of the ratio 'length of the prementary / length of the dentary' reflects the small size of the prementary, while in ceratopsids, it rather reflects the important elongation of the dentary.

PLATE 1

Skull of the holotype of *Protoceratops hellenikorhinus* (IMM 95BM1/1) from Bayan Mandahu. A: left lateral view; B: right lateral view; C: rostral view. Scale bar = 20 cm.

PLATE 2

Skull of the holotype of *Protoceratops hellenikorhinus* (IMM 95BM1/1) from Bayan Mandahu. A: caudal view; B: dorsal view. Scale bar = 20 cm.

PLATE 3

Fig. 1 — Skull of the paratype of *Protoceratops hellenikorhinus* (IMM 96BM1/4) from Bayan Mandahu. A: left lateral view; B: rostral view; C: dorsal view. Scale bar (for A and B) = 10 cm.

Fig. 2 — Isolated teeth found with the skull pieces of *Protoceratops hellenikorhinus* IMM 96BM5/2 from Bayan Mandahu. A and C: lingual or labial views (we don't know if these teeth belong to dentary or maxilla); B and D: rostral or caudal views. Scale bar = 2 cm.

PLATE 4

Fig. 1 — Skull of a juvenile of *Protoceratops hellenikorhinus* (IMM 96BM5/3). A: left lateral view; B: detail of the left infratemporal fenestra showing the long and thin (slightly broken) ventral projection of the squamosal along the quadrate. Scale bar for A = 2 cm.

Fig. 2 — Skull of a young adult male of *Protoceratops hellenikorhinus* (IMM 96BM2/1). Left lateral view. Scale bar = 10 cm.

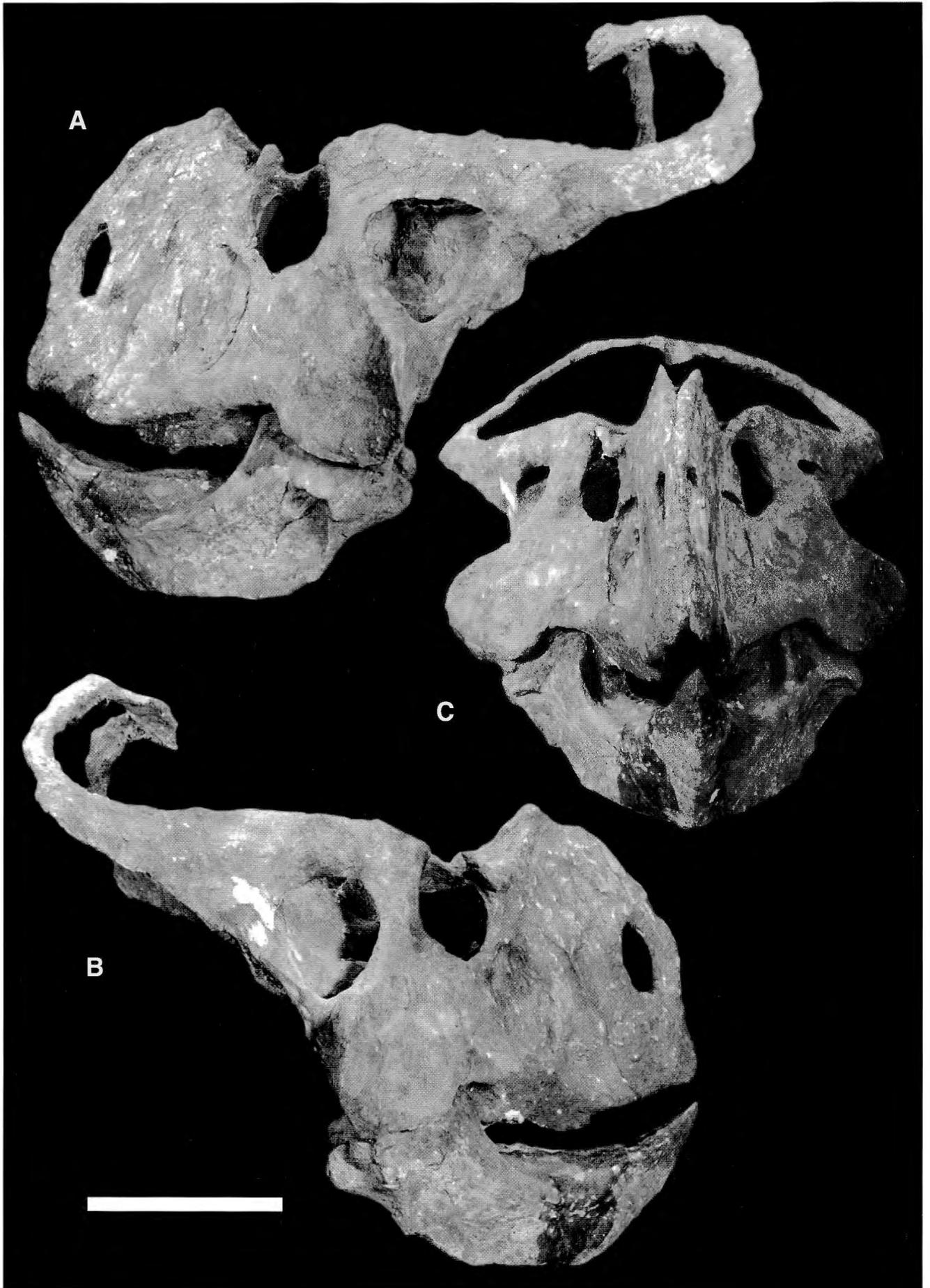


PLATE 1

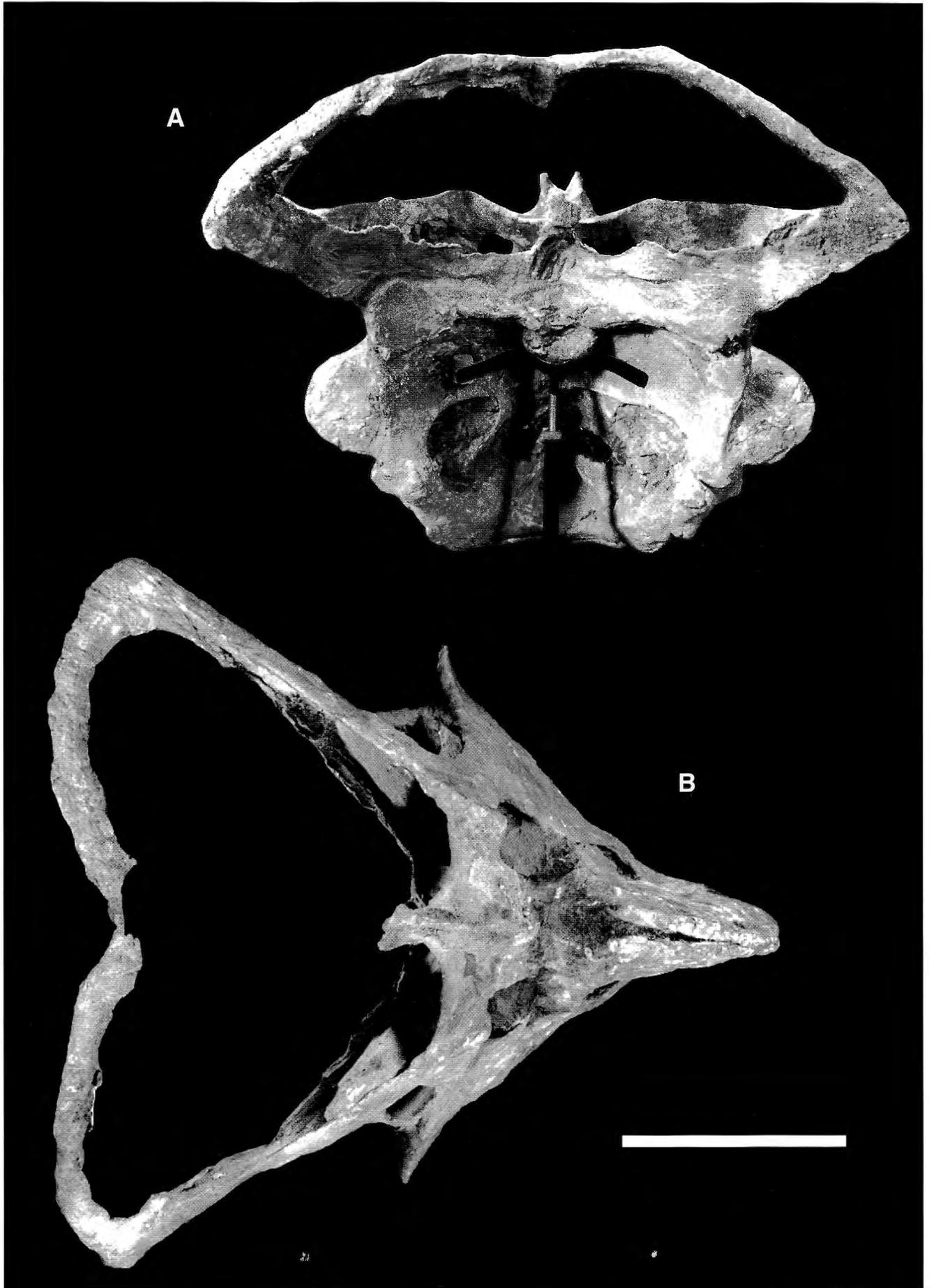


PLATE 2

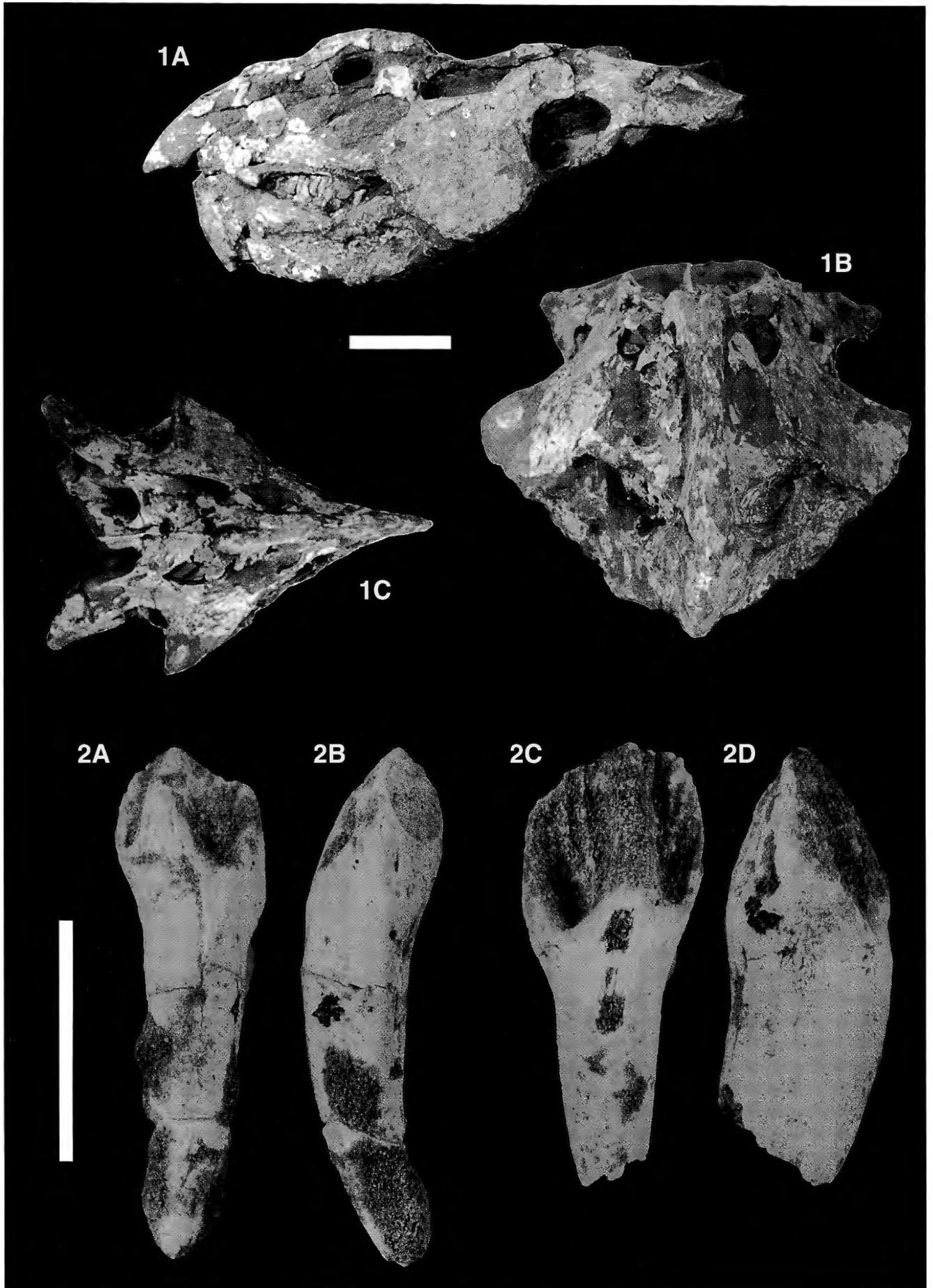


PLATE 3

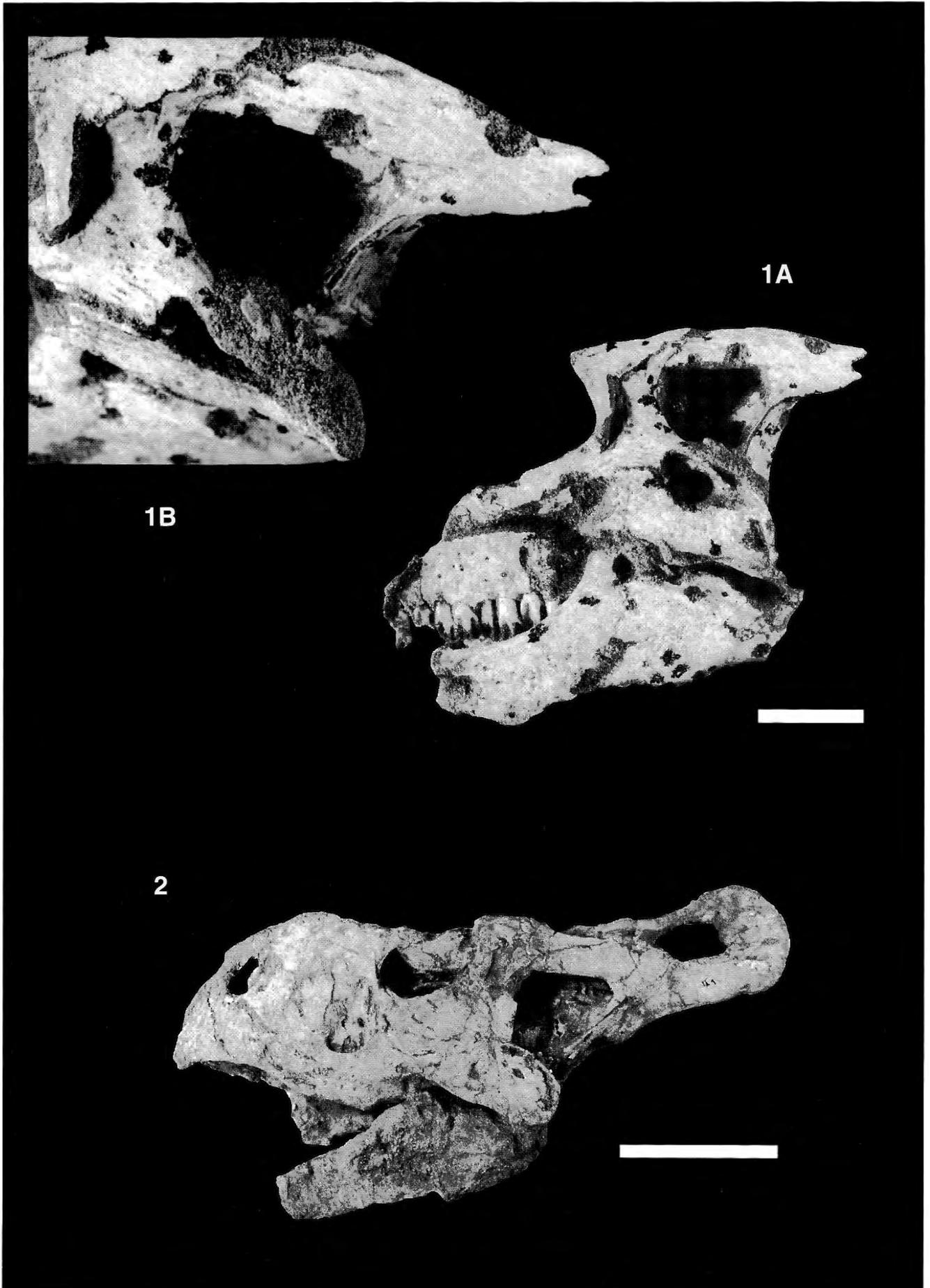


PLATE 4