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PACHYCEPHALOSAURIA, A NEW SUBORDER OF ORNITHISCHIAN DINOSAURS

(Plates XXII-XXXI)

Contents

Abstract. — The present paper deals with the dinosaurs assigned to the family Pachycephalosauridae STERNBERG, 1945. The new material, which was recently recovered in the Upper Cretaceous of Mongolia, is described. It includes three new genera and species: *Tylocephale gilmorei* from the Barun Goyot Formation, *Prenocephale prenes* and *Homalocephale calathocercos*, both from the Nemegt Formation. This material as well as that known from North America show that the Pachycephalosauridae form a separate group within the Ornithischia, and a new suborder Pachycephalosauria is erected to include this family. Pachycephalosauria are characterized: by the strongly thickened bones of the skull roof; by the complete ossification of the orbit, comparable only to that in some birds and mammals; by the presence of the epipterygoid, which was never reported in any ornithischian dinosaur. The structure of the pachycephalosaurid pelvic region is unusual for the dinosaurs: the pubis is practically excluded from the acetabular rim; the ischium contacts the ilium twice and additionally it contacts also the sacrum by means of the sacral ribs; the juncture between the sacrum and ilium is weak. The present paper brings the diagnoses of new taxa and the systematic descriptions as well as the osteology of the skull and that of the postcranial skeleton in this group. Some aspects of the myology, cranial neurology and circulation are discussed, as well as the adaptations, mode of life, sexual dimorphism and the supposed phylogeny of this group. It is believed here that the pachycephalosaurids were the animals with keen sense of vision and good olfactory sensitivity which fed on plants and insects; their cursorial abilities were limited; they held horizontally the dorsal portion of the vertebral column during the gait, using the fleshy and protected by tendons tail as the prop during the rest; the dome might be used as the defensive weapon; a significance of the dome in pachycephalosaurids as a sexual character seems to be still disputable.

INTRODUCTION

The Pachycephalosauridae are a comparatively rare and scarce group of ornithischian dinosaurs from the Upper Cretaceous. Until recently only two genera were recognized: *Stegoceras* LAMBE, 1902 and *Pachycephalosaurus* BROWN & SCHLAIKJER, 1943, both known mainly from North American continent (the only described Asian species — "*Stegoceras*" *bexelli* BOHLIN, 1953 — is represented by a scanty and incomplete material). The new genus *Yaverlandia* GALTON, 1971 from the Lower Cretaceous (Wealden) of England was lately added to the Pachycephalosauridae. During the Polish-Mongolian Paleontological Expeditions to the Gobi Desert in 1965, 1970 and 1971 (KIELAN-JAWOROWSKA & DOVCHIN, 1969; KIELAN-JAWOROWSKA & BARSBOLD, 1972) three skulls, two of them with the fragmentary postcranial skeletons, were recovered in the Barun Goyot Formation and Nemegt Formation in the localities Khulsan and Nemegt, within Nemegt Basin (GRADZIŃSKI *et al.* 1969; GRADZIŃSKI & JERZYKIEWICZ, 1972). This material, mostly excellently preserved, is described in the present paper under the new generic and specific names: *Tylocephale gilmorei* n. gen. et sp., *Prenocephale prenes* n. gen. et sp., *Homalocephale calathocercos* n.gen.et sp. The skull of *Tylocephale gilmorei* with the mandible attached was recovered at Khulsan, laying among loose weathered blocks on the sayr channel surface. No other skeletal elements of this species were present. The specimen of *Prenocephale prenes* was found in a weakly cemented sandstone at the Nemegt locality, in situ. The head was in a nearly horizontal position. Posterior to it, the rock was damaged and the anterior portion of the postcranial skeleton was not preserved. Slightly below, the sacrum with the right side of the pelvis and both femora were found. Several damaged centra of caudals and numerous free caudal tendons were present in the weathered rock around the caudals. The most complete specimen was that of *Homalocephale calathocercos*. It was also found in situ at the Nemegt locality. The skeleton was articulated laying on a shelf above the bottom of the sayr, with the abdomen placed ventrally. The anterior portion of the skull, as well as the anterior portion of the postcranial skeleton were lacking due to an extensive cleavage of the sandstone block in this site. The mode of preservation of the Mongolian pachycephalosaurids is exceptional; they show no traces of transport. The opposite is true for the American pachycephalosaurids known up to date, which are mostly restricted to the skull roofs (except for one specimen of *S. validus* and that of *P. grangeri*) and as was noticed by STERNBERG (1933) they "show more or less wear, as if they had been rolled along by water".

The systematic position of the Pachycephalosauridae within the order Ornithischia has often caused and still causes discussion. They used to be assigned within the suborders: Stegosauria (LAMBE, 1918), Ceratopsia (NOPCSA, 1904), Ankylosauria (ROMER, 1927; NOPCSA, 1928, 1929), Ornithopoda (GILMORE, 1924; BROWN & SCHLAIKJER, 1943). In 1945 STERNBERG established a new family: Pachycephalosauridae, which was assigned by the author to the Ornithopoda, the latter systematic position being nowadays generally accepted although not absolutely (i.e. ROZHDESTVENSKY, in 1964, assigned them within Incertae subordinis, and in 1972 to the suborder Ankylosauria).

The new material of the pachycephalosaurids which was collected in Mongolia convinced us that the establishment of a new suborder Pachycephalosauria within the Ornithischia is fully justified. The representatives of this suborder are bipedal, similarly as the ornithopods but they possess a pelvis, in which the pubis is practically excluded from the acetabulum. This feature is unique among the dinosaurs. Several separate ossifications are present in the sphe-

nethmoidal region of the pachycephalosaurids. No similar structure of this region has ever been reported in any reptile. The new suborder Pachycephalosauria includes for the time being but one family Pachycephalosauridae with the following genera: *Stenopelix* MEYER, 1859, *Yaverlandia* GALTON, 1971, *Stegoceras* LAMBE, 1902, *Pachycephalosaurus* BROWN & SCHLAIKJER, 1943, *Tylocephale* n. gen., *Prenocephale* n. gen., *Homalocephale* n. gen. *Stenopelix*, which is here assigned to the Pachycephalosauridae, was thus far placed either within the Hypsilophodontidae (NOPCSA, 1928; ROZHDESTVENSKY, 1964) or within the Psittacosauridae (ROMER 1956; STEEL, 1969). KOKEN (1887) noticed the unusual structure of the pelvis of *Stenopelix*. The same structure of pelvis, unique among the dinosaurs, we find in the pachycephalosaurids. This is why we think that *Stenopelix* cannot be assigned to any ornithopod family. This structure of the pelvis and the presence of the strong caudal ribs make *Stenopelix* close to the Pachycephalosauridae [1].

Because of its excellent preservation, the new pachycephalosaurid material here described enables us to provide much additional osteological data on the skull and on the postcranial skeleton. For this reason, the present paper is divided into three parts. The first one is devoted to systematic considerations, the establishing of new taxa and to general descriptions and comparisons. The second part deals with the detailed comparative osteology of the Pachycephalosauridae based on the new and partly on the old materials, while in the third part the possible adaptations and the mode of life as well as the pachycephalosaurid phylogeny are discussed. All the comparisons we have made in this paper, which concern the North American materials, are essentially limited to the complete skulls of *Stegoceras validus* LAMBE, 1902 (UA No. 2) and *Pachycephalosaurus grangeri* BROWN & SCHLAIKJER, 1943 (A.M.N.H.No. 1696). We had at our disposal the plaster cast of the skull of *S. validus* (UA No. 2) as well as the skull roof of the specimens NMC Nos. 138, 8816. We have not revised the species within *Stegoceras* and *Pachycephalosaurus*, lacking the adequate materials, and we do not discuss the specific range of these genera in this paper.

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Abbreviations used:

A.M.N.H.   — American Museum of Natural History,
G.I. SPS   — Geological Institute Section of Palaeontology and Stratigraphy, the Academy of Sciences of the Mongolian People's Republic,

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[1] SCHMIDT (1969) redescribed the holotype of *Stenopelix valdensis* MEYER and stated among others that the pubis takes part in the formation of the acetabulum to the small extent (*l. c.*, p. 197). However, the pubis is still insufficiently illustrated on the drawing given by this author (*l. c.*, Fig. 1) to state for sure which is the normal articulation of the pubis in this specimen.

NMC   — National Museum of Canada,
UA   — University of Alberta,
Z.Pal.   — Palaeozoological Institute of the Polish Academy of Sciences.

The described material is housed in the Palaeozoological Institute of the Polish Academy of Sciences, Warsaw, and in the Geological Institute of the Academy of Sciences of the Mongolian People's Republic, Ulan Bator.

SYSTEMATICS

SYSTEMATIC POSITION OF THE PACHYCEPHALOSAURIDAE WITHIN THE ORNITHISCHIA

The new pachycephalosaurid material from the Upper Cretaceous of Mongolia again raises the problem of the systematic position of this group within the Ornithischia. The unusual structure of the pachycephalosaurid pelvis with the pubis almost excluded from the acetabulum, the sagittal shortening of the basicranium and its separation from the palatal and suborbital regions, the presence of the accessory sphenethmoidal ossifications which close the orbit anteromedially, separate them from all dinosaurs described to date. This last character is probably the most exceptional feature of the Pachycephalosauridae. The complete ossification of the lamina orbitonasalis and of the planum supraseptale has never been reported in any reptile, but it is sometimes present in certain birds (ectethmoid and uncinate bone — *fide* de BEER, 1971, p. 443). However, the ossification of the orbitonasal region went much further in the Pachycephalosauridae, where the bones which can be homologized with these two mentioned in birds are accompanied by three additional orbitonasal ossifications (p. 68). Another character which was never reported in any ornithischian dinosaur, is the presence of the well developed epipterygoid, which is in the contact with the prootic, similarly as it is in the Squamata. The exclusion of the pubis from the acetabulum is characteristic of the Pachycephalosauridae and among the archosaurs this is present only in the crocodiles. It was also reported in one other dinosaur — *Stenopelix* MEYER, 1859 (KOKEN, 1877)[2]. Another character of the Pachycephalosauridae which is unique for a dinosaur is the articulation of the second and third sacral ribs with the ischium in the anterior part of the latter. The pubis is strongly reduced in certain ankylosaurs in which it is practically excluded from the acetabulum. However, the ilium in ankylosaurs is quite different and the acetabulum is closed so that really there is no close resemblance between the pelves of the two groups. Some resemblance exists between the pelvis of the Pachycephalosauridae and that of the Protoceratopsidae, as was already mentioned by BROWN & SCHLAIKJER (1943, p. 145). They deal especially with the shape of the ischium. However, in the Protoceratopsidae the pubis is strongly reduced and takes part in the formation of the acetabulum. The pre- and postzygapophyses in the dorsal vertebrae of pachycephalosaurids have the tongue and groove articulation that among dinosaurs was reported only in *Protoceratops* (*fide* BROWN & SCHLAIKJER, 1943, p. 145). The tail of pachycephalosaurids is characterized by the strong development of the caudal ribs which are present on several anterior caudals. Similar long caudal ribs are not reported so far in any other dinosaurs, but it should be mentioned here that they were present in *Stenopelix*.

The Pachycephalosauridae were undoubtedly bipedal animals and most probably of ornithopod origin (p. 100), but they cannot be assigned to the suborder Ornithopoda as is

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[2] Compare foot-note on p. 47.

usually done. They differ from the ornithopods in numerous characters such as the presence in the Pachycephalosauridae of a heavy skull with a thick roof and a marked tendency for the closure of the supratemporal fenestra. These features, which would be regarded as "normal" in the ankylosaurs, are never found in any ornithopod. Another character, most probably being the consequence of the thickening of the skull roof, is the vertical extension of the occipital region, which is not found in ornithopods. A slightly similar structure of the occiput is present in the Ceratopsia but there the basicranium is placed in quite a different plane to that of the occiput, which is not the case with the Pachycephalosauridae. The quadratojugal/quadrate relation in the Pachycephalosauridae is quite different from that of ornithopods, where the two bones only contact each other for a short distance, the quadratojugal never descending very near to the lower articular surface of the quadrate as in the pachycephalosaurids. There are also the distinctive differences in the mandibles of both groups. The coronoid process is generally better developed in the Ornithopoda than it is in the Pachycephalosauridae. The Pachycephalosauridae have a very strongly pronounced retroarticular process but generally this is not the case in ornithopods. Among the characters of the skull common to the pachycephalosaurids and the ornithopods is the presence of the premaxillary teeth which are more or less different from the maxillary dentition. The heterodont dentition in ornithopods is most strongly pronounced in *Lycorhinus* HAUGHTON, 1924 (= *Heterodontosaurus* CROMPTON & CHARIG, 1962, according to THULBORN 1970) in which the premaxillary teeth are of the carnivorous type and there is a diastema between the premaxillary and maxillary teeth to receive the enlarged mandibular canine. A similar condition is found in some Pachycephalosauridae (p. 54).

There are also certain similarities in the postcranial skeleton of the Pachycephalosauridae and the Ornithopoda, but they are due to bipedalism of both grups. The similarities in the skull as well as in the postcranial skeleton concern the characters which are primitive in the Pachycephalosauridae and their presence can be explained by the fact that these latter derived most probably from a primitive ornithopod group (p. 100). Moreover, it should be mentioned here that Pachycephalosauridae display some similarities to all the suborders of the Ornithischia which was already noticed by many authors (GILMORE, 1924; BROWN & SCHLAIKJER, 1943, and the present paper). However, the essential characters of the skull and the postcranial skeleton prevent the assignment of the Pachycephalosauridae to any known ornithischian suborder. For these reasons we believe that the establishment of a new suborder Pachycephalosauria is most reasonable and fully justified.

The systematics of the Ornithischia differs significantly from that accepted in the Saurischia where the infraorders are recently recognized within the suborders. To the suborder Theropoda, which includes the bipedal forms, three infraorders are assigned: Coelurosauria, Carnosauria and Deinonychosauria (COLBERT & RUSSELL, 1969). Were the same practice applied to the Ornithischia, our new suborder Pachycephalosauria could be regarded as an infraorder within the suborder Ornithopoda. Although the unification of systematics of the two dinosaurian orders mentioned seems to be necessary, we are not able to decide at the moment whether or which infraorders should be recognized within the Ornithopoda.

DESCRIPTIONS

Order ORNITHISCHIA
Suborder PACHYCEPHALOSAURIA nov.

Diagnosis. — As for the family.
Family assigned: Pachycephalosauridae STERNBERG, 1945.
Stratigraphical and geographical distribution. — Cretaceous of Eurasia and North America.

Family PACHYCEPHALOSAURIDAE STERNBERG, 1945
(= TROÖDONTIDAE GILMORE, 1924, not TROÖDONTIDAE *sensu* RUSSELL, 1948)

Revised diagnosis. — Bipedal, highly specialized ornithischians, small to moderate in size. Pubis does not take part in formation of acetabulum. Skull roof thickened, flat to dome-like. Supratemporal fenestra usually closed in highly domed forms. Antorbital fenestra occasionally present. Maxilla penetrated by extensive intramaxillary sinus. Epipterygoid present and being in contact with the prootic. Orbits anteriorly and medially closed by accessory sphenethmoidal ossifications. Quadrate with tendency to oblique position of its dorsal portion. Jugal excluded from posterior boundary of infratemporal fenestra and together with quadratojugal strongly expanded ventrally to level of articular surface of quadrate. Basicranial region strongly shortened (sag.), nearly completely separated from palatal and suborbital regions by extension of quadrate and pterygoid and by juncture of basisphenoid and prootic with quadrate wing of the pterygoid. Basal tubera thin, plate-like. Occipital and basicranial regions usually placed almost in the same vertical plane. Premaxillary dentition present, heterodonty more or less pronounced. Dentition weak, teeth arranged in one row, enameled on both sides. External skull bones strongly ornamented. Dorsal vertebrae mostly with tongue and groove articulation of zygapophyses. Caudal ribs strongly developed on anterior caudals. Tibia shorter or equal in length to femur. Pes tetradactyl.

Genera assigned: ?*Stenopelix* MEYER, 1859, *Yaverlandia* GALTON, 1971, *Pachycephalosaurus* BROWN & SCHLAIKJER, 1943, *Stegoceras* LAMBE, 1902, *Tylocephale* n. gen., *Prenocephale* n. gen., *Homalocephale* n. gen.

Stratigraphical and geographical distribution. — Lower Cretaceous (Wealden) of Great Britain and Germany, Upper Cretaceous of North America and Asia.

Remarks. — The Upper Cretaceous representatives of the Pachycephalosauridae show the advanced specialization as compared with their Wealden predecessors — *Stenopelix* and *Yaverlandia*. The new elements which separate the frontal from the orbital margin are added to the skull roof. The postcranial skeleton becomes more lightly built. The sacrum includes three additional vertebrae, the femur shortens relatively and the shortening of the forelimb is more advanced. It seems that the possibility exists for excluding the two Lower Cretaceous forms from the Pachycephalosauridae and erecting for them a separate family. They are, however, thus far too poorly known and represented by too scanty material. The abdominal ribs, which are never present in any ornithischian, were often reported in the diagnoses of the family Pachycephalosauridae given by the different authors. The Mongolian material here described made us possible to state that the supposed segmented abdominal ribs are, in fact the ossified caudal tendons which formed a kind of a basket around the posterior portion of the tail.

Genus **TYLOCEPHALE** n.gen.

Type species: Tylocephale gilmorei n.sp.
   Derivation of the name: Gr. *tyle* = swelling on the skin, *cephale* = head; because of the thickening of the skull roof.
   Genus monotypic: diagnosis, stratigraphic and geographic distribution — as for the species.

Tylocephale gilmorei n.sp.
(Pl. XXII, Fig. 3; Text-fig. 1 *B*)

Type specimen: One specimen (Z. Pal. No. MgD-I/105) including: damaged skull with several maxillary teeth, lacking braincase, palate and anterior portion of snout; mandible with several mandibular teeth, lacking anterior portion of dentary, as well as articular and prearticular.
   Type horizon: Upper Cretaceous, Barun Goyot Formation, zone of *Djadochtatherium catopsaloides* KIELAN-JAWOROWSKA, *Nemegtbaatar gobiensis* KIELAN-JAWOROWSKA and *Chulsanbaatar vulgaris* KIELAN-JAWOROWSKA.
   Type locality: Khulsan, Nemegt Basin, Gobi Desert, Mongolian People's Republic (see GRADZIŃSKI & JERZYKIEWICZ, 1972, Text-fig. 4, No. 10).
   Derivation of the name: in honour of the late Ch. W. GILMORE, who first gave the detailed description of a pachycephalosaurid species.

Diagnosis. — Cranial roof thickened, highly elevated, the highest point situated far posteriorly. Postorbital and both supraorbitals incorporated into domed part. Infratemporal fenestra very narrow, long and placed nearly vertically. Orbit elongate, oblique, rising upwards posteriorly. Quadrate nearly vertical. Occipital region narrow, very faintly depressed. Tooth-bearing edge of maxilla straight nearly to the very posterior end. Crowns of maxillary and mandibulary teeth large. Surface of the external bones strongly ornamented, domed part rough. Surface of the jugal at the orbital margin, as well as this of the quadratojugal nearly smooth.
   Dimensions — see Table 1.
   Description. — The skull is extremely high and narrow posteriorly. The postorbital portion of the skull is very short. The dome is very highly elevated and its highest point is placed very close to the posterior margin of the skull, so when the skull is viewed posteriorly the dome is visible above the dorsal edge of the occipital region. The squamosal in its dorsal portion forms the thick margin of the skull, which is sharp and not swollen. The ventral portion of the squamosal contacting the exoccipital is thin. The squamosals are separated on the margin of the skull by a very narrow wedge of the parietals. The latter widen on the occipital face of the skull and become slightly concave where they meet the supraoccipital. All the bones forming the occipital surface of the skull are comparatively thin. The quadrate is relatively long so that its length is nearly equal to the distance between both quadrates as measured between the mandibular joints. The quadrate is nearly vertical; its lower third is perpendicular to the lower edge of the maxilla and its upper portion is only slightly inclined backwards. The ventral portions of the quadrates are directed slightly medially. The jugal, from its juncture with the maxilla posteriorly, is directed distinctly laterally. When seen ventrally, the lateral wall of the splanchnocranium is angularly bent in its posteriormost region along the jugal, quadratojugal and the quadrate, so that the space between the lateral wall and the pterygoid is relatively very broad transversally. The infratemporal fenestra is nearly vertical and its posterior portion is only slightly oblique. It is equally narrow along its entire length. The orbit is nearly twice as long as broad and its upper boundary is flat. The postorbital bar is narrow and parallel to the quadrate. The postorbital overlaps the jugal anterodorsally along the oblique suture. The anterior

4*

and the posterior supraorbitals are relatively steeply placed and they were most probably incorporated into the domed part of the skull roof.

Dentition. The maxilla has 9 posterior teeth preserved. They are arranged in a straight row but the last tooth is placed slightly outwards from the straight line formed by the other teeth. The teeth are badly damaged and the denticulation of the crowns is hardly visible. The teeth are relatively large. There are seven mandibular teeth preserved. They display high crowns and their cutting edges are arched rather than conical in lateral view. The labial face of the tooth is concave dorsoventrally and anteroposteriorly. On the inner, lingual face there is a strong vertical ridge with 4 parallel ridges anterior to it and 3 ridges posterior to it. All the ridges are visible along the entire height of the crown. They end on the cutting edge of the crown and form its denticulation. The similar pattern of the ridge arrangement is present on the labial face of the crown, but it is less distinct there. The lingual face of the maxillary teeth is worn out.

Ornamentation. The external surface of the supraorbitals and the postorbital are quite regularly ornamented with the tubers of moderate size. The outer surface of the jugal near the mandibular joint is covered by large, prominent and irregularly spaced tubers. The preserved posterior part of the domed roof is rough. Eight nodes are present on the squamosal along the posterior margin of the skull roof. A single large node is present below the outermost node of the squamosal series. A row of the large nodes mentioned continues forwards laterally across the squamosal and the postorbital; farther anteriorly the nodes diminish and merge together continuing in the form of a sharp crest along the supraorbitals which constitutes the dorsal margin of the orbit. Another not so prominent crest is present along the postorbital bar.

Mandible. The coronoid is weakly elevated above the upper contour of the jaw. The adductor fossa is very deep in transverse direction.

Remarks. — The skull of *Tylocephale gilmorei* was recovered in Khulsan, Barun Goyot Formation. The age of this formation is determined by KIELAN-JAWOROWSKA (1974) as the ?Middle Campanian, and may be vaguely compared with that of the Belly River Formation, which yielded the specimens of *Stegoceras validus*. The skull of *T. gilmorei* is comparable in size to the complete skull of *S. validus* described by GILMORE (1924). It differs from the latter in having the highest point of the dome placed very far posteriorly, close to the posterior margin of the skull. The skull of *T. gilmorei* is the only pachycephalosaurid in which the elevation of the dome is visible when the skull is seen from the back. The nearly vertical position of the quadrate and of the infratemporal fenestra also distinguish *T. gilmorei* from the other Pachycephalosauridae in which the infratemporal fenestra is usually more or less horizontal. The posterior plane of the skull which includes in the Pachycephalosauridae the basicranial and basioccipital regions, is proportionally narrower and higher than it is in *S. validus* and other Pachycephalosauridae. The poorly preserved occipital region of *T. gilmorei* is only slightly concave centrally while it is always distinctly depressed in all the other representatives of the family. *Tylocephale gilmorei* has the posterior cheek region, bounded by the jugal and quadratojugal, very strongly expanded laterally to an extent never reported in any other pachycephalosaurid. The poor state of preservation of the maxillary and mandibulary teeth in the specimen of *T. gilmorei* makes it impossible to make detailed comparisons. However, it can be stated that the teeth are relatively larger than in other Pachycephalosauridae and not conical as they are in *Stegoceras validus*. The mandible of *T. gilmorei* is delicate and devoid of ornamentation, when compared with the mandible of *S. validus*, which has so far been the only known mandible in this group. The character of the ornamentation of the skull of *T. gilmorei* is similar to that of *S. validus* but it

differs in details. Taking into account all the significant differences from the other representatives of the family, we are of the opinion that the species above described should be assigned to the new genus.

Genus **PRENOCEPHALE** n.gen.

Type species: Prenocephale prenes n. sp.
Derivation of the name: Gr. *prenes* = inclined, sloping, *cephale* = head; because of the anterior sloping profile of the head.
Genus monotypic: diagnosis, stratigraphic and geographic distribution — as for the species.

Prenocephale prenes n.sp.
(Pl. XXII, Fig. 2, Pl. XXIII, Pl. XXV, Figs 2, 3, Pl. XXXI, Fig. 2; Text-figs 1 C, 2, 3, 6)

Type specimen: One specimen (Z. Pal. No. MgD-I/104) including perfectly preserved skull with dentition, without mandibles, several fragmentary dorsal vertebrae, one caudal vertebra, fragmentary dorsal ribs, badly damaged left femur, right femur lacking greater and lesser trochanters and lateral condyle, numerous free caudal tendons, several of them in natural arrangement.
Type horizon: Upper Cretaceous, Nemegt Formation, zone of *Tarbosaurus bataar* (MALEYEV) and *Saurolophus angustirostris* ROZHDESTVENSKY;
Type locality: Nemegt, Nemegt Basin, Gobi Desert, Mongolian People's Republic (see GRADZIŃSKI & JERZY-KIEWICZ, 1972, Text-fig. 1, No. 19).
Derivation of the name: see this for the genus.

Diagnosis. — Skull with highly domed frontoparietal roof with its highest point situated above the postorbital bar. Parietosquamosal shelf not developed. Outline of orbit subcircular with dorsal margin flattened. Postorbital portion of skull long. Premaxillary portion of snout separated from the maxillary portion by a long and deep diastema. Three caniniform premaxillary teeth present with a serrated crest developed along their posterior faces. Seventeen maxillary teeth arranged in a straight line which is bent outwards at the posterior end. Crowns of maxillary teeth small, ventral edges of crowns worn down. There is no supratemporal fenestra. Infratemporal fenestra short and broad. Antorbital fenestra present. Upper margin of orbit formed by two supraorbital bones. Frontal and prefrontal excluded from orbital margin. Uppermost portion of quadrate distinctly deflected backwards. The occipital region is overhung dorsally by the strongly swollen squamosals and its central part is deeply depressed. Foramen magnum small and round. Occipital condyle small. Basal tuber flat, its ventral edge close to quadrate wing of pterygoid. Basisphenoid deeply wedged dorsally between basal tubera and pterygoids. Surface of dome rough; row of conspicuous nodes developed along posterolateral and posterior margins of skull.
Dimensions — see Tables 1 and 3.

Description. — The cranial roof is very highly domed. The upper outline of the skull slopes steeply forwards and slightly less steeply backwards, in lateral view. The parietosquamosal shelf is not developed and the domed part reaches backwards to the posterior margin of the skull. The supratemporal fenestra is completely closed and only a weak depression in the place where the postorbital, squamosal and frontoparietal meet marks its former position. Laterally the dome incorporates the postorbital and the two supraorbitals.Each of these elements mentioned is strongly thickened and convex. They are separated from each other by deep pits, which are present on the suture with the frontoparietal mass. The prefrontal is flat, although also thick.

The nasal is weakly convex and even somewhat concave close to the suture with its fellow. The premaxillary portion of the snout is distinctly differentiated and narrow transversely. The internarial bridge was presumably formed from the premaxillae but it is broken off. The anterior portion of the premaxilla in front of the external nares is relatively long. The premaxilla reaches far posteriorly on the lateral wall of the skull. The infratemporal fenestra is comparatively high. The orbit is large subcircular. A rather small antorbital fenestra is present. The quadrate along about two thirds of its length is perpendicular to the lower margin of the maxilla, but its upper portion is deflected backwards. The foramen magnum and occipital condyle are relatively small. The occipital region is extremely expanded dorsally and laterally. It includes the posterior portion of the squamosals and parietals. The dorsal margin of the occipital region is very strongly thickened across the squamosals. The region of the base of the skull is very much compressed in connection with the extreme development of the occipital region. The basal tuber is so strongly flattened anteroposteriorly that it forms a thin plate, which is placed very closely to the basisphenoid process. The basicranial plane, anterior to the basal tubera, is located in the deep, narrow cleft which is vertically extended. In posterior view, the quadrate is very strongly developed in the medial direction and it overlaps anteriorly the broad and thin quadratic wing of the pterygoid. Together they form a very broad plate, extended transversely to the long axis of the skull, onto which is plastered the lateral portion of another flat plate which is built from the prootic and the basisphenoid. The prootic-basisphenoid plate is placed anteriorly to the flat basal tuber and forms the anterior boundary of the cleft-like basicranial region. As a result of the transverse extension and the union of the bones mentioned above, the posterior region of the skull, including the occiput and the basis cranii, is completely separated from palate region. The latter is also placed in the plane perpendicular to the posterior region. The palate is highly vaulted. The both wings of the pterygoid are well developed. The small postpalatal fenestra are present. The internal nares are large.

Dentition. The three premaxillary teeth are distinctly caniniform, conical and oval in cross section. Their roots are strong and have a greater diameter than the crowns which are enamelled and bear densely arranged vertical ridges. One of the ridges present on the posterior face of the crown is serrated and there are about 8 minute denticles on 1 mm. This serrated ridge is visible on two premaxillary teeth but it was presumably present on all three canines. The crowns of the premaxillary teeth bear on their posteromedial faces the relatively broad, vertical trace of being worn down. It is evidence that there were also caniniform teeth along the anterior portion of the mandible. Between the premaxillary and the maxillary series of the teeth there is a long diastema. It is very deep and situated on the suture between the two tooth-bearing bones. The presence of the diastema suggest that there was a strong, caniniform tooth in the mandible, which fitted into the deep pit present ventrally on the juncture premaxilla-maxilla. The seventeen maxillary teeth are arranged in a straight line, which is slightly bent outwards only at the very end. The crowns of the maxillary teeth are low and enamelled on both sides as is well shown on the replacement teeth. The lingual surface of the crown is convex dorsoventrally and anteroposteriorly. The labial surface is concave dorsoventrally and convex anteroposteriorly. The crown is vertically and parallelly ridged. The central ridge on the lingual side is the strongest. There are 4 ridges anterior to it and the anteriormost edge of the crown is also sharply serrated. All the ridges reach a cingulum-like swelling at the base of the crown. Three ridges are present posterior to the medial one but they are thinner than the anterior ridges. The posteriormost edge of the crown is serrated. All the ridges end on the cutting edge of the crown to form the denticulation. The median ridge is less pronounced on the labial face of the crown. Other details of the structure of the labial face of crown are not

visible. The ventral edge of each maxillary tooth is worn down. The roots of the maxillary teeth are generally of the smaller diameter than the crowns. Although the maxillary teeth are very densely arranged they overlap each other only very slightly. The first two or three maxillary teeth have their crowns slightly pointed, while on the more posterior teeth the ventral margins of the crowns are flat. Each third tooth is the replacement one.

Ornamentation. A prominent line of the dermal, pointed nodes is developed along the posterior margin of the cranial roof which passes downwards onto the postorbital bar. In this part the nodes are less prominent. The convex ridge is present above the orbit which continues forwards along the lateral margin of the nasal in the form of separate tubercules. The entire surface of the external bones is covered by irregular tubercles, except the frontoparietal dome which is rough and bears scarce, fine stiches.

The preserved elements of the *postcranial skeleton* differ only slightly from those of *Homalocephale calathocercos* n. gen. et sp. (p. 58). The sacrum consists of 6 vertebrae. The sacral ribs are slender. The pelvis has the acetabulum closed by the ilium and ischium. The caudal ribs are very long, the first two of them touch the posterior part of the ilium ventrally. The femur is curved. Its head is long in medial direction, but it is weakly differentiated from the shaft ventrally. The fourth trochanter is weakly pendant. The caudal tendons were arranged in a form of the basket.

Remarks. — The skull and fragmentary postcranial skeleton of *Prenocephale prenes* were recovered in the Nemegt Formation which, according to ROZHDESTVENSKY (1971) and OSMÓLSKA *et al.* (1972), may correspond with the Lower Edmonton Formation in North America. It more closely resembles *Pachycephalosaurus grangeri* BROWN & SCHLAIKJER, which occurs in the higher, Lancian strata in North America, in: the presence of comparably high dome, lack of the supratemporal fenestra and the parietosquamosal shelf, the considerable length of the snout, the presence of the extensive diastema between the premaxillary and maxillary teeth and the general structure of the teeth, than any representative of the genus *Stegoceras*, which in North America is known from the Edmonton Formation and the older, Belly River Formation. The species described above cannot be assigned to the genus *Pachycephalosaurus* BROWN & SCHLAIKJER, because it shows the presence of numerous and essential differences. Among them should be mentioned in *P. prenes*: the more extensive doming of the cranial roof, with the prefrontals, supraorbitals and postorbitals included, the presence of the antorbital foramen, the significant backward extension of the premaxilla laterally, the much deeper antorbital portion of the snout. The upper part of the quadrate is less horizontal and the infratemporal fenestra is more obliquely placed in *P. prenes* than in *Pachycephalosaurus grangeri*. The ornamentation of the skull is also much weaker in *P. prenes*. BROWN & SCHLAIKJER (1943) suggested that the premaxillary portion of the snout in *Pachycephalosaurus grangeri*, which was not preserved, was devoid of any teeth. However, it is very likely, in our opinion, that the toothless portion of the maxilla corresponds to the diastema, as it is the case in *Prenocephale prenes*. We assume that most probably *Pachycephalosaurus grangeri* possessed premaxillary teeth of the canine type. The small diastema on the juncture between the premaxilla and maxilla is present in *Stegoceras validus* LAMBE. However, the premaxillary teeth in the latter species, although they differ slightly from the maxillary dentition, are not canine-like. In the number of the maxillary teeth, which is 17 in *P. prenes*, this species is closer to *Stegoceras validus*, in which 16 teeth are present, than to *Pachycephalosaurus grangeri*, where the number of teeth is 20. The dental arch of the upper jaw in *P. prenes* is narrower and longer than that in *S. validus*. The maxillary teeth of *P. prenes* are worn in quite a different manner to those of the majority of ornithischians. The wear surface in this species is placed along the ventral

edge of the tooth, instead of on the lingual side as it is in *Tylocephale gilmorei, Homalocephale cala-thocercos* and *S. validus*. BROWN & SCHLAIKJER did not mention how the teeth were worn down in *Pachycephalosaurus grangeri. Stegoceras edmontonensis* (BROWN & SCHLAIKJER, 1943), described from the Edmonton Formation on the basis of the frontoparietal area, exposes some similarities to *Prenocephale prenes* in the narrow fronto-nasal contact, and probably also in the presence of the vertically broad infratemporal fenestra. *S. edmontonensis* exposes, however, the presence of the narrow parietosquamosal shelf, which is absent in *P. prenes*. The striking difference which is apparent between the skulls of *P. prenes* and *Pachycephalosaurus grangeri* is the much larger orbit in the former species. This character can be connected with the difference in the individual age of the specimens, *P. prenes* being, may be, younger because its skull is much smaller (KRAMER & MEDEM, 1955). The distinctive character of *P. prenes* is the very deep medial depression on the occipital region. The basicranial region in this species is also significantly pushed forwards in its central portion. This results in the anteromedial tilting of the prootics, as well as in the fact that the occipital condyle does not protrude backwards behind the posterior edges of the quadrate wings of the pterygoids. Thus, the condylar surface was also very deeply placed and the joint between the condyle and the atlas occurred almost in the same vertical plane as the joint between the skull and the mandible. The relation above mentioned is not recorded in any pachycephalosaurid known. The palatal wings of the pterygoids are more highly vaulted in *Prenocephale prenes* than in *Stegoceras validus* and *Homalocephale calathocercos*. This region cannot be compared in *Pachycephalosaurus grangeri* in which is incompletely preserved. The preserved fragments of the postcranial skeleton of *P. prenes* do not show any significant difference to the other pachycephalosaurids and are typical for the family.

Genus **HOMALOCEPHALE** n.gen.

Type species: Homalocephale calathocercos n.sp.
Derivation of the name: Gr. *homalos* = even, *cephale* = head; because of the flat skull roof.
Genus monotypic; diagnosis, geographic and stratigraphic distribution — as for the species.

Homalocephale calathocercos n.sp.
(Pl. XXII, Fig. 1, Pl. XXIV, Pls XXVI-XXX, Pl. XXXI, Fig. 1; Text-figs 1 D, 4, 5)

Type specimen: One specimen (G. I. No. SPS 100/51) including skull, without mandibles, lacking nasals, anterior portion of frontals, supraorbitals, prefrontals and right jugo-maxillar arch; left maxillary dentition preserved posteriorly; two sternal plates; 10 posterior dorsal vertebrae with ribs attached; 6 sacral vertebrae with nearly complete right side sacral ribs and fragmentary left side ribs, neural arches of sacrals lacking; 29 postsacral vertebrae with caudal ribs; several incomplete chevrons; right ilium, left ilium in articulation with proximal portion of right ischium; distal parts of prepubes; left femur with damaged distal articular surface lacking greater and lesser trochanters, fragmentary right femur; distal ends of left and right tibia and fibula; left astragalus; left and right distal tarsal III; right metatarsal II and distal portion of metatarsal III; distal parts of left metatarsals I, II, III; phalanx 1 of digit? IV of left pes; numerous free caudal tendons and a basket work of tendons woven around distal caudals of preserved series.
Type horizon: Upper Cretaceous, Nemegt Formation, zone of *Tarbosaurus bataar* (MALEYEV) and *Saurolophus angustirostris* ROZHDESTVENSKY.
Type locality: Nemegt, Nemegt Basin, Gobi Desert, Mongolian People's Republic (see GRADZIŃSKI *et al.,* 1969. Text-fig. 2, No. 8).
Derivation of the name: Gr. *kalathos* = basket, *kerkos* = tail; because of the caudal tendons arranged in a kind of a basket.

Diagnosis. — Cranial roof thick but completely flat. Supratemporal fenestra large. Interfrontal and frontoparietal sutures distinct. Infratemporal fenestra low and long. Orbit

large and nearly round. Quadrate deflected backwards along the upper half of its length. Occipital region moderately concave, deepened centrally. Foramen magnum round and large. Occipital condyle large. Basal tubera flat anteroposteriorly, their ventral edges very close to quadratic wings of pterygoids. Ventral maxillary edge arched outwards posteriorly. Maxillary teeth with small crowns. Cranial roof roughly ornamented.

Dimensions — see Tables 1—3.

Table 1

Measurements of the skulls (in mm)

| | Tylocephale gilmorei | Prenocephale prenes | Homalocephale calathocercos |
| | Z. Pal. Nos. | | G. I. No. SPS 100/51 |
	MgD-I/105	MgD-I/104	
Length of skull (premaxilla-upper end of quadrate)	—	218.0	—
Greatest width of skull	99.0	169.0	138.0
Greatest height of skull	133.0	170.0	118.0
Orbit length	38.0	50.5	53.5
Orbit height	16.5	31.5	—
Antorbital length of skull	—	100.0	—
Postorbital length of skull	35.5	66.5	54.0

Description. — The cranial roof is completely flat, being formed from thick parietals and frontals, and it slopes forwards. The interfrontal and frontoparietal sutures are very distinct but the interparietal suture is obliterated. The supratemporal fenestra is large. The infratemporal fenestra is long and low. The orbit is very large and round. The quadrate along its lower half is perpendicular to the lower edge of the maxilla, in its upper half the quadrate is declined backwards. The occipital region is very strongly extended vertically and transversely. It bears a deep central depression. The posterior portions of the squamosals and parietals are included in the occipital region. The occipital condyle and the foramen magnum are large. The basicranial region is compressed and the flat basal tubera nearly touch the quadratic wing of the pterygoids ventrally. Both wings of the pterygoid are strongly developed. The cleft is present anteriorly between two palatal wings of the pterygoids. The small foramen is present on the contact of the maxilla, ectopterygoid and palatine. The tooth-bearing edge of the maxilla is arched outwards posteriorly.

Dentition. The maxillary teeth are arranged in one row and the posterior margin of each tooth slightly overlaps laterally the anterior margin of the successive tooth. The crowns are low. The labial surface of the crown is concave dorsoventrally and the lingual surface is convex anteroposteriorly. On the lingual surface of the crown a thick medial ridge is present. Six ridges are developed anteriorly to it and four ridges posteriorly to it. The posteriormost edge of the crown is additionally serrated. The preserved maxillary teeth are strongly worn out, the worn out surfaces being placed on the lingual side of the crown. They tend to form a common plane over the whole maxillary series.

Ornamentation. The surface of the external cranial bones is very rough, the skull roof bears centrally a small, smooth field, placed on the parietals close to the frontoparietal suture. The cranial roof is covered on its periphery by deep large pits, towards the medial line the or-

Table 2

Measurements of the vertebral column of *Homalocephale calathocercos* n. gen. et sp. (in mm)

(G. I. No. SPS 100/51)

Vertebrae	Length of centrum	Width of centrum (anterior)	Height of centrum (anterior)
D_{n+1}	22	23	20
D_{n+2}	22	22	—
D_{n+3}	22	24	—
D_{n+4}	23	25	—
D_{n+5}	24	26	—
D_{n+6}	26	26	—
D_{n+7}	27	26	—
D_{n+8}	28	28	26
D_{n+9}	29	29	—
D_{n+10}	29	31	29
S_1	33	31	—
S_2	27	—	—
S_3	25	25	—
S_4	25	—	—
S_5	23	23	—
S_6	24	24	—
C_1	27	20	—
C_2	26	24	—
C_3	24	24	—
C_4	23	23	22
C_5	23	22	—
C_6	23	23	23
C_7	23	23	20
C_8	24	23	—
C_9	23	22	—
C_{10}	23	22	—
C_{11}	23	21	—
C_{12}	24	20	16
C_{19}	24	20	16
C_{20}	24	19	—
C_{21}	24	19	—
C_{22}	24	19	—
C_{23}	24	17	—
C_{24}	24	17	—
C_{25}	24	18	15
C_{26}	25	17	15
C_{27}	24	17	—

namentation becomes weaker and denser. The node-like ornamentation is developed along the posterolateral and posterior edges of the cranial roof, but it is moderate in the size.

The anterior portion of the *postcranial skeleton* is represented only by two sternal bones. Each one consists of the thickened, shaft-like process and the thin expanded portion. The posterior dorsals are short and amphiplatyan and possess relatively low neural spines. The zygapophyses of successive dorsals articulate by means of the groove and tongue articular surfaces. The diapophyses rise steeply outwards. They articulate with the rod-like dorsal ribs,

Table 3

Measurements of the pelvis and hind limbs (in mm)

	Homalocephale calathocercos G. I. No. SPS 100/51	Prenocephale prenes Z. Pal. No. MgD-I/104
Length of ilium	230·0	225·5e
Length of ischium	—	185·0e
Length of prepubis	65·6e	—
Femur:		
Length	218·0	221·5e
Proximal transverse width	57·5	62·0e
Distal transverse width	46·5e	—
Least diameter of shaft	25·2	26·0
Tibia:		
Distal· transverse width	59·5 (dext.) 57·5 (sin.)	—
Fibula:		
Distal transverse width	18·8	—́
Pes:		
Length of metatarsal II	95·0	
Length of metatarsal III	99·5e	
Length of phalanx IV_1	32·0	

contacting both the capitulum and the tuberculum. The sacrum includes six vertebrae, all with the ribs preserved. The fourth sacral rib is strongly expanded vertically and flattened anteroposteriorly. The second, third and the ventral part of the fourth rib contact the ischium. The caudals are amphiplatyan and bear the long neural spines. The proximal caudals have long, rod-like caudal ribs. The articular surfaces of the prezygapophyses on the anterior caudals are concave and dorsomedially directed, behind the tenth caudal they are facing medially. The acetabulum is completely closed by the ilium and the ischium. The prepubis is short, laterally flattened. The femur is recurved inwards and its articular head is elongated medially. The ventral edge of the head is weakly dinstinguished from the medial edge of the shaft. The fourth trochanter is weakly pendant. The tibia is strongly broadened distally. The pes was probably tetradactyl, with a weak first digit. The posterior portion of the tail is surrounded by a basket work of the ossified tendons.

Remarks. — The completely flat skull roof with the distinct sutures distinguishes *Homalocephale calathocercos* from all the pachycephalosaurids described to date. Even those Pachycephalosauria which are known as being relatively flat-roofed: *Yaverlandia bitholus* GALTON, 1971 and the specimen A.M.N.H. No. 5450 of *Stegoceras validus* (figured in GALTON, 1971 a) expose the slight convexity of the cranial roof, and the sutures in this region are not visible in these forms. The flatness of the cranial roof and the presence of the sutures, characteristic for *H. calathocercos*, cannot be regarded as being due to the juvenile stage, the skull in question being larger than that of any known skull of *S. validus*. The pitted ornamentation of the skull in *H. calathocercos* is most similar to that of *Yaverlandia bitholus* from the Wealden of England. It should be emphasized in this place that in spite of the differences in the structure of the cranial roof, the other cranial regions are developed according to the typical pachycephalo-
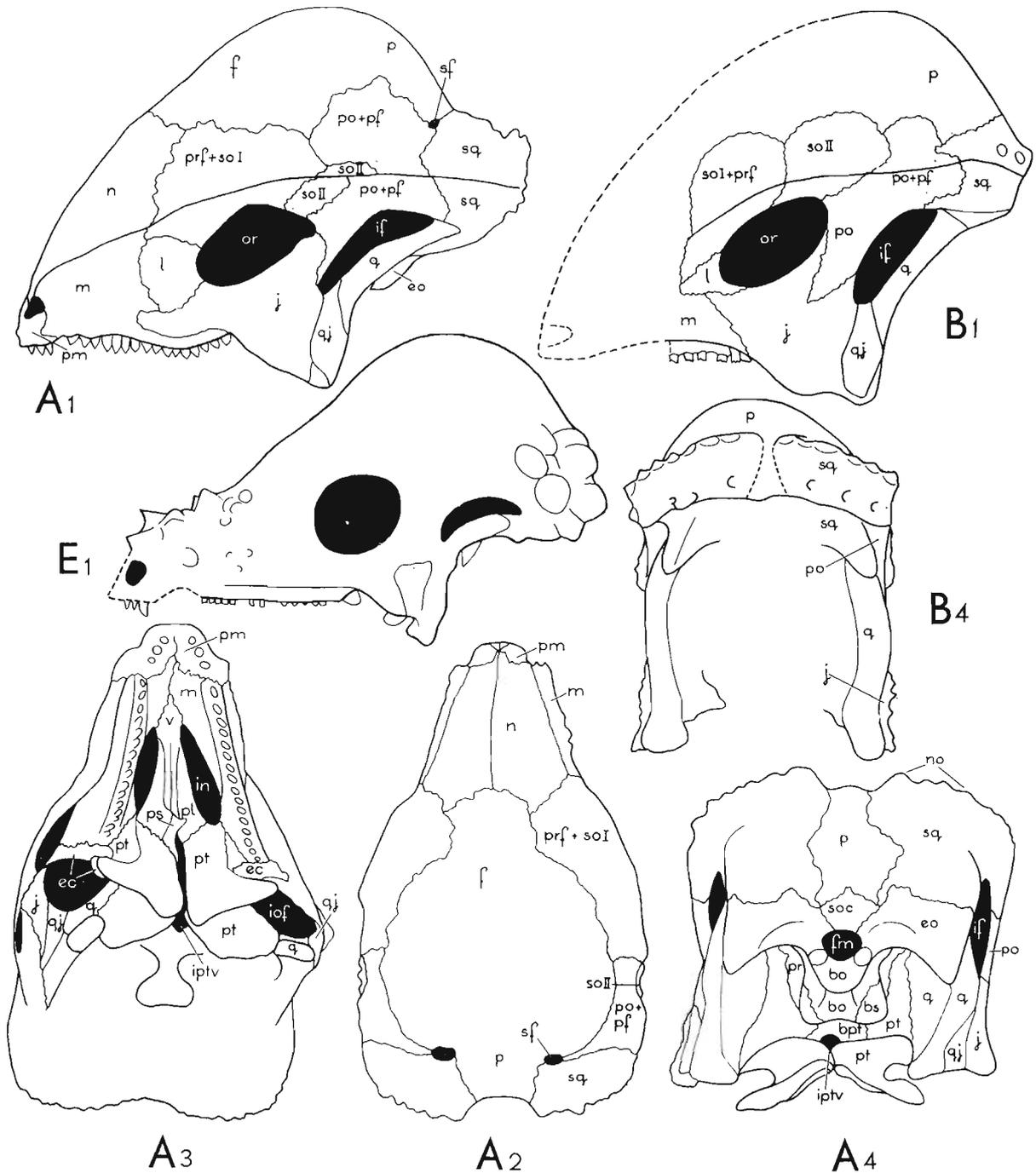
Fig. 1

Diagrammatic drawings of the skulls of the Upper Cretaceous Pachycephalosauria; *A Stegoceras validus* LAMBE, *B Tylocephale gilmorei* n. gen., n. sp., *C Prenocephale prenes* n. gen., n. sp., *D Homalocephale calathocercos* n. gen., n. sp., *E Pachycephalosaurus grangeri* BROWN & SCHLAIKJER; *1* left lateral view, *2* dorsal view, *3* palatal view, *4* occipital view. Abbreviations: *aof* antorbital foramen, *bo* basioccipital, *bpt* basipterygoid, *bs* basisphenoid, *ec* ectopterygoid, *en* external naris, *eo* exoccipital, *f* frontal, *fm* foramen magnum, *if* infratemporal fenestra, *in* internal naris, *iof* infraorbital fossa, *iptv* interpterygoid vacuity, *j* jugal, *l* lacrimal, *m* maxilla, *n* nasal, *no* nodes, *op* opisthotic, *or* orbit, *p* parietal, *pf* postfrontal, *pl* palatine, *pm* premaxilla, *po* postorbital, *ppf* postpalatal foramen, *p* prootic, *prf* prefrontal, *ps* parasphenoid, *pt* pterygoid, *q* quadrate, *qj* quadratojugal, *sf* supratemporal fenestra, *sq* squamosal, *so* supraorbital, *soc* supraoccipital, *v* vomer. Not to scale.
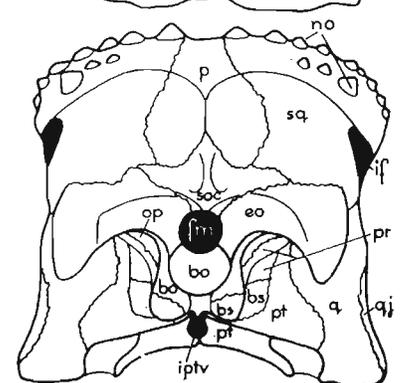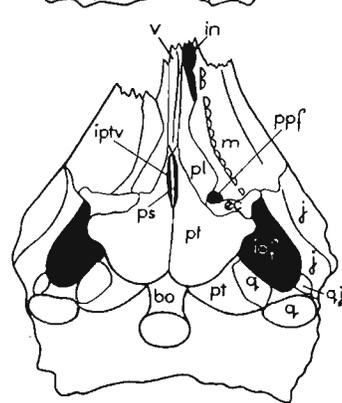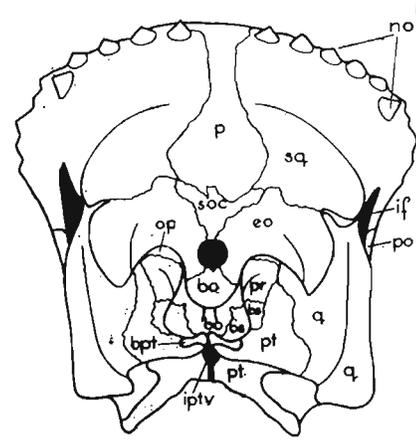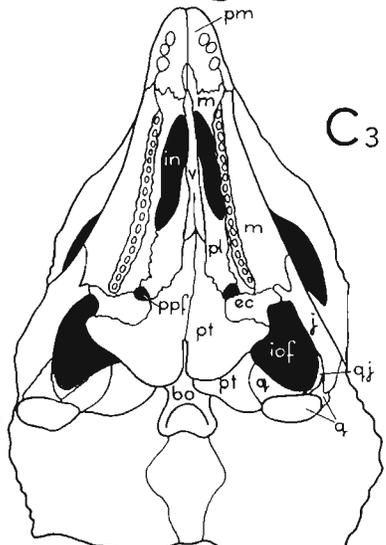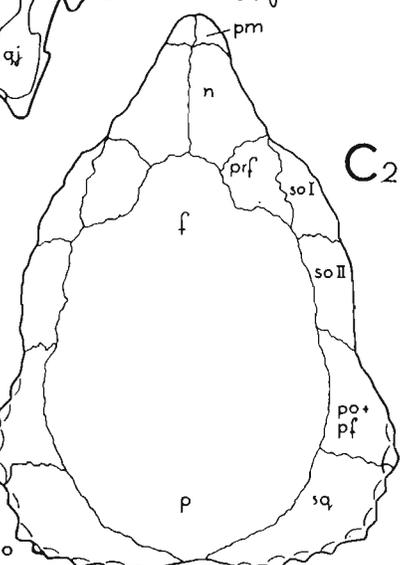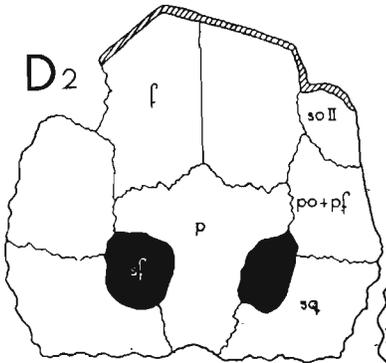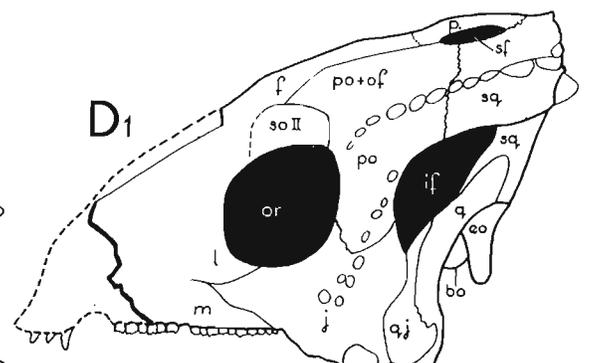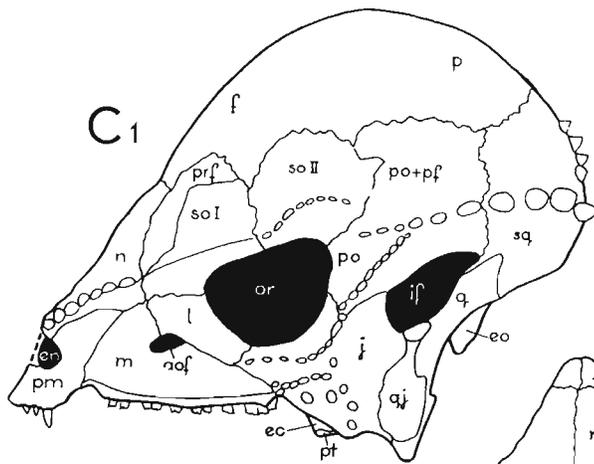
saurid pattern. *H. calathocercos* comes from the same locality and formation (Nemegt) as *Prenocephale prenes*. The latter form has the frontoparietal dome most strongly developed among the Pachycephalosauridae known to date. The skulls of both these species are of about the same size and when their occipital regions are compared the difference is to be noticed in the size of their foramina magna and of the occipital condyles with both being larger in *H. calathocercos*. The cranial roof of *H. calathocercos* is narrower in the posterior view and does not overhang the occipital region as in *P. prenes*. However, the ventral portion of the squamosal and the exoccipital is much broader transversely in *H. calathocercos*. This is partly caused by the more steep inclination of these bones towards the medial line in *P. prenes*. The central depression which is present in the occipital region of all the Pachycephalosauridae, in *H. calathocercos* is the broadest transversely but it is much shallower than in *P. prenes* and about as shallow as it is in *Stegoceras validus*. This depression in *H. calathocercos* is divided medially by a low, vertical ridge; this feature is very weakly pronounced in the two species compared. The basal tubera in *H. calathocercos* are flattened anteroposteriorly as it is the usual case with all the pachycephalosaurids, but they are still thicker than those in *P. prenes* and may be only compared to these in *S. validus*. However, in the latter species the basal tubera are not so close to the quadratic wing of the pterygoid as they are in *H. calathocercos*. The basioccipital portion of the basal tubera in our species is strongly developed, comparable to that in *Pachycephalosaurus grangeri*. In the palatal view, the ventral margin of the maxilla in *Homalocephale calathocercos* is distinctly arched outwards in its posterior section, and it is nearly straight in *Stegoceras validus* and *Tylocephale gilmorei*, very slightly arched in *Prenocephale prenes* and recurved inwards in *Pachycephalosaurus grangeri*. The general structure of the maxillary teeth is similar in *Pachycephalosaurus grangeri* and *Prenocephale prenes* (although the teeth were used in different ways, judging from the different position of the worn out surfaces in the latter species, p. 55). The maxillary teeth in *H. calathocercos* have less ridges on the crowns than the teeth in *P. prenes*. The structure of the maxillary teeth in *H. calathocercos* and *S. validus* is incomparable, because the crowns are conical in the latter species.

ANATOMY OF THE PACHYCEPHALOSAURIDAE

OSTEOLOGY OF THE SKULL
(Pls. XXII-XXIV, Pl. XXV, Fig. 2; Text-figs 1-3)

The following detailed description of the bones of the skull is based on the skull of *Prenocephale prenes* (Z.Pal.No.MgD-I/104) from the Nemegt Formation (Upper Cretaceous) of Nemegt in the Gobi Desert. The state of preservation of this skull is by far the best known in this family, and it has allowed us to obtain some new informations about the skull structure in the Pachycephalosauridae. The sutures are for the most part clearly visible and for this reason we decided to base the description of cranial osteology of the family on the skull of the specimen. In addition to this skull we have two other less complete specimens — that of *Homalocephale calathocercos* (G. I. No. SPS 100/51) from the same beds and locality and that of *Tylocephale gilmorei* (Z.Pal.No.MgD-I/105) from the older, Barun Goyot Formation of the locality Khulsan in the Gobi Desert. We had also the opportunity to consult a plaster cast of the skull of *Stegoceras validus* LAMBE 1902 (UA. No. 2) described by GILMORE (1924) as well as the cranial roofs of this species (N.M.C. Nos. 138, 8816) described by LAMBE (1918) from the Belly River Formation in Alberta. Unfortunately the skull of *Pachycephalosaurus grangeri* BROWN &

SCHLAIKJER, 1943 from the Lance Formation in Montana is not accesible to us at the moment. Based on the above material, we are able to state that the basic structure of the pachycephalosaurid skull is very peculiar, although generally a very uniform one. The following cranial osteology is completed by some new data dealing with the structure of: the orbit, the upper jaw and the middle ear cavity, which were not formerly described. The comparisons of the bones of skull of *Prenocephale prenes* with those of other pachycephalosaurids from the Upper Cretaceous are given at the end of the description of each particular bone. The comparisons of the cranial regions, as well as the descriptions of the dentition are given in the systematic part of this paper (p. 50). The bones of the mandibular segment are not considered here because the most complete lower jaw known so far is that of *Stegoceras validus* and it was already sufficiently described by GILMORE (1924). The new Mongolian material at our disposal displays only a fragmentary mandible of *Tylocephale gilmorei* and this is described in the systematic part of the present paper.

Neurocranium

The bones forming the brain case are firmly united in the Pachycephalosauridae. Some of them are strongly thickened or domed i.e. those of the skull roof, which gave a very strong protection to the brain. The union of the neurocranium with the splanchnocranium is very strong so the skull was akinetic.

Supraoccipital. — The supraoccipital takes part in the formation of the dorsal margin of the foramen magnum, but it is very narrow there. The supraoccipital gives laterally two narrow wings on the occipital surface of the skull, each of them deeply wedged between the exoccipital and the squamosal. In the midline, the supraoccipital is elongated in the dorsal direction and it gives a tongue which deeply invades the parietal. The supraoccipital forms the bottom of the deep central depression and bears medially a vertical keel, on the both sides of which a pair of short deep grooves is present. The supraoccipital forms the narrow portion of the roof of the medulla oblonga and anteriorly it expands and bounds the inner ear cavity posteromedially. The supraoccipital takes part in formation of the upper margin of the foramen magnum in *Homalocephale calathocercos* and shows strongly pronounced medial, vertical keel. The supraoccipital is similarly developed in *Stegoceras valius*. LAMBE (1918, Pl. 1, Figs. 1, 2) mistakingly named in *Stegoceras validus* the supraoccipital as the exoccipital. This most probably was caused by the presence of the vertical clevage through the supraoccipital. BROWN & SCHLAIKJER (1943) stated that the supraoccipital in *Pachycephalosaurus grangeri* was excluded from the boundary of the foramen magnum. Thus, in this respect, the species mentioned would be different from all other known Pachycephalosauridae.

Exoccipital. — The exoccipital forms the major part of the sharp margin of the foramen magnum and gives the pedicle which participates in the formation of the occipital condyle. Laterally this pedicle is perforated by the foramen for the exit for the nerve XII. On the margin of the foramen magnum and within the medulla oblonga it contacts the basioccipital ventrally and the supraoccipital dorsally. It bounds mediolaterally the inner ear cavity. It forms the flat, wing-like paroccipital process which meets the squamosal dorsolaterally. The suture between the squamosal and the exoccipital is folded in its more medial portion and gives upwards the small embayment of the exoccipital within the squamosal. The exoccipital contacts the opisthotic under the proximal part of the ventral edge of the paroccipital process. The suture is distinct, reaches the upper margin of the foramen ovale and it is very apparent that the entire distal portion of the paroccipital process was formed only by the exoccipital. The condylar

pedicle of the exoccipital gives the short process lateroventrally, along the occipital condyle, which forms the upper half of the edge of the basal tuber. This process contacts the basioccipital medially in the region of the condylar neck and the basisphenoid ventrally. The suture between the exoccipital and the basisphenoid extends here upwards on the anterior face of the flat basal tuber. At the lower margin of the foramen ovale, the exoccipital contacts the horizontal ridge of the prootic laterally, and bounds the foramen ovale ventroposteriorly. An extensive depression is present on the posterior face of the exoccipital above the foramen magnum which is transversely elongated. A strongly arched ridge extends above this depression in the lateral direction and it reaches the ventral edge of the paroccipital process short before its lateroventral extremity. The distal ends of the paroccipital processes are longer and narrower in *Homalocephale calathocercos* than in *Prenocephale prenes*. They are very much shorter in *Stegoceras validus*. In all representatives of the Pachycephalosauridae they are closely attached to the squamosals and quadrates laterodorsally, except *P. prenes* where their upper distal edges are broadly separated from the bones mentioned. BROWN & SCHLAIKJER (1943) mentioned that the contact of the exoccipital with the prootic is extensive in *Pachycephalosaurus grangeri*. This contact is very limited in *P. prenes* and *Homalocephale calathocercos* and it is present only at the lower margin of the foramen ovale. Most probably these authors had in minds the ventral contact of the exoccipital below the lower edge of paroccipital process. Here however, the exoccipital is ventrally separated from the prootic by the narrow posterior inclusion of the opisthotic as it is distinctly visible in both Mongolian species mentioned and also in *Stegoceras validus*.

Basioccipital. — The basioccipital forms nearly the entire occipital condyle. It forms the narrow portion of the bottom of the medulla oblonga and in the ventroanterior direction it forms the central portion of the basal tubera, marked medially by a sharp keel. The keel is most strongly pronounced in its anterior part. The condylar neck is extremely short. The articular surface of the condylus is developed on its posterior face, and it continues ventrally, where it forms a comparatively extensive triangular area. There is a pair of short grooves present on both sides of the keel mentioned above. The basioccipital contacts the exoccipitals dorsally in the region of the occipital condyle, laterally within the medulla oblonga, as well as laterodorsally outside the condyle. Here on the boundary the foramen for exit of the nerves X and XI is present. The basioccipital contacts the basisphenoid on the posteroventral portions of the basal tubera. The ventral suture with this bone extends transversely close to the bases of the basipterygoid processes within the deep cleft between the basal tubera posteriorly and the pterygoids anteriorly. The occipital condyles in all the Pachycephalosauridae are similar in being formed mostly by the basioccipital, but they differ in the degree of ventral inclination, which is strongest in *Stegoceras validus*. The condyle is nearly perpendicular to the line of the maxillary teeth in *Homalocephale calathocercos* and it has the large articular surface facing ventrally. The similar surface seems to be present in *Pachycephalosaurus grangeri*. It is also developed in *Prenocephale prenes* but it is much smaller here. The neck-like portion of the basioccipital, anterior to the occipital condyle, is very well developed and deep dorsoventrally in *Pachycephalosaurus grangeri*, bearing the thick keel in its anteriormost portion. It differs from that in *Prenocephale prenes*, which has only a sharp keel present in this place, and the neck-like portion is nearly absent in the latter species. This portion seems to be deepest and narrowest in *Pachycephalosaurus grangeri*.

Opisthotic. — The opisthotic is a comparatively small, flat bone. Its posterior extension is wedged between the exoccipital dorsally and the prootic ventrally, and its anteromedial edge reaches the boundary of the foramen ovale. Within the infratemporal fossa, it takes part in

the formation of its posteromedial wall. It is hidden laterally by the quadrate, and a narrow space is present between these bones. The opisthotic meets the prequadratic process of the squamosal dorsoposteriorly and dorsomedially. It contacts and is slightly overlain by the prootic anteromedially. The opisthotic is visible in all the skulls at our disposal, between the exoccipital and prootic but the sutures between these bones extend differently in all the specimens. The suture between the exoccipital and the opisthotic is placed immediately at the ventral margin of the paroccipital process in *Stegoceras validus*, it is placed slightly more anteriorly in *Prenocephale prenes* and still more anteriorly in *Homalocephale calathocercos*, in which the ventral
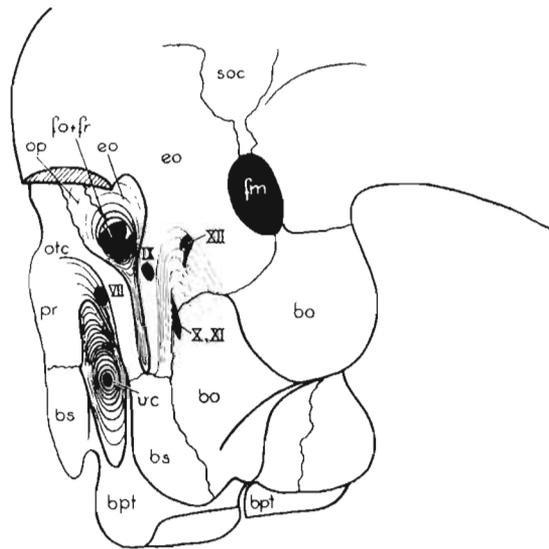
Fig. 2

Prenocephale prenes n. gen., n. sp. Diagrammatic, drawing of the left side of the otic and basicranial region of the skull in posterolateral view (see also Pl. XXV, Fig. 2a). Abbreviations: *fo* fenestra ovalis, *fr* fenestra, rotunda, *otc* otosphenoidal crest, *vc* opening to Vidian canal; Roman numbers indicate exits of cranial nerves, other abbreviations as in Fig. 1. About natural size.

portion of the exoccipital gives anteriorly the narrow horizontal process which takes part in the formation of the roof of the middle ear cavity. The opisthotic was not described by GILMORE (1924) or BROWN & SCHLAIKJER (1943).

Prootic. — The prootic in the Pachycephalosauridae is a very complicated bone that to date has not been described. It is developed according to the quite different pattern than that known so far in the dinosaurs. It has developed the extensive external wing which lies transverse to the long axis of the skull, instead of being placed longitudinally. The upper part of the anterior surface of this wing forms the medioventral wall of the infratemporal fossa, while the lower part of the posterior surface underlies the quadrate wing of the pterygoid. The strong crest runs outwards across the latter portion of the prootic, which bounds the middle ear cavity dorsoanteriorly. This crest, in spite of its unusual position, most probably corresponds to the otosphenoidal crest of other dinosaurs. It continues towards the basal tuber ventrally and meets the basisphenoid, immediately at the contact of the latter bone with the exoccipital. The prootic contacts the opisthotic dorsally. It meets the basisphenoid once more below the horizontal portion of the crest. Here, the flat lateral extension of the basisphenoid overlaps slightly the prootic posteriorly, the two bones forming a common plate, which is placed very close to the

quadrate wing of the pterygoid and only a very narrow slit separates the two plates. In this way, the basicranial region is nearly completely separated from the suborbital and palatal regions. The prootic-basisphenoid plate bounds anteriorly the comparatively broad and very deep cavity which corresponds to the strongly shortened basicranial region and is limited backwards by the plate-like basal tuber. Within the infratemporal fossa the prootic contacts the opisthotic posteriorly, the quadrate laterally and dorsally, the pterygoid laterally and ventrally. The contact with the laterosphenoid medially is an extensive one. The contact with the basisphenoid anteriorly is only partly visible dorsally and it is nearly completely hidden by the pterygoid and epipterygoid ventrally. The prootic meets the epipterygoid anteroventrally and immediately below the contact with the laterosphenoid. The prootic is similarly constructed in *Homalocephale calathocercos*. The nearly complete separation of the basicranial and the suborbital regions as well as the presence of the horizontal crest on the posterior surface of the transverse wing of the prootic in *Stegoceras validus*, both characteristic of *Prenocephale prenes* and *Homalocephale calathocercos*, indicate that the general structure of the bone was similar in this species. The crest mentioned seems but slightly more weakly pronounced in *Stegoceras validus*, but it seems to be quite strong in *Pachycephalosaurus grangeri*.

Basisphenoid. — The basisphenoid is very complicated in the pachycephalosaurids thanks to the very strong anteroposterior compression of the basicranial region. Not all its contacts with the adjoining elements could be observed and intepreted. This is especially true for the anterolateral contacts of the basisphenoid, which can be observed in the medioventral part of the wall of the orbit, where many additional bony elements are added. In the posterior view, the basisphenoid forms the lateroventral extension of the flat, plate-like basal tubera, and it contacts here the exoccipitals dorsally and basioccipital medially. The basisphenoid is invaginated medially on both side of the basicranium and forms the deep lateral cavities bounded by the basal tubera posteriorly and anteriorly by the plates which are formed by the basisphenoid ventrally and the prootic dorsally. The bottom of this cavity is pierced in the medioventral direction by the entrance to the Vidian canal. The basisphenoid sends medially and anteroventrally a pair of the thick basipterygoid processes which attach to each other medially, roofing the posterior portion of the interpterygoid cavity. In posterior view, the prootic-basisphenoid plate is underlain along its margin by the quadrate wing of the pterygoid. It appears within the infraorbital fossa anteriorly, and here the suture between the prootic and basisphenoid is not exposed. The suture of the basisphenoid is here visible dorsally with the presphenoid backwards and with some additional ossifications forwards. The anteriormost edge of the basisphenoid forms the posterior boundary of the space which joins the two orbits transversely (the interorbital fissure, p. 77). The dorsal rim of this fissure is formed by two additional bony elements and dorsally a pocket is present between them. It is bounded by the palatal wing of the pterygoid anteriorly and ventrally. The interorbital fissure communicates ventrally with the interpterygoid vacuity. The basisphenoid is pierced by the exit for nerve VI and below it by the small foramen which was probably the exit for the palatine artery. The basisphenoid is generally very similar in all the Pachycephalosauridae where it was described. The part of the basisphenoid which forms the ventral portions of the basal tubera is most extended ventrally in *Homalocephale calathocercos* in which it nearly reaches the pterygoids; it is the shortest vertically in *Stegoceras validus* in which the comparatively wide space separates the basisphenoid from the pterygoids. The interorbital fissure mentioned above in *Prenocephale prenes* and present in front of the basisphenoid is nearly closed in *Homalocephale calathocercos* and *Stegoceras validus* where this bone seems to be more expanded forwards. The basisphenoid of *Pachycephalosaurus grangeri* was never described.

Parasphenoid. — The parasphenoid in the Pachycephalosauridae is well developed and differentiated from the basisphenoid, although it overlaps the latter bone ventrally. The parasphenoidal rostrum is developed but it seems to be short in *Prenocephale prenes*, and is visible within the interorbital fissure. The posterior part of the parasphenoid distinctly overlaps ventrally the basisphenoid in *Homalocephale calathocercos* and it closes nearly completely the lumen of the interorbital fissure. The parasphenoidal rostrum is long in this species, being visible in the palatal view in the slit between the two pterygoids. The parasphenoid seems also to close the lumen of the interorbital fissure in *Stegoceras validus*. The parasphenoidal rostrum is developed in this species similarly as it is in *Homalocephale calathocercos*, but it extends ventrally in its most anterior part as the pendant process which was tentatively called the presphenoid by GILMORE (1924, p. 22).

Laterosphenoid. — The laterosphenoid is coalesced with the adjoining elements except those of the skull roof and most of its sutures are but weakly visible. It forms the dorsomedial portion of the crest which marks the boundary between the infratemporal fossa and the orbit. It is expanded mostly on the dorsomedial wall of the infratemporal fossa, and only a small portion is present within the orbit. The entire posterior boundary of the laterosphenoid contacts the parietal. It meets the postorbital posterodorsally and the frontal anterodorsally. It contacts the orbitosphenoid anteriorly, the basisphenoid anteroventrally and the prootic ventrally. The narrow tongue of the laterosphenoid makes the dorsal margin of the exit for cranial nerve V_1 close to the contact of the basisphenoid and prootic. The laterosphenoid in *Homalocephale calathocercos* does not differ from that in *Prenocephale prenes*, but its contact with the adjoining bones seems to be looser. The laterosphenoid in *Stegoceras validus* (alisphenoid of LAMBE 1918 and GILMORE 1924) is less extended vertically because of the much lower orbit and infratemporal fossa. In this species it forms the upper anterior boundary of the infratemporal fossa rather than the lower anterior one as was mistakingly stated by GILMORE (1924, p. 21). Judging from the description of the bone given by BROWN & SCHLAIKJER (1943) for *Pachycephalosaurus grangeri* it is similar here to that bone of other pachycephalosaurids.

Presphenoid. — It is difficult to indicate the presphenoid in the pachycephalosaurid skull because of the many additional ossifications present in the orbital region. We think that it is most reasonable to consider as the presphenoid the small bone which bounds ventrally and slightly anteriorly the exit of the optic nerve. This bone contacts the prootic posteroventrally on the lateral wall of the braincase, the basisphenoid ventrally and a separate element of the additional orbital ossification anteroventrally. The dorsal contact of the presphenoid is exclusively with the orbitosphenoid. The foramen is present in the posterior suture between the presphenoid and orbitosphenoid which represents the exit for the third nerve. The exit of sixth nerve is present at the presphenoid/basisphenoid suture. The usual contact between the presphenoid and the parasphenoid which can be observed in many ornithischian dinosaurs on the lateral wall of the braincase is not present in the pachycephalosaurids. It is caused by the presence of the additional ossifications which separate the two bones and by the peculiar compression and folding of the basicranial region in this family. The presphenoid is very similar in *Homalocephale calathocercos*.

Orbitosphenoid. — The orbitosphenoid is small and forms the dorsoposterior boundary of the exit for the second nerve. The orbitosphenoid is suturally connected with the presphenoid on both sides of the optic foramen. It contacts the additional orbital ossifications anteriorly and dorsally, and the laterosphenoid posteriorly. There are separate exits for the fourth and third nerves. That for the fourth nerve is placed in the orbitosphenoid, that for the third nerve in the suture with the presphenoid, immediately posteriorly to the exit for the second nerve.

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The external surface of the orbitosphenoid is very uneven, furrowed irregularly and deeply. The orbitosphenoid is also very small occupying the same position with respect to the adjoining elements in *Homalocephale calathocercos* and in *Stegoceras validus*. The surface of this bone in *Homalocephale calathocercos* is smoother than in *Prenocephale prenes*.

Frontoparietal. — The frontal and parietal are not separated by sutures dorsally and they are extremely strongly domed. The frontoparietal contacts anteriorly the nasal by means of a short suture. Laterally it meets the prefrontal along an arched suture. It gives the short wedge which meets the supraorbital I laterally. More posteriorly it is bounded laterally by the supraorbital II, postorbital, and the squamosal. At the juncture of the sutures between the frontoparietal from the one side and the prefrontal, supraorbitals from the other side there is a deep pit. Two other such pits, the anterior deeper and the posterior shallower, are present at the frontoparietal suture on the juncture with the supraorbital II-postorbital and the postorbital-sqamosal. Within the orbit the frontal contacts the prefrontal, the accessory orbital ossification *3,* the orbitosphenoid, the laterosphenoid, the supraorbitals and the postorbital. The narrow tongues of the parietal are wedged between the sqamosals on the posterior margin of the skull. They widen on the occipital surface of the skull and contact the squamosals laterally, and the supraoccipital ventrally. The parietal ridge is well pronounced along the ventral portion of the parietals and it reaches into the central depression. The parietals take part in formation of the central depression. The preserved portion of the frontoparietal shows that the dome in *Tylocephale gilmorei* was placed very much posteriorly in the comparison with other pachycephalosaurids (p. 52). The parietal is nearly vertically placed on the occipital face of the skull, as a result of the lack of the deep central depression present here in other Pachycephalosauridae. The frontoparietal is very variable in the specimens assigned to *Stegoceras validus,* which is connected with the various development of the dome within this species. The frontal portion of the dome in *Stegoceras validus* is more convex and better distinguished from the adjacent bones than it is in *Prenocephale prenes.* The parietals are similarly placed in *Stegoceras validus* as in *Prenocephale prenes* in connection with the presence of the deep central depression on the occipital face of the skull. They are, however, relatively broader on the margin of the skull and are devoid of the parietal ridge in *Stegoceras validus.* One of the specimens of *Stegoceras validus* (NMC No. 2379) exposes dorsally the presence of the distinct interfrontal and fronto-parietal sutures (LAMBE 1918, Fig. on p. 25). A similar course of these sutures is exposed in *Homalocephale calathocercos,* the species which possesses an entirely flat skull roof. A weak trace of the interparietal suture is preserved in the latter species. The parietals are broader on the margin of the skull in *Homalocephale calathocercos* and the occipital portions of these bones are flatter transversely in connection with the broader central depression than in *Prenocephale prenes.* They bear also a thinner but sharper parietal ridge. The parietals bear a large, round protuberance in *Pachycephalosaurus grangeri* on their occipital portion, which is absent in *Prenocephale prenes,* and other pachycephalosaurids. The ornamentation of the frontoparietal varies distinctly in the species within this family. It was sometimes regarded as the character of the sexual dimorphism (p. 100). The most distinct ornamentation of this region was observed in *Homalocepha lecalathocercos,* where the irregular coarse granulation is present on the frontals and parietals. The granules are much larger on the posterior portion of the parietals, while the anterior portion is smooth, close to the medial section of the frontoparietal suture. The fronto-parietal is more or less smooth and more or less densely pitted in *Prenocephale prenes* and *Stegoceros validus.* The surface of the dome is smooth in the species of *Pachycephalosaurus* but also exposes the perforations.

Accessory orbital ossifications (Text-fig. 3). — The medial and anterior wall of the orbit

is completely ossified in the Pachycephalosauridae. The numerous additional ossifications are surrounded periferally by the bones usually present in this region: the frontal, prefrontal, lacrimal palatine, basisphenoid, presphenoid, orbitosphenoid, laterosphenoid. These additional elements form a mosaic of bones which are suturally separated but are often very small. For this reason they are rather difficult to describe. However, three of them are more regular, larger and present in the same place in different specimens. The notations *1—3* are given to them on Text-fig. 3 and they are described below. This complete ossification of the anteromedial region of the orbit means that the nasal cavity was completely separated from the orbital region and that the nerves and vessels for the snout had to issue through special openings which are present in the anterior wall of the orbit. Such extensive ossification of the orbital region has not been described in any other reptile but slightly similar conditions are present in mammals and some birds. Some
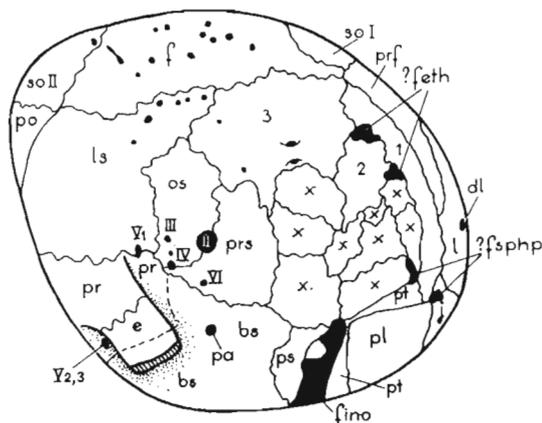
Fig. 3

Prenocephale prenes n. gen., n. sp. Diagrammatic drawing of the right orbit (see also Pl. XXV, Fig. 2*b*). Abbreviations: *dl* lacrimal duct, *e* epipterygoid, *feth* foramen ethomoidale, *fino* interorbital fissure, *fsphp* foramen sphenopalatinum, *ls* laterosphenoid, *os* orbitosphenoid, *pa* opening for exit of palatine artery, *prs* presphenoid, *1, 2, 3,* × accessory orbital ossifications; other abbreviations as in figs. 1 and 2. About natural size.

of these bones most probably represent the separate ossifications within the planum antorbitale (= lamina orbitonasalis of de BEER, 1971), planum supraseptale and comissura ethmoidalis. Another possible interpretation is that ossifications 2 and 3 arose within the trabecula communis and consequently they could be interpreted as the separate ossifications of the presphenoid. Others are certainly the membranous bones formed within the membranes of the orbital region.

Accessory orbital ossification 1. — This bone is the most anterior one and the largest of the accessory elements. It forms the major part of the anterior wall of the orbit and contacts anteriorly the prefrontal with its upper portion, the lacrimal and jugal below, and the palatine most ventrally. It meets the accessory ossifications 2 and 3 and the narrow upward extension of the pterygoid posteriorly. Two openings are present on the suture between the accessory ossifications *1* and *2* and they most probably represent the foramina ethmoidale. Another opening is present here, at the most ventral extension of the accessory ossification *1* between the latter and the palatine with the jugal. It may be interpreted as the sphenopalatine foramen. It also leads to the nasal cavity. When seen anteriorly, from the nasal cavity, the accessory ossification *1* forms the extensive posterior wall of the nasal cavity. This wall is convex anteriorly and contacts the maxilla and prefrontal laterally, the palatine ventrally, the accessory ossification 2 medially and the accessory ossification 3 posteriorly. The latter, together with accessory

ossifications *2* and *3*, take part in the formation of the floor of the olfactory tract with accessory ossification *1* composing its most anterior part. The accessory ossification *1* seems to be a homologue of the lateral ethmoid of fishes and of the ectethmoid+uncinate bone of some birds. DE BEER (1971) discussing the ossifications of the lamina orbitonasalis suggests that the uncinate bone of birds "apears to be a portion of the ectethmoid segmented off...". The bone described above in *Prenocephale prenes* is well distinguishable also in *Homalocephale calathocercos* and *Stegoceras validus* but in the latter species it is distinctly smaller, which is most probably related to the much lower orbit of *Stegoceras validus*. It seems, that the small fragment of the bone named by LAMBE (1918, Pl. 1, Figs. 1, 2) as parasphenoid corresponds to our accessory orbital ossification *1*.

Accessory orbital ossification 2. — This ossification is a small bone, which bounds the upper foramen ethmoidalis ventrally and lower foramen ethmoidalis posteriorly. It meets accessory ossification *1* anteriorly, accessory ossification *3* dorsally, one bone of other accessory elements posteriorly and several others ventrally. It takes part in the formation of the floor of the olfactory tract. This bone is slightly smaller in *Homalocephale calathocercos*, otherwise being similar in the shape. A bone, which most probably represents accessory ossification *2*, is present posteriorly to the lower foramen ethmoidalis in *Stegoceras validus*, but it is larger here.

Accessory orbital ossification 3. — It is another large bone of the accessory orbital ossifications. It is elongated in the sagittal direction and contacts the frontal with a long suture dorsally, the laterosphenoid posteriorly and, with its posterior half, the orbitosphenoid ventrally. It meets accessory ossification *1* above the upper foramen ethmoidalis and slightly below the latter, it is suturally connected with accessory ossification *2* anteriorly. One of the small accessory elements is placed anteroventrally to accessory ossification *3*. The latter forms the lateral wall to the most anterior portion of the cerebrum, the coronal sulcus and the olfactory tract. The accessory ossification *3* is also well visible in *Homalocephale calathocercos* and *Stegoceras validus* and it is similarly large in both species. In the specimen NMC No. 138 of *S. validus* this bone was determined by LAMBE (l. c.) and GALTON (1971*a*, Text-fig. 4*b*) as the presphenoid.

Splanchnocranium

The splanchnocranium includes, as here conceived, all the skull elements which are not directly involved in the formation of the brain case. They are, however, attached directly or indirectly to the neurocranium and all the contacts with the neurocranium seem to be extremely firm, except, perhaps, that between the upper portion of the quadrate and the skull roof. The squamosal has a rounded, deep articular socket for the head of the quadrate, which would be for an amortization rather than due to the kineticism of the skull.

Premaxilla. — The premaxilla is relatively large, its lateral wing is wedged far posteriorly between the nasal and maxilla and separating these bones for a very long distance. This wing is placed in the vertical plane and is flat. The anterior portion of the premaxilla is long and thickened, sloping steeply down laterally. The alveolar margin of the premaxilla is comparatively thick and bears three deep alveolae. The very tip of the premaxilla is devoid of dentition. Ventrally the premaxilla forms the anterior part of the slightly concave snout. More posteriorly it forms the roof of the deep pit for the enlarged dentary tooth, and medially its posterior process underlies the maxilla. The premaxilla bears anteriorly, opposite the first premaxillary tooth, a small foramen. It presumably leads to the slit-like opening placed above and anteriorly to the bottom of the nasal cavity. It seems probable that both openings were connected with the

Jacobson's organ. The internarial bridge was probably formed from the premaxillae, because each of them gives posteriorly, on the dorsal side, a process which is broken off. The anterior portion of the nasal cavity is large and deep medially. The side walls of the medial depression are formed by the premaxillae, while its bottom is built from the maxillae. Within the Pachycephalosauridae the premaxillary portion of the snout is only known in *Stegoceras validus* and in the here described *Prenocephale prenes*. The essential difference between the two species in this region involves the degree of its development, which is much more extensive in *Prenocephale prenes* in connection with the development of the relatively strong canine-like premaxillary teeth. In *Stegoceras validus* the premaxillary portion of the snout is not differentiated from the posterior portion, and the notch for receiving of the enlarged mandibular tooth is lacking, although the short and very slightly deepened diastema is present. The anteriormost portion of the premaxilla in *Stegoceras validus* is very low and its lateral wing is very short, not separating the nasal and the maxilla as in *Prenocephale prenes*. One would expect a similar structure of the anterior portion of the premaxilla in the other long-snouted form, *Pachycephalosaurus grangeri*. This portion of the premaxilla is not preserved in this species, and its lateral wing is excluded from the nasal according to BROWN & SCHLAIKJER (1943, p. 134), as in *Stegoceras validus*. The authors mentioned above suggested that such development of the lateral premaxillary wing might be typical of the family, which has appeared to be untrue.

Maxilla. — The maxilla is penetrated along nearly its entire length by the extensive sinus, which is here called the intramaxillary sinus [3]. It is entirely surrounded by the maxilla in its anteriormost section. The medial lamina of the maxilla is here pierced dorsally by a very extensive fenestra, above the maxillary teeth 3—6. This fenestra connects the intramaxillary sinus with the nasal cavity. More posteriorly, the lateral wall of the sinus is perforated by the antorbital foramen. The sinus is bounded in this region dorsally by two separated laminae of the lacrimal, and by the two laminae of the maxilla. The caudal section of the intramaxillary sinus extends under the lower margin of the orbit. It is bounded here by the jugal dorsally and by the maxilla ventrally, close to the contact of the latter bone with the ectopterygoid. The sinus opens posteriorly through a comparatively small foramen into the pterygopalatine fossa. The lateral wing of the maxilla is very high and placed vertically. It contacts the premaxilla anterodorsally, along the extensive, oblique suture, the lacrimal posterodorsally and the jugal posteroventrally. Its dorsal contact with the nasal is short. The alveolar margin of the maxilla bends weakly backwards, near the place where it meets the jugal and the ectopterygoid. It bears seventeen teeth. A broad narrowing anteriorly, shelf is present, which is external to the row of the teeth. It is pierced by a row of larger and smaller vascular canals. The lingual wing of the maxilla is placed vertically and it forms the medial wall of the intramaxillary sinus. It gives the short palatinal process in its posterior part. The row of large fenestra, which open into the alveolae, is present immediately below the teeth. The anterior portion of the maxilla is thick and medially contacts its fellow, but ventrally and slightly posteriorly the vomer is wedged between the two maxillae. The narrow, anteriormost process of the maxilla is overlapped dorsally and ventrally by the processes of the premaxilla. The maxilla is widened in front of the first maxillary tooth, and posterior to the contact with the premaxilla. It has ventrally developed an extensive pit, which is bordered laterally by the sharp, toothless margin of the maxilla. This margin rises upwards anteriorly, when seen from the side. The alveolar margin of

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[3] It corresponds, partly at least, to the antorbital recess in *Hypsilophodon* (GALTON, 1970a), but it is more extensive in the Pachycephalosauridae and seems to be present also in the forms devoid of the antorbital foramen. This is why we decided to introduce here the term "intramaxillary sinus".

the maxilla is straight to the very end in *Tylocephale gilmorei*. The lateral maxillary shelf is in this species very narrow. The alveolar margin is arched outwards posteriorly in *Homalocephale calathocercos*, and the shelf is still more extensive in this species than it is in *Prenocephale prenes*. The maxilla has a long contact with the nasal laterally in *Stegoceras validus*, and it borders the external naris posteriorly, which is not the case in *Prenocephale prenes*. The maxillary teeth come to the contact between the maxilla and the premaxilla in *Stegoceras validus* and there is no pit developed in this place. The maxilla bears sixteen teeth in the latter species. The anterior portion of the maxilla is here broad and flat in the ventral view, in which this species differs from *Prenocephale prenes*. Otherwise the maxillae of the two species compared are alike. The maxilla in *Pachycephalosaurus grangeri* is different from that in *Prenocephale prenes* in having a much longer backward process, which contacts the lacrimal ventrally and reaches nearly to the level of the orbit. The difference is also marked in the development of the anterior, ventral margin of the maxilla in the two species compared. This in *Pachycephalosaurus grangeri* does not rise upwards anteriorly, as can be judged from the ilustration given by BROWN & SCHLAIKJER (1943, Pl. 38, Fig. 2), but it is similarly sharp as in *Prenocephale prenes*. There may be also a difference between the species compared in the contact between the maxilla and the nasal, but it cannot be stated basing on the description and ilustrations given by BROWN & SCHLAIKJER (l. c.). The lateral wing of the maxilla is convex outwards in *Pachycephalosaurus grangeri* and *Stegoceras validus*, while it is flat and vertically placed in *Prenocephale prenes*.

Lacrimal. — The lacrimal is a relatively large bone bounded dorsally by the supraorbital I and anteriorly to the latter, by the small wedge of the nasal. It contacts the maxilla anteriorly and slightly ventrally along an extensive suture, except for the part, where it bounds posteriorly the antorbital fenestra. More backwards, it is bounded by the jugal ventrally, along a short suture. Inside the orbit, it forms the anterior margin of the latter. The lacrimal duct is located immediately at the margin of the orbit and it leads into the intramaxillary sinus. The lacrimal contacts the jugal ventrally, within the orbit, the accessory orbital ossification *1* posteriorly, the prefrontal posterodorsally and the postorbital 1 dorsally. The lacrimal gives a separate medial lamina in the region of the antorbital foramen, and this lamina bounds dorsomedially the intramaxillary sinus. The lacrimal is subcircular in *Stegoceras validus* when seen on the lateral wall of the snout, and forms but the ventral part of the anterior margin of the orbit. It does not contact the nasal. The lacrimal of *Pachycephalosaurus grangeri* is more similar to that of *Prenocephale prenes*, and it occupies the entire anterior margin of the orbit, as in *Prenocephale prenes*. The lacrimal occupies, however, one third of the orbital margin in *Pachycephalosaurus grangeri* and less than one fourth in *Prenocephale prenes*. The antorbital foramen seems to be absent in all the species here compared, except *Prenocephale prenes*.

Jugal. — The jugal is a large and long bone, when wiewed from the side, and it forms the entire ventral margin of the orbit. The thin tongue of the jugal underlies medially the postorbital. The jugal forms a short wedge between the lacrimal dorsally and the maxilla ventrally, and its apex does not extend further than the anterior margin of the orbit. The posterior margin of the bone is strongly expanded vertically, and it bounds the infratemporal fenestra anteriorly. It contacts the quadratojugal ventrally overlapping the latter bone and contacting the quadrate, above the mandibular joint. In ventral view, the jugal contacts the maxilla anteriorly, and it overlaps the maxilla laterally along a short suture. The short tongue of the jugal is wedged medially between the maxilla and the ectopterygoid. The epijugal (= infrajugal of GILMORE 1924) was not observed in *Prenocephale prenes*. The jugal forms the major portion of the posterior margin of the orbit in *Tylocephale gilmorei*, when viewed laterally. It is strongly convex

laterally below the ventral margin of the orbit in this species, and in both these features the jugal differs from that of *Prenocephale prenes*. The jugal is similar in *Homalocephale calathocercos*, but it comes very close to the mandibular joint ventrally. The jugal in *Stegoceras validus* differs from that in *Prenocephale prenes* in having a very long anterior process, which reaches much further forwards than the anterior suture of the lacrimal. The jugal overlaps laterally in *Stegoceras validus* the anterior margin of the postorbital along the extensive surface. *Pachycephalosaurus grangeri* has the jugal very different from that described in *Prenocephale prenes*. It is small and has a long anterior process; it overlaps the anterior portion of the postorbital slightly laterally, and it does not take part in the formation of the anterior margin of the infraorbital fenestra. The posteroventral margin of the jugal of *Pachycephalosaurus grangeri* is situated well above the mandibular joint of the quadrate, even higher than it is in *Prenocephale prenes*. The lower, posterior part of the jugal is strongly ornamented in all species of the Pachycephalosauridae known from the Upper Cretaceous.

Quadratojugal. — The quadratojugal consists of two laminae, which overlap the jugal anteriorly and the quadrate posteriorly. The lateral lamina has its quadrate wing strongly developed, while the medial lamina, which is larger than the former, has its jugal wing more strongly developed. The quadratojugal is constricted centrally between these two laminae. The bone is pierced by the quadrate foramen. The lateral lamina of the quadratojugal is drop-shaped, being very narrow dorsally and broad ventrally. It reaches the infratemporal fenestra above the contact of the jugal and quadrate. The medial lamina of the quadratojugal is comparatively narrow ventrally and broad dorsally. The quadratojugal is extremely strongly ornamented in *Prenocephale prenes*. The quadratojugal does not have two laminae in *Homalocephale calathocercos*. It forms a thin plate of bone, the posterior wing of which overlaps the quadrate laterally and the anterior wing underlies the jugal medially. Its external surface is quite smooth. Otherwise, the quadratojugal in *Homalocephale calathocercos* resembles that of *Prenocephale prenes*. The two laminae of the jugal are less distinctly developed in *Stegoceras validus* than they are in *Prenocephale prenes*. The bone is not so strongly expanded ventrally on the lateral surface of the skull as it is in *Prenocephale prenes*. It is also smoother externally than it is in *Prenocephale prenes*. The bone is shorter vertically in *Pachycephalosaurus grangeri* and it is connected with the weaker vertical expansion of the jugal in its posterior part.

Quadrate. — The quadrate has the strong shaft and the thin, extensive medial wing for the overlapping contact with the pterygoid. The lower part of the shaft, which meets the quadratojugal anteriorly, is nearly vertical to the line of the teeth and its upper part is inclined backwards and inwards. The upper margin of the quadrate is wedged between the prequadratic and postquadratic processes of the squamosal. A sharp crest is present along the posterior face of the shaft; it begins above the articular condyle and fades away above half the length of the shaft. The medial wing of the quadrate overlaps the quadrate wing of the pterygoid dorso-anteriorly, and it meets the prootic posteromedially. The medial wing of the quadrate, close to its posterior contact with the squamosal, lies above the opisthotic but a narrow cleft is left between the two bones, and it is only posteroventrally, where the two bones contact each other. The quadrate is incompletely preserved in *Tylocephale gilmorei* and only its shaft is present. It is not deflected backwards in its upper portion, when seen from the side. Its dorsal and ventral portions are directed inwards, in posterior view. In these characters it differs from the shafts of the quadrates known in other representatives of the family. The posterior face of the quadratic shaft is flat in *Tylocephale gilmorei* and its lateral margin is crest-like. The quadrate of *Homalocephale calathocercos* is generally similar to that of *Prenocephale prenes*, but it has slightly more slender shaft, and its posteriorly declined dorsal portion is longer.

The posteromedial and anterolateral margins of the shaft of the quadrate are sharp and crest-like in *Stegoceras validus*. The posteriorly deflected dorsal portion is very long in this species. Ventrally, only the articular surface for the mandible protrudes below the lower margin of the cheek region. Otherwise the quadrate is generally similar in *Stegoceras validus* and *Prenocephale prenes*. The quadrate has a strong shaft in *Pachycephalosaurus grangeri* in which it is similar to that of *Prenocephale prenes*. The differences between the two species are distinctly visible in the position of the dorsal portion of the shaft, which is placed nearly horizontally in *Pachycephalosaurus grangeri*, as well as in the lack of any crest on the posterior face of the shaft in this latter species.

Squamosal. — The squamosal is a very thick bone. Its posterior margin is strongly swollen and overhangs the occipital region of the skull. In dorsal view, the medial portion of the squamosal is incorporated into the dome, while the lateral portion is slightly inclined downwards and outwards and it is placed at an angle to the side of the dome. The squamosal meets the postorbital anteriorly on the dorsal and lateral surface of the roof and it overlaps this bone with a long tongue on the ventral surface. Laterally the squamosal gives two thin processes in the anteroventral direction, which overlap the dorsal end of the quadrate on its anterior and posterior face. The prequadratic process of the squamosal contacts the opisthotic and laterosphenoid anteromedially, and the parietal medially. The squamosal is strongly expanded on the posterior face of the skull. The deep and broad groove is developed under the swollen posterior edge of the squamosal. It is arched and extends transversely, invading the parietal in the medial direction and meeting its fellow within the central depression of the occipital region. A thick ridge is developed below and parallel to this groove. The squamosal contacts the parietal medially on the posterior face of the skull, along the extensive suture. It meets the exoccipital ventrally and gives a small tongue which contacts the supraoccipital and is wedged between the parietal and the exoccipital. The end of the postquadratic process of the squamosal is thin and overlain laterally by the paroccipital process. A sharp edge is developed across the postquadratic process in the lateral prolongation of the suture between the squamosal and exoccipital. This edge is parallel to the upper margin of the paroccipital process but does not contact the latter. The squamosal is incompletely preserved in *Tylocephale gilmorei*, but apparently its posterior and lateral margins formed a narrow shelf. The occipital portion of the squamosal is very narrow in respect to that of *Prenocephale prenes*. The posterior margin of this bone is not overhung and it is not swollen in *Tylocephale gilmorei*, and the ventral portion of the squamosal is relatively thin and does not have any ridge or groove. The squamosal is very different in the dorsal view in *Homalocephale calathocercos*, what is connected with the entire lack of the dome and with the presence of the large supratemporal fenestrae. It is small, when viewed dorsally, and anteriorly contacts the postorbital. The large supratemporal fenestra separates the squamosal from the parietal for most of its length and the two bones contact only posteriorly along a short suture. The posterior margin of the squamosal is not swollen and does not overhang the occipital region as in *Prenocephale prenes*. Similarly as in *Tylocephale gilmorei* there are no grooves and ridges on the posterior face of the squamosal. The postquadratic process is placed very close to the upper margin of the paroccipital process in *Homalocephale calathocercos*, in which it differs from *Prenocephale prenes*. There are no other important differences between the squamosals of the species above mentioned. The squamosal is completely incorporated into the dome in *Pachycephalosaurus grangeri*. The posterior margin of the squamosal is here swollen and overhung similarly as it is in *Prenocephale prenes*. The relation between the postquadratic process of the squamosal and the upper margin of the paroccipital process is similar in these two species. In the various forms assigned within *Stegoceras validus* the squamo-

sal varies in the connection with the different development of the shelf. The bone in question is completely preserved but in one specimen of *Stegoceras validus* (UA. No. 2) and it is not incorporated there into the dome being instead placed nearly in the horizontal plane. The posterior margin is in this specimen much less swollen than in *Prenocephale prenes*, but there is a similar arched groove present below the posterior margin of the bone. The postquadratic process of the squamosal is entirely contacted by the paroccipital process. In specimens of *Stegoceras validus* which are known but from the skull roofs (NMC Nos. 138, 8816; LAMBE 1918, Pl. 1, Fig. 1) there is a deep "cotylus" visible which receives the dorsal extremity of the quadrate. It is most probably present also in other representatives of the family, because in both *Prenocephale prenes* and *Homalocephale calathocercos* the juncture between the squamosal and the quadrate seems to be the loosest within the skull. We think that it is developed for the purposes of the amortization rather than for the movements. The posterior and lateral margins of the squamosal bear a row of dermal spines or nodes which are suturally attached. Those in *Pachycephalosaurus grangeri* are the most strongly developed. The dorsal and lateral surfaces of the squamosal are covered in *Stegoceras validus* and *Tylocephale gilmorei* by the irregular tubercles. The dorsal surface of the squamosal is rough and covered by the sparse stiches in *Prenocephale prenes* and it is deeply pitted in *Homalocephale calathocercos*.

Postorbital. — The postorbital is large and its dorsal portion is quadrangular in shape, being incorporated into the dome. It forms the entire upper margin of the infratemporal fenestra laterally, and slightly less than a half of the postorbital bar. It contacts the supraorbital II anteriorly on the dorsal and lateral face of the skull. It meets the frontoparietal medially and the squamosal posteriorly. The suture with the jugal extends obliquely downwards and forwards on the surface of the postorbital bar. The postorbital is underlain by the jugal along the posterior margin of the orbit. It gives a stout, sharply crested process medially which makes the contact with the laterosphenoid and dorsally and laterally marks the boundary between the orbit and the infratemporal fossa. The postorbital is bounded by the frontoparietal posteromedially and it is underlain posteriorly by a long tongue of the squamosal. It has a very limited contact with the frontal within the orbit. The postorbital is generally similar in *Tylocephale gilmorei*, but it is separated laterally from the posterior margin of the orbit by the ascending process of the jugal, along a significant distance. The postorbital reaches medially the supratemporal fenestra in *Homalocephale calathocercos*, but otherwise is similar to that in *Prenocephale prenes*. The postorbital does not form the external margin of the orbit in *Stegoceras validus* because dorsolaterally there is a continuation of the supraorbital and squamosal shelf along the postorbital bar, which is not present in *Prenocephale prenes*. A similar shelf across the postorbital is present in *Pachycephalosaurus grangeri* but there it is but a continuation of the shelf-like ridge on the supraorbital. The postorbital is not incorporated into the dome in *Pachycephalosaurus grangeri*. The dorsal surface of the postorbital is very rough and pitted in *Prenocephale prenes* and laterally it bears the continuation of the squamosal row of nodes. In this species a row of smaller tubercles passes obliquely downwards along the postorbital bar. The more or less similar pattern of ornamentation of the postorbital is present in all representatives of the family. The postorbital was described in *Stegoceras validus* by GILMORE (1924) as the complex bone including the postfrontal. After the examination of the plaster cast of the specimen UA. No. 2, which was the subject of GILMORE'S description, as well as of the other skulls of the Pachycephalosauridae (excluding that of *Pachycephalosaurus grangeri*) we are able to state that there was no postfrontal present in the representatives of the family. The bone determined by LAMBE (1918) as the postfrontal in *Stegoceras validus* represents in fact the supraorbital II (p. 76).

Supraorbitals. — There are two distinctly separated dermal ossifications forming the heavy upper margin and the roof of the orbit and they represent the supraorbitals I and II. The supraorbital I sends a narrow process anteriorly which contacts the nasal. The contact with the lacrimal is present on the lateral wall of the snout and inside the orbit, where the supraorbital I is bounded by the prefrontal anterodorsally, and by the frontal more posteriorly on the medial wall of the orbit. The posterior margin of the supraorbital I makes the contact with the supraorbital II both inside the orbit and on the dorsal surface. The supraorbital I is bounded by the prefrontal medially, on the dorsal surface of the skull and by the corner of the frontal posteriorly. The supraorbital II forms the posterior part of the orbital roof, contacting the supraorbital I anteriorly and the frontal medially. The posterior and ventral margins of the supraorbital II make contact with the postorbital. This bone meets the postorbital posteriorly also inside the orbit, contacting there the frontal medially and the supraorbital I anteriorly. Only the posterior portion of the supraorbital II is preserved in *Homalocephale calathocercos* in which it contacts the same bones as in *Prenocephale prenes*, but it is placed in the horizontal plane of the skull roof being only slightly elevated and thicker with respect to the other bones of the skull roof. Both supraorbitals are present in *Tylocephale gilmorei* and they do not show any significant difference to *Prenocephale prenes*. LAMBE (1918) indicated in the specimen NMC No. 138 of *Stegoceras validus* the sutural facet for the supraorbital and he distinguished a small bone posteriorly to it, which he regarded as the postfrontal (*l. c.*, Pl. I, Fig. 1, 2). Recently GALTON (1971a, Text-fig. 4b) gave an ilustration of the same specimen and he determined the "postfrontal" of LAMBE (1918) as the prefrontal, in which he partly followed GILMORE (1924). The latter author recognized this bone as being in the union with the supraorbital (*l. c.* Text-figs. 1, 2) in the specimen UA. No. 2 of *S. validus*. The specimens above mentioned were at our disposal and we were able to state that two supraorbitals, suturally separated from each other, are present in *Stegoceras validus*, the supraorbital I being fused with the prefrontal as it was already noticed by GILMORE (l. c.). The supraorbital II corresponds to the bone named as the "postfrontal" by LAMBE (1918) and as the "prefrontal" by GALTON (1971a) in the specimen NMC No. 138 of *Stegoceras validus*. The supraorbital II is much smaller in the specimen UA. No. 2 of *Stegoceras validus* (Text-fig. 1A) than it is in *Prenocephale prenes*. Both supraorbitals are not incorporated into the dome in *Stegoceras validus*, in which they differ from *Prenocephale prenes*. One supraorbital bone was distinguished in *Pachycephalosaurus* by BROWN & SCHLAIKJER (1943) and it is distinctly separated from the prefrontal, similarly as in *Prenocephale prenes*. Two supraorbitals may also be present in *Pachycephalosaurus grangeri*, but the state of the preservation of this region of the skull in the species in question does not allow us to be sure. The supraorbitals are rough in *Prenocephale prenes* and *Pachycephalosaurus grangeri* and densely tuberculated in *Stegoceras validus* and *Tylocephale gilmorei*. The tubercles are more regularly arranged in this latter species. The supraorbital II is densely pitted and granulated in *Homalocephale calathocercos*. A sharp ridge is present along the supraorbitals above the orbit in all species of the family, with the possible exception of *Pachycephalosaurus grangeri*.

Prefrontal. — The sutural boundaries of the prefrontal are well defined. It is a thick but comparatively flat bone. On the dorsal surface of the skull it contacts the frontal posteriorly and posteromedially, the nasal anteromedially and the supraorbital I laterally. It is also visible inside the orbit, where it meets the lacrimal anteriorly, the supraorbital I dorsally, and the accessory ossification *I* (p. 69) posteriorly along an extensive suture. This bone is not preserved in *Homalocephale calathocercos*, and it is fused with the supraorbital I in *Stegoceras validus*. The prefrontal is extensive and separated from the adjoining bones in *Pachycephalosaurus grangeri*.

Nasal. — The nasal is a thick and ornamented bone displaying in dorsal view a sharply marked lateral edge. It is roughly triangular, having its longest side medially, along the suture with its fellow. It makes contact with the premaxilla anteriorly at the internarial bridge. It meets the maxilla and lacrimal posteroventrally along a short suture on the lateral face of the snout, and the prefrontal lateroposteriorly along an extensive suture on the dorsal surface of the skull. The narrow, posterior process of the nasal reaches the supraorbital I. The contact of the bone described with the frontal is relatively short. Both nasals are slightly concave anteriorly along the internasal suture in *Prenocephale prenes*, being only weakly convex near their comparatively narrow contact with the frontals. The longitudinal and transverse profiles through the nasals are here nearly flat on the top. A similar condition is found in *Pachycephalosaurus grangeri* but the ornamentation of the nasal is more strongly developed, consisting of nodes and spines, while the nasal of *Prenocephale prenes* is rather moderately and evenly granulated and only the tubercles along the lateral edge of the bone are slightly larger. The region of the nasals is quite different in *Stegoceras validus*, their posterior contact with the frontals being broader in this species, the crest along the lateral margin of the nasal not pronounced, the nasals taking part with their anterior processes in the formation of the internarial bridge. The contact of the nasal with the maxilla is very long in *Stegoceras validus*. The longitudinal and transverse profiles across the nasals are distinctly convex in this species.

Pterygoid. — The pterygoid is a complicated and broadly expanded bone in the pachycephalosaurids and it is developed in several different planes. It consists of two broad wings: the palatal wing (roughly horizontal) which is developed mostly in the ventral plane of the skull and the quadrate wing, developed for its most part in the vertical plane. The palatal wing of the pterygoid exposes a nearly horizontal, broadly expanded posterior portion and a tapering anterior portion which is developed in the vertical plane. The latter, vertical portion meets its fellow medially in the ventral direction. Slightly posteriorly it is applied along the posterior margin of the palatine in the dorsal direction being seen within the orbit at its medial wall, slightly anteroventrally. The most dorsal tongue of the bone takes part in the formation of the medial wall of the orbit. It is very narrow here and contacts the accessory orbital ossification *1* anteriorly. The ventral portion of this tongue of the pterygoid forms the anterior boundary of the slit (interorbital fissure) separating the brain case from the palatal region and communicating with the interpterygoid cavity. The latter corresponds to the interpterygoid vacuity, but as it is laterally closed by the vertical walls of the palatal wings of the pterygoids, which attach each other ventrally, it has the form of a sagittal cavity. The palatal wing of the pterygoid is overlapped dorsally along its lateral margin by the ectopterygoid and the palatine. The most anterior, medial process of the palatal wing of the pterygoid is overlapped by the vomer ventrally. The close medial contact of the two palatal wings is slightly reduced posteriorly. The posterior margin of the palatal wing is free. The quadrate wing of the pterygoid is developed dorsal to the palatal wing, and the portion of the pterygoid connecting both wings is short and very stout. The quadrate wing has its small, anterior portion developed in a roughly horizontal plane and a much more extensive posterior portion, which is developed in the vertical plane. The posterior margin of the horizontal portion is free and at the anteromedial edge a short, stout process is developed for close contact with the basipterygoid process. An entrance to interpterygoid cavity mentioned above is present between these two processes and their fellows of the other side. Posteriorly the quadrate wing of the pterygoid bends upwards at 90° angles. This vertical plate is directed backwards and outwards, where it broadly overlaps posteriorly, along its entire height, the pterygoid wing of the quadrate. The anterior surface of the vertical portion of the quadrate wing forms the medioposterior wall of the infraorbital

fossa. The quadrate wing of the pterygoid broadly overlaps anteriorly the anterolateral portion of the basisphenoid, above the basipterygoid process and the prootic. The most dorsal portion of the pterygoid is wedged between the two wings of the prootic, the posterior one, mentioned above, and the anterior one which is visible on the posteromedial wall of the orbit. Ventrally the pterygoid bounds the bottom and a part of the posterior edge of the interorbital fissure. Medially the palatal wing of the pterygoid rises very steeply upwards in *Prenocephale prenes*, but it is not so steep in *Stegoceras validus* and is only slightly inclined in *Homalocephale calathocercos*. Its posterior part is narrowest longitudinally in *Stegoceras validus* and broadest in *Homalocephale calathocercos*, where it covers anteriorly a significant portion of the ectopterygoid. The anterior, vertical portions of the palatal wings of both pterygoids are closely attached in *Prenocephale prenes*, while they are separated by the interpterygoid vacuity in *Homalocephale calathocercos* and the cultriformis process of the parasphenoid is visible above. The posterior portions of the palatal wings are more distinctly separated in *Stegoceras validus*. More anteriorly, the pterygoids are separated in this species by the pendant process of the parasphenoid The horizontal portion of the quadrate wing is very close to the basal tuber in *Homalocephale calathocercos*, where it nearly contacts the latter. It is well distant in *Stegoceras validus* and slightly less distant in *Prenocephale prenes*. The horizontal portions of the quadrate wings of both pterygoids are separated from each other medially in *Prenocephale prenes* and *Homalocephale calathocercos* by a space leading to the interpterygoid cavity. They are joined medially in *Stegoceras validus*, but it is not clear whether the latter condition was not caused by the lateral deformation of the skull. The description of the pterygoid in *Pachycephalosaurus grangeri* (BROWN & SCHLAIKJER, 1943) is short and the illustration are insufficient for any comparisons.

Epipterygoid. — The bone which is flattened laterally and directed anteroventrally from the prootic towards the quadrate wing of the pterygoid is here interpreted as representing the epipterygoid. It meets the prootic posteriorly, immediately below the contact of this bone with the laterosphenoid. The distal end of the epipterygoid is divided into two lips; the broader one overlaps laterally the anterior surface of the pterygoid, while the much narrower, medial lip covers the pterygoid dorsally. The epipterygoid is more completely preserved in *Homalocephale calathocercos* than in *Prenocephale prenes* (in the latter species the distal end of the bone being broken off) but otherwise it does not differ. The epipterygoid has not been described so far in any ornithischian dinosaur, and the homology of the bone named as the "epipterygoid" in the present paper with the epipterygoid of saurischians may be dubious. However, the bone is well developed in both Mongolian species above mentioned and most probably also in the skull of the specimen UA. No. 2 of *Stegoceras validus*; its contacts with the adjacent elements are the same as of the epipterygoid in some other reptiles; it had presumably played the same role here as in other reptiles, thus we think it reasonable to describe the bone under the name of the epipterygoid.

Ectopterygoid. — The ectopterygoid is a small, triradiate bone, which contacts the maxilla posteriorly and posterolaterally. It overlaps dorsally the lateral part of the palatal wing of the pterygoid. The anterior margin of the ectopterygoid forms the hind boundary of the posterior palatine fenestra. The jugal process of the ectopterygoid is stout. The lateral margin of the bone bounds the infraorbital fossa medially. The jugal process is still more stout in *Homalocephale calathocercos* than in *Prenocephale prenes*. The ectopterygoid is relatively smaller in *Stegoceras validus*, but it does not differ from that in *Prenocephale prenes* and the same is true for *Pachycephalosaurus grangeri*.

Palatine. — The palatine is small, flat and it strongly tapers anteriorly. Medially the bone

rises very steeply upwards and it contacts the vomer anteriorly. Its maxillary wing contacts the pterygoid medially and posteriorly. The maxillary wing of the palatine takes part in the formation of the ventroanterior wall of the orbit. It overlaps here the pterygoid laterally and its upper margin meets the accessory orbital ossifications. In the region of the infra-orbital fossa the palatine contacts the ectopterygoid over an extensive surface. The palatine forms the posteromedial boundary of the internal naris and the anterior boundary of the posterior palatine fenestra. The palatines are placed obliquely and convergently upwards to each other within the nasal cavity. They continue dorsally above the vomer, when seen from the front, but they do not meet each other medially. The anterior extremity of the pointed process of the palatine is located opposite the fifth maxillary tooth, in the mid-length of the internal naris. It seems to end further anteriorly in *Homalocephale calathocercos*, in which the snout is not completely preserved. The anterior process of the palatine forms most of the medial boundary of the internal naris in *Stegoceras validus*, ending anteriorly immediately before reaching the cojoined maxillae. The maxillary wing is broader in *Prenocephale prenes* and *Homalocephale calathocercos*, its anterior margin reaching above the sixth/seventh maxillary tooth (counting from the back) while it is comparatively narrow in *Stegoceras validus* and *Pachycephalosaurus grangeri*, reaching above the fourth/fifth maxillary tooth. The depth of the maxillary wing is greater in *Prenocephale prenes*, *Homalocephale calathocercos* and *Pachycephalosaurus grangeri*, than it is in *Stegoceras validus*. The posterior portion of the palatine, at the boundary with the pterygoid, is concave dorsally in *Stegoceras validus*, which is not the case in any other known pachycephalosaurid species.

Vomer. — The vomer is very long and Y-shaped, being unpaired anteriorly, where it separates the maxillae, while its two posterior laminae overlap laterally the anterior processes of the pterygoids. Laterally the dorsal margins of the laminae of the vomer meet the medial surfaces of the palatines. The anterior, unpaired part of the vomer, which is free from contact with the palatines, is longer in *Prenocephale prenes* than it is in *Stegoceras validus* GILMORE (1924) suggested that the pendant process visible posteriorly between the pterygoids may represent the vomer or the presphenoid. It seems to us more probable that this bone represents the anterior portion of the parasphenoid. The skull of *Homalocephale calathocercos* allowed us to observe that the posterior laminae of the vomer bound the cultriformis process of the parasphenoid lateroventrally.

SOME ASPECTS OF CRANIAL NEUROLOGY AND CIRCULATION

Endocranial cavity. — The complete endocranial cast is known only in *Pachycephalosaurus grangeri* as described and illustrated by BROWN & SCHLAIKJER (1943, Pl. 41). The upper half of the brain cavity is preserved in *Stegoceras validus* (specimen NMC No. 138), which was described by LAMBE (1918). A latex cast of the latter specimen has been made and is illustrated in the present paper (Pl. XXV, Fig. 1). The differences between the upper portions of two brain cavities of the specimens mentioned are striking, and they involve the shorter and the less sloping stalks of the olfactory lobes, plus the steeper slope of the posterior portion of the brain in *Stegoceras validus*. The cerebrum and cerebellum, as well as the optic lobes are separated neither in *Pachycephalosaurus grangeri* nor in *Stegoceras validus*. The latter species lacks the anterodorsal processes of the cerebrum, which are well developed in *Pachycephalosaurus grangeri*, having on the other hand, in the posterior portion of the cerebellum several small backward projections:

two of them are dorsally located along the midline of the endocranial cavity, a pair of the projections is present slightly more ventrally on the posterior wall of the endocranial cavity. They most probably represent features of the endolymphatic system. These projections are evidently absent in *Pachycephalosaurus grangeri*. The dorsal surface of the rhombencephalon of *Stegoceras validus* is marked ventrally by the thick longitudinal ridge which divides downwards, behind the ear region, into two laterally directed ridges. They may be interpreted as the median dorsal longitudinal sinus and the posterior cerebral veins. Endocranial casts of the Mongolian species *Prenocephale prenes* and *Homalocephale calathocercos* could not be made. However as far as the anterior and the posterior portion of the brain cavity could be penetrated, the brains of these specimens were very like that of *Stegoceras validus*, having in common the olfactory lobes located closely to the cerebrum, and the rhombencephalon sloping steeply downwards and backwards to the ear region. As far as can be stated, the brain cavity is comparatively even deeper in the upward direction in *Prenocephale prenes* and *Homalocephale calathocercos* than it is in *Stegoceras validus*. The floor of the cavity of the rhombencephalon is formed in *Prenocephale prenes* by the very narrow basioccipital posteriorly and the broad basisphenoid anteriorly. The basisphenoid rises forwards forming the *dorsum sellae*. The roof of the cavity is formed posteriorly by the supraoccipital which widens forwards. Posteriorly the supraoccipital forms the posteromedial wall of the inner ear. The exoccipital contacts the supraoccipital dorsally within the cavity of the rhombencephalon, immediately at the wall of the inner ear. The anterior portion of the lateral wall of the cavity of the rhombencephalon is formed by the prootic. The endocranial cavity seems to be similarly constructed in *Homalocephale calathocercos* except that it is much more extensive than it is in *Prenocephale prenes*, emerging outwards by the much larger foramen magnum. The midline groove extends in the sagittal direction in *Homalocephale calathocercos* along the floor of the endocranial cavity in the region of *dorsum sellae*. It represents the tract of the *arteria basilaris*. This groove is not marked in *Prenocephale prenes*.

Ear. — The middle ear cavity is very deep, vertically elongated and broad dorsally. It is bounded anteriorly by the high otosphenoidal crest and posteriorly by the ventrolateral wing of the exoccipital (Pl. XXV, Fig. 2a; Text-fig. 2). The roof of the middle ear cavity is formed by the exoccipital and its floor by the thin tongue of the opisthotic. In the ventral portion of the middle ear cavity the medial wall is pierced by two foramina which are separated by a very thin bridge of bone. The upper foramen is the *fenestra ovalis* and the lower the *fenestra rotundum*. This bridge is partly damaged in *Prenocephale prenes*, but it is complete in *Homalocephale calathocercos*. The middle ear cavity is much broader in this latter species than in *Prenocephale prenes*. The middle ear cavity in *Stegoceras validus* (so far as can be judged from the plaster cast of the specimen UA. No. 2) seems to be not so deep. The inner ear is not completely preserved in any pachycephalosaurid specimen except *Pachycephalosaurus grangeri* (BROWN & SCHLAIKJER, 1943). The posteromedial wall of the inner ear is well preserved in the Mongolian species and together with the wall of the opposite ear they significantly narrow the lumen of the brain cavity posteriorly, as seen through the foramen magnum (Pl. XXII, Fig. 2b). The semicircular canals were described in *Stegoceras validus* by LAMBE (1918).

Olfactory nerve (I). — The olfactory lobe is relatively large but the olfactory stalk is short. The olfactory lobes were separated, at least dorsally. The anterior openings, from which the olfactory nerves emerge to the nasal cavity, are the largest of all the nerve foramina. They are observed in *Prenocephale prenes* from the nasal cavity, and they seem to be separated by the dorsal septum. The olfactory lobes in this species are similar to those describe by LAMBE (1918) in *Stegoceras validus*. The olfactory nerve in *Pachycephalosaurus grangeri* displays an

olfactory stalk that is longer with respect to the olfactory lobe (BROWN & SCHLAIKJER 1943, Pl. 41) than is the case in all so far known brains of the Pachycephalosauridae.

Optic nerve (II). — The exit for the optic nerve is large, round and its edge is thickened. It is placed behind the centre of the orbit, in the suture between the orbitosphenoid and the presphenoid. As seen from the brain cavity, the entrances for both optic nerves are very close to each other and located immediately in front of the pituitary fossa. The position and course of the optic nerves are the same in *Prenocephale prenes* and *Homalocephale calathocercos* as in *Pachycephalosaurus grangeri*, but the relative size of the nerve is larger in the Mongolian pachycephalosaurids.

Oculomotor nerve (III). — The oculomotor nerve pierces the orbitosphenoid. The entrance for the nerve III is common with that for the nerve IV as are the exits, and the nerves are separated externally by a thin bridge of bone. The exit for the nerve III was not visible in *Homalocephale calathocercos*.

Trochlear nerve (IV). — The exit for the trochlear nerve is located close to and posterior to the exit for the optic nerve, in the suture between the orbitosphenoid and the presphenoid. The entrance for the trochlear nerve is present in the brain cavity above and laterally to the pituitary fossa. It is visible in *Prenocephale prenes* only on the right side, where the *dorsum sellae* is damaged. The entrance is comparatively large and slit-like. BROWN & SCHLAIKJER (1943) did not find the entrance for the fourth nerve on the endocranial cast of *Pachycephalosaurus grangeri*. May be, also in this species the fourth nerve runs through the common passage with the third nerve as it is in *Prenocephale prenes*, and most probably in *Homalocephale calathocercos*.

Trigeminal nerve (V). — There are two separate openings which are here interpreted as the exits for three branches of the fifth nerve. That for the *ranus ophthalmicus* (V_1) is small, located posteriorly and slighty below the exit for the third nerve, in the suture between the prootic and laterosphenoid. The groove runs dorsally from the exit of V_1, which was occupied by the ophthalmic branch. There is a common exit for the emergence of the *ramus maxillaris* and the *ramus mandibularis*. It is large and located in the prootic close to the basisphenoid, immediately below the base of the epipterygoid the latter bridging above it. The surface of the basisphenoid is deeply furrowed ventrally to the exit for V_2 and V_3. The entrance for the fifth nerve is very large, located in the brain cavity on the prootic/basisphenoid contact, latero-dorsally and slightly forwards to the entrance for the sixth nerve. The position of the entrance and the exits for the trigeminal nerve seem to be similar in *Pachycephalosaurus grangeri* judging from the endocranial cast of this species (BROWN & SCHLAIKJER, 1943, Pl. 41).

Abducens nerve (VI). — The exit for the sixth nerve is present in the presphenoid below the exit for the second nerve. The entrance for the abducens nerve is well visible in the brain cavity. It is small and pierces the *dorsum sellae*. Further forward, the abducens nerve passed laterally through the pituitary fossa. The exit and the entrance for the sixth nerve are similarly located in *Homalocephale calathocercos*. BROWN & SCHLAIKJER (l. c.) mentioned the presence of the abducens nerve on the endocranial cast of *Pachycephalosaurus grangeri*, but its exact position is not clear in the latter species.

Facial nerve (VII). — The exit of the facial nerve is very small, located immediately in front of the *fenestra ovalis*, medioventrally to the supposed otosphenoid crest This exit is placed on the external edge of the posterior wall of the slit developed as the result of the medial invagination of the basisphenoid (p. 66), in the suture between the latter bone and the prootic dorsoposteriorly. The broad and deep groove runs obliquelly downwards and forwards from the exit for the seventh nerve, along the lateral side of the basipterygoid process. The

groove presumably transmitted the palatine ramus of the facial nerve. Further forwards, the palatine ramus runs ventrally to the basipterygoid process to enter the interpterygoidal cavity together with its fellow. The entrance for the facial nerve within the brain cavity, is very small and located immediately posterior and slightly ventrally to the entrance for the trigeminal nerve. The exit and the entrance for the seventh nerve are in about the same position in *Prenocephale prenes* and in *Homalocephale calathocercos*, as is the entrance in *Pachycephalosaurus grangeri*.

Auditory nerve (VIII). — The entrance for the auditory nerve cannot be easily observed in any specimen in our disposal, because it is hidden posteriorly by the internal wall of the otic capsula, which here constricts the cranial cavity.

Glossopharyngeus nerve (IX). — The exit for the glossopharyngeus nerve is placed in the exoccipital, lateral to the occipital condyle. It is located on the edge of a sharp crest which is developed parallel to the basioccipital in the dorsal prolongation of the basal tuber. The passage for the nerve pierces the exoccipital and is separated from the middle ear by a thin bony wall. The entrance for the ninth nerve is located very close to the inner ear cavity, but its precise position cannot be determined, because of the damage of this portion of the brain cavity. The passage and the exit of the ninth nerve is comparatively large and it is possible that it also contained the jugular vein. The exit for the glossopharyngeus nerve is in the same position in *Homalocephale calathocercos* but the position of the entrance cannot be determined. BROWN & SCHLAIKJER (1943) suggested a common exit for nerves IX—XI in *Pachycephalosaurus grangeri*. The illustration of the endocranial cast given by these authors (*l. c.*, Pl. 41) does not allow to observe the position of these nerves.

Vagus and accessory nerves (X—XI). — There is a narrow slit present in the suture between the exoccipital and basioccipital placed laterally to the neck-like portion of the occipital condyle which locates a common exit for the vagus and accessory nerves. Two grooves lead from the exit of the nerves, across the basioccipital. One of them, directed ventrally is slightly broader than the other which is directed anteriorly. The common entrance for these two nerves is located in the exoccipital immediately above the suture with the basioccipital. The exit for the vagus and accessory nerves is also common and slit-like in *Homalocephale calathocercos* and *Stegoceras validus*. The slit is placed slightly more vertically in these two species than it is in *Prenocephale prenes*.

Hypoglossal nerve (XII). — The exit for the hypoglossal nerve is large, funnel-like and it pierces the exoccipital. It is located on the lateral side of the condyle, posterodorsally to the exit for the tenth and eleventh nerves. Two grooves lead from the exit, one of which is deeper, broader and is directed ventrally, the other-slightly anteriorly. The entrance is well visible within the cavity of the medulla oblonga, and is located laterodorsally. The position of this nerve in other known pachycephalosaurid skulls is about the same as it is in *Prenocephale prenes*.

In addition to the cranial vessels described above and connected with the brain, there are several openings on the lateral walls of the brain case and in the orbitonasal region in *Prenocephale prenes*, which should be interpreted as locating the arteries and veins.

Internal carotid artery. — The entrance for the Vidian canal is located at the very bottom of the invaginated portion of the basisphenoid, dorsal to the basipterygoid process and anteroventral to the exit for the seventh nerve (Text-fig. 2). Within the passage in the basisphenoid posteriorly to the pituitary fossa, the internal carotis gives outwards the palatine artery which emerges through the basisphenoid ventral to the exit for the sixth nerve. Two grooves extend from the exit for the palatine artery, one of which is directed ventrally and the other posteriorly. They might contain the branches of the palatine artery. The septum between

the orbit and the nasal cavity is pierced by several foramina which resemble the relations known in mammals (Text-fig. 3). Two of these foramina, suggested here as representing the foramina for the ethmoidal artery, are located between accessory orbital ossifications *1* and *2*. Dorsally, their exits into the nasal cavity are placed immediately at the midline, and on the suture between these bones mentioned. Two other foramina are placed more ventrally. One of them pierces the accessory ossification *1* at the suture between the palatine and jugal and emerges into the nasal cavity laterodorsally, immediately above the palatine. It may represent the sphenopalatine foramen for the entrance of the sphenopalatal artery. The second foramen is located slightly above the tongue of the pterygoid which underlies the palatine. It is bounded dorsally by several small ossifications of the orbital region. Its exit is invisible because it is located more medially, and is completely hidden by the palatal wing of the pterygoid. The foramen leading to the intramaxillary sinus is located in the maxillary portion of the orbit within the fossa pterygopalatina and it could conduct forwards the infraorbital artery as well as the infraorbital branch of V_2. In the bottom of the infratemporal fossa two foramina are present which are separated by the broad bridge of the prootic that contacts laterally the quadrate. A distinct groove leads from the lower of these two foramina forwards and downwards, under the epipterygoid, and towards the exit of V_2 and V_3 nerves. A broad and shallow recessus is present on the bottom of the infratemporal fossa which is confluent with the upper of the foramina mentioned above. Both foramina communicate posteriorly with two foramina located below the paroccipital process, in the slit between the prootic-opisthotic and quadrate. These structures most probably should be also interpreted as the passages for the blood vessels. The numerous vascular foramina penetrate the bones of the orbital roof and they are especially aboundant on the frontal.

OSTEOLOGY OF THE POSTCRANIAL SKELETON
(Pl. XXV, Fig. 3, Pls XXVI-XXXI; Text-figs 4, 5)

The pachycephalosaurid postcranial skeleton was until recently known only in *Stegoceras validus* LAMBE, 1902, and although being incomplete, it has provided much important information, particularly that dealing with the bipedal posture of the animal. The discovery of another incomplete postcranial skeleton of *Homalocephale calathocercos* n.gen.et sp. (Pls XXVI—XXX, Pl. XXXI, Fig. 1; Text-figs 4, 5) with most of the preserved bones in the articulated conditions as well as some postcranial fragments of *Prenocephale prenes* n.gen.et sp. (Pl. XXV, Fig. 3, Pl. XXXI, Fig. 2) allowed us to complete the data given by GILMORE (1924). It enabled us also to conclude, that the essential characters of the postcranial skeleton were probably very similar in all representatives of the family. The description below, is based on the postcranial skeleton of *Homalocephale calathocercos*, but we have tried, as far as it was possible, to compare the bones of the latter species with the postcranial elements of *Prenocephale prenes* and with those described by GILMORE (l. c.) in *Stegoceras validus*. The reasons for basing the osteological description on the Mongolian species *Homalocephale calathocercos* is not its completeness, which is generally lesser than in *Stegoceras validus*, but the fact that the preserved portion of the vertebral column is complete, and was recoverd in the natural arrangment, with the ribs, pelvic girdle and the tail-basket articulated.

Vertebral column. (Pls XXIV—XXVIII; Text-fig. 4). — The preserved part of the vertebral column shows its natural curvature. It rises slightly backwards along the first three presacral dorsals preserved, and then it slopes towards the last dorsal and the sacrum, which are

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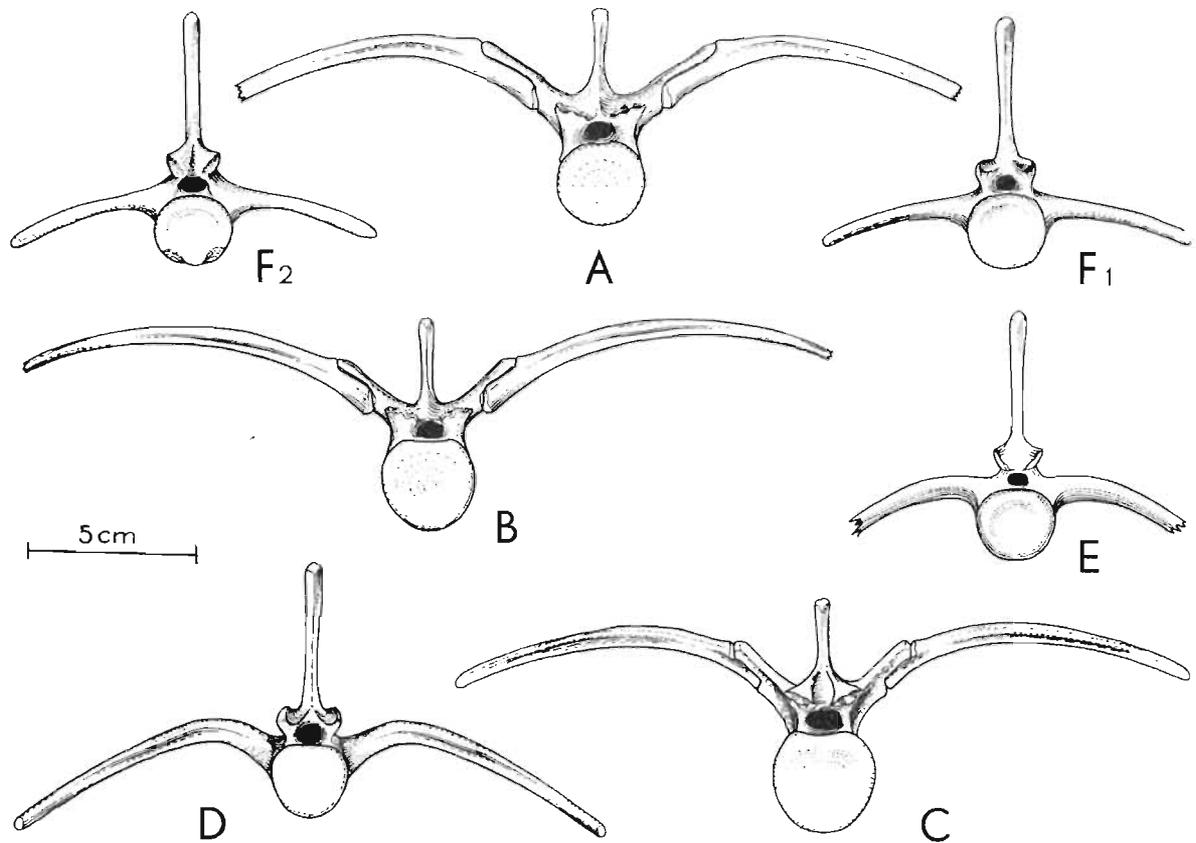
Fig. 4

Homalocephale calathocercos n. gen., n. sp. (G. I. No. SPS 100/51). Presacral and caudal vertebrae: *A* dorsal n+4 (seventh counted from the sacrum) with dorsal ribs attached, anterior view, *B* dorsal n+8 (third counted from the sacrum) with dorsal ribs attached, anterior view, *C* dorsal n+9 (second counted from the sacrum) with dorsal ribs attached, posterior view, *D* caudal 4, anterior view, *E* caudal 5, posterior view, F_1 caudal 6, anterior view, F_2 same caudal, posterior view.

horizontal. Immediately behind the sacrum, the vertebral column slopes relatively steeply downwards, beginning with the first caudal, and the lateral profile of the vertebral column becomes still more steep, along the series between caudal 6 and caudal 13; more posteriorly the tail is horizontally placed. The dorsal vertebrae are amphiplatyan (Pl. XXVI, Fig. 1; Text-fig. 4*A-C*). Their centra distinctly increase in size posteriorly. The centra of the first three vertebrae of the preserved series are slightly compressed laterally and have a median keel along their ventral surfaces. The centra are concave ventrally in lateral view. The successive posterior dorsals are devoid of the ventral keel and are more deeply concave in lateral profile. The sutures between the centra and the neural arches level with the neural canal in the first three preserved dorsals, and are slightly lower in the successive dorsals. The neural arch is about twice as high as the centrum in the three anterior dorsals of the preserved series and it is about one and a half times as high in the posterior dorsals. The diapophyses on these more anterior dorsals are directed upwards at an angle which is less than 45° to the horizontal level of the neural canal. This angle increases posteriorly so the diapophyses of the posterior dorsals (except the last one) are very steep. The diapophysis in the last dorsal is nearly horizontal. The diapophyses become shorter and broader towards the sacrum. They bear two articular surfaces for the ribs. The part of the diapophysis which contacts the tuberculum becomes short-

er in successive dorsals and as a result the two articular surfaces become closer to each other. The capitular part of the diapophysis is placed vertically on the last dorsal and the capitular surface is very close to the tubercular one. The zygapophyses of the dorsals are short and broad and they show a tongue and groove articulation. The prezygapophyses bear two grooves each, and the postzygapophyses two ridges, which fit into each other. The articular surfaces of the zygapophyses are almost horizontal. The articular surfaces of the prezygapophyses face slightly inwards and those on the postzygapophyses slightly outwards. A deep depression is developed below each postzygapophysis, on the posterior face of the pedicel of neural arch. The neural spines are subrectangular and strong, although relatively low. They are slightly inclined backwards.

The sacrum (Pl. XXVII, Pl. XXVIII, Fig. 1; Text-fig. $5A_1$, A_2) is composed of six vertebrae, which have their centra fused. One former dorsal and two former caudals are incorporated into the sacrum, plus the three basic sacrals. The ventral margin of the sacrum is very slightly arched. The sacral 1 bears a normal diapophysis, but its rib is fused to the diapophysis, and the capitular and tubercular surfaces are joined. The first sacral rib is very short and broad, and its distal extremity is thin and flattened dorsoventrally. It attaches loosely to the shallow embayment on the medial edge of the ilium. The ventral surface of the centrum of the sacral 1 is devoid of any keel. The centrum widens posteriorly and its posterior articular surface fuses to the successive sacral. The ventral surfaces of sacrals 2—4 bear a keel, which is well pronounced, although comparatively low. Their sacral ribs are situated in the upper half of the centrum, those of sacral 2 are placed intervertebrally between the sacral 1 and 2, those of the sacrals 3 and 4 are placed in the anterior part of each centrum, close to the line of fusion of the sacrals. The sacral ribs 2—4 are strong and flattened anteroposteriorly; the strongest one is that of sacral 4 and it forms a vertical plate. A distinct suture is visible between its dorsal part and the diapophysis. The rib of sacral 2 is directed posteriorly, that of sacral 3 anteriorly and that of sacral 4 slightly forwards. The sites of articulations between the sacral ribs and the centra are very well marked. The sacral ribs 2 and 3 converge distally and both contact the anterior process of the ischium. Sacrals 5 and 6 have their centra fused but their neural arches are very similar to those of the caudal vertebra. The keel on the ventral surfaces of the centra of sacrals 5 and 6 is very low, in the comparison with those on sacrals 2, 3, 4 which are the primary ones. Sacrals 5 and 6 have very distinctly marked sutures between their centra and the neural arches. Short and stout diapophyses are also characteristic of these sacrals. The rib of sacral 5 is flattened anteroposteriorly. The site of its attachment with the diapophysis forms a vertically elongated articular surface somewhat constricted in the middle. The suture between this rib and the diapophysis is well visible. The shape of the rib of the sacral 6 is similar to that of the succeeding caudal rib, and its suture with the diapophysis is distinct. This rib is flattened dorsoventrally for the most of its length, and it is the broadest behind half of its length. Its most distal portion is thickened and strongly narrowed. Proximally, the rib rises steeply.

The centra of the caudal vertebrae are spool-like (Pl. XXVI, Fig. 2, Pl. XXVIII, Figs 2—4; Text-fig. 4 D-F). Those of the anterior caudals are somewhat concave ventrally, in lateral view. The anterior articular surface of the centrum of caudal 1 is slightly protruded forwards dorsally and it overlies the upper part of the posterior articular surface of the centrum of the last sacral. Several caudals from the medial portion of the tail posterior to caudal 4 have centra that are very deeply concave ventrally. The centra of these medial caudals are shortened both in respect to the centra of preceding and succeeding caudals. The first sites for the articulation of chevrons are present on the ventral, posterior margin of caudal 5 and on the ventral, anterior margin of caudal 6. They are here smaller than the articular facets for the successive chevrons. A pair

of longitudinal ridges appears on the ventral surface of the each chevron-bearing caudal, and the ventral face of the centrum, between these ridges, is flat. The posterior articular surface of the centrum of caudal 6 is more vertically placed than the others. The chevrons were still present on caudal 29, judging from the presence of the articular facets on the ventral margins of the centra. The transition point (RUSSELL, 1972) in the caudal series is present on caudal 9. Behind it, each caudal bears a ridge along the side of its centrum. These ridges become longer on the successive centra. The cross-section of the centra changes posteriorly along the entire caudal series from being round to hexagonal, which is caused by the appearance of the lateral and ventral ridges along the centra. The zygapophyses are relatively short. The caudal prezygapophyses are much longer than the postzygapophyses. The prezygapophyses on the anterior caudals have their articular surfaces concave and directed dorsomedially. They become gradually flatter and face more medially on the successive caudals, and at about caudal 10 they face entirely medially. The eight anterior caudals bear the caudal ribs, and the distinct sutures are visible where the ribs contact the vertebrae. The first four ribs are placed on the boundary between the centrum and the neural arch, more posteriorly their attachment is lower and the two last caudal ribs are exclusively on the sides of the centra. The ribs on the most anterior caudals are very long. The rib of the first caudal differs from the successive ones in shape. The distal end of this rib is thickened and it has an articular surface which loosely contacts the upper margin of the ilium on the very end of the latter. The shaft of the rib is flattened, being the broadest close to the distal end. This flattening diminishes on the three successive caudal ribs and the last ones are more rod-like. The arching of the caudal ribs changes along the caudal series. The first four ribs are more strongly arched and they rise upwards along their proximal halves; they become nearly straight and directed downwards, beginning with the caudal 5; the last, eight caudal rib is the shortest and is developed as a short process; there is only a tubercle developed, instead of the rib, on the caudal 9. The neural spines in the caudal vertebrae are very long. The first four spines are broader than the others. They are very slightly inclined backwards in the proximal vertebrae and the inclination becomes stronger in the more posterior caudals.

The portion of the vertebral column preserved in *Homalocephale calathocercos* is thus far the most complete in the family Pachycephalosauridae. GILMORE (1924) had at his disposal but the two dorsals and the eight caudals from the different parts of the tail, in the specimen of *Stegoceras validus*. He suggested that the vertebra illustrated by him (*l. c.* Pl. 12, Figs 8, 9) represents the medial dorsal, because of the strong upward direction of its diapophyses. This, however, should not be necessary true, because the preserved portion of the presacral vertebral column shows in *Homalocephale calathocercos* that the diapophyses on the several penultimate dorsals display the most upwards direction. The diapophyses are similarly directed as these in *Homalocephale calathocercos*, in *Thescelosaurus edmontonensis* STERNBERG 1940, although, it seems that the relation is reversed in *Thescelosaurus neglectus* where the more posterior dorsal diapophyses are less steep than those anterior ones. Two sacral bones are present in the material recovered in Mongolia and that of the above described species, *Homalocephale calathocercos*, is more complete. The sacrum and the sacral ribs of another Mongolian species, *Prenocephale prenes*, do not show any important differences, except for being, perhaps, slightly more slender. The caudal vertebra illustrated by GILMORE (*l. c.*, Pl. 12, Fig. 2) in *Stegoceras validus*, was considered by him as the third one. It exposes the presence of the articular facet for the contact with chevron, on the lower posterior margin of the centrum. The first articular facet for the chevron in *Homalocephale calathocercos* is present on the caudal 5. Thus, the caudal in question,

illustrated by GILMORE (l. c.) more probably represents the caudal 5, because also the centra of the two vertebra here compared have the similar shape.

Sternum (Pl. XXX, Fig. 1). — Both sternal plates are not fused medially. The sternum is 74.5 mm long and has its posterior, shaft-like process directed outwards and thickened distally. It broadens and thins medially. The lateral margin of the expanded portion is thickened, especially at the proximal end, where it exposes a rough surface. The medial margin of the expanded portion sends the hook-like process, close to the shaft. The process is directed posteriorly. The sternal plates of *Homalocephale calathocercos* described above were for the first time recovered within the Pachycephalosauridae. They resemble very closely in the shape the sternal plates of *Anatosaurus annectens* (MARSH, 1892) and are one more evidence for the bipedality of the pachycephalosaurids.

Ribs. — Nine posterior dorsal ribs are preserved in *Homalocephale calathocercos* [4]. They rise slightly outwards in the proximal portion, and are gently arched more distally, except the last dorsal rib, which is more strongly vaulted than the others. The ribs become broader more posteriorly. The fifth and the tenth rib of the preserved presacral series are complete. They are correspondingly 83 mm and 73 mm long across the curve and 142 mm and 117 mm long along the curve when measured from the capitulum. Both the capitulum and the tuberculum articulate with the diapophysis, but they are distinctly separated. They are closer to each other in the more posterior ribs. The penultimate dorsal rib has the capitulum and the tuberculum still well separated, but the last dorsal rib has the articular facets separated only when the rib is seen ventroposteriorly. The tuberculum is placed outwards and posteriorly with respect to the capitulum on all the ribs, the last one excluding. Here, the two facets are nearly equidistant from the median line of the body, and the tuberculum is placed above the capitulum. The dorsal ribs are directed slightly posterolaterally but the last rib has its long axis about normal to the line of the vertebral column. The more anterior ribs of the preserved series are narrower than the posterior ones. The last rib, which contacts the ilium freely by its medial portion, is here the flattest and the broadest, while its distal extremity is rounded in cross-section. The distal ends of the more anterior ribs are oval in cross-section. Only five fragmentary dorsal ribs are preserved in *Prenocephale prenes*, and as far as can be stated, they do not differ from those in *Homalocephale calathocercos*. The same seems be true for *Stegocercas validus*.

Pelvic girdle (Pl. XXV. Fig. 3, Pl. XXIX, Pl. XXX, Fig. 2; Text-fig. 5 *A*, *B*). — The pelvic girdle is broad and widens posteriorly. The ilium has its anterior portion dorsoventrally flattened. The posterior portion is developed in the form of a vertical blade and it bears dorsally a flat, subtriangular inward extension, immediately behind the acetabulum. There is no antitrochanter developed. A shallow embayment for the reception of the distal end of the first sacral rib is present on the medial edge of the anterior portion of ilium, close to its anterior extremity. The pubic peduncle is exceptionally wide and flattened dorsoventrally. It is directed forwards and downwards and bears the narrow, transversely elongated articular surface for the prepubis. The medial corner of the pubic peduncle contacts the ischium. The ischiac peduncle is very heavy, thick and expanded transverselly. It is long, extending below the ventral margin of the posterior portion of the ilium. Laterally it exhibits a strong, rough protuberance above the articular facet for the ischium. In posterior view, the ischiac peduncle is a strong, transverse plate. It continues upwards and merges dorsally with the anteromedial border of the inward extension of ilium. The dorsal acetabular rim is very broad transversely. A vertically elongated depression is present

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[4] For the description of sacral and caudal ribs see p. 85.

C_1

C_2
- IS TROC
- IL-TROC
- OBT
- CA-FEMBR
- FEM-T
- ADD

A_1

C_3
- P-I-FINT
- FEM-T
- G

C_4
- P-I-FINT
- IL-TROC
- CA-FEMBR
- FEM-T
- ADD
- G

A_2
- d
- is
- 2s
- 3s
- 4s
- 5s
- 6s
- c
- ppd
- is

C_5
- P-I-FINT
- CA-FEMBR
- FEM-T
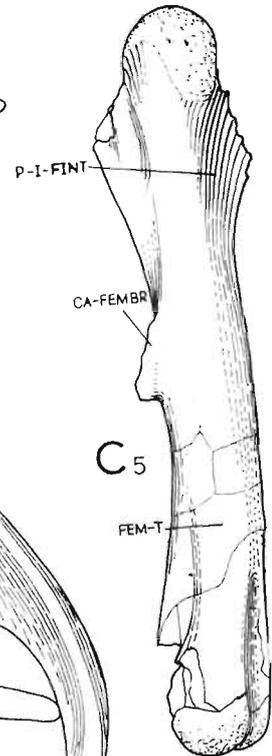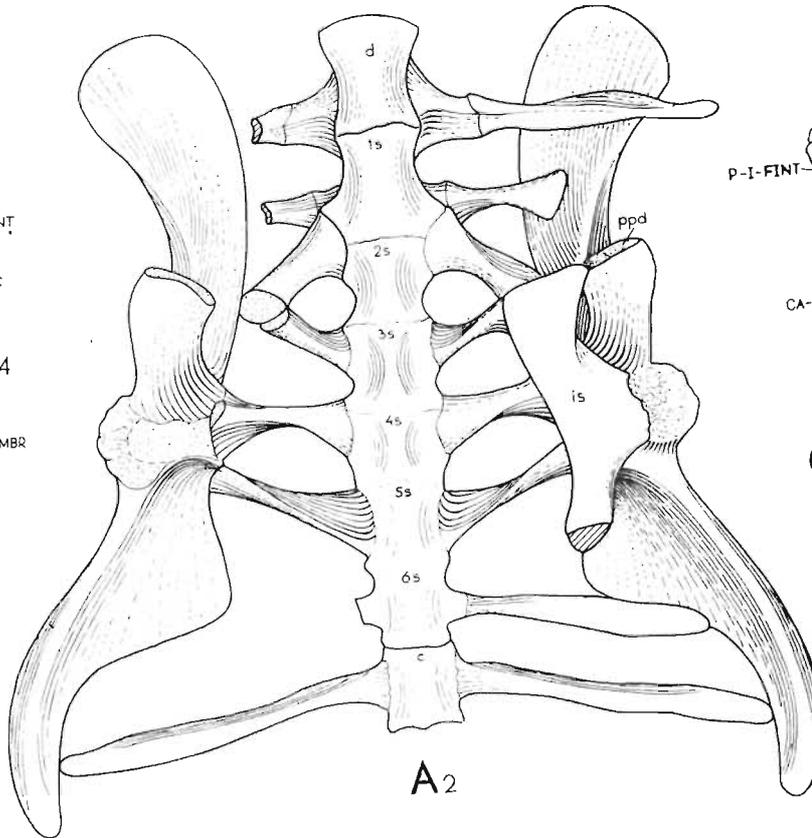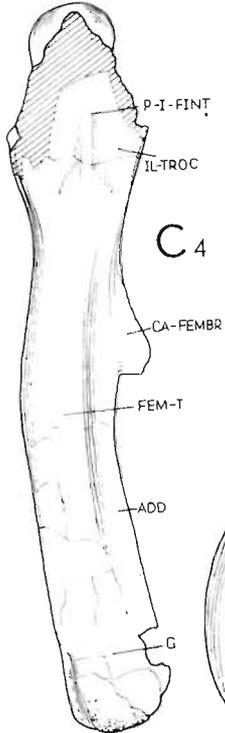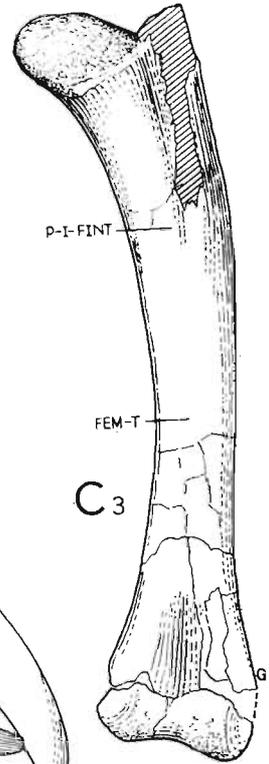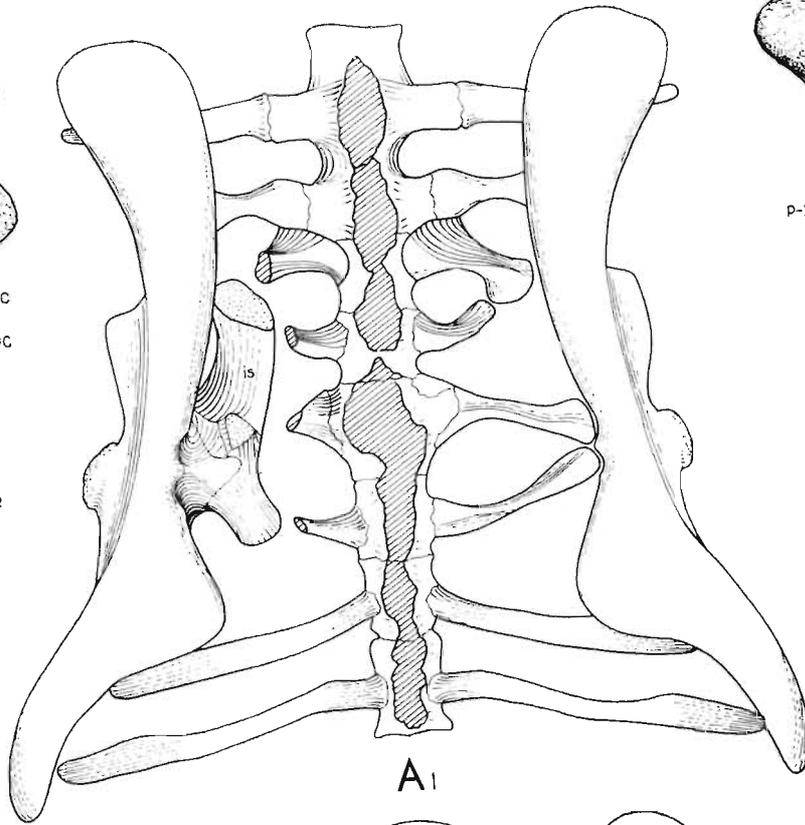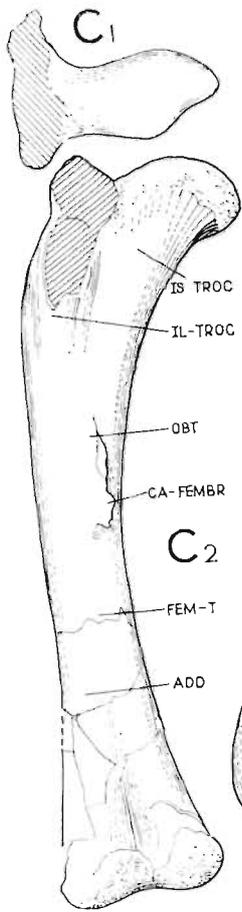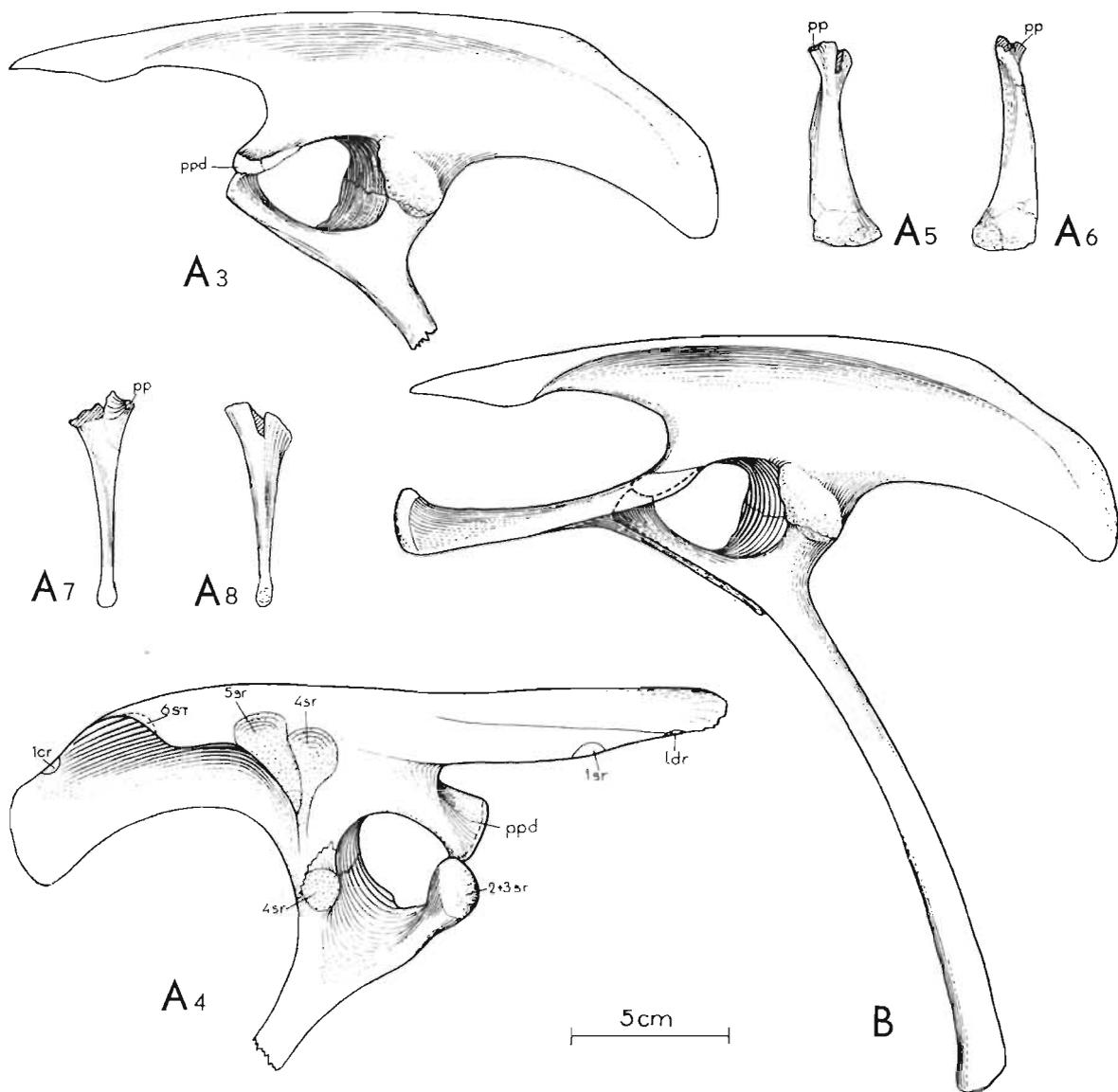
Fig. 5

Homalocephale calathocercos n. gen., n. sp. (G. I. No. SPS 100/51). A_1 pelvic region partly reconstructed, with last dorsal and first caudal vetebrae attached, dorsal view, A_2 same specimen, ventral view, A_3 left ilium and ischium in natural articulation, lateral view, A_4 same specimen, medial view, A_5 left prepubis, medial view, A_6 same specimen, lateral view, A_7 same specimen, ventral view, A_8 same specimen, dorsal view, B reconstruction of the pelvis, lateral view, C_1 left femur, articular head in dorsal view, C_2 same bone, posterior view, C_3 same bone, anterior view, C_4 same bone, lateral view, C_5 same bone, medial view. Abbreviations: *ADD* M. adductor femoralis, *CA-FEMBR* M. caudi-femoralis brevis *FEM-T* M. femoro--tibialis, *G* M. gastrocnemius, *IL-TROC* M. ilio-trochantericus, *IS-TROC* M. ischio-trochantericus, *OBT* M. obturatur internus, *P-I-FINT* M. pubo-ischio-femoralis internus, *c* first caudal vertebra, *1cr* contact for the rib of the first caudal, *d* last dorsal vertebra, *is* ischium, *ldr* contact for the rib of the last dorsal, *pp* postpubis, *ppd* pubic peduncle of the ilium, *s* sacrals 1-6, *sr* contacts for the sacral ribs 1-6.

on the medial surface of the ilium, above the ischiac peduncle. It is the attachment site of the fifth sacral rib. Another, broad and triangular depression is present anterodorsally to that for the fifth sacral rib. It is larger than the latter and the upper portion of the fourth sacral rib fits into it. The shallow depression for the end of the sixth sacral rib is present on the medial margin of the postacetabular portion of ilium. It is situated ventrally and immediately to the posterior boundary of the medial extension of this bone. The site for the free contact with the first caudal rib is marked some distance behind the depression for the sixth sacral rib.

The ilium of *Prenocephale prenes* (Pl. XXV, Fig. 3) is the same size as in *Homalocephale calathocercos*. The slight difference between the ilia of these species can be observed in the structure of the lateral wall, above the acetabulum, which in *Prenocephale prenes* is less concave and somewhat higher. Another difference deals with the anterior process of the ilium which is transversely narrower in *Prenocephale prenes*, and the posterior process of this bone which is less arched in the lateral view, in the latter species. The posterior extremity of the postacetabular portion of the ilium is more curved inwards in *Homalocephale calathocercos* than in *Prenocephale prenes*. The ilium of *Stegoceras validus* is slightly smaller than these bones in the two Mongolian species, but it was evidently not complete. Its depth at the centre of the acetabulum is between that in *Homalocephale calathocercos* and that in *Prenocephale prenes*, but it can be easily accepted that they are of the same size, as the range equals 5 mm. GILMORE (1924) emphasized, while describing the ilium of *Stegoceras validus*, the exceptional width of the pubic penducle, in the anteroposterior direction. It seems that even more striking is its extensive transverse width, which is characteristic of all pubic peduncles in the ilia within this family. The most important difference observed between the ilium of *Homalocephale calathocercos* and that of *Stegoceras validus* is the presence "on the internal side at the center above the acetabular border" (GILMORE, 1924, p. 35) of three sites for the articulation of the sacral ribs in *Stegoceras validus*, while there are only two depressions in *Homalocephale calathocercos*, and probably also in *Prenocephale prenes*. The sacral ribs which could articulate with the ilium in *Homalocephale calathocercos* and *Prenocephale prenes* in the acetabular region are these of the second to fifth sacrals. Out of these, the two first run convergently to each other and are comparatively narrow (in vertical direction). They are also directed decidely downwards, so contact with the ilium a b o v e the acetabulum was in these two species impossible. In fact these ribs contact, or at least the second rib does, the articular surface present dorsally on the preacetabular process of the ischium. Unfortunately, GILMORE (*l. c.*) did not give any illustration of the inner side of the ilium in *Stegoceras validus*, and we had not any occasion to see the bone.

The ischium (Pl. XXV, Fig. 3*b*) is long and slender. It has two articular peduncles proximally, but they both contact the ilium, and there is no articular facet present for the contact with the pubis. The posterior articular peduncle of the ischium is very stout and short and it makes the broad and firm contact with the corresponding ischiac peduncle of the ilium. A rounded, flat articular facet is placed on the medial border of the posterior peduncle of the ischium, immediately below its sutural union with the ilium. The lower portion of the fourth sacral rib fits onto this facet. The unusually long process, wide transversely and flattened dorsoventrally, extends anteroventrally from the posterior peduncle of the ischium. This process constitutes the anterior peduncle of this bone. It bounds the acetabulum ventrally, contacting laterally the anteromedial articular surface of the pubic peduncle of the ilium. In this manner, the pubis is almost entirely excluded from the acetabulum. The lower boundary of the acetabulum, built from the anterior peduncle of the ischium, is not placed opposite the dorsal rim of the acetabulum but is shifted much inwards. The anterior peduncle of the ischium bears on its

anterior extremity, a large rounded articular facet, which faces slightly medially. It makes the contact with the distal end of the second, and most probably also with the third sacral ribs. The lateroventral surface of the anterior peduncle of the ischium is flat and its lateral margin, below the anterior portion of the acetabulum, is sharp. The shaft of the ischium is very slender and it broadens slightly distally. Its lateroventral face is flat. The shaft is slightly bent inward towards its fellow.

GILMORE (1924), while describing the ischium of *Stegoceras validus* noticed that the anterior peduncle is long and that its extremity is opposite the pubic peduncle of the ilium. He did not observe these two bones in the articulated position, as we did, and moreover, he did not have the pubis in the material at his disposal. Our material allowed us to state that the unusual length of the anterior peduncle of ischium is connected with the closure of the acetabulum by means of the ischium and the ilium exclusively. It may serve as the evidence that the same structure of the pelvic girdle was the case in *Stegoceras validus*. When the ischia of *Stegoceras validus*, *Homalocephale calathocercos* and *Prenocephale prenes* are compared, the slight difference is observed in the curvature of their shafts. The portion of the ischium preserved in *Homalocephale calathocercos* shows that the shaft was less curved inwards in this species.

The prepubis (Pl. XXIX, Fig. 2; Text-fig. $5A_{5-8}$) is flattened dorsoventrally in its proximal portion, and laterally in the distal one. Its articular surface, which contacted the pubic peduncle of the ilium, is damaged, as well as the pubis (or postpubis). The dorsal margin of the prepubis is slightly rised up distally. The very distal extremity is thickened and rough. The base of a thin, broken off process, which corresponded to the pubis, is proximally present at the medial margin of the prepubis. This is the only pubis thus far recovered in this family.

Hind limb (Pl. XXX, Figs. 3—6, Pl. XXXI; Text-fig. 5C). — The femur is recurved inwards. The articular head is slightly compressed anteroposteriorly and its articular surface faces slightly forwards. It is separated from the anterior face of the shaft by a sharp ridge, and from the greater trochanter dorsally by a deep groove. The fourth trochanter is moderately developed and faintly pendant. It lies entirely in the proximal half of the femur. The distal end has two condyles separated by a shallow intercondylar groove. The lateral condyle is stronger than the medial one. Along the posterolateral face of the femur extends the relatively sharp ridge, which disappears towards the proximal end, on the level of the fourth trochanter. The smooth, flat surface is present on the posterior face of the shaft. It extends downwards and laterally to the fourth trochanter, and is separated from the anterior face of the shaft by the sharp ridge. The furrow extends upwards, on the lateral surface of the proximal end, above the fourth trochanter. The femur of *Prenocephale prenes* (Pl. XXXI, Fig. 2) is slightly more recurved inwards than this in *Homalocephale calathocercos* (Pl. XXXI, Fig. 1). Its articular head is still less distinctly distinguished from the medial and anterior faces of the shaft. The articular head is slightly longer and more slender in *Prenocephale prenes*, when viewed from the top. The greater and the lesser trochanters are lacking in both Mongolian species, but their bases are preserved. These latter are much thicker in *Prenocephale prenes* than in *Homalocephale calathocercos*, and consequently the trochanters should be stronger in the species first mentioned. The femur of *Stegoceras validus* was damaged and its description and illustration (GILMORE, 1924) are insufficient for the detailed comparisons.

The preserved distal half of the tibia in *Homalocephale calathocercos* (Pl. XXX, Figs. 3, 4) shows that its shaft was slender and the distal part strongly broadened lateromedially. The internal margin of the distal end is sharp and the posteromedial face of this bone is flat behind this margin. The lateral condyle is the more prominent of the two. The flattened surface for contact with the distal end of the fibula is present on the anterior face of the tibia, immediately

above the lateral condyle. The medial condyle has its articular surface elongate anteroposteriorly. The broad, shallow groove extends along the lateral side of the tibia, above the lateral condyle. It does not continue upwards on the shaft. The preserved distal portion of the fibula is slightly broadened lateromedially and thickened. The incompleteness of the two bones in *Homalocepahale calathocercos* makes impossible any comparisons with these in *Stegoceras validus*. The proximal tarsals are represented by but the astragalus, which is attached to the tibia (Pl. XXX, Fig. 3). It is thick, and has the rough distal articular surface. Its upper margin mounts a little the anterior face of the tibia centrally. The third distal tarsal is preserved in the left and right limb. Its distal articular surface is divided into two parts, one of them, the larger, fitting onto proximal articular surface of the metatarsal III, the smaller one and the shallower articular surface fits onto metatarsal II. Metatarsal II (Pl. XXX, Fig. 5) has the ridge marked along the outer margin of its upper half, which most probably indicates the position of the metatarsal I. Metatarsal III (Pl. XXX, Fig. 5) exposed the flattened surface on its anterolateral side. This surface extends obliquely upwards in the medial direction. It seems probable that it represents the surface of the attachment of metatarsal IV. In such case, metatarsal III would be slightly wedged between the metatarsal II and IV, in its upper part. This would result in the comparative narrowness of the pes. The distal articular surfaces of the preserved metatarsal are rough. The foveae ligamentosae on metatarsal III are broad and shallow. The phalanx 1 of the supposed digit IV of the left pes (Pl. XXX, Fig. 6) is preserved in both hind limbs. It is flattened dorsoventrally, short and distinctly constricted close to the distal articular surface. The proximal articular surface is undivided, large and shallow. The caput has distinctly separated condyles. The foveae ligamentosae are deep. The pes in *Homalocephale calathocercos* is very incompletely preserved, and it is incomparable to the pes of *Stegoceras validus* as different bones are present in the two species.

Chevrons. — The chevrons are few and very incompletely preserved. The articular surfaces for their attachment with the vertebrae are present beginning with the caudal 6 so they were absent on the first five caudals.

Caudal tendons (Pl. XXVIII, Figs 3, 4). — A basket-work of tendons is preserved around the hind part of the tail, beginning with the caudal 12. The tendons have roughly fuselar shape. Their median, thickened portions are placed outwards, forming the outer wall of the "basket", while the long and thinning extremities are directed posteriorly and anteriorly towards the backbone and they are not visible exteriorly. The tail is slightly flattened laterally along the portion which was surrounded by the "basket". The two halves of the "basket" are separated by the neural spines dorsally and the chevrons ventrally, both the extramities of the spines and of the chervons standing somewhat out from the "basket". Within each half of the "basket" six rows of the tendons can be distinguished, these of each particular row differing in shape. The first row, counted from the neural spines, consists of the tendons, which are slender, long and loosely arranged on the outer wall of the "basket"; their thinning anterior extremities meet those of the next row. The posterior extremities seem to run parallel and close to the neural spines. The thickened medial portions of the second row of tendons are also loosely arranged and they are slightly thicker than those of the preceding row. Their thinning posterior extremities meet those of the third row along the line situated opposite the boundary between the arch and the centrum of the caudals. The tendons of the third row are the mirror images of the tendons of the second row. Their anterior extremities slant downwards and meet the anterior extremities of the fourth row tendons. The tendons of the ventral, fourth to sixth, rows are more stout and very closely arranged. The thickened medial portion of the tendons of the fourth and fifth row are shorter and have the stronger curvature. The posterior extremities

of the fourth row of tendons approach the tendons of the more ventral row, opposite the medial line of the thickened portions of the latter, and they are directed more inwards towards the back. The tendons of the fifth row are the most strongly curved inwards. Their anterior, thinning extremities meet those of the next row while the posterior extremities rise slightly and approach the median portions of the tendons of the more dorsal row. The last, sixth row of tendons is placed entirely ventrally and it flanks the chevrons. Its tendons are very stout, their thickened, medial portions being comparatively long and closely attached to each other. The posterior extremities of the sixth row of tendons are directed inwards and run parallel to the sides of the chevrons. It seems, judging from the preserved fragments, that the tendons within each row become more slender towards the end of the tail. One can noticed on cross-section of the tail, that the thin extremities of all tendons, in all the rows, are arranged parallel to the backbone. Sometimes the extremities of the tendons, especially these anterior ones of the first and second row, are fused together. Similar, ossified were recovered together with the postcranial skeleton of *Prenocephale prenes*, although mostly they were not in their original arrangement. As the specimens of *Homalocephale calathocercos* and *Prenocephale prenes* here described have proved, the elements described by GILMORE (1924, p. 31) in *Stegoceras validus* as the abdominal ribs, represent in fact the caudal tendons. On the other hand, the ossifications described by this author (l. c.) as the tendons are but the thinned extremities of the tendons. The caudal tendons in the three species mentioned, where they were recovered, do not differ, and, most probably, the presence of the "basket" around the major part of the tail is characteristic of the family Pachycephalosauridae.

REMARKS ON MYOLOGY

Muscle scars are visible on most of the bones and especially on the skull. We do not provide the present paper with any reconstruction of the musculature, but interpretations of the attachment sites are here presented. In the interpretation of the muscle attachments on the head we mainly followed OELRICH (1956) and OSTROM (1961), while our interpretations of the muscle scars of the pelvic region and the hind limbs are based on ROMER (1927) and GALTON (1969).

Mandibular musculature. — Several scars corresponding to the origins of the mandibular adductors can be distinguished on the skull of the pachycephalosaurids. Their position does not deviate from that found in other ornithischian dinosaurs i.e. in the hadrosaurs (OSTROM, 1961) except perhaps, that they are generally placed more posteriorly in relation to their insertions on the mandible than in the latter group, in which they slightly resemble the conditions in *Protoceratops* (HASS, 1955; OSTROM, 1964, 1966). *Internal adductors.* The attachment of the *M. pterygoideus dorsalis* is visible on the dorsal surface of the ectopterygoid and partly on the ventral wing of the pterygoid. The attachment of the *M. pterygoideus ventralis* is visible on the dorsal surface of the ventral wing of the pterygoid along its posterior margin. The attachment of the *M. pseudotemporalis* is present within the infratemporal fossa, on the ventral surface of the postorbital and partly on the lateral surface of the parietal. The posterior boundary of the attachments is indicated by the comparatively sharp crest present on the squamosal, along its contact with the parietal. The origin of the *M. pseudotemporalis* is present in *Homalocephale calathocercos* just in front of the anterior boundary of the supratemporal fenestra. *External adductors.* The origin of the *M. adductor externus superficialis* is visible on the laterodorsal surface of the prequadratic process of the squamosal. The origin site of the *M. adductor externus*

medialis is present medially to the *M. adductor externus superficialis*, within the infratemporal fossa, and separated from scar of the latter muscle by an elevation of the prequadratic process. The sharp ridge on the dorsoposterior surface of the squamosal separates medially the attachment site of the *M. adductor externus medialis* from that of the *M. adductor externus profundus*, which is partly placed on the parietal. This muscle attaches to the skull just below the posterior margin of the supratemporal fenestra in *Homalocephale calathocercos. Posterior adductor.* The attachment site of the *M. adductor posterior* is comparatively broad transversely but restricted in its vertical dimension. It occupies the lower anterior surface of the quadrate.

Branchial musculature. — There is some doubt about the attachment area of the *M. de-*
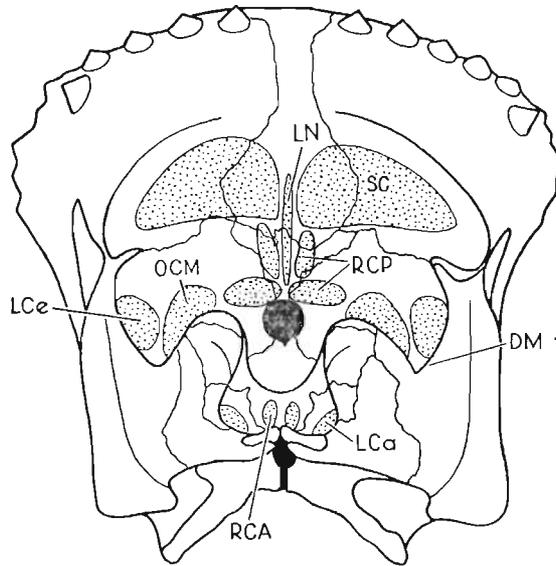
Fig. 6

Prenocephale prenes n. gen., n. sp. Diagrammatic drawing of the skull in posterior view with the insertion scars of muscles marked. Abbreviations: *DM* M. depressor mandibulae, *LCa* M. longissimus capitis, *LCe* M. longissimus cervicis, *LN* ligamentum nuchae, *OCM* M. obliquus capitis magnus, *RCA* M. rectus capitis anterior, *RCP* M. rectus capitis posterior, *SC* M. spinalis capitis.

pressor mandibulae (Text-fig. 6) on the skull of the pachycephalosaurids. Two sites are observed which eventually could prove to be the surface for the origin of the *M. depressor mandibulae.* One of them is visible in the form of a rugosity on the very end of the paroccipital process. This position is suggested by OSTROM (1961) as the origin site of the depressor muscle in the *Corythosaurus casuarius* (*l. c.*, Text-fig. 50). Another possibility is to locate the origin of this muscle along the posterolateral margin of the squamosal (as in the Ceratopsia, *fide* HASS 1955), and such a narrow surface is visible in *Homalocephale.* However, the latter position of the depressor would interfere with the superficial tympanum, behind the quadrate and it does not seem very probable. OSTROM (1961) drew the attention to the fact that the paroccipital process in hadrosaurs is deflected ventrally, in which it might parallel the fibers of the *M. depressor mandibulae.* The same deflection of the paroccipital process is present in the Pachycephalosauridae, so OSTROM'S suggestions may be valid also here.

Axial musculature (Text-fig. 6). — The very distinct scars left by the axial muscles are present on the occipital surface of the skull. Their position does not deviate from the general

reptilian pattern, but some of them are more strongly developed than usually, and this is connected with the heavy skull roof of the Pachycephalosauridae. *Extensors.* The *M. capitis spinalis*, which occupies the most dorsal position, had to be especially powerful and the site of its insertion is very extensive, limited dorsally in *Prenocephale prenes* by the thick, arched ridge across the parietal and squamosal. This ridge may correspond to the attachment of the aponeurotic *fascia colli superficialis*. A vertical ridge is present medially which corresponds to the attachment of the *ligamentum nuchae*. This ridge is differently developed in the various pachycephalosaurids and it is the sharpest in *Homalocephale calathocercos* and less pronouced in *Prenocephale prenes*. But, in the latter species a pair of deep pits is present in the centre of the occipital depression, on both sides of the ridge mentioned, which may correspond to the extremely strong *ligamentum nuchae*. The insertion site of the *M. rectus capitis posterior* seems to be divided into two parts: one of them, in the form of the cup-like depression is located within the exoccipital immédiately above the foramen magnum and separated from its fellow by the very narrow ridge of the supraoccipital; the other, more dorsal, is placed on the ventral portion of the central occipital depression. The attachment site of the *M. obliqus capitis magnus* is present on the exoccipital, above the medial part of the ventral edge of the paroccipital process. It is delimited dorsolaterally by the arcuate ridge, which separates it from the insertion site of the *M. longissimus cervicis* (according to OERLICH 1956; = *pars transversalis capitis* of the *M. longissimus*, according to OSTROM, 1961), the latter occupying the posterior surface of the paroccipital process. *Flexors.* The impressions of both flexors are very characteristic by their comparatively small sizes and the position which is very close to the medial axis of the skull. The insertion site of the *M. rectus capitis anterior* is placed on the basioccipital, immedietely ventral to the occipital condyle and is separated from its fellow by means of the median ridge. The insertion of the *M. longissimus capitis* (according to OELRICH, 1956; = *pars transversalis cervicis* of the *M. longissimus* according to OSTROM, 1961) is placed lateral to the insertion of the *M. rectus capitis anterior*, on the posterior face of the plate-like basal tubera. Quite unusual ridges are present on the posterior surface of the plate formed by the pterygoid wing of the quadrate, close to its contact with the dorsal wing of the pterygoid. The lateral edge of the prootic-basisphenoid plate which nearly attaches to the pterygoid (p. 65) displays also the distinct impressions. It is difficult to explain to which structures both these impressions correspond, because they were not reported so far in other reptiles. They may correspond to the aberrant position of the insertions of the ventral or lateral cervical muscles, which matched the strong development of the axial extensors, or may be, they represented the attachments of some fasciae.

Pelvic and *appendicular musculature* (Text-fig. 5). Several muscle scars can be observed on the external surface of the ilium of *Homalocephale calathocercos*. The supposed origin site of the *M. ilio-tibialis 1* is present on the narrow lateral surface of the anterior process of the ilium. The rough crest, which lowers postriorly extends along the dorsal margin of the ilium. It most probably formed the origin site of the posterior portion of the *M. ilio-tibialis*. It is difficult to determine where the boundary between the *ilio-tibialis 1* and *2* should be placed. The supposed origin site of the *M. ilio-caudalis* is located slightly dorsally on the posterior end of the post-acetabular portion of the ilium and it is comparatively extensive. The posterior boundary of the origin site of the *M. ilio-fibularis* is visible below and anteriorly to the origin of the *M. ilio-tibialis*. The posterior edge of the inward extension of the postacetabular portion of the ilium bears ventrally numerous and strong longitudinal striations which correspond to the origin of the *M. dorsalis caudae*. The similar striations are present on the anterior process of the ilium and they formed the insertion site for the portion of the *M. dorsalis trunci*. ROMER

(1927) and GALTON (1969) located on the external surface of the ilium the origins of the *Mm. ilio-trochantericus, ilio-femoralis, caudi-femoralis brevis,* and *flexor tibialis externus*; however, these areas are impossible to determine in *Homalocephale calathocercos*. There are striations present on the dorsal surface of the pubic peduncle of the ilium which however cannot be interpreted as being left by muscles and they may mark the former presence of the cartilaginous tissue which connected the illium and the pubis (THULBORN, 1972, p. 39). A narrow and deep longitudinal scar is present dorsally on the lateral surface of the prepubis, close to its proximal end which may represent the insertion of the tendon of the *M. ambiens.* A distinct scar is visible along the middle section of the ventral edge of the prepubis. It seems probable that it may be for the origin of the *M. pubo-ischio-femoralis internus,* similarly as was postulated by GALTON (1969) in *Hypsilophodon.* The lateral surface of the prepubis is finely striated longitudinally, at its distal end. It is difficult to state, which muscle left this scar. The only muscle scar distinctly marked on the ischium of the pachycephalosaurids is visible in the form of a long, rough groove present proximally on the lateral surface of the ischium, close to its anterior margin. It seems that it corresponds to the *M. adductor femoralis* in other ornithischians. A weak scar corresponding to the origin of the *M. ischio-trochantericus* is visible more distally, along the posterior margin of the shaft of the ischium. There is no shelf developed for this muscle in the pachycephalosaurids.

The interpretation of the pelvic musculature in the Pachycephalosauridae is difficult because of the unusual structure of pelvis in this group. The anterior process of the ilium is flattened dorsoventrally and it does not display much lateral surface for the attachments of the limb muscles (even the surface for the origin of the *M. sartorius* is comparatively narrow) as it does i.e. in *Hypsilophodon* or in *Stegosaurus.* It is slightly similar in its structure to the anterior process of the ilium in *Triceratops.* On the other hand, the anterior part of the prepubis is flattened in the plane perpendicular to the plane of the flattening of the anterior process of the ilium, displaying ventrally a sharp margin instead of the broad surface for the muscular attachments. In this it resembles the prepubis of *Triceratops,* but it is still much less expaned dorsoventrally than the latter form. In the lack of the antitrochanter the pelvis of the Pachycephalosauridae differs from that in the Ceratopsia and other quadrupedal ornithischians. As far as the distribution of the muscles on the prepubis is concerned, ROMER (1927, 1956) was of the opinion that the longitudinal course of the striations, as well as the laterally compressed shape of the prepubis in some ornithischian dinosaurus are the evidence that the lateral surface of the anterior portion of the prepubis provided the surface for the insertion of the *M. obliquus abdominis.* GALTON (1969) disagreed with this opinion, arguing that the latter muscle more probably inserted on the ventral surface of the prepubis and on the anterior part of the postpubis. According to the latter author the lateral surface of the prepubis was occupied anteriorly by the origin of the *M. pubo-tibialis* (which ROMER believed to be lacking in ornithischians) in *Hypsilophodon.* The problem seems still unclear to us. However, the abdominal cavity must have been large and extended much backwards in the pachycephalosaurids, taking into account the weak curvature of the dorsal ribs and the very broad pelvic as well as postsacral region. It needed the strong support, so the insertion of the *M. obliquus abdominis* on the anterior part of the ischium seems to be more likely.

The muscle scars are plainly visible on the femur (Text-fig. 5C) and the pattern of their distribution is very similar to that presented by GALTON (1969, fig. 9, 10) in *Hypsilophodon.* The partly preserved distal part of the femur in *Homalocephale calathocercos* and *Prenocephale prenes* allows us to observe a distinct tuberosity above the lateral condyle which most probably represent the origin of the *M. gastrocnemius.* The deep and broad groove present distally along

the lateral margin of the tibia posteriorly to its attachment with the fibula, may represent the origin of the muscles moving the halux.

Tail musculature. — Very little is known about the musculature of the tail in dinosaurs and any comparison with that of the pachycephalosaurids is difficult. The rather strange skeletal structure of the tail in the latter group with extremely long caudal ribs in the anterior part of the tail and the basket-like arrangement of the tendons in the posterior part indicate that the caudal musculature was extremely strongly developed and played an important role. Distinct, vertically arranged striations are present on the lateral surfaces of the high spinal processes of the proximal caudal vertebrae. They cover the entire lateral surface of the spine on its top part, and are grouped at the anterior margin more ventrally. The striations are also present on the caudal ribs close to the centra and along the external surface of the shafts of the anterior caudal ribs. It indicates that the epaxial musculature of the tail was well developed. These striations may correspond to the attachments of the muscles of the: transversospinalis system (*Mm. interspinales, M. spinalis, M. dorsomedialis*), longissimus system (*M. sacro-coccygeus dorsolateralis*) and iliocostalis system (*M. sacrococcygeus lateralis*) of the mammals. The striations corresponding to the ventral musculature of the tail are generally distinct. They are located along the centra and along the internal surfaces of the flattened shafts of the caudal ribs close to their anterior margin. These striations seem to correspond to the *M. caudi-femoralis* and the *M. ilio-ischio-caudalis.*

CONCLUSIONS

ADAPTATIONS AND MODE OF LIFE

The suggestions made below dealing with the possible habits of the Pachycephalosauridae are of a speculative nature although in our opinion they seem to be generally consistent with what is known of their morphology. The habits of the Pachycephalosauridae were previously the subject of discussions by several authors, among others GILMORE (1924) and STERNBERG (1933). Recently GALTON (1970 *b*, 1971 *a*) has discussed the possible function of the pachycephalosaurid dome.

Feeding habits. — Attention should be drawn to the fact that in spite of the general structure of the teeth which is similar in all the pachycephalosaurids, the pattern of wear of the teeth varies very much within this group. This implies that the mode of using the teeth had to vary, which is reflected by the different position of the wearing surfaces in the different genera I.e. *Homalocephale* exposes the extensive, worn out lingual surfaces of the maxillary teeth, and these surfaces over the whole maxillary series tend to form a common plane. Consequently, the cutting edges of all the maxillary teeth are horizontal and they form here almost continuous line over the entire series. A similar pattern is present in *Tylocephale*, although the teeth are here much larger with respect to the size of the skull. Each maxillary tooth in *Stegoceras* bears the surface of wearing antero-medially, and the cutting edges over the full maxillary series produce the "megaserration", the teeth being conical (GILMORE, 1924, p. 27). There are no sharp cutting edges on the maxillary teeth in *Prenocephale*, because the narrow wearing surface of each tooth is present along its ventral margin. This, together with the canine-like premaxillary teeth presumably of prehensile function make the dentition of this genus quite unique among the late ornithischians, except perhaps *Pachycephalosaurus*. This wide variation in the dentition of the Pachycephalosauridae speaks for different kinds of food, which might include the plants (leaves, fruits and seeds) and the insects as well. In spite of the very variable dentition,

the construction of the suspensorium is very alike in all the Pachycephalosauridae (p. 62.) The functional analysis of the mandibular joint in this group is limited by the fact, that the complete mandible is known only in one specimen (*Stegoceras validus*). Thus we are only able to offer some vague suggestions. The striking character of the pachycephalosaurid suspensorium is the complete external covering of the insertion area of the main adductors on the mandible (*M. adductor externus* and *M. pseudotemporalis*, p. 93). It is achieved by the high position of the precoronoidal portion of the surangular and especially by the strong downward development of the jugal and quadratojugal. As a result the space for upward passage of the main adductors was very narrow, and was the broadest in *Tylocephale*, where the outward protrusion of the jugal and quadratojugal region is the strongest (p. 51). The narrow passage for these adductors indicates that the bulk of the muscles was not very large. The relatively high position of the insertion of *M. adductor externus* would have produced a shortening of this muscle, were not its origins shifted slightly backwards (p. 93). However, the length of the adductor externus can by no means be compared to that in the advanced Ceratopsia, but to some extent it resembled the length of the superficial portion of the *M. adductor externus* in *Protoceratops*. The mandibular joint in the Pachycephalosauridae did not allow for any protraction and retraction, as can be deduced from the small glenoid facet in *Stegoceras validus*. Additional evidence for the lack of such a motion is found in the mutual relation between the dorsal, posterior portion of the mandible and the suborbital fossa of the skull which excluded any aft and fore motion in this species. The presence of premaxillary teeth and the toothed anterior portion of the dentary (at least in *Stegoceras* and *Prenocephale*) as well as the character of the wear on these teeth, also speak against protraction of the mandible. Judging from the mutual relation of the origin site of the *M. adductor posterior* and its insertion (around the Meckelian fossa), the course of the fibers of this muscle was nearly parallel to that of the main adductors, so it generated an adductive force in the same direction, rather than retraction of the mandible. The premaxilla has a thick, rounded ventral margin which is in our opinion the evidence against the presence of a beak and suggests the development of the soft and comparatively extensive lip around the tip of the snout. This lip might have been larger in *Prenocephale* than in *Stegoceras*.

Vision. — Vision presumably played an important role in the life of the Pachycephalosauridae. The orbits are very large and deep and their bony walls gave perfect protection to the eye. The orbits are facing laterally, but there is a strongly marked tendency to extend the field of vision more anteriorly. It is realized during phylogeny by the gradual narrowing forwards of the snout in its preorbital portion and by the enlargment (especially in the vertical direction) of the orbit. This tendency reaches its climax in *Prenocephale*, where additionally the orbit is also facing slightly anteriorly. The optic nerve is one of the largest, which speaks for the high degree of the visua perception.

Olfaction. — The endocranial casts of the pachycephalosaurid skulls are characterized by the enormous size of the first nerve, which speaks for good olfactory abilities. There is a well developed external nasal cavity in the pachycephalosaurids, which displays the extensive floor. It might have been covered by mucous membrane for the increasing of olfactory sensitivity.

Posture. — The cervical vertebrae are known in no pachycephalosaurid specimen, which makes impossible the reconstruction of the neck region and of the exact position of the head in these animals. However, the very strong development of the extensors of the head was necessary for keeping the heavy skull in the horizontal position while the animal was walking. Such a position of the skull during the normal gait seems to us the most reasonable one, because the development of the laterally extending shelves above the eyes would limit (at least in *Prenocephale* and *Stegoceras*) the forwards vision if the head is kept vertically. We think that

the position with the lowered head and the anteriorly directed dome was attained when the head (and the dome) was used as the defensive weapon. The battering role for the dome in the pachycephalosaurids was suggested by GALTON (1970b, 1971a). This assumption seems to us well founded and logical. Interpretation of the dome as being connected with sexual dimorphism seems to us still disputable. The need for the development of a defensive weapon seems to be very essential in animals which, like the pachycephalosaurids, were comparatively slow (judging from the tibia/femur ratio, p. 101) and unprotected by armour. The flexors of the head are weak in the Pachycephalosauridae in contrast to the strong development of the extensors. Moreover, they insert on the very weak, plate-like basal tubers. This indicates that the action generated by these muscles was less powerful than that of the extensors. The location of the main flexors immediately on the medial axis of the skull might result in stronger development of the lateral or ventral cervical musculature to match the transverse development of the extensors. We suppose that the neck in the Pachycephalosauridae was fleshy, broad and short. The anterior dorsal region is also unknown in the Pachycephalosauridae. The weak curvature of the posterior dorsal ribs, the broad pelvis, and the presence of unusually long ribs on the anterior caudals mean that the animal was very broad in top view. The groove and tongue articulation of the zygapophyses on the (at least) posterior dorsal vertebrae completely eliminated lateral flexions of the trunk. A similar lack of lateral flexion is found in the posterior portion of the tail, where it is prevented by the vertical position of the articular surfaces of the zygapophyses. The only laterally flexible part of the tail was its anterior portion, where the zygapophyseal articular surfaces are horizontal. Here however, the lateral flexion was limited by the long caudal ribs. A slightly stronger lateral flexions of the tail was possible in the point placed immediately behind the rib-bearing portion of the tail, between the eight and ninth vertebra, where the zygapophyses have small, but completely horizontal articular surfaces, which are not only more horizontal than the zagypophyses of the succeeding caudal, but also than those of the preceding ones. Vertical movements were possible along the tail, but they were limited by the very high spinal processes. The basket-work of tendons gave perfect protection to the tail, being at the same time relatively light and elastic in the vertical direction. The arrangement of the thickest tendons along the ventral surface of the tail, as well as the numerous traces of damages present on these very tendons prove that it was the "working surface" of the tail. As was already mentioned above the structure of the pachycephalosaurid pelvis is most unusual. It is not only very broad (for a bipedal animal), but the acetabulum practically lacks its lower rim, as a result of the inward shifting of the anterior articular process of the ischium towards the sacrum. Moreover, the ischium contacts the sacrum at two points by means of the sacral ribs, one in front and the other behind the acetabulum. The contact between the ilium and the sacrum is weakened in the anterior portion of the pelvis, and it is restricted to a loose attachment between the anterior process of the ilium and the first sacral rib. The only firm union between the sacrum and ilium is that behind the acetabulum, by means of the upper portion of the fourth sacral rib and the fifth sacral rib. This latter contact seems to be additionally strenghtened by the vertical extension of the ilium in the medial direction which closely attaches to the posterior surface of the fifth sacral rib. Most probably this aberrant structure of the widenning backwards pelvic region was caused by the development of the large (also posteriorly) abdominal cavity. It may suggest that the Pachycephalosauridae were viviparous. The generally loose contact between the pelvis and sacrum might be important for the amortization of the abdomen when the animal was fighting and blows were conducted backwards along the rigid vertebral column. The rigid structure of the vertebral column may indicate that it was held nearly horizontal while the animal walked (GALTON, 1970b), but the deeper acetabulum

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and the stronger pubic peduncle in the Pachycephalosauridae, than they were i.e. in the hadrosaurs, indicate that the more inclined upwards posture of the vertebral column and the ilium could be also achieved during the rest, with the tail acting as the prop and with the centre of gravity placed behind the acetabulum.

REMARKS ON THE SEXUAL DIMORPHISM AND THE SUPPOSED PHYLOGENY OF THE PACHYCEPHALOSAURIA

The first authors who discussed the problem of the sexual dimorphism in the Pachycephalosauridae were BROWN & SCHLAIKJER (1943). In their opinion, the degree of development of the parietosquamosal shelf and the surface of the domed part of the skull roof are the characters connected with the sexual dimorphism; the forms with the smooth frontoparietal dome, which nearly lacked the shelf, were regarded by these authors as females, while the forms with the rough dome and the extensive shelf represented males. Recently GALTON (1971 a) reconsidering this problem, drew attention to the fact that the development of the shelf is connected with the development of the dome. He also reversed BROWN & SCHLAIKJER'S sex designation suggesting that forms with the relatively larger domes could be males. Although the majority of the Pachycephalosauridae have their skull roofs domed, among them the two forms are known which have them flat. They are: *Homalocephale calathocercos* from Mongolia and the skull No. A. M. N. H. 5450 of *S. validus* from Canada (GALTON, 1971 a, Text-figs 5, 6). Were the latter Canadian specimen the female, the only other unquestionable female should be the specimen of *H. calathocercos*. If the hypothesis about the sexual dimorphism within the pachycephalosaurids were applied to our Mongolian material, *Prenocephale prenes* and *H. calathocercos* have to be considered as male and female (or vice versa) of the same species because they were contemporary, being recovered in the beds of the same age (Nemegt Formation). But, the differences between the "flatly roofed" *H. calathocercos* and domed *P. prenes* are not restricted to the structure of the skull roof. They also deal with many other characters of the skull and the postcranial skeleton as well. Certainly, some of these differences are connected with the change in the thickness of the skull roof, or caused by their different mechanic promoted by the dissimilar position of the weight centres. There exists, however, still a number of differences between the two skulls compared, which seem to be independent: e.g. the differences in the size and shape of the foramen magnum and the medulla oblonga, in the shape of the arch of upper teeth and in their being worn out in the different manner, in the shape and the mutual relation between the pterygoids, etc. They speak, in our opinion, for the taxonomical separation of the two specimens in question rather than in favour of their sexual dimorphism. Nevertheless, the problem of the sexual dimorphism of the Pachycephalosauridae can be definitively solved only on the basis of a large sample, such as that from Belly River Formation of Alberta, which is far the richest in this family, as suggested by GALTON (1971a). We fully agree here with GALTON (*l. c.*) that the characters regarded by BROWN & SCHLAIKJER (1943) as of sexual value are far from being convincing, and a revision of the North American species, especially of "*Stegoceras validus*" is badly needed.

The earliest Pachycephalosauria known, represented by the *Stenopelix* and *Yaverlandia*, were reported from the Lower Cretaceous of Europe (MEYER, 1859; GALTON, 1971a). The Pachycephalosauria most probably should be derived from the Jurassic Hypsilophodontidae, as they have the premaxillary dentition still preserved, and they expose the similar general structure of the skull (GALTON, 1971a). However, the earliest hypsilophodontid with the known

postcranial skeleton — *Fabrosaurus australis* GINSBURG, 1964 from the African Upper Triassic (Thulborn, 1972) — has already the tibia distinctly longer than the femur, which relation is the constant character within the main hypsilophodontid lineage. The relation between the femur and the tibia is more primitive in the Pachycephalosauria. In the Wealden *Stenopelix* MEYER, and in the Upper Cretaceous Pachycephalosauridae as well, the femur is never shorter than the tibia. This fact, and the extensive differences in the pelvic structure, indicate that the Pachycephalosauria might have arisen very early (Triassic?) from the Hypsilophodontidae, before their advanced, cursorial trend was achieved. However, as already noticed above (p. 48), there are similarities in the structure of the pelvis, as well as some in the skull, between the Pachycephalosauria and the Ceratopsia. These two suborders had appeared in the ornithischian history very late (Cretaceous). In our opinion, both groups can be derived from the common, side line of the Hypsilophodontidae. It could be easily presumed that their separation took place during the Jurassic. Pachycephalosauria occur from the Belly River Formation to the Lance Formation in North America inclusively (Upper Campanian to Upper Maastrichtian, according to Russell; personal communication). In Asia, their earliest representative "*Stegoceras*" *bexelli* BOHLIN, 1953 (BOHLIN, 1953) is known from the Tsondolein-Khuduk locality in Inner Mongolia, and these beds are, perhaps, an equivalent of the Djadokhta Formation according to ROZHDESTVENSKY (1971, Table 2). The age of the Djadokhta Formation is Coniacian or Santonian according to KIELAN-JAWOROWSKA (1970). Recently, the Polish--Mongolian Expeditions recovered pachycephalosaurid representatives in Barun Goyot Formation (?Middle Campanian, according to KIELAN-JAWOROWSKA, 1974), and in the Nemegt Formation (Maastrichtian, according to ROZHDESTVENSKY, 1971, and Upper Campanian or Maastrichtian, according to OSMÓLSKA *et al.*, 1972). If the beds in Tsondolein-Khuduk may really be correlated with the Djadokhta Formation, the poorly known species "*Stegoceras*" *bexelli*, which occurs in these beds, is the oldest known representative of this family in Asia.

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T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXII

Fig. 1. Stereo-photograph of the damaged skull in right lateral view. Type specimen (G. I. No. SPS 100/51); about 1/3 of natural size.

Fig. 2. Stereo-photographs of the skull in: *a* — palatal view, *b* — occipital view. Type specimen (Z. Pal. No. MgD-I/104); about 1/3 of natural size.

Fig. 3. Skull in: *a* — dorsal view, *b* — right lateral view (with the mandible attached), *c* — palatal view, *d* — occipital view. Type specimen (Z. Pal. No. MgD-I/105); about 1/3 of natural size.
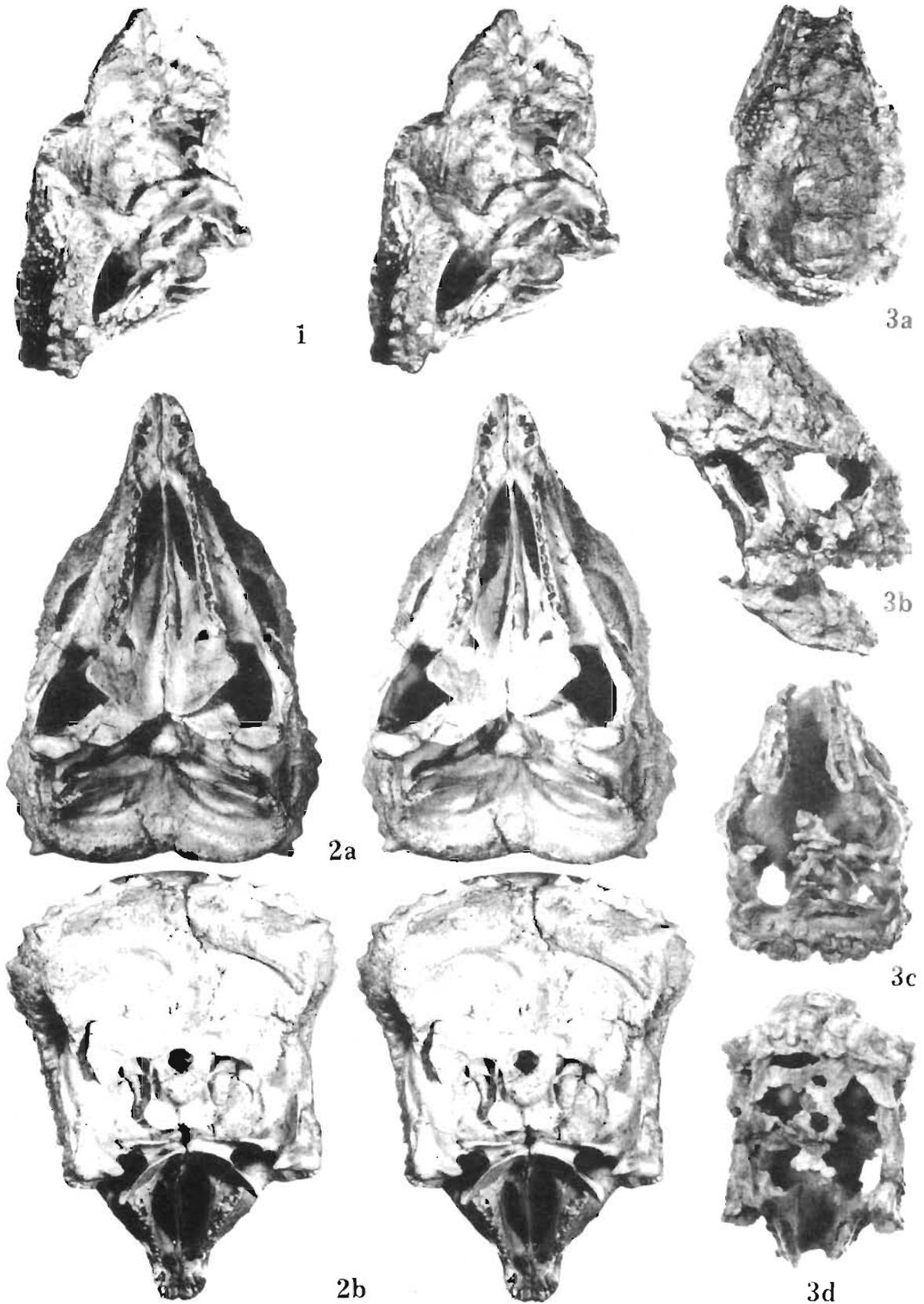
Photo: M. Kleiber, W. Skarżyński

1

2a

2b

3a

3b

3c

3d

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXIII

(see also Plates XXII, Fig. 2; XXV, Figs. 2, 3; and XXXI, Fig. 2)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Stereo-photographs of the skull in: *a* — dorsal view, *b* — right lateral view, *d* — anterior view, *c* — left lateral view. Type specimen (Z. Pal. No. MgD-I/104); about 1/3, of natural size.
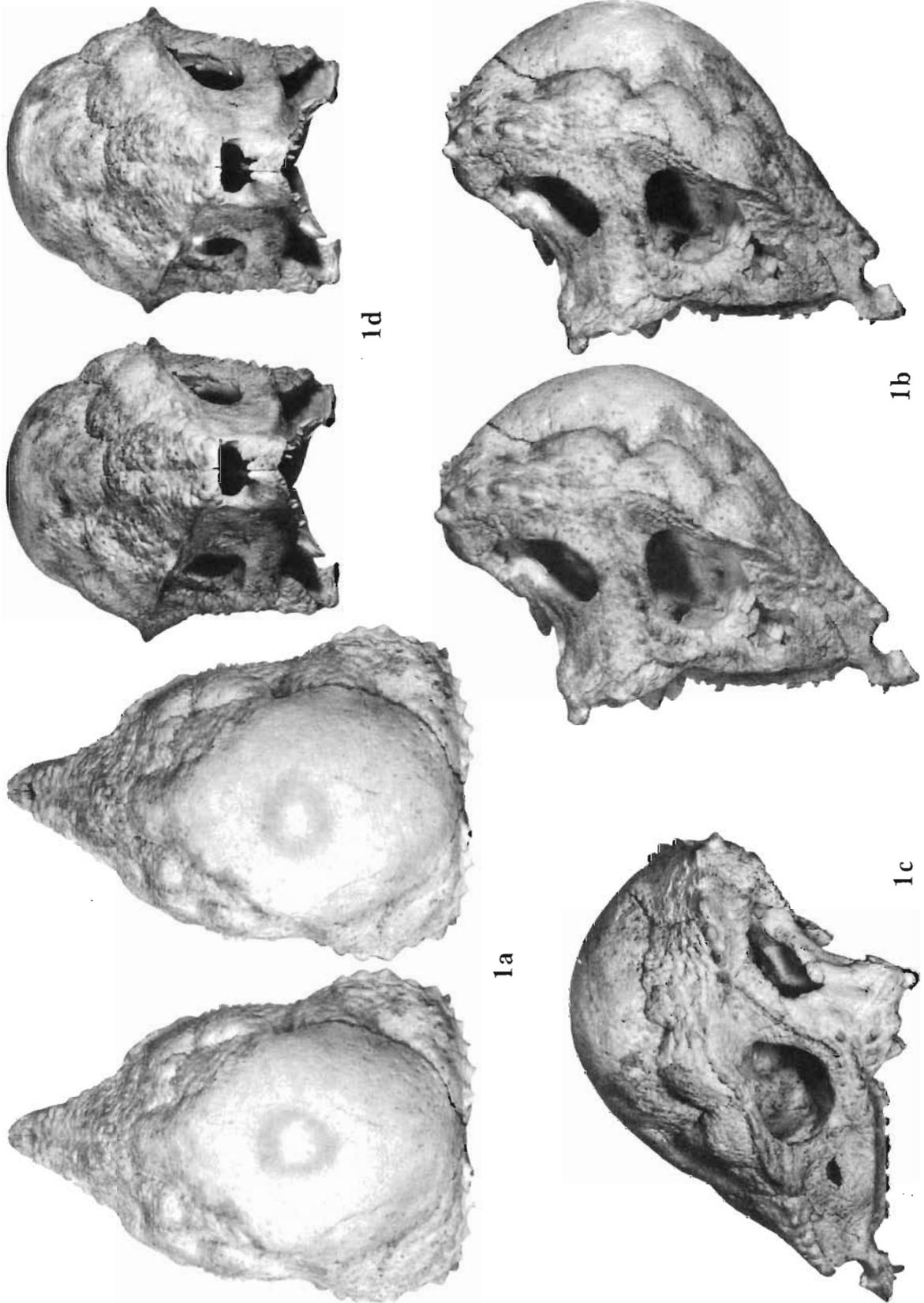
Photo: W. Skarżyński

1a

1b

1c

1d

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXIV

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Stereo-photographs of the damaged skull in: *a* — dorsal view, *b* — left lateral view, *c* — occipital view, *d* — palatal view. Type specimen (G. I. No. SPS 100/51); about 1/3 of natural size.

Photo: W. Skarżyński
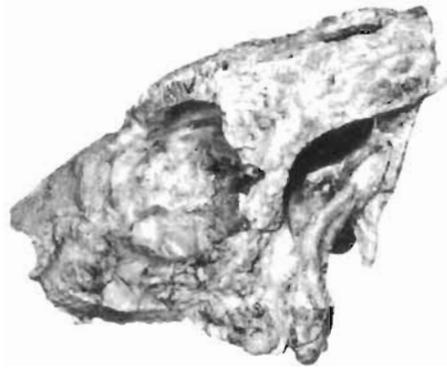
1b

1d

1a

1c
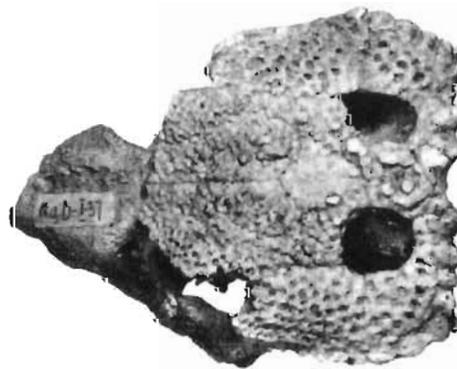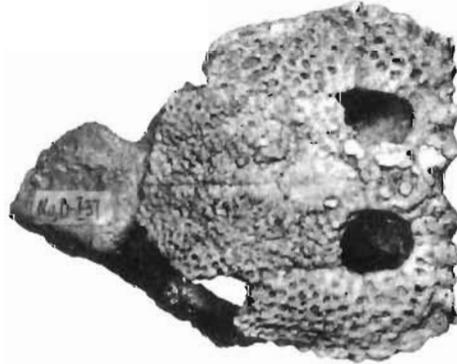
T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXV

Upper Cretaceous, Belly River Formation, Red Deer River, Alberta, Canada

Fig. 1. Latex cast of the endocranial cavity of specimen NMC No. 138: *a* — stereo-photograph in dorsal view, *b* — posterior view (medulla oblonga), *c* — left lateral view. Specimen illustrated also by LAMBE, 1918, Pl. 1, Fig. 1; ×1.

(see also Plates XXII, Fig. 2, XXIII and XXXI, Fig. 2)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 2*a*. Left middle ear and basicranial region in oblique, posterolateral view (see also Text-fig. 2). Type specimen (Z. Pal. No. MgD-I/104); ×1.

Fig. 2*b*. Medial wall of the right orbit with accessory ossifications visible (see also Text-fig. 3). Same specimen; ×1.

Fig. 3*a*. Dorsal view of the sacral and caudal ribs with ilium in natural articulation. Same specimen; about 1/3 of natural size.

Fig. 3*b*. Ventral view of the sacral region, right ilium and ischium, the latter shifted slightly in horizontal direction from the natural position. Same specimen; about 1/3 of natural size.
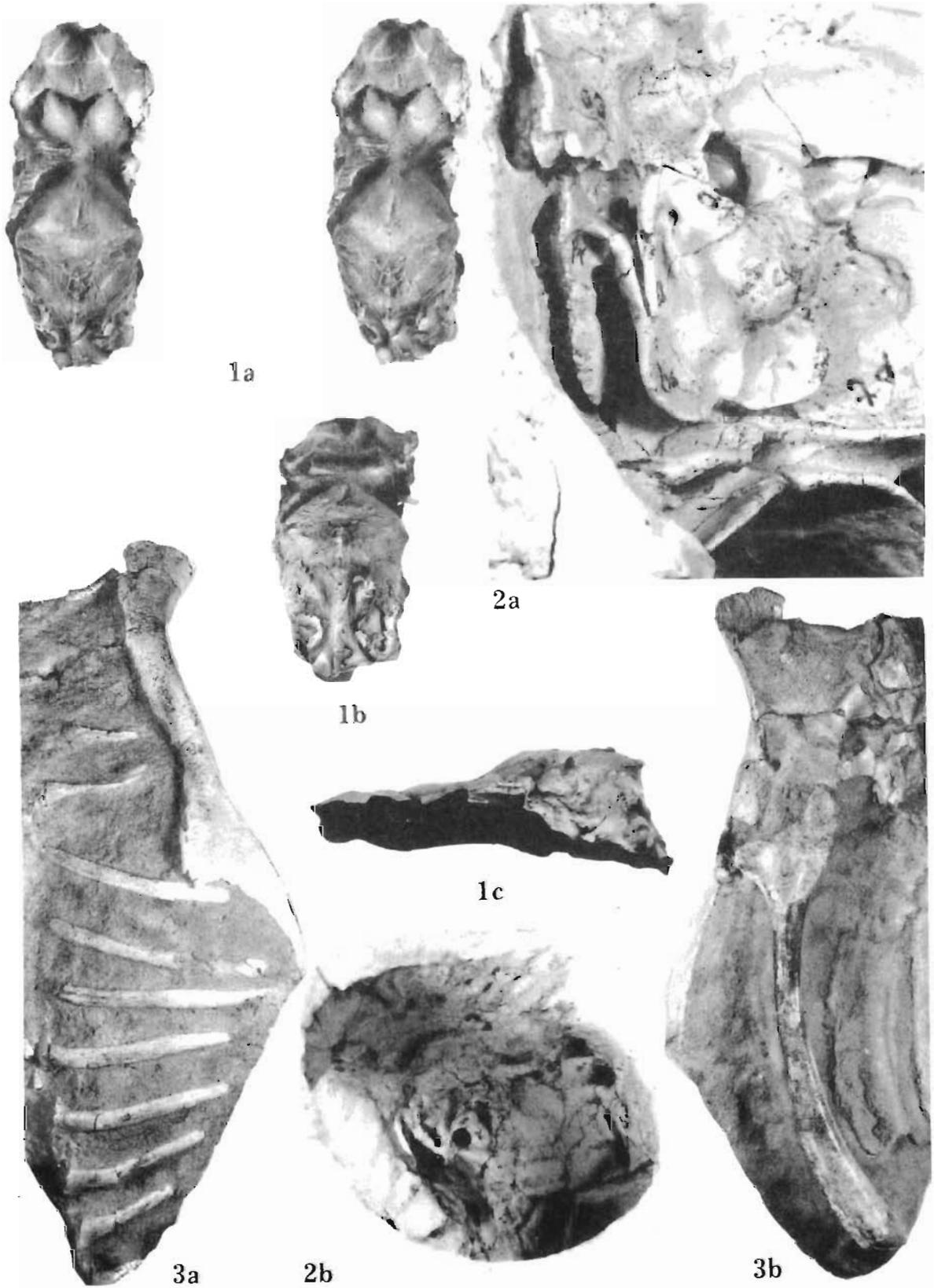
Photo: W. Skarżyński

1a

2a

1b

1c

3a   2b   3b

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXVI

Page

Homalocephale calathocercos n.gen., n.sp. 56

(see also Plates XXII, Fig. 1; XXIV, XXVII-XXX and XXXI, Fig. 1)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Posterior dorsal portion of the vertebral colum, the penultimate dorsal lacking, in: *a* — right lateral view, *b* — dorsal view. Type specimen (G. I. No. SPS 100/51); about 1/2 of natural size.

Fig. 2. Postsacral portion of the vertebral column in dorsal view. Same specimen; about 1/2 of natural size.
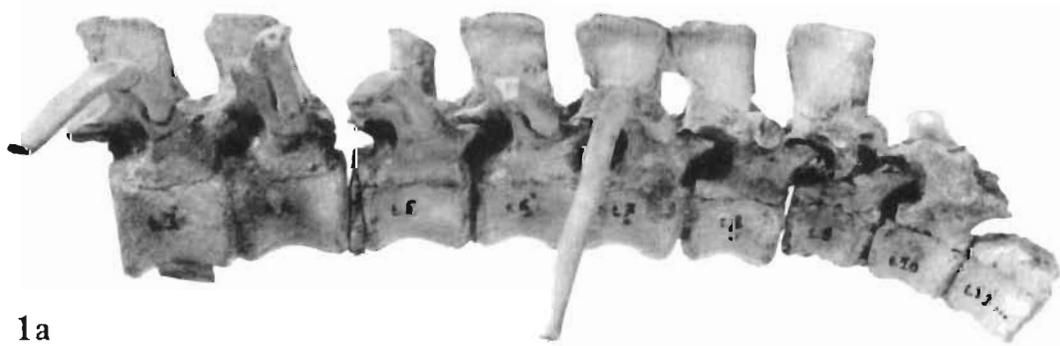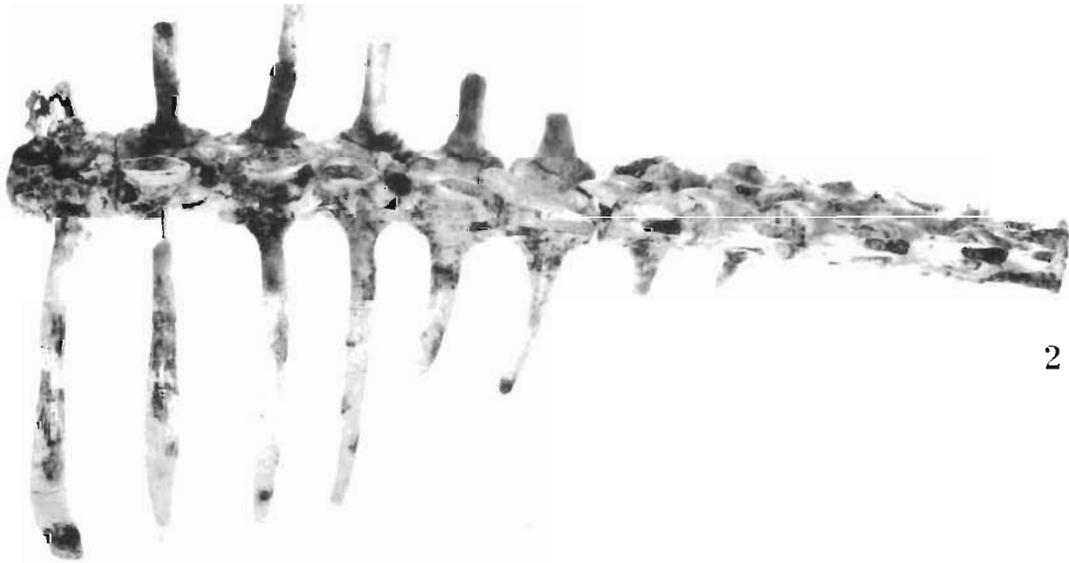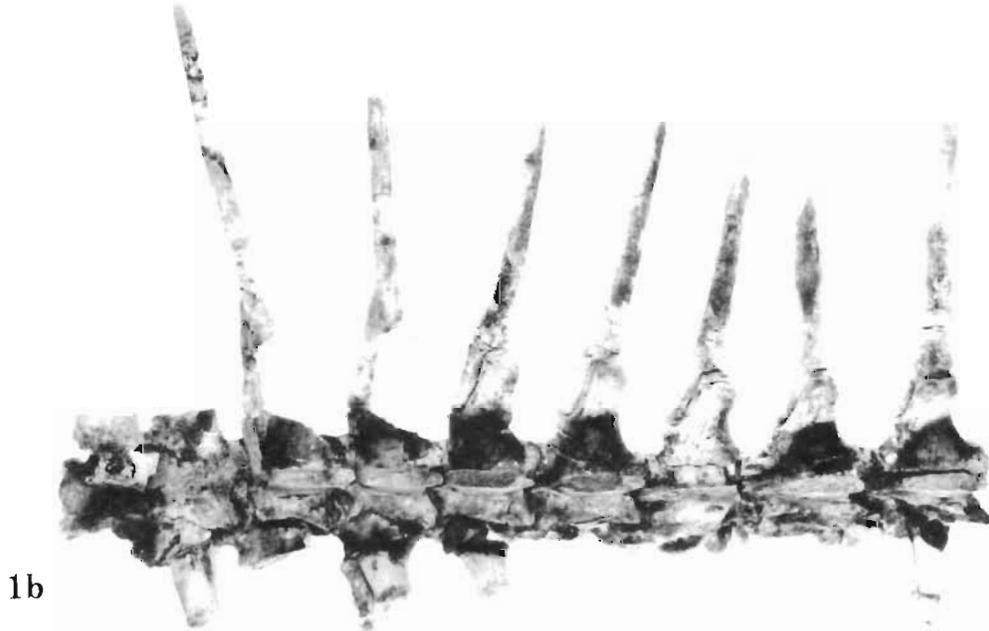
Photo: M. Kleiber

1b

2

1a

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXVII

(see also Plates XXII, Fig. 1, XXIV, XXVI, XXVIII-XXX and XXXI, Fig. 1)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Stereo-photograph of the damaged sacrum, with the last dorsal attached, in: *a* — dorsal view, *b* — ventral view. Type specimen (G. I. No. SPS 100/51.); about 1/2 of natural size.

Photo: W. Skarżyński
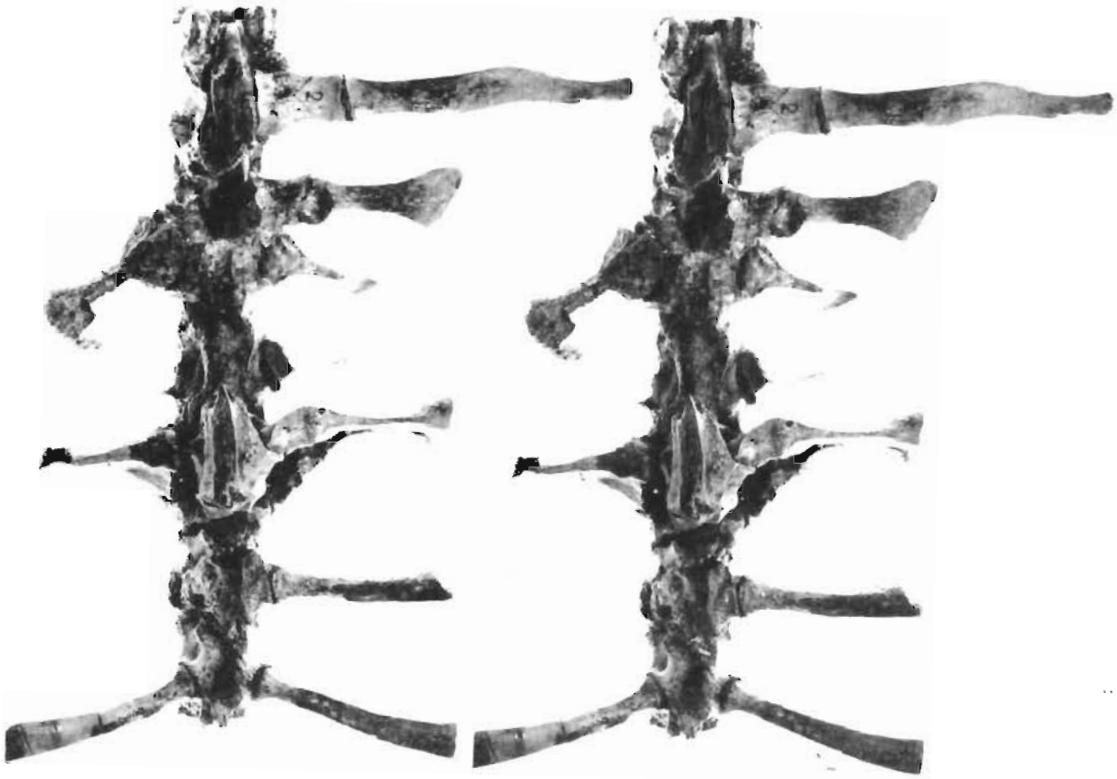
1a
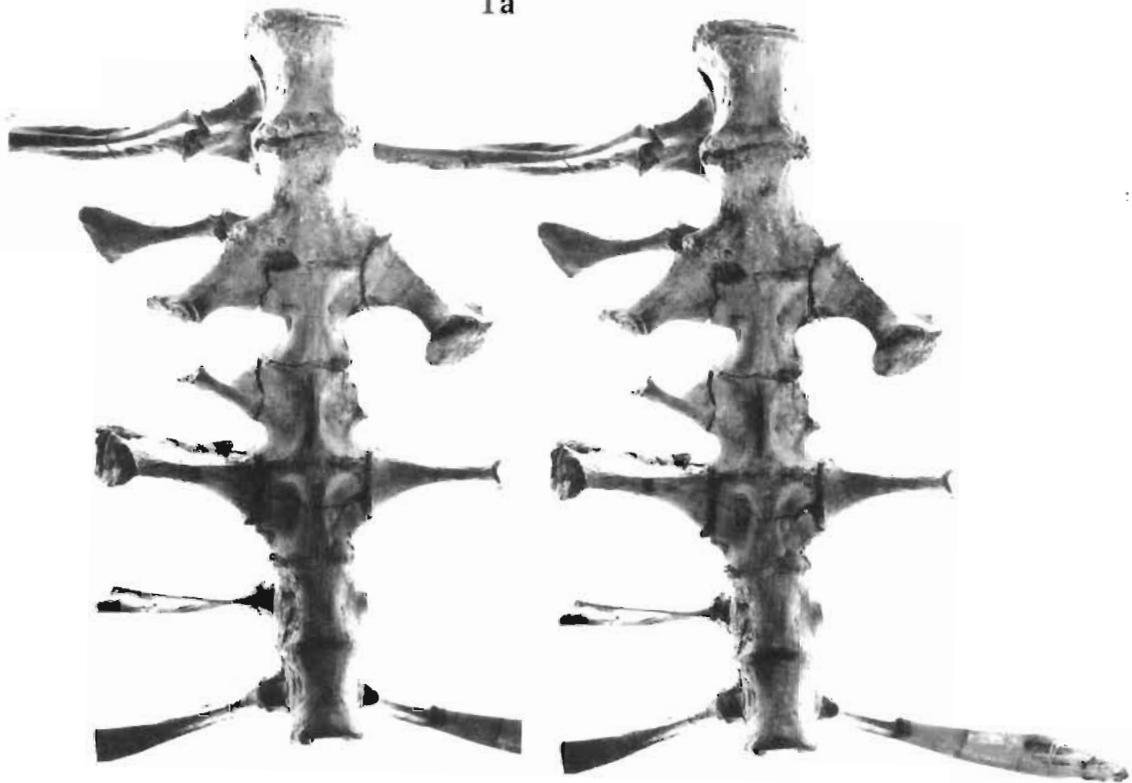
1b

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXVIII

Page

Homalocephale calathocercos n.gen., n.sp. 56
(see also Plates XXII, Fig. 1, XXIV, XXVI, XXVII, XXIX, XXX and XXXI, Fig. 1)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Sacrum in right lateral view. Type specimen (G. I. No. SPS 100/51); about 1/2 of natural size.
Fig. 2. Postsacral portion of the vertebral column in left lateral view. Same specimen; about 1/2 of natural size.
Fig. 3. Posterior portion of the tail, with the basket-work of tendons visible, in left lateral view. Same specimen; about 1/2 of natural size.
Fig. 4. Posteriormost preserved portion of the tail, partly with tendons, in left lateral view. Same specimen; about 1/2 of natural size.

Photo: M. Kleiber
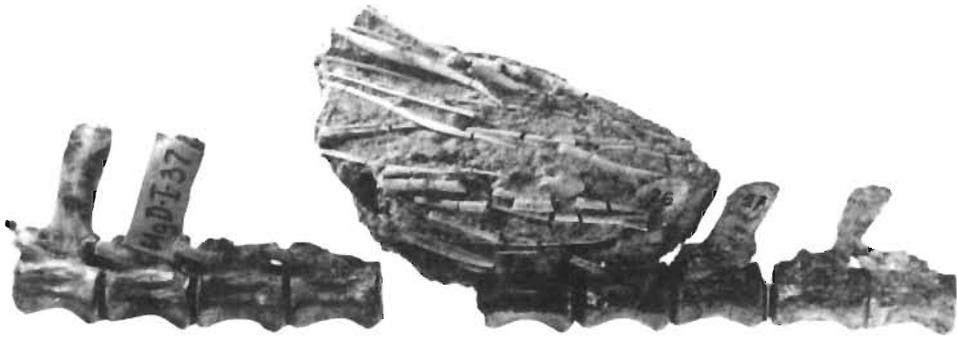
4
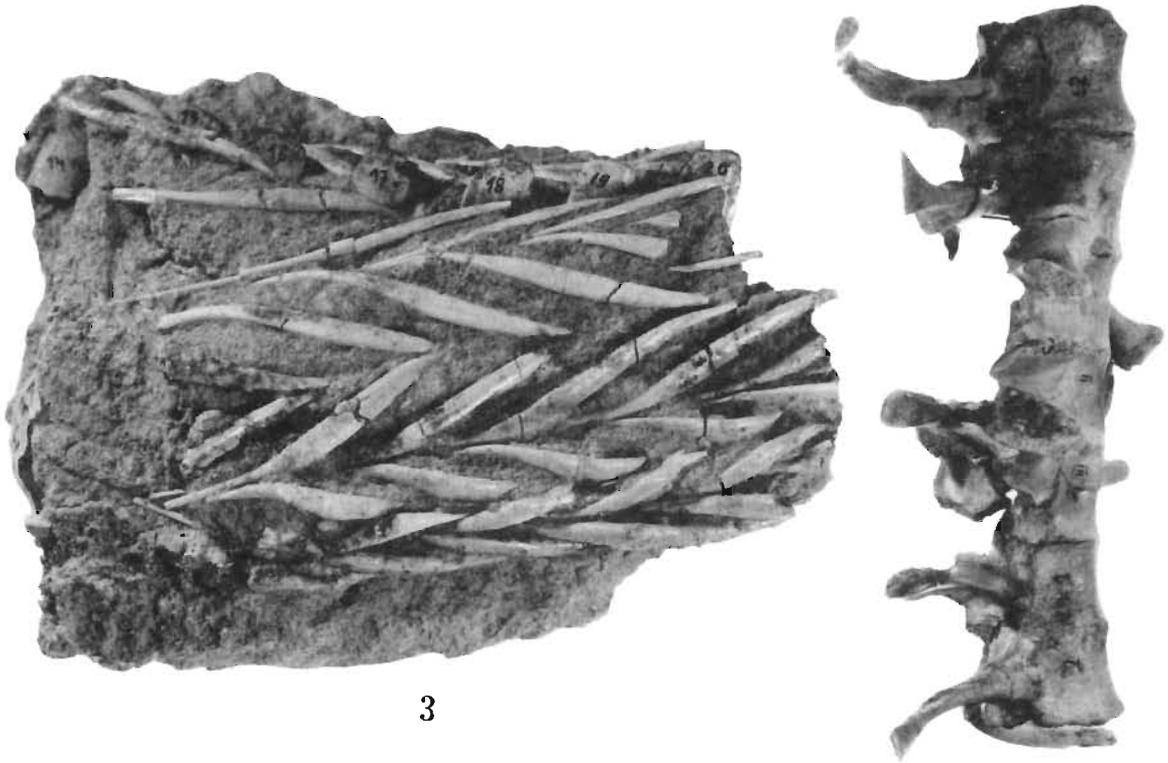
3

1

2

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXIX

Page

Homalocephale calathocercos n.gen., n.sp. 56

(see also Plates XXII, Fig. 1, XXV, XXVI-XXVIII, XXX and XXXI, Fig. 1)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Left ilium with proximal portion of the ischium in natural articulation: *a* — stereo-photograph in lateral view, *b* — stereo-photograph in medial view, *c* — dorsal view. Type specimen (G. I. No. SPS 100/51); about 1/2 natural size.

Fig. 2. Left prepubis in: *a* — lateral view, *b* — medial view. Same specimen; about 1/2 of natural size.
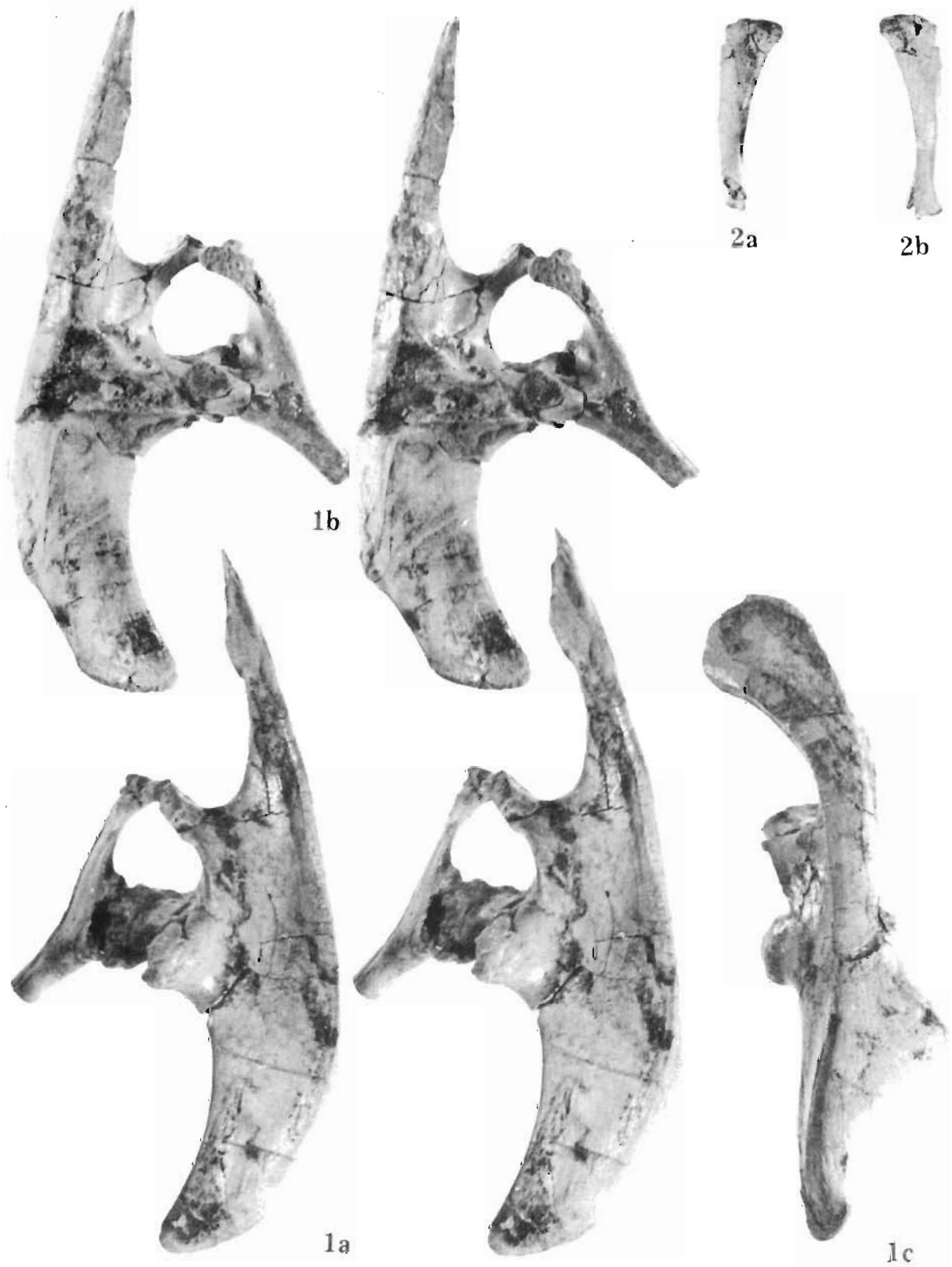
Photo: M. Kleiber

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXX

Page

Homalocephale calathocercos n.gen., n.sp. 56

(see also Plates XXII, Fig. 1, XXIV, XXVI-XXIX and XXXI, Fig. 1)

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Sternal bones in ventral view. Type specimen (G. I. No. SPS 100/51); about 1/2 of natural size.

Fig. 2. Stereo-photograph of the left ilium with fragment of the ischium, in natural articulation, ventral view. Same specimen; about 1/2 of natural size.

Fig. 3. Distal portion of the right tibia and fibula, with astragalus attached, in: *a* — posterior view, *b* — anterior view. Same specimen; about 1/2 of natural size.

Fig. 4. Distal portion of the left tibia, in: *a* — posterior view, *b* — anterior view. Same specimen; 1/2 of natural size.

Fig. 5. Left metatarsal II and damaged metatarsal III in: *a* — anterior view, *b* — posterior view. Same specimen; about 1/2 of natural size.

Fig. 6. Phalanx 1 of the left digit IV (?) in: *a* — dorsal view, *b* — ventral view. Same specimen; about 1/2 of natural size.
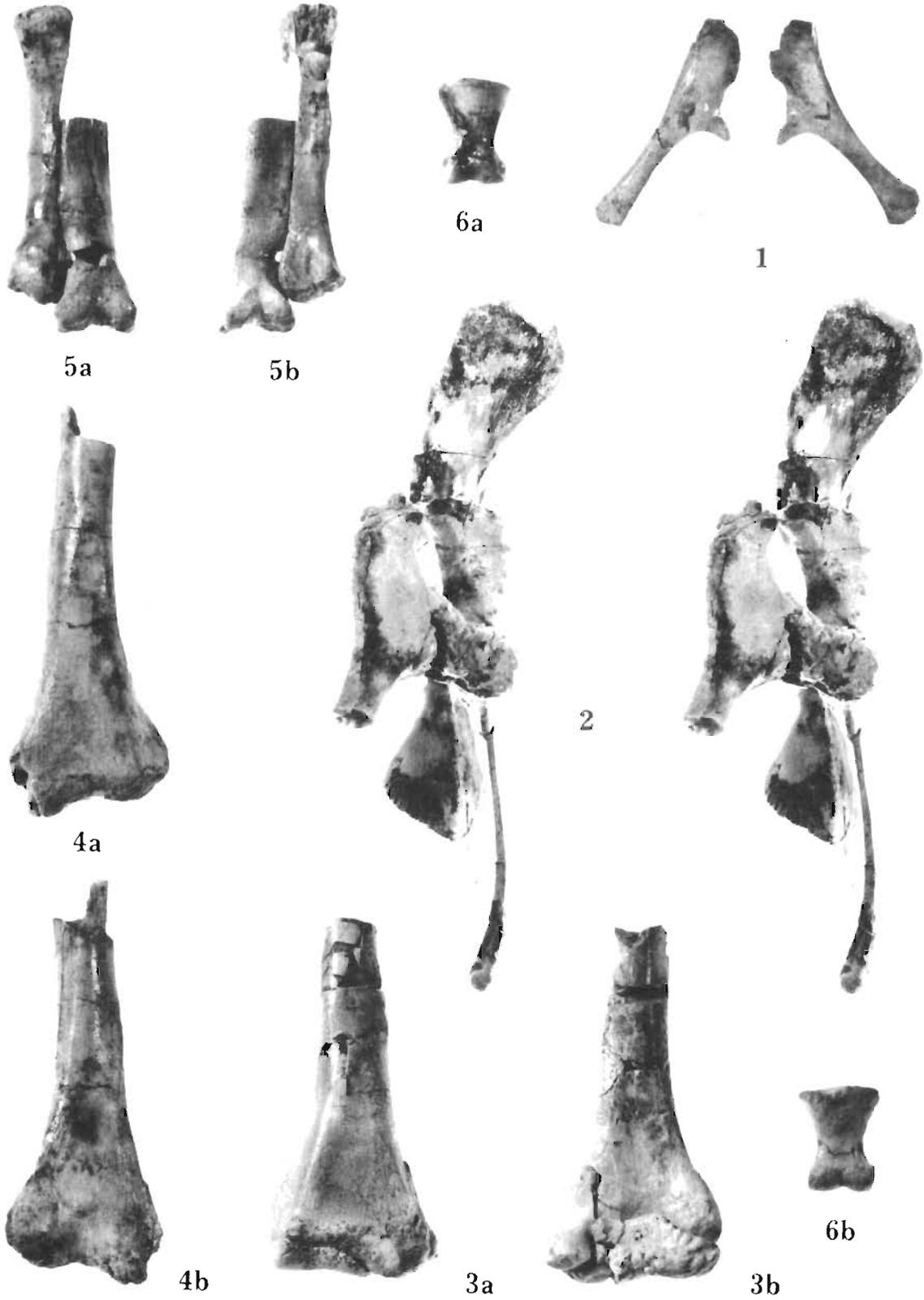
Photo: M. Kleiber, W. Skarżyński

5a   5b   6a   1

4a   2

4b   3a   3b   6b

T. MARYAŃSKA & H. OSMÓLSKA: PACHYCEPHALOSAURIA, NEW SUBORDER

PLATE XXXI

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 1. Stereo-photograph of the left femur in: *a* — anterior view, *b* — posterior view. Type specimen (G. I. No. SPS 100/51); about 1/2 of natural size.

Upper Cretaceous, Nemegt Formation, Nemegt, Gobi Desert, Mongolia

Fig. 2. Right femur in: *a* — anterior view, *b* — posterior view, *c* — medial view. Type specimen (Z. Pal. No. MgD-I/104); about 1/2 of natural size.

Photo: M. Kleiber, W. Skarżyński