A STUDY OF THE TROÖDONT DINOSAURS WITH THE DESCRIPTION OF A NEW GENUS AND FOUR NEW SPECIES

BARNUM BROWN AND ERICH M. SCHLAIKJER

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INTRODUCTION

DISCOVERY AND GEOLOGICAL OCCURRENCE

THE ORIGINAL DISCOVERY of a troödont was made by Dr. F. V. Hayden. The specimen consisted of a single, little-worn tooth from the Judith River Beds of Montana and was described as *Troödon formosus* by Leidy in 1856. No additional material was referred to Leidy's genus and species until 1902 when Lambe noted the occurrence of isolated teeth in the Belly River formation of Canada. In 1905 Hatcher reported similar teeth from the Lance formation of Converse County, Wyoming. Gilmore (1924, p. 39) has quite rightfully questioned the authenticity of this observation. No further assignment of material to Leidy's genus was made until Gilmore (1924) correctly demonstrated that *Stegoceras*, described by Lambe in 1902, and *Troödon* were synonymous. Lambe based his *Stegoceras validus*, from the Belly River formation of Alberta, Canada, on the frontoparietal areas of two skulls, which he at first suggested (1902, p. 69) were from the median line of the skull in front of the nasals, possibly of a ceratopsian. This misidentification was partially corrected by Nopcsa (1903), who interpreted the bones as frontals and fused nasals, and entirely corrected by Hatcher (1907, p. 98) who said, "They appear to me rather as representing the superior portion of the occipital, parietal, and frontal segments of the skull . . . ." This was substantiated by additional material collected by Lambe in the Belly River formation, and in 1918 he described or listed a dozen or more specimens which he referred to *Stegoceras validus*, and one specimen which he designated as *S. brevis*, a new species. These specimens consisted principally of frontoparietal areas, which occasionally had portions of adjacent elements united with them, and isolated skull fragments. All were collected from the same formation and from the same general locality along the Red Deer River, Alberta, Canada. *S. brevis* is undoubtedly the same as *S. validus*, as Gilmore has pointed out (1924, pp. 10–11). Lambe lists a large specimen (No. 192) which is quite different from the others. In 1928 Sternberg collected another very similar specimen from the same locality. These two specimens represent a new species, which is described below.

In 1924 Gilmore referred to the frontoparietal areas of three skulls and described in detail a complete and excellently preserved skull and jaws, and partial skeleton in the collection at the University of Alberta. These specimens were collected from the Belly River formation along the Red Deer River in the same vicinity from which all the *Stegoceras* material had been collected. In this paper Gilmore recorded the first and only troödont postcranial elements known and established the fact that Lambe's *Stegoceras* and *Troödon* were synonymous.

Sternberg (1926) included *Troödon* in a list of fossil reptiles from the Edmonton formation. This was the first report of this genus from the Edmonton and was based on his discovery of the frontoparietal areas of three skulls. These specimens represent a new species, which is described in this paper.

A fragmentary skull cap of a large troödont was described by Gilmore in 1931 as *Troödon wyomingensis*. This specimen was from the Lance formation in Niobrara County, Wyoming. In the same paper Gilmore described for the first time a fragment of a squamosal, presumably representing the same species, which was found in the Lance by Hatcher in 1890. Gilmore also described a fragmentary portion of a skull cap collected by Hatcher in 1888 from the Judith River formation not far from the type locality of *Troödon formosus*. It seems probable that Gilmore's reference of this specimen to Leidy's species is correct. This specimen is significant, therefore, in that it is the only known skull material referable to this species, and it appears as corroborative evidence that *Stegoceras* and *Troödon* are synonymous. In 1936 Gilmore described another large skull cap from the Lance of Wyoming, which he referred to *T. wyomingensis*.

There are four other Lance specimens known. One consists of a fragment of the left squamosal from the type locality of Gilmore's *Troödon wyomingensis* and may represent a new species. This specimen has been described and figured on two previous occasions, once

by Marsh (1896, p. 214, pl. 70) who considered it as dermal ossification of *Triceratops*, and once by Hatcher (1907, p. 65) who was doubtful about its affinity but implied that it belonged to either a trachodont or a ceratopsian. The other three Lance specimens are as yet undescribed. Two of these are in the Colorado Museum of Natural History and were collected in Corson County, South Dakota. They represent distinct species. One is undoubtedly Gilmore's *Troödon wyomingensis*, and the other represents a new species described below. The third specimen, now in the collection of the American Museum, is a beautifully preserved, nearly complete skull from north of Ekalaka, Carter County, Montana. This specimen represents a new genus and species, and its description and study constitute a considerable portion of this paper. All the Lance species are referable to this new genus.

Forty-six troödont specimens are now known. In this assemblage two genera and seven species are represented. Their geologic and geographic distribution is shown in the following tabulation:

Number of Specimens	Formation	Locality	Genus and Species
2	Judith River	Montana	*Troödon formosus*
34	Belly River	Alberta	All assignable to *T. validus* except 2 which represent a new species
3	Edmonton	Alberta	Represent a new species of *Troödon*
7	Lance	Montana, South Dakota, and Wyoming	All belong to a new genus. They represent 2 new species and Gilmore's "*Troödon*" *wyomingensis*

PREVIOUS WORK

There are between 40 and 50 references on the troödonts in palaeontological literature. A great number of these are merely references in faunal lists which are occasionally accompanied by very brief comments. Most of the others are but very brief statements and descriptions, and less than a half dozen are of any real significance.

After Leidy's original description of *Troödon formosus* in 1856, based on a single tooth, and his subsequent notes in 1860 on the same species, there was no important contribution to our knowledge of *Troödon* until the appearance of Gilmore's excellent and authoritative paper on *Troödon validus* in 1924. During the intervening years there were some who followed Leidy's original suggestion that *Troödon* was a lizard. Nopcsa (1901), however, regarded it as a carnivorous dinosaur, and after that most writers classified it with the dinosaurs, but on the question of just what kind there seemed to be no unanimity of opinion. Lambe's two papers (1902 and 1918) on "*Stegoceras*" were important contributions, although he did not regard this form as a troödont. Since 1924 Gilmore has published two other shorter papers devoted exclusively to troödonts, one in 1931 on a new species from the Lance formation, and one in 1936 which was a description of another specimen from the Lance. Other short papers or brief comments which deal especially with the affinity of the troödonts are by Romer (1927), Gilmore (1930), Nopcsa (1931), Russell (1932), and Sternberg (1933).

THE PRESENT STUDY

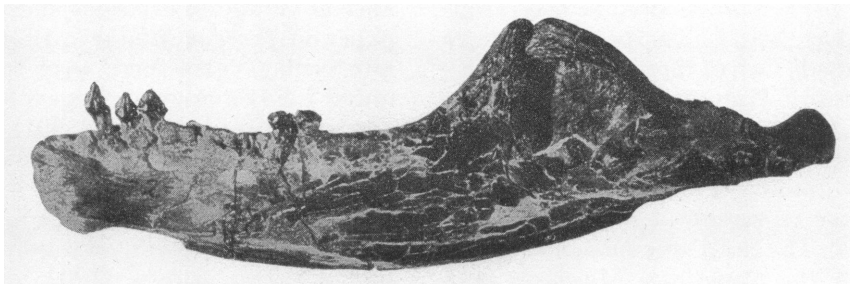
When the very splendid and complete troödont skull from the Lance formation of Montana (A.M.N.H. No. 1696) came to the American Museum, we planned to confine the present paper to a description and comparative study of this specimen. It soon became evident, however, that a complete revision of the troödonts would be necessary, especially because so many additional specimens

PLATE 33

Lower jaw and premaxillary teeth of *Troödon validus* (Lambe), from Gilmore, 1924, plate 6.

1. Lower jaw, internal lateral view, ×¾.

2. Three anterior teeth, external lateral view, more than ×4; insert, tooth of *Troödon formosus* Leidy, lateral view, ×3.



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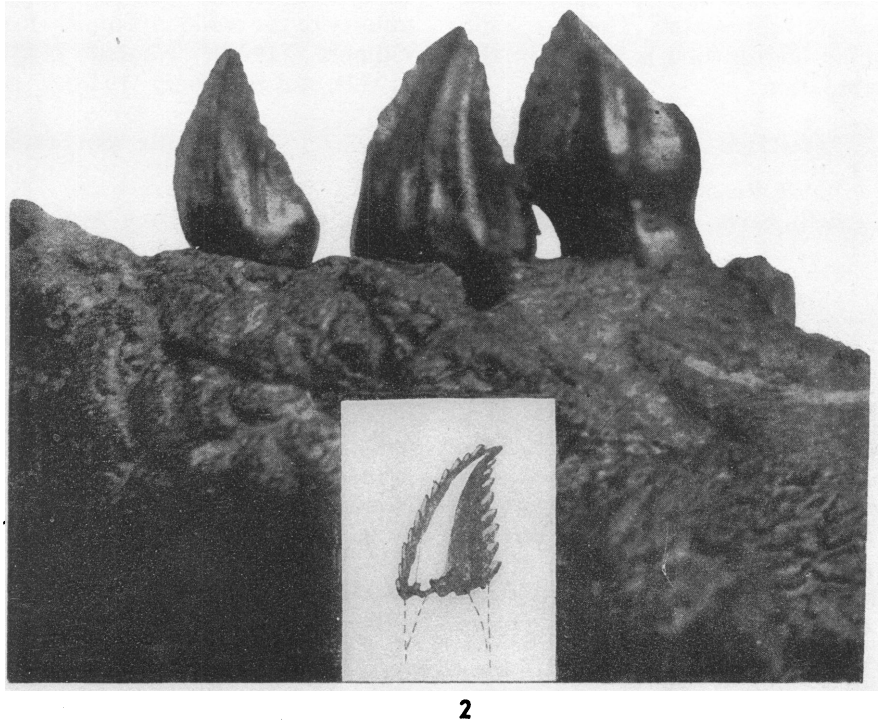

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had been discovered since the publication of Lambe's 1918 paper and Gilmore's authoritative 1924 description of the material in the University of Alberta. We now have before us all the known troödont specimens, and in this paper we present a comparative study of them. This study involves a redefinition of the family Troödontidae, the description of one new genus and four new species, and a discussion of the affinities of the troödonts. The problem of the affinities of the troödonts is one on which there has been considerable disagreement. The problem was mainly whether this group was more closely related to the nodosaurs or to the ornithopodous dinosaurs. We favor assignment to the latter group. While we have now shown that the troödonts are not nodosaurs, we still feel that this paper falls in line with our more extensive studies on the Nodosauria, for which we received a grant-in-aid from the Geological Society of America. A small part of this grant has been used in partial support of the preparation of this paper.

MATERIALS STUDIED

Of the 46 troödont specimens known to science, only two are complete skulls. One is the *Troödon validus* skull described by Gilmore (1924) from the Belly River formation, and the other is the new genus and species herein described from the Lance formation. Associated with the former are some limb bones, some of the pectoral and pelvic elements, and some vertebrae and ribs. This is the only troödont postcranial material known. The rest of the specimens consists of partial skulls, principally of the frontoparietal area, and a few skull fragments. All this material has been seen and studied by us except the frontoparietal areas of three skulls in the University of Alberta. The 43 specimens studied and a brief description and the locality of each are given in the following list. They are considered according to the institutions wherein they are deposited.

THE AMERICAN MUSEUM OF NATURAL HISTORY:

A.M.N.H. No. 1696, the nearly complete skull of a new genus and species described below. Hell Creek Beds of the Lance formation, sec. 17, T. 1 S., R. 55 E., William Winkley Ranch, Powder Hill, north of Ekalaka, Carter County, Montana. Found by William Winkley and collected by W. H. Peck and Thomas G. Nielsen, 1940.

A.M.N.H. No. 5388, *Troödon validus*, frontoparietal area, fairly large, excellent condition, sutures distinct on roof of endocranial cavity. Adult. Belly River formation, about 6 miles above Sand Creek, Red Deer River, Alberta, Canada. Collected by Barnum Brown, 1915.

UNITED STATES NATIONAL MUSEUM:

U.S.N.M. No. 7806, two incomplete bones tentatively referred to troödonts by Gilmore (1931). Lance formation, Niobrara County, Wyoming. Collected by J. B. Hatcher, 1890.

U.S.N.M. No. 8295, *"Troödon" wyomingensis*, referred to the new genus herein described, fragment of a squamosal. Lance formation, Seven Mile Creek, Niobrara County, Wyoming. Collected by C. H. Sternberg, 1909.

U.S.N.M. No. 11954, *Troödon formosus*?, frontal bones showing part of the endocranial cavity. This is the only other troödont known from the type locality of the genus and species. Judith River formation, Cow Island, Montana. Collected by J. B. Hatcher, 1888.

U.S.N.M. No. 12031, *"Troödon" wyomingensis*, referred to the new genus herein described, type of this species. Upper posterior half of the skull including part of the occipital region. Lance formation, 9 miles southwest of Warren P.O., Buck Creek, Niobrara County, Wyoming. Collected by G. F. Sternberg, 1930.

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA:

A.N.S.P. No. 9259, *Troödon formosus*, complete

PLATE 34

Three "male" frontoparietal areas representing young, early mature, and fully adult growth stages of *Troödon validus* (Lambe).

1–3. Dorsal, lateral, and ventral views of young specimen, G.S.C. No. 1108.

4–6. Dorsal, lateral, and ventral views of early mature specimen, G.S.C. No. 515.

7–9. Dorsal, lateral, and ventral views of adult specimen, A.M.N.H. No. 5388.

All figures approximately ×½.

and well-preserved tooth. This is the genoholotype. Judith River formation, Montana. Collected by F. V. Hayden, 1856.

CARNEGIE MUSEUM:

C.M. No. 3180, *"Troödon" wyomingensis*, referred to the new genus herein described, greater portion of the dome-like part of the skull. Younger than the type of this species. Field data incomplete. Lance formation, Wyoming. Collected by W. H. Utterbeck.

COLORADO MUSEUM OF NATURAL HISTORY:

Colo. Mus. No. 469, the frontoparietal area with parts of the squamosals and nasals preserved. Represents a new species, described below. Lance formation, level unknown, probably Hell Creek Beds, near southwest corner of sec. 25, T. 20 N., R. 21 E., Corson County, South Dakota. Collected by Philip Reinheimer, 1922.

Colo. Mus. No. 470, *"Troödon" wyomingensis*, referred to the new genus herein described, portion of the frontoparietal area. Lance formation, level unknown, probably Hell Creek Beds, sec. 25, T. 20 N., R. 21 E., Corson County, South Dakota. Collected by Philip Reinheimer, 1922.

UNIVERSITY OF ALBERTA:

Univ. A. No. 2, *Troödon validus*, splendid skull and jaws, with associated skeletal remains. Adult. Belly River formation, Red Deer River, near Steveville, Alberta. Collected by G. F. Sternberg, 1920–1921.

ROYAL ONTARIO MUSEUM:

R.O.M. No. 808, *Troödon validus*, frontoparietal area with portions of the postorbitals and squamosals. Young. Belly River formation.

GEOLOGICAL SURVEY OF CANADA:

G.S.C. No. 121, *Troödon validus*, frontoparietal area. Young. Belly River formation, Red Deer River, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. No. 138, *Troödon validus*, frontoparietal area with the squamosals and postorbitals. Belly River formation, below the mouth of Berry Creek, Red Deer River, Alberta, Canada. Collected by L. M. Lambe.

G.S.C. No. 158, *Troödon validus*, left squamosal. Belly River formation, below the mouth of Berry Creek, Red Deer River, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. No. 192, *Troödon* sp., frontoparietal area. This specimen is of a large adult. It is low and broad and has other characters which show that it represents a new species to which G.S.C. No. 8817 is also referable. Belly River formation, below the mouth of Berry Creek, Red Deer River, Alberta, Canada. Collected by C. G. Sternberg, 1913.

G.S.C. No. 193, *Troödon validus*, frontoparietal area without the posterior tips of the parietals. Young. Belly River formation, below the mouth of Berry Creek, Red Deer River, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. No. 194, *Troödon validus*, frontoparietal area without the posterior tips of the parietals. Young. Belly River formation, below the mouth of Berry Creek, Red Deer River, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. No. 515, *Troödon validus*, frontoparietal area. This is Lambe's type of *Stegoceras validus*. Young. Belly River formation, Red Deer River, Alberta, Canada.

G.S.C. No. 1107, *Troödon validus*, parietals. Water-worn. Young adult. Belly River formation, south of Steveville, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. No. 1108, *Troödon validus*, frontoparietal area. Young. Belly River formation, from Sand Creek, Alberta, Canada. Collected by C. H. Sternberg, 1915.

G.S.C. No. 1423, *Troödon validus*, frontoparietal area. Young. This is Lambe's type of *Stegoceras brevis*. It presents no characters which do not come well within the range of *T. validus* and undoubtedly belongs to that species. Belly River formation, east side of Red Deer River below Berry Creek, Alberta, Canada. Collected by L. M. Lambe, 1901.

G.S.C. No. 1914, *Troödon validus*, right prefrontal. Adult. Belly River formation, from Sand Creek, Alberta, Canada. Collected by C. H. Sternberg, 1915.

G.S.C. No. 2369, *Troödon validus*, most of the frontoparietal area. Young adult. Belly River formation, south of Steveville, Red Deer River, Alberta, Canada. Collected by C. H. Sternberg, 1913.

G.S.C. Nos. 2370–2373, *Troödon validus*, skull fragments of young to fully adult individuals consisting of the posterior lateral border of a left postorbital, a left squamosal, a portion of a parietal(?), and a portion of a left postorbital. Belly River formation, south of Steveville, Red Deer River, Alberta, Canada. Collected in 1913.

G.S.C. Nos. 2374–2377, *Troödon validus*, skull fragments of young to fully adult individuals consisting of a basicranial fragment, the posterior border of a right squamosal, a portion of a left prefrontal(?), and the posterior border of parietals showing the suture with the left squamosal. Belly River formation, Red Deer River, Alberta, Canada. Collected in 1917.

G.S.C. No. 2378, *Troödon validus*, posterior lateral border of a left postorbital(?). Young. Belly River formation, from Sand Creek, Alberta, Canada. Collected by C. M. Sternberg, 1917.

G.S.C. No. 2379, *Troödon validus*, frontoparietal area. Young adult. Belly River formation, from Sand Creek, Alberta, Canada. Collected by C. M. Sternberg, 1917.

G.S.C. No. 8816, *Troödon validus*, frontoparietal area with squamosals and postorbitals. Young. Belly River formation, 2½ miles east of Happy Jack Ferry, upper 50 feet of beds, Red Deer River, Alberta, Canada. Collected by C. M. Sternberg, 1921.

G.S.C. No. 8817, *Troödon* sp., frontoparietal area of a large adult. Its large size and low broad form together with other features show that it represents a new species, described below, to which G.S.C. No. 192 is also referable. Belly River formation, southeast of Steveville, Alberta, Canada. Collected by C. M. Sternberg, 1928.

G.S.C. No. 8818, *Troödon validus*, frontoparietal area. Fully adult. Belly River formation, south Saskatchewan River, 3 miles below Bow Island ferry, 200–300 feet below the top of the formation. Collected by E. J. Whittaker, 1923.

G.S.C. No. 8819, *Troödon validus*, frontoparietal area. Young. Belly River formation, below the mouth of Berry Creek, Red Deer, River, Alberta, Canada. Collected by C. M. Sternberg.

G.S.C. Nos. 8830–8832, *Troödon* sp., frontoparietal areas of three specimens. Fully adult. These are the only troödont specimens known from the Edmonton formation. They are unquestionably referable to the genus *Troödon* but represent, as is shown later in this paper, a distinct species. Edmonton formation, opposite the mouth of Big Valley Creek below Scollard ferry, Red Deer River, Alberta, Canada. Collected by C. M. Sternberg, 1926.

COLLECTIONS OF MR. ROY L. FOWLER OF ALDERSYDE, ALBERTA, CANADA:

No. 684, *Troödon validus*, frontoparietal area. Young. The locality and geologic level of this specimen are unknown. It is almost identical with the Belly River specimens of *Troödon validus*, and its only feature of interest is the presence of carnivore tooth marks on the posterior portion of its dorsal surface.

YALE PEABODY MUSEUM:

No. 335, troödont, a portion of the left squamosal. This specimen is too incomplete for specific determination. It undoubtedly belongs to the new genus herein described and probably represents a new species. Lance formation, Lance Creek, Niobrara County, Wyoming. Collected by J. B. Hatcher.

ACKNOWLEDGMENTS

The very splendid and unusually complete skull, herein described as a new genus and species, was obtained by the American Museum of Natural History through exchange with the Carter County Geological Society, Elkalaka, Montana. The arrangements for this exchange were brought about by the generous cooperation of Mr. W. H. Peck of that society, with the late Dr. Walter Granger and Mr. Albert Thomson when they were in the field for the Museum in 1939.

The excellent preparation of this specimen and the obtaining from it of an unusually fine endocranial cast were skillfully accomplished by Mr. Otto Falkenbach.

The following institutions have been generously cooperative in lending to us their troödont collections for study and description: Carnegie Museum; Colorado Museum of Natural History; National Museum of Canada; Peabody Museum, Yale University; Royal Ontario Museum of Palaeontology; University of Alberta; and the United States National Museum.

Funds necessary for bibliographic work, for sectioning the cranium of *Troödon validus*, and for the execution of the very fine drawings of teeth by Miss Marie C. O'Brien were used from the grant to us by the Geological Society of America for our monographic study, now under way, of the low-plated dinosaurs.

SYSTEMATIC DESCRIPTION AND COMPARATIVE STUDY

ORDER ORNITHISCHIA
SUBORDER ORNITHOPODA
FAMILY TROÖDONTIDAE GILMORE, 1924

When Gilmore established this family, it included one genus and three species. One of the three species, as shown by Gilmore, was of doubtful validity. All the material known was assignable to these species, and it all came from the Belly River or Judith River formations. Considerable material is now known from the Lance formation and some from the Edmonton. The family now includes two genera and seven species. The following family characters were given by Gilmore:

"Abdominal cuirass of segmented ribs; premaxillaries with teeth; teeth in a single row; dome-like thickening of parietal and frontal bones; dorsal vertebrae having zygapophyses with tongue and groove articulation; pelvic bones resembling the Ceratopsia in the horizontal widening of the preacetabular portion of the ilium and ischium without obturator process, and with an elongated pubic process" (Gilmore, 1924, p. 8).

It becomes necessary to modify and extend this definition as follows:

Small to rather large bipedal dinosaurs. Skull with moderate to extreme thickening of the frontoparietal area, and with irregularly shaped, node-like ornamentations on the face and around the margins. Supratemporal openings nearly or completely closed. Premaxillaries with or without teeth. Maxillary teeth in a single row. Crowns quite pointed, vertically ribbed, concave externally and convex internally. Abdominal cuirass of segmented ribs. Zygapophyses of dorsal vertebrae with tongue and groove articulation. Ilium and ischium very similar to those elements in primitive Ceratopsia.

In 1918 (p. 35) Lambe suggested the family name Psalisauridae and included his "*Stegoceras*" *validus* and "*S.*" *brevis* in it. As Gilmore has shown (1924, p. 9), this family name was not founded on the name of a generic type and, therefore, cannot be accepted.

GENUS TROÖDON LEIDY, 1856

Troödon LEIDY, 1856, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 72; LEIDY, 1860, Trans. Amer. Phil. Soc., new ser., vol. 11, p. 147, pl. 9, figs. 53–55; LAMBE, 1902, Contrib. Canadian Palaeont., Geol. Surv. Canada, vol. 3, pt. 2, art. 2, pp. 68–69, figs. 1–5, pl. 21; LAMBE, 1918, Trans. Roy. Soc. Canada, ser. 3, vol. 12, sect. 4, pp. 23–36, pls. 1, 2; GILMORE, 1924, Bull. Univ. Alberta, Dept. Geol., no. 1, pp. 1–43, figs. 1–3, pls. 1–15.

GENERIC TYPE: *Troödon formosus* Leidy.

AUTHOR'S DIAGNOSIS: "The specimen consists of a compressed curved conical crown with trenchant edges. The outer side is more convex than the inner, which is worn off towards the apex from friction of the opposing tooth. The trenchant edges are coarsely denticulate; the denticulations themselves being compressed conical, with trenchant edges, and are bent in such a manner that their apices are directed towards the summit of the crown" (Leidy, 1856, p. 72).

GILMORE'S DIAGNOSIS: "Premaxillae having teeth; skull with large dome-like mass developed above by the thickening of the parietals and frontals; external surfaces of skull highly ornamented; occiput and quadrates strongly inclined forward ventrally; parietal and squamosal bones forming a heavy overhanging posterior crest; supratemporal fossa nearly closed externally; infratemporal fossa much reduced; orbits large; premaxillary nearly excluded from lateral view of face; post-coronoid part of mandible much short-

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PLATE 35

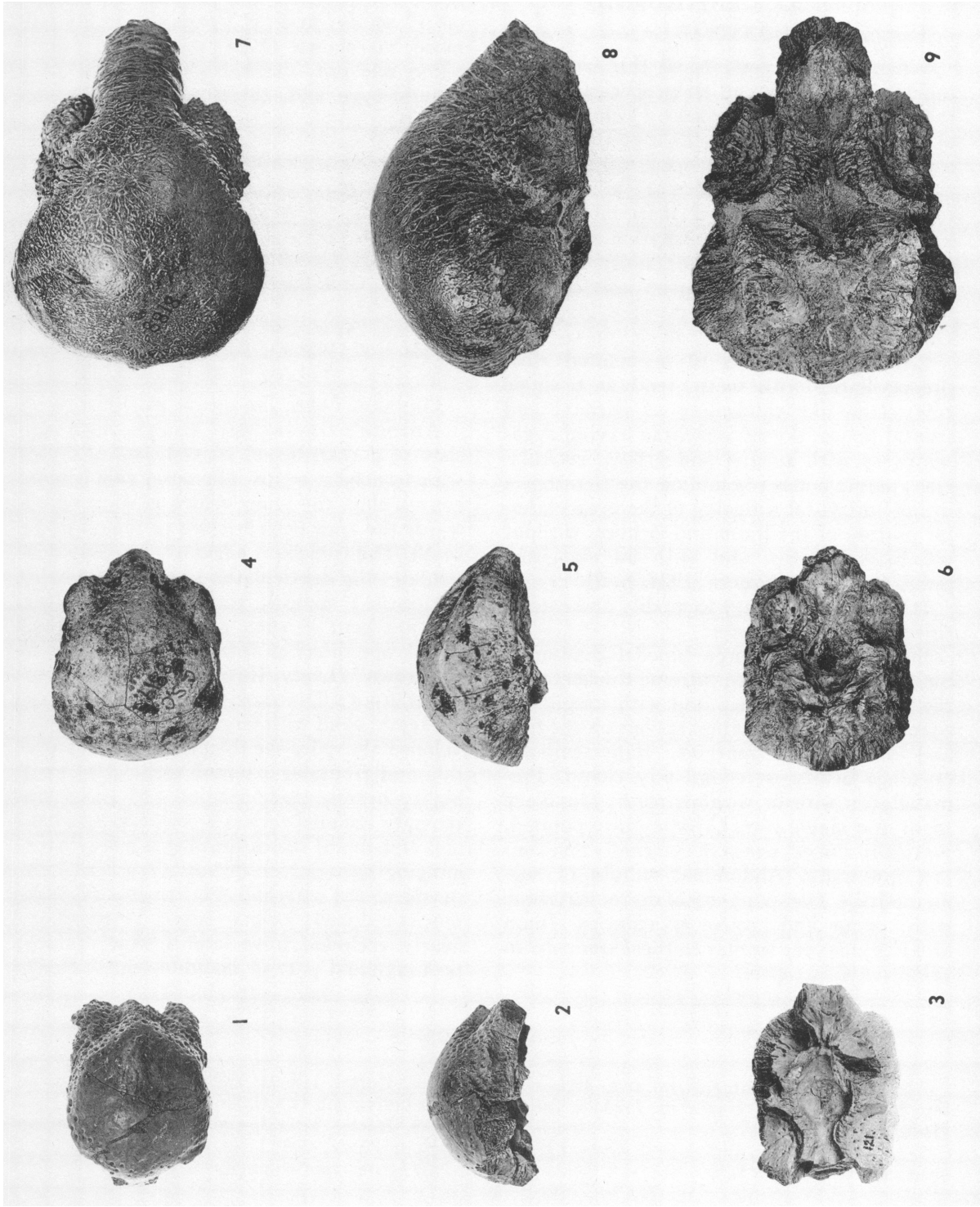
Three "female" frontoparietal areas representing different growth stages in *Troödon validus* (Lambe).

1–3, Dorsal, lateral, and ventral views of young specimen, G.S.C. No. 121.

4–6. Dorsal, lateral, and ventral views of an older individual, G.S.C. No. 8819.

7–9. Dorsal, lateral, and ventral views of an adult specimen, G.S.C. No. 8818.

All figures approximately ×½.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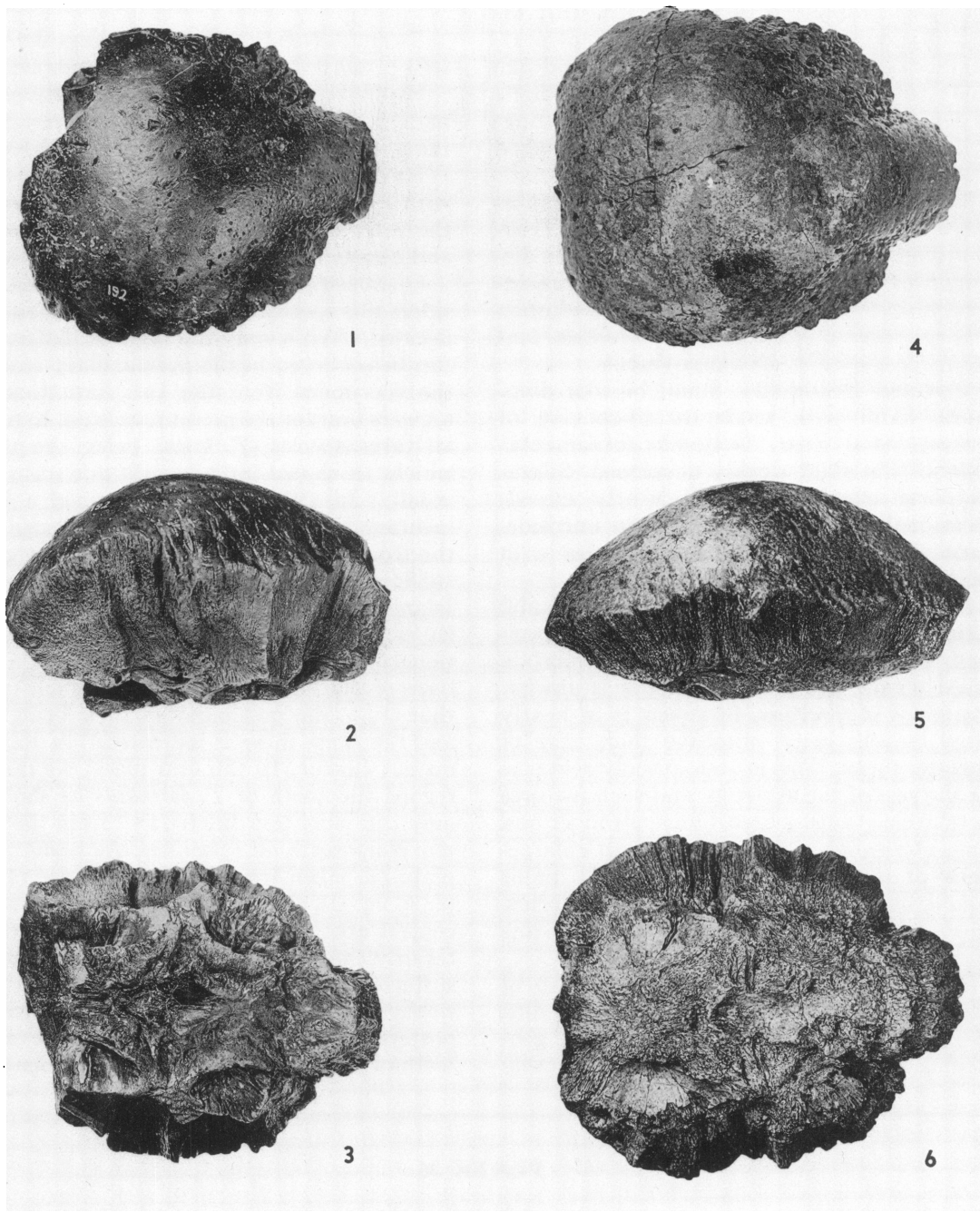
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ened; fore limb much reduced; scapula long, narrow, with elongate obliquely developed anterior plate; ilium with expanded horizontal preacetabular portion; wide inwardly directed process from superior surface of postacetabular position; ischia curved, rod-like shaft without obturator process; four digits in pes, first reduced, fifth apparently wanting; abdominal cuirass of segmented ribs; ossified tendons" (Gilmore, 1924, p. 11).

From this diagnosis it is obvious that as there was only one genus in the family Troödontidae, Gilmore made little attempt to distinguish between family and generic characters. Also, this characterization is based upon the conclusion that Leidy's *Troödon* and Lambe's *Stegoceras* are synonymous.

REVISED DIAGNOSIS: Small bipedal dinosaurs. Skull with moderate thickening of frontoparietal area. Node-like ornamentations of the skull weakly developed. Supratemporal openings usually nearly closed; occasionally completely closed on one side. Face short and deep. Premaxillaries with teeth.

DISCUSSION: Because troödont postcranial skeletal parts are known only from one specimen of *Troödon*, generic characterization based on the postcranial skeleton is unwise. The skull of *Troödon*, however, is in nearly every respect more primitive than that of the later forms. This is undoubtedly also true for the rest of the skeleton, and such features as relatively longer hind limbs, stronger and more elongated metatarsus, and an enlargement of the anterior process of the pubis should be characteristic of the later forms. Verification of this must await future discovery of more complete specimens.

This genus contains four species, two of which are new. Its geological range is Judith River-Belly River to Edmonton, and geographically it occurs in Alberta and Montana.

Troödon formosus Leidy, 1856

Troödon formosus, LEIDY, 1856, Proc. Acad. Nat. Sci. Philadelphia, vol. 8, p. 72.

TYPE: A.N.S.P. No. 9259, a complete and well-preserved tooth, probably premaxillary.

HORIZON AND LOCALITY: Judith River formation. Badlands of the Judith River, Montana.

REVISED DIAGNOSIS: Premaxillary tooth with smoothly curved convex central area of the outer side. Marginal denticulations strong and clearly defined.

DISCUSSION: Gilmore (1924, p. 10) considers this species very close to *T. validus* but decided, "While only the slightest differences can be observed in the premaxillary teeth in the specimens from the two formations, it appears best for the present, at least, to retain all three species [*T. brevis* being the third, which, as shown later, we do not regard as valid]." In 1931 Gilmore described a fragmentary skull portion, consisting mostly of the frontals, which Hatcher had collected in 1888 from the Judith River formation on Cow Island, Montana, not far from the type locality of *T. formosus*. This specimen is unquestionably very similar to *T. validus*. On the basis of this new specimen Gilmore felt (p. 6) that " . . . the possibility of their being one and the same thing is indicated." In this we do not concur. In the first place, we do not regard the tooth of *T. formosus* as showing only the "slightest differences" from the premaxillary teeth of *T. validus*. As is shown in plate 33, taken from Gilmore's paper (1924, pl. 6, fig. 2), the *T. formosus* tooth has the central area of the outer surface anteroposteriorly convex, while in *T. validus* the outer surfaces of the premaxillary teeth are vertically ribbed. It also lacks the conspicuous posterior "heel" which is characteristic of the teeth of *T. validus*, and the marginal denticu-

PLATE 36

Type and paratype specimens of *Troödon sternbergi*, new species.

1–3. Dorsal, lateral, and ventral views of frontoparietal region of the paratype specimen, G.S.C. No. 192.

4–6. Dorsal, lateral, and ventral views of frontoparietal region of the type specimen, G.S.C. No. 8817.

All figures approximately ×½.

lations are much better developed. It is also a fact that the cheek teeth of both *T. validus* and the later Cretaceous forms, which are unquestionably generically distinct, conform to a given pattern and certainly present no greater dissimilarity than do the premaxillary teeth of *T. validus* and *T. formosus*. In the second place it is true that the fragmentary frontal area from the same formation and from the same general locality as *T. formosus* is indeed very similar to, and as far as known seems indistinguishable from, *T. validus*. This evidence, however, may be interpreted in several ways. (1) As Gilmore has suggested, this fragmentary skull part may be that of *T. formosus*, in which case *T. validus* is synonymous with *T. formosus*, providing, of course, that the now unknown skull parts showed equal similarity. (2) The skull fragment may be that of "*Stegoceras*" *validus* occurring in the same beds with *T. formosus*, the two being distinct genera. (3) The specimen may be *T. formosus* and when completely known may prove to have characters in the other parts of the skull that show it to be as distinct from *T. validus* as does the premaxilllary tooth. What the occurrence of this fragmentary specimen in the Judith River of Montana really presents is corroborative evidence that there is a close correlation between the Judith River and the Belly River formation. We believe that the evidence strongly suggests that *Troödon* and *Stegoceras* are synonymous, but on the basis of the premaxillary teeth, which after all are the only real evidence available, we believe that *T. formosus* and *T. validus* are at least specifically distinct.

Troödon validus (Lambe), 1902

Stegoceras validus, LAMBE, 1902, Contrib. Canadian Palaeont., Geol. Surv. Canada, vol. 3, pt. 2, art. 2, pp. 68–69, figs. 1–2, pl. 21; LAMBE, 1918, Trans. Roy. Soc. Canada, ser. 3, vol. 12, sect. 4, pp. 23–36, pls. 1–2.

Stegoceras brevis, LAMBE, 1918, *ibid.*, ser. 3, vol. 12, sect. 4, p. 35.

Troödon validus, GILMORE, 1924, Bull. Univ. Alberta, Dept. Geol., no. 1, pp. 1–43, figs. 1–3, pls. 1–15.

TYPE: G.S.C. No. 515, well-preserved frontoparietal area.

HORIZON AND LOCALITY: Belly River formation. East side of Red Deer River below the mouth of Berry Creek, Alberta, Canada.

AUTHOR'S DIAGNOSIS: Lambe made no distinction between generic and specific characters.

DIAGNOSIS: A rather small species. Frontoparietal area relatively narrow and quadrangular in outline when viewed from above; low and gently arched in the immature stage, but strongly arched and deep in the adult. Prominent parieto-squamosal shelf behind the arched portion of the parietal. Frontals narrow where in contact with the nasals.

DISCUSSION: The type of this species consists of a well-preserved frontoparietal area. In 1918 Lambe described a somewhat more complete specimen which he correctly referred to this species. In the same paper he described an additional species which he named *Stegoceras brevis*. As stated above, Gilmore (1924) placed these species in the genus *Troödon* and described an unusually complete skull and jaws, accompanied by some skeletal parts, which are specimen No. 2 in the University of Alberta collections. This is the most complete specimen and the only complete skull known of *Troödon*. Gilmore's description is so extensive that only a few additional comments are necessary.

There are now 32 specimens known which are referable to this species. All are from the Belly River formation and the same general locality along the Red Deer River in Alberta, Canada. Of these 32 specimens, about 20 are complete enough for definite specific determination. Even though this number is fairly small, it is possible to determine what are specific characters, what are growth changes, and what, possibly, are sexual differences. All the specimens show clearly the specific characters listed above. In addition to these, all are narrow between the orbits, as measured across the base of the frontals, and all have the base of the parietal behind the endocranial cavity curved downward. Both of these may be specific characters. There is a considerable amount of variation in the doming of the frontoparietal area. Since, as is shown in table 1, the increase in height of dome accompanies increase in size, this seems, unquestionably, to be an age character. In all the small skull roofs, the sutures are quite open on the roof of the endocranial cavity

TABLE 1

MEASUREMENTS AND INDICES OF THE FRONTOPARIETAL AREAS OF NINE SPECIMENS OF *Troödon validus*
(Measurements in millimeters)

Specimen numbers	G.S.C. 8816	G.S.C. 138	G.S.C. 1108	G.S.C. 515	A.M.N.H. 5388	G.S.C. 1423	G.S.C. 121	G.S.C. 8819	G.S.C. 8818
Greatest length (=L)	89	93	95	105	122	65	67	74	122
Greatest width (=W)	56	58	55	61	83	44	50	59	90
Height above endocranial cavity (=H)	30	31	36	36	64	24	28	33	71
Width of frontals where in contact with nasal =N−FW)	26	23	20	23	33	17	20	20	33
Median thickness of frontals where in contact with nasals (=T)	12	17	18	20	33	10	13	11	29
$\frac{W \times 100}{L}$	62.921	62.365	58.947	58.095	68.032	67.692	74.627	79.729	73.770
$\frac{H \times 100}{L}$	33.708	33.333	37.894	34.285	52.459	36.923	41.791	44.594	58.196
$\frac{H \times 100}{W}$	53.571	53.448	65.454	59.016	77.108	54.545	56.000	55.932	78.888
$\frac{T \times 100}{N\text{-}FW}$	46.154	73.913	90.000	85.956	100.000	58.823	65.000	55.000	87.878

and frequently on the outer surface of the dome, and the dome is low and gently curved. In the large specimens, the sutures in the frontoparietal area are almost, or entirely, obliterated, and the dome is very high.

With this upgrowth of the frontoparietal area with age, there is a reduction in the parietal shelf behind the dome, and the posterior projection of the parietals enters into and forms more of the posterior margin of the skull. This is shown in a number of specimens. In G.S.C. No. 8816 the posterior tip of the parietals has not reached the posterior margin of the skull, and even though the squamosals are broken away in this vicinity, the parietals show very clearly the sutural surfaces for contact with them. In G.S.C. No. 138 the parietals have entered into the formation of, and in the University of Alberta specimen No. 2 they form a considerable portion of, the posterior margin. (See pl. 44.)

Another change that takes place from the immature to the adult stage is that the portion of the frontal which is in contact with the nasal becomes proportionately deeper and more constricted. In some specimens, as G.S.C. No. 8818, a deep groove on either side of this central area sets it off even more prominently from the rest of the low anterior region of the frontals.

Gilmore (1924, p. 10) attributes variation in roughening of the external surface of the frontoparietal to age. A considerably larger number of specimens, not available to Gilmore at the time, now show this not to be the case. Some of the smaller specimens are smoother, some are equally as roughened, and some are even more rugose than the larger

specimens. Some of this is undoubtedly individual variation, but most of it, we believe, may be attributed to sexual difference. This conclusion is based on the following facts. While all the specimens exhibit some roughness on the domed portion, there are both immature and mature specimens that are definitely smoother than others. There is only one other character of any importance which is found with this smoothness. In all such skulls, the dorsal surface of the parietal immediately behind the domed area curves downward quite abruptly, while in the specimens with the rugose dorsal surface of the dome this area of the parietals extends out into a prominent shelf. These two types of frontoparietal areas are represented in both the immature and mature stages. There are 17 specimens in which the frontoparietal area is complete enough to determine these features. Of these, seven show the smoothness of the dome and the lack of a prominent shelf behind it. This is suggestive of the 1:1 sex ratio. Arbitrarily we select these as representing females, the others males.

The facts given above have an important bearing on the question of the validity of *Troödon brevis*. When Lambe described this species as *Stegoceras brevis* (1918, pp. 35–36), he cited the following six characters to show wherein this species was distinct from his *Stegoceras validus* (=*Troödon validus*):

1. "The parieto-frontal mass is shorter in comparison with its breadth.

2. "The upper parietal surface between the squamosals instead of extending backward almost horizontally or at a moderately inclined downward slope to the posterior border curves convexly downward so as to become almost vertical posteriorly.

3. "The parieto-squamosal sutural facets are relatively deeper and are more nearly parallel to each other, providing a relatively larger entry of the parietal into the posterior border.

4. "The supratemporal fossae are apparently closed or nearly so.

5. "A greater compactness in the parietofrontal mass throughout as a result of its abbreviation.

6. "In *S. brevis* the upper outline, in lateral aspect, is almost semicircular, the posterior curve in particular continuing evenly downward from the central elevation" (Lambe, 1918, pp. 35–36).

From what has been stated above, it is obvious that the type specimen of this species is a "female" specimen of *Troödon validus*. The only two features wherein it differs from the latter are the lack of a prominent parietal shelf and the smoothness of the dome. Lambe did not mention the latter. Character 1, cited by Lambe, is true, but that is because of the reduced shelf, his second character. Number 3, as shown above, is an age character. It is true that the skulls shown in plate 34 are "male," with the extended parieto-squamosal shelf. Since the "female" skulls (pl. 35) have the reduced shelf, naturally the parietals will enter the central portion of the posterior margin of the skull earlier in life, or even from the very beginning, because the shelf-like portions of the squamosals are not in that vicinity to exclude them. Number 4 is not a distinct character for two reasons. First, the specimen is not complete enough for one to determine definitely whether or not the supratemporal openings are closed. It would not be surprising, however, even if they were closed, because the lack of a prominent parietosquamosal shelf in the early growth stage and, therefore, a disproportionately rapid upgrowth of the parietals in the posterior region could easily result in the closing of these openings. Second, there is a considerable

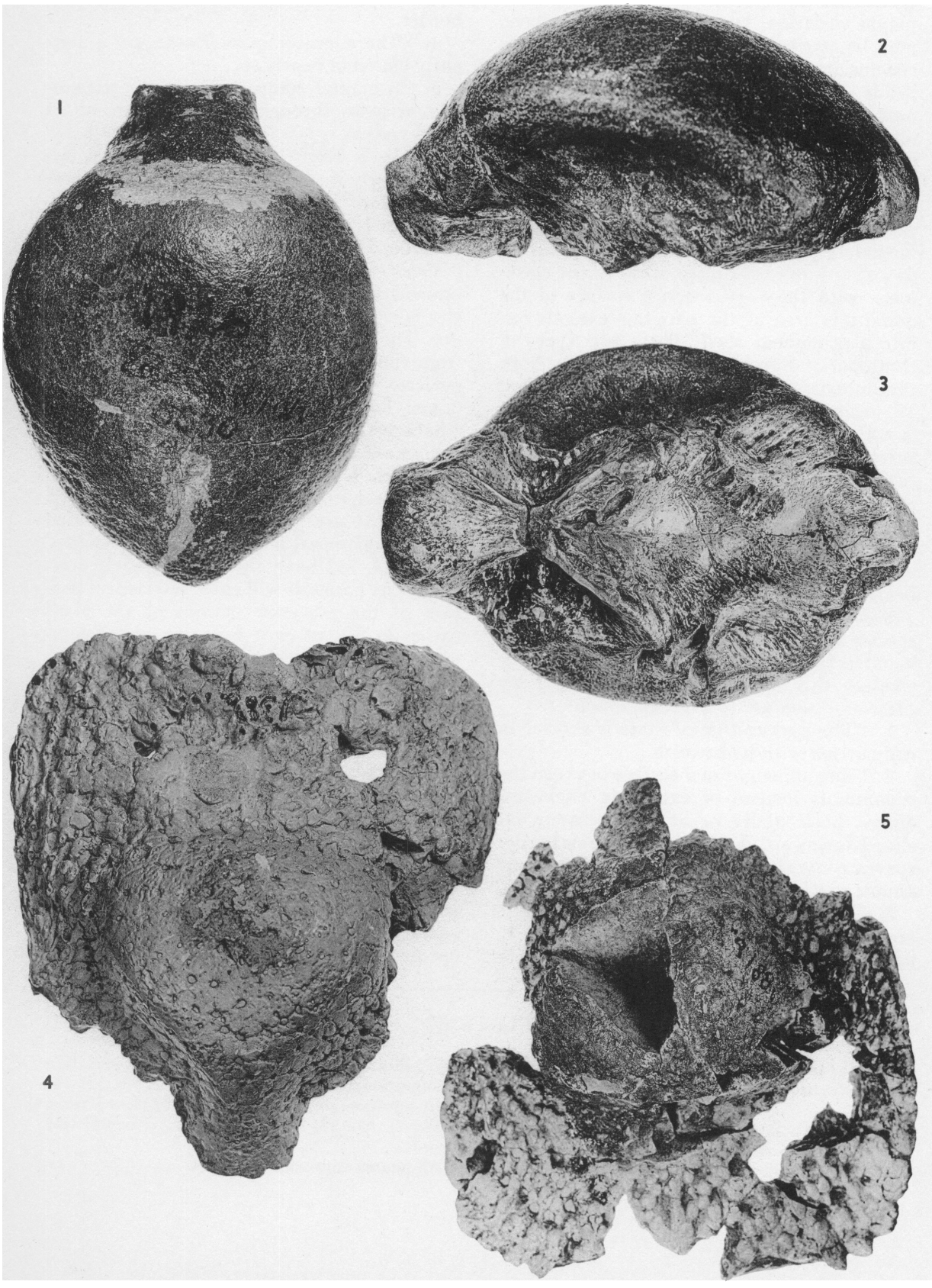
PLATE 37

Frontoparietal regions in the type of *Troödon edmontonensis*, new species, and in *Troödon validus* (Lambe).

1–3. Dorsal, lateral, and ventral views of the type of *Troödon edmontonensis*, G.S.C. No. 8830.

4–5. Dorsal views of *Troödon validus*, G.S.C. No. 138 and G.S.C. No. 8816, to show variation in supratemporal openings. In G.S.C. No. 138 the right supratemporal opening is nearly closed, while in G.S.C. No. 8816 the left opening is completely closed.

All figures approximately ×1.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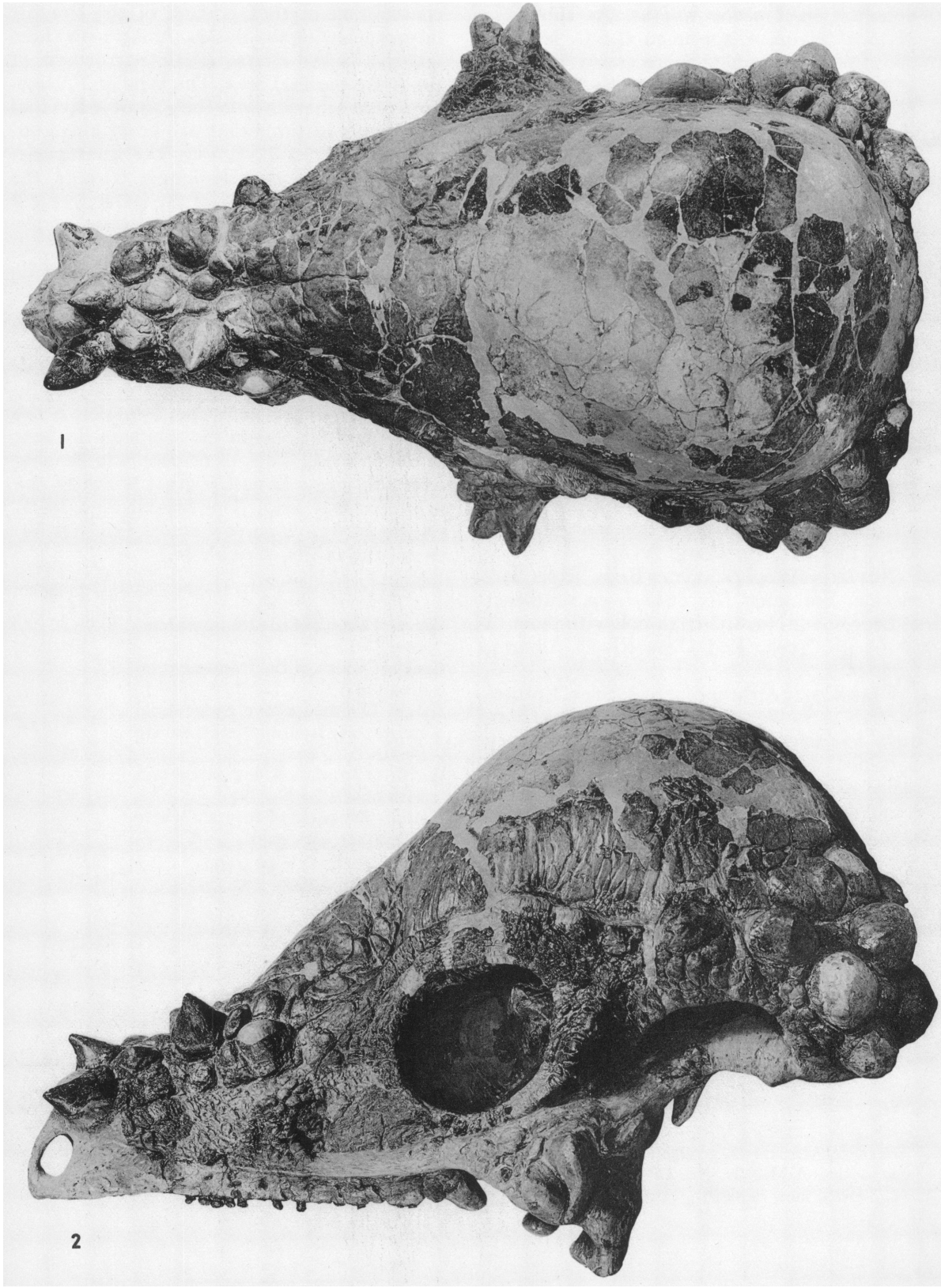
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amount of variation in the supratemporal openings in *Troödon validus*. As shown in plate 37, figure 4, specimen G.S.C. No. 138 has the right opening more closed than the left, and in G.S.C. No. 8816 the left supratemporal opening is entirely closed, while the right is still open. Characters number 5 and number 6 are likewise not distinctive because of the reasons cited above.

The postcranial elements of *Troödon validus* described by Gilmore (1924) are, at present, not available for study. We have had to rely, therefore, upon Gilmore's illustrations and very thorough description. Our comments on these elements are included in a later section of this paper on the affinities of the troödonts.

Troödon sternbergi,[1] new species

TYPE: G.S.C. No. 8817, a nearly complete frontoparietal area. Collected by C. M. Sternberg, 1928.

PARATYPE: G.S.C. No. 192, a frontoparietal area lacking the posterior margin. Collected by C. H. Sternberg, 1913.

HORIZON AND LOCALITY: Belly River formation. Specimen No. 8817 from southeast of Steveville; No. 192 from below the mouth of Berry Creek, Red Deer River, Alberta, Canada.

DIAGNOSIS: A rather large species. Frontoparietal area relatively broad, proportionately low even in the adult stage, and very flattened over the parietals. Parieto-squamosal shelf not prominent and about in the same plane as the dorsal surface of the parietals. Frontals proportionately low and broad where in contact with the nasals.

DISCUSSION: As shown above, some of the growth changes that take place in the frontoparietal area of *T. validus* are marked increase in height of the dome, a complete, or nearly complete, obliteration of the sutures, and the marked proportionate increase in depth and constriction of that portion of the frontals in contact with the nasals. Along with these features is the characteristic narrowness of the frontoparietal area. The type of *T. sternbergi* represents a nearly fully adult individual and shows features that are in striking contrast to those of *T. validus*. The frontoparietal area is but slightly longer than in the largest known specimen of the latter, yet it is nearly one-third wider. The portion of the frontals in contact with the nasals is broad, low, and lacks the abrupt constriction of its lateral margins so characteristic in *T. validus*. The uppermost portion of the dome in both the type and paratype is quite smooth, and the rest of the frontoparietal area is moderately rugose. Another feature, especially well shown in the paratype, No. 192, is the great breadth between the orbits on the base of the frontals. This, of course, is in keeping with the proportionately great width of the frontoparietal area. The frontal area in *T. validus* is always narrow across the base between the orbits. (See pl. 36.)

[1] Named for Mr. C. M. Sternberg, discoverer of the type.

MEASUREMENTS AND INDICES OF THE TYPE

Greatest length of the frontoparietal area (=L)	131 mm.
Greatest width of the frontoparietal area (=W)	110
Height of dome above endocranial cavity at frontoparietal suture (=H)	62
Width of frontals where in contact with nasals (=N-FW)	40
Median thickness of frontals where in contact with nasals (=T)	25
Frontoparietal area $\frac{W \times 100}{L}$	84.733
Frontoparietal area $\frac{H \times 100}{L}$	47.328
Frontoparietal area $\frac{H \times 100}{W}$	56.364

PLATE 38

Pachycephalosaurus grangeri, new genus and new species, A.M.N.H. No. 1696, type.

1. Dorsal view of skull.
2. Lateral view of skull.

Both figures approximately $\times \frac{1}{4}$.

Frontals where in contact with nasals	$\frac{T \times 100}{N\text{-}FW}$	62.500

Troödon edmontonensis, new species

TYPE: G.S.C. No. 8830, a frontoparietal area of an adult. Collected by C. M. Sternberg, 1926.

PARATYPES: G.S.C. No. 8831, a frontoparietal area with the anterior margin broken away; G.S.C. No. 8832, the anterior two-thirds of a frontoparietal area. Collected by C. M. Sternberg, 1926.

HORIZON AND LOCALITY: Edmonton formation. Opposite the mouth of Big Valley Creek below Scollard ferry, Red Deer River, Alberta, Canada.

DIAGNOSIS: A small species. Frontoparietal area oval in outline when viewed from above; low and gently arched in the adult stage. Parieto-squamosal shelf only slightly developed. Frontals low and narrow where in contact with the nasals and not set off from the rest of the frontals by lateral grooves.

DISCUSSION: These three specimens are the only representatives of *Troödon* from the Edmonton and are the only ones known above the Judith River-Belly River formations. Since the sutures are completely obliterated in all three specimens, they probably represent fully adult individuals. There is some variation in size among them. The type is the smallest, No. 8832 somewhat larger, and No. 8831 intermediate between them. With the larger size there is a slight relative increase in thickening of the dome. In all three specimens the outer surfaces of the domes are smooth. The largest one (No. 8832), however, although quite water-worn, is slightly rugose.

Apart from the diagnostic features listed above, the specimens of *T. edmontonensis* exhibit a combination of features in the base of the frontoparietal area that is distinct. The dorsal region of the endocranial cavity is relatively longer, and actually wider than in the other species. The width across the base of the frontals between the orbits is proportionately greater. The base of the parietals behind the endocranial cavity is not downcurved. In these features *T. edmontonensis* is more advanced. Another feature peculiar to this species is that the inner walls of the lateral temporal openings seem to indicate that those openings were not so compressed dorsoventrally as in the others. (Pl. 37, figs. 1–3.)

MEASUREMENTS AND INDICES OF THE TYPE

Greatest length of the frontoparietal area (=L)	95 mm.
Greatest width of the frontoparietal area(=W)	67
Height of dome above endocranial cavity at frontoparietal suture (=H)	38
Width of frontals where in contact with nasals (=N-FW)	20
Median thickness of frontals where in contact with nasals (=T)	12
Frontoparietal area $\frac{W \times 100}{L}$	70.526
Frontoparietal area $\frac{H \times 100}{L}$	40.000
Frontoparietal area $\frac{H \times 100}{W}$	56.716
Frontals where in contact with nasals $\frac{T \times 100}{N\text{-}FW}$	6.000

GENUS **PACHYCEPHALOSAURUS,** NEW GENUS

GENERIC TYPE: *Pachycephalosaurus grangeri,* new species.

DISTRIBUTION: Upper Cretaceous, Lance formation, Montana, South Dakota, and Wyoming.

DIAGNOSIS: Rather large bipedal dinosaurs. Skull with extreme thickening of the frontoparietal area. Node-like ornamentations of the skull strongly developed. Supratemporal openings always completely closed. Face narrow and shallow. Premaxillaries probably without teeth.

DISCUSSION: Gilmore (1931) recorded the first material from the Lance formation which could unquestionably be considered as troödont. He described a new species, based on a fragmentary frontoparietal area, which he designated as *Troödon wyomingensis.* He later referred another skull cap from the Lance to this same species. Gilmore (1931, p. 1) recognized the striking dissimilarities between this species and *Troödon validus,* but, because of inadequate material, preferred to place it in *Troödon* rather than erect a new genus. Since

Gilmore's work, the Lance formation has produced two additional frontoparietal areas and an unusually complete skull. That all this Lance material represents a new genus is beyond question.

This new genus includes three species, two of which are new.

Pachycephalosaurus grangeri, new species

TYPE: A.M.N.H. No. 1696, a nearly complete and excellently preserved skull. Found by William Winkley and collected by W. H. Peck and Thomas G. Nielsen, 1940.

HORIZON AND LOCALITY: Hell Creek Beds, Lance formation. Sec. 17, T. 1 S., R. 55 E., William Winkley Ranch, Powder Hill, north of Ekalaka, Carter County, Montana.

DIAGNOSIS: Frontoparietal area high arched and extremely thickened. Posterior surface of the parietal extends abruptly upward from the posterior margin of the skull, thus eliminating all trace of the parieto-squamosal shelf. Frontals deep and narrow where in contact with the nasals. Distance from occipital condyle to posterior margin of skull great. (See pls. 38, 39.)

DISCUSSION: No other known specimens are referable to this species. The following is a comparative study of the unusually complete and excellently preserved type.

THE SKULL

The skull is, in linear dimensions, more than three times the size of the *Troödon validus* skull described by Gilmore (1924) from the Belly River formation. Only part of the left jugal, the anterior portion of the border of the right orbit, and the very tip of the nose are missing.

When viewed from above, the skull is long and triangular in general form. The posterior border, formed by the posterior margins of the squamosals and parietals, is broad and straight, and the front of the skull is narrow and pointed. The high vaulting in the frontoparietal area, which posteriorly extends abruptly upward from the posterior margin of the occipital area, is carried to a greater extreme than in any other known form. The skull is nearly a foot thick above the occipital condyle. Three-fourths of this thickness is above the endocranial cavity and is caused by the dome-shaped upgrowth of the frontoparietal area.

The antorbital area is relatively short, low, and narrow. It is not over 3½ inches deep at the anterior ends of the maxillaries. The postorbital area is proportionately long, principally as a result of the posterior growth of the parieto-squamosal area. This has resulted also in the dragging backwards of the upper parts of the exoccipitals, quadrates, and, of course, the lateral temporal openings. Because of this shifting, the distal ends of the quadrates, although the articular surfaces are broken away, seem to have shifted forward more than they actually have. They are under the orbits and are, therefore, proportionately in a more anterior position than in *Troödon validus*. This means that the lower jaw was also relatively shorter.

At the postero-external corners of the squamosals, on the surfaces of the jugals below the orbits and on the dorsal surface of the nose, there are large, irregularly shaped, node-like ornamentations. The elevated dome-like area of the frontoparietal region is perfectly smooth, but on the rest of the skull the surface presents a welt-like roughening. The skull, therefore, is more highly ornamented than is that of any of the other known troödonts.

As the premaxillaries are missing, the form and size of the external nares cannot definitely be determined. From the preserved portions of the front of the maxillaries, however, it seems reasonable to conclude that they were small and directed forward, occupying relatively the same position as in *Troödon validus*.

Any indication of the supratemporal openings has been completely obliterated by the very marked development of the dome-like mass and the abrupt upward growth of its posterior surface. In *T. validus* they are still present as perforations in the shelf-like structure, formed by the squamosals and the posteromedian portions of the parietals at the base of the frontoparietal mass. In the type of *Pachycephalosaurus wyomingensis* (Gilmore) from the Lance formation, they are completely closed but are indicated by ovate depressions. In a specimen of a fairly immature individual in the Carnegie Museum (No. 3180), described by Gilmore (1936), also from

the Lance formation, they are closed, but their margins are clearly indicated by rather deep grooves. In another specimen from the Lance of Corson County, South Dakota (Colorado Mus. Nat. Hist. No. 469), to be described later in this paper, there is no indication at all of the supratemporal openings. Through the great doming of the skull roof, the lateral temporal opening has become much reduced and has become slit-like in form with the posterior margin rotating down to an almost horizontal position and the slightly arched anterior margin rotating back almost parallel with it above.

The foramen magnum is round and proportionately small. In *Troödon validus* it is transversely elliptical in form and is about one-half as large, while the skull is only approximately one-third the size of *Pachycephalosaurus grangeri*.

The subtemporal openings are much reduced and are rounded in form. Since most of the prevomers and palatines are broken away, the inner margins of the internal nares cannot be determined. They occupied the same position and presumably were about the same shape as in *Troödon validus*, although they are proportionately shorter. The posterior palatine openings, which are much reduced in *T. validus*, seem to be entirely eliminated in *Pachycephalosaurus grangeri*.

The skull is probably that of an old individual. It is the largest known troödont skull, and the sutures are quite closed or entirely obliterated.

None of the premaxillary is preserved. The sutural surface on the front of the maxillary is preserved, however, and shows that the relationship between the two elements is approximately the same as in *Troödon validus*. The lateral wing of the premaxillary must have been short and was situated on the anterolateral surface of the maxillary, at the ventral margin, under a slightly bulbous overhang, and was thus excluded from contact with the nasal behind the external narial opening. Gilmore (1924, p. 18) has emphasized the unusualness of this character in *T. validus*. Its presence in *Pachycephalosaurus*, which is considerably more specialized and later in time, would seem to suggest that it is a family character. In front of the tooth row, the maxillary extends forward 25 mm. to form a sharp ventral margin which becomes thinner and less prominent anteriorly. The lateral wing of the premaxillary overlapped this ridge on the outer surface throughout most of its length. This is convincing evidence that premaxillary teeth were absent. In *T. validus*, where they are present, there is practically no space between them and the maxillary teeth, and the premaxillary butts against the maxillary with only a slight amount of overlap.

In its general form the maxillary is very similar to that of *Troödon validus*. It is proportionately somewhat longer, however, and its posterosuperior projection extends backward over the lacrimal to a point almost above the anterior margin of the orbit. Also, it has 20 alveoli instead of 16, as in *T. validus*. Although it is similar to the latter in its relationship with the premaxillary, prevomer, palatine, extopterygoid, and jugal, the anterior ridge-like extension of the jugal does not overlap the maxillary so far. In front of this process there is a ridge on the side of the maxillary that extends forward to above the first tooth. Below this ridge the surface of the bone is smooth and has numerous foramina. Above the ridge the surface of the maxillary is very rugose and along the union with the nasal there are five large nodes. The anterior of these is the smallest, and the last is the largest and has the form of a blunt projection. On the inner surface just above the alveolar border is a series of foramina, one for each vertical series of teeth. They are connected

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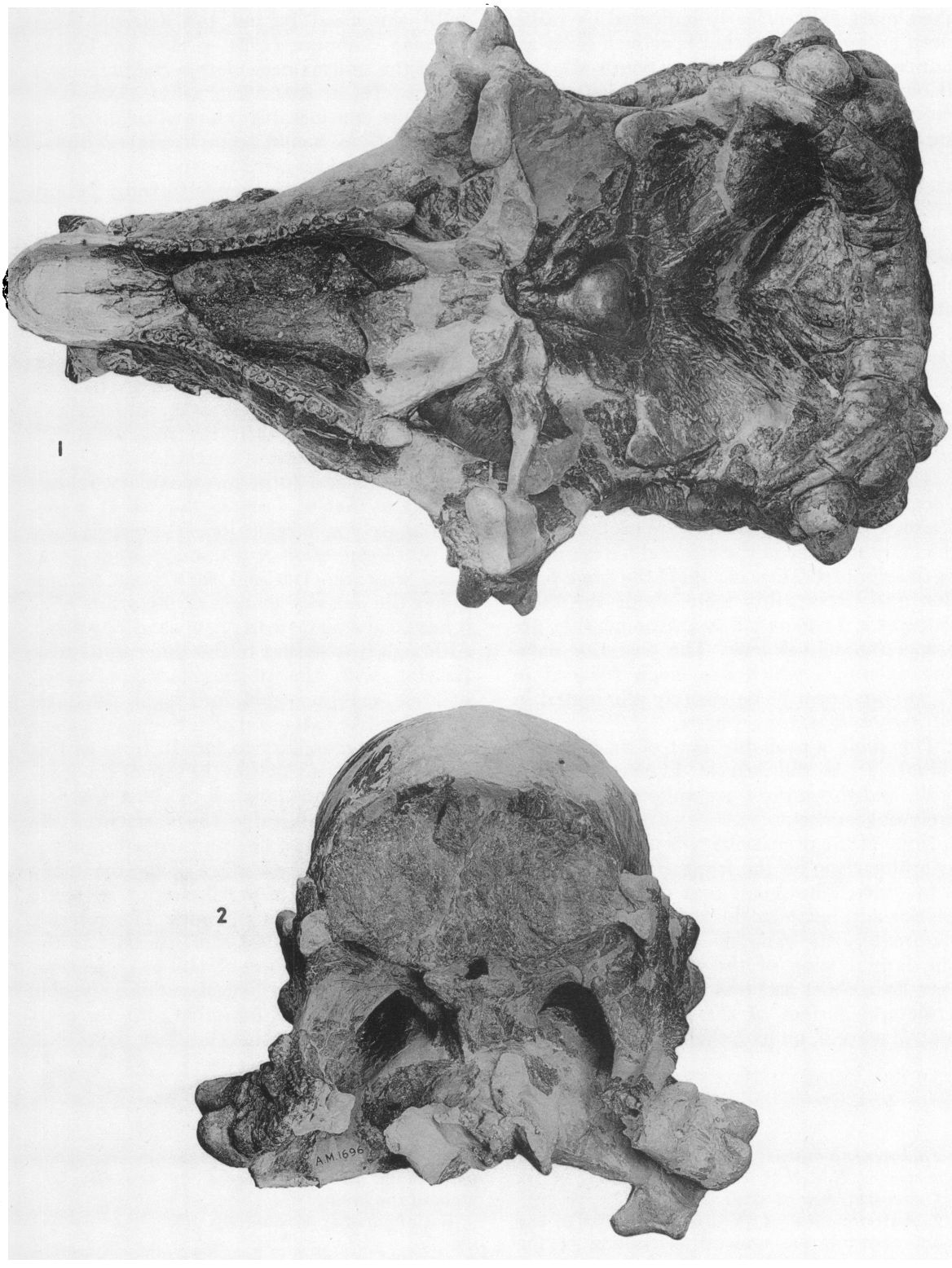
PLATE 39

Pachycephalosaurus grangeri, new genus and new species, A.M.N.H. No. 1696, type.

1. Ventral view of skull.

2. Anterior view of skull in the region of the orbit, showing the unusual thickening of the anterior part of the frontals above the area of the endocranial cavity, occupied by the olfactory stalk of the brain.

Both figures approximately $\times\frac{1}{4}$.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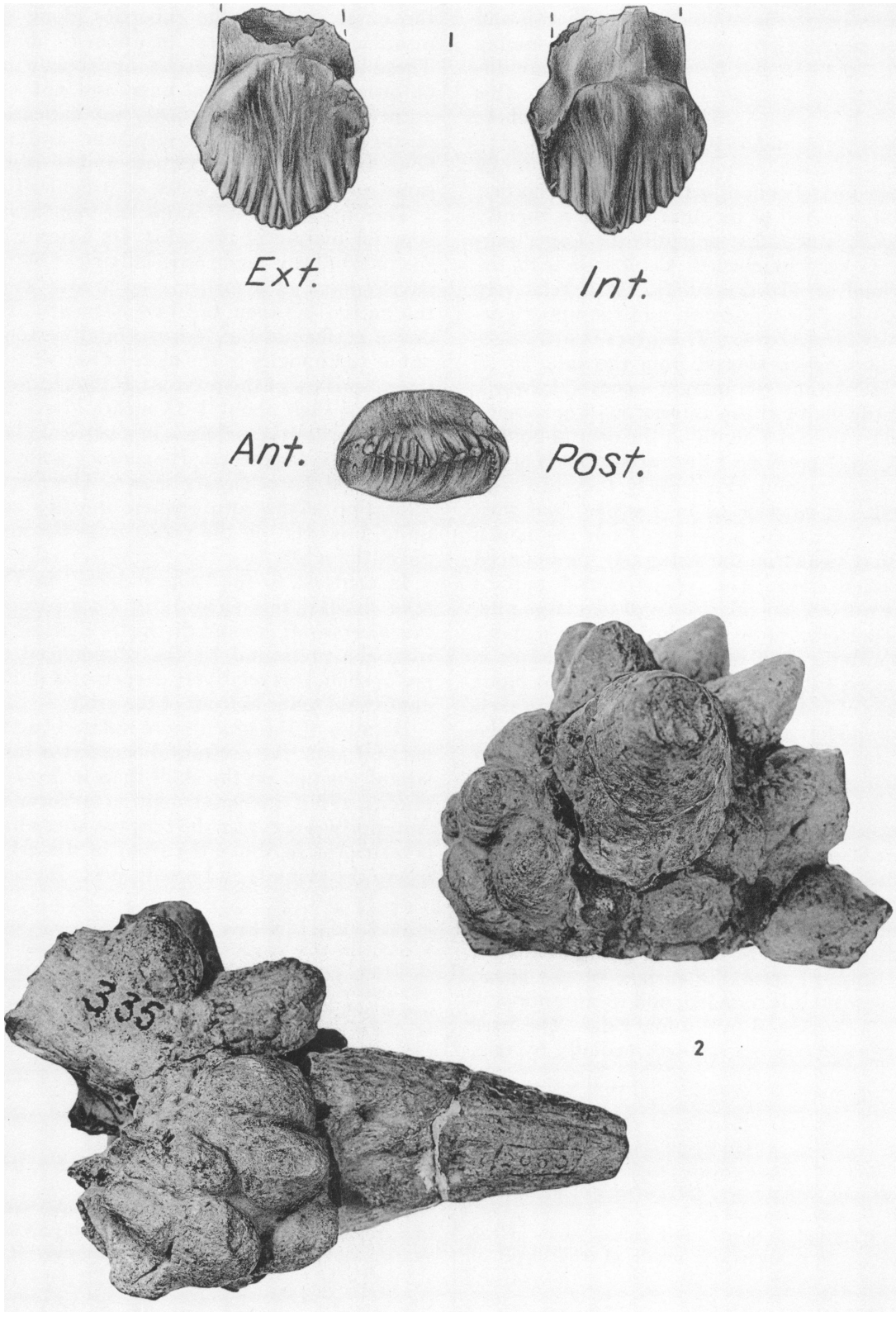
A.M. 1696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by a shallow groove. The margins of most are broken away, the others are oval-shaped and quite small. There is no reason for assuming that the origin and function of these are different from that in the ceratopsians. This problem has been discussed by us elsewhere (1940a, p. 7, and 1940b, p. 146).

The lacrimal is relatively large. It forms approximately one-third of the orbital border. The lower half of its outer surface is slightly concave and rather smooth; the upper portion is very roughened. Compared with the lacrimal of *Troödon validus*, it is relatively much shallower in front, and the upper portion is quite narrow. This gives it a triangular form when viewed from the side. In *T. validus* the anterior margin is curved forward, and the depth at the anterior margin is much greater than the depth on the orbital border.

A small portion of the anterior ends of the nasals is missing. Posteriorly they are relatively not so wide as in *Troödon*, and they differ even more strikingly from the nasals of that genus in the extremely pronounced ornamentation. The posterodorsal surface presents low irregularities and two large pits. The posterior of these is the largest. On about the anterior half of the nasal the surface is crowded with low welts and prominent blunt spikes of bone. One low spike, about an inch in diameter at its base, is situated on the midline at the very front end in a position which presumably is just above the process which divided the narial orifice. At the antero-external corner of this area is a somewhat larger, though less pointed, spike which is directed forward. A large boss is at the posterior juncture of these two spikes, and immediately behind this is a third spike which is the largest of the three. It extends outward and upward from the surface of the nasal. Posteriorly it is rounded, and its anterior surface is developed into a low ridge. The base of this spine is surrounded medially by one, and posteriorly by three, low tubercles. On the outer side are the tubercles along the maxillary-nasal suture mentioned above. These spines and tubercles apparently are outgrowths of the nasal bone and not separate elements. There is never any indication of their being separate elements, and the bone structure of the largest spikes is the same as the smallest welts or irregularities.

The "supraorbital"[1] forms the very heavy superior margin of the orbit. Its union with the prefrontal is made especially clear by the development of a rather deep groove along the suture between the two elements. The dorsal surface of the "supraorbital" extends out at right angles to the more or less vertical lateral surface of the prefrontal, thus forming a narrow shelf about 1–1½ inches above the orbit. The lateral surface is in a vertical plane and is very roughened. Its contact with the postorbital is not clearly shown. There is an indication of the suture where the two may unite, however, on the posterosuperior margin of the orbit.

In contrast to the "supraorbital" in *Troödon validus*, this element in *Pachycephalosaurus grangeri* is more distinctly marked off from the prefrontal by the pronounced superior shelf, it is relatively deeper, and it does not extend so far in front of the orbit.

Because of the much more inflated frontoparietal area, the prefrontal occupies a more lateral position on the skull than in *Troödon validus*, and it does not extend so far forward. Anteriorly it occupies the concave area which is restricted to above the front of the orbits where the frontals and nasals meet. Immedi-

[1] The word "supraorbital" is here placed in quotation marks because, as we have pointed out elsewhere (1940b, p. 155) the true supraorbital is found in certain fish skulls and not in the higher vertebrates. Here, as in the ceratopsians, it probably originated as a palpebral bone and is homologous with the "supraorbital" in the skull of *Camptosaurus*, which has already become partially incorporated in the skull roof.

PLATE 40

Tooth of *Pachycephalosaurus grangeri*, new genus and new species, and portion of squamosal of *Pachycephalosaurus* sp.

1. External, internal, and crown views of the fifteenth left maxillary tooth of the type of *Pachycephalosaurus grangeri*, A.M.N.H. No. 1696, ×3.

2. Posterior (above) and lateral (below) views of a fragmentary left squamosal of *Pachycephalosaurus* sp., Y.P.M. No. 335, approximately ×1.

ately behind this area it becomes pronouncedly convex anteroposteriorly and slightly so dorsoventrally. The lateral surface of this posterior area is almost vertical. This condition is very different from that in *T. validus* where the surface of the skull is deeply concave lateral to the anterior and much arched extension of the frontal. Most of this lateral region is occupied by the prefrontal. The dorsal surface has only a few transverse shallow grooves, whereas in *T. validus* it is covered with prominent nodes.

The postorbital is short and heavy. It forms the anterior and superior borders of the lateral temporal opening. Its dorsal surface forms a shelf-like ridge continuous with the shelf in front that is developed on the "supraorbital." It differs markedly from the postorbital of *Troödon validus* in that it does not extend up onto the side of the vaulted portion of the frontoparietal area. There is no indication that a postfrontal was present.

The frontal and parietal have become so firmly coalesced that there is no remaining indication of sutural contact between them. The development of these two bones into a very much enlarged dome-like mass is the most striking single feature of the skull. So extreme is the vaulting in this area that more than 6 inches of solid bone lie above the portion of the endocranial cavity that was occupied by the olfactory stock of the brain, and 9 inches above the region of the cerebellum. In no other reptile has the skull roof become so thickened. The structure of the bone that forms this dome seems to be identical with that in *Troödon*. Most of the mass is composed of a compact fibrous structure made up of many small columns of bone which radiate out from a thin dense ventral zone and terminate in an equally dense thin outer zone. The outer surface is without ornamentation and presents numerous perforations that lead into canals which penetrate into the fibrous zone. As Gilmore has suggested (1924, p. 12), these are undoubtedly nutrient canals.

The problem of the composition of bone which forms this dome-like mass in the troödonts will be discussed later in this paper.

The frontoparietal mass of *Pachycephalosaurus grangeri*, when compared with that of *Troödon validus*, shows the following differences:

1. It is proportionately much more vaulted.
2. Broadening is carried to a much greater degree, and thus the postorbital and prefrontal bones are much more lateral in position. Also the concave area above the orbit is restricted to above the anterior of the orbit because of the widening of the anterior portion of the frontal.
3. The supratemporal openings have been obliterated entirely by the remarkable vaulting of the parietals.
4. The shelf behind the frontoparietal mass has been completely eliminated, and the dome extends abruptly upward from the posterior margin of the occipital area.

This last character and the extreme vaulting are features that are unique in this species. In all the other Lance specimens, the dome is more flattened and there is always a posterior shelf, although it is never so well developed in these as in *Troödon validus*.

Ventrally the parietal forms the central portion of the very heavy, saddle-shaped, postero-inferior margin of the skull. From this margin it extends forward to form a very heavy, raised, and solid V-shaped mass. In the center of this mass is a large round protuberance. This undoubtedly is where the ligamentum nuchae was inserted. The pronounced development of this protuberance certainly means that the ligament was large, and from this we infer that the tip of the neural spine of the axis must have been heavy and rugose. On either side of the V-shaped area is a deep slit-like concavity where the parietals and squamosals are in contact. These are confluent posterolaterally with the larger concave areas on the ventral surfaces of the squamosals, and together with them probably mark the areas of insertion of the large rectus capitis posterior muscle masses.

In none of the other known troödonts is there a protuberance for the insertion of the ligamentum nuchae. In the other specimens of *Pachycephalosaurus* the V-shaped mass is not nearly so prominent, and in *Troödon* it is only weakly developed.

The squamosal forms the posterolateral corner of the skull and has approximately the same relationship with the other elements as in *Troödon validus*. The exaggerated upgrowth of the parietal, however, has eliminated all traces of a dorsal shelf. The entire

external surface is, therefore, almost wholly in a vertical plane. The squamosal forms the posterior border of the lateral temporal opening, and the proximal end of the quadrate is buried deeply in its anteroventral portion, so firmly that there is scarcely any trace of the sutures between them. The external surface is more highly ornamented than in any other known troödont. It has eight large, welt-like nodes, which are somewhat differently arranged on the right and left squamosals. They are arranged in three more or less transverse rows. On the left there are two in the lower row. The outer of these is the smaller. In the middle row there are three large subequal nodes, and in the upper row three smaller ones. The latter are also subequal in size, and the middle one has a tendency to become vertically divided. On the right squamosal there are three instead of two in the lower row, and two instead of three in the upper row. The inner one of the upper row has become vertically separated into three equal portions. Around the bases of these nodes, where they are not in contact with one another, there are numerous smaller welts which have no definite arrangement. In *Pachycephalosaurus wyomingensis* (Gilmore), these nodes are known only on the somewhat immature individual in the Carnegie Museum (No. 3180). They, too, are arranged in three transverse rows, but they are much smaller and more numerous. There are five in the upper row, four in the middle row, and three are preserved in the lower row. When the squamosal of *Pachycephalosaurus grangeri* is compared with that of *Troödon validus*, it shows the following main differences. It is proportionately much shorter and deeper; the dorsal shelf has been almost entirely eliminated; and the external surface is nearly in a vertical plane and is more highly ornamented.

The most outstanding feature of the jugal is its relatively small size. The posterior ascending wing is low, overlaps but slightly the postorbital behind the orbit, and apparently does not enter into the formation of the anterior margin of the lateral temporal opening. The portion beneath the orbit is very shallow. Its surface presents many small and medium-sized nodes. The ventral margin where the jugal and quadratojugal meet is very heavy.

There is no indication of what Gilmore (1924, p. 19) described in *Troödon validus* as an infrajugal. Some such element may be represented, however, by two large nodes which occupy the entire surface of the ventral projection of the jugal. The suture between the anterior projection of the jugal and the maxillary is not distinct. This projection is long and thin and extends to a point about halfway forward on the maxillary, approximately as in *T. validus*. In other respects the jugal is very different from that of *T. validus*. It does not extend upward so far behind the orbit, it apparently does not form part of the anterior margin of the lateral temporal opening, and, most important of all, it is very much shallower and more nodose beneath the orbit.

The form and position of the quadratojugal are about the same as in *T. validus*. It is proportionately somewhat shorter, and it is of more uniform width throughout its length.

The usualness of the forward inclination of the quadrate in *Troödon* has been noted by Gilmore (1924, p. 20). In *Pachycephalosaurus grangeri* this is even more exaggerated. The whole element is thick and heavy in contrast to the thin and light quadrate of *T. validus*. The upper end is deeply buried in the squamosal at the lateral margin of the skull at the posteroventral margin of the lateral temporal opening. The posterior margin presents no thin, crest-like margin as in *T. validus*. It is flat and heavy. Proximally it merges into the strong and short internal lateral wing which is mostly overlain by the distal end of the exoccipital. Distally it narrows and is braced against the posterior descending wing of the pterygoid. The articulation for the lower jaw is not preserved.

Shortening of the basicranial area in the troödonts is climaxed in *Pachycephalosaurus grangeri*. This, of course, has resulted from the great expansion of the frontoparietal area, which has affected particularly the position of the exoccipitals. Their dorsal areas and lateral extensions, instead of being vertical, are in an almost horizontal position. The exoccipitals are robust, and their transverse diameter is short. They form the lateral and dorsal border of the foramen magnum. The suture between them and the supraoccipital is not entirely distinct, but the portion clearly

shown indicates that the exoccipitals meet above the foramen magnum, thus eliminating the supraoccipital from the border. The lateral extension is heavy and is much expanded distally. Most of the external margin is firmly united with the squamosal and quadrate. The anteroventral corner is free and extends downward and forward to opposite the middle of the condyle. The dorsal margin is in contact with the supraoccipital throughout most of its length. Just how much is in contact with the parietal cannot be determined. The ventral margin is heavy. Just anterior to this margin, where the exoccipital extends down to form the lateral wall of the foramen magnum, are two foramina. The posteroinferior of these undoubtedly transmitted the twelfth nerve, for it enters the endocranial cavity just inside the foramen magnum. The other foramen passes forward and inward and enters the fenestra ovalis. This probably is the foramen lacerum posterius. The union of the exoccipital with the proötic is extensive. The other boundaries of the latter element cannot be determined accurately. The superolateral surface of the occipital condyle is developed on the lower portion of the exoccipital.

The supraoccipital is large and is nearly vertical in position. Its lateral wings are directed considerably backward, and its median surface has a low vertical ridge. Its boundaries are not entirely distinct, but evidently it has become quite removed from the superior boundary of the foramen magnum by the union of the exoccipitals above the foramen.

The only portion of the laterosphenoid that is suturally distinct from the other elements is the superolateral wing. It is triangular in cross section, being flattened above and keel-like below, and is braced over the frontoparietal suture above. This relationship of the laterosphenoid to the other cranial elements is more or less typical of all the ornithischians.

The basioccipital has approximately the same form as in *Troödon validus*. The neck-like portion in front of the occipital condyle is somewhat deeper and narrower, and the condyle itself is relatively narrower. The exoccipitals contribute proportionately less to the formation of the condyle than in *T. validus*, and the main portion is more convex, both transversely and anteroposteriorly. The surface of the condyle shows that a considerable amount of lateral head motion was possible, but an even greater mobility in a vertical dimension is indicated. The condyle faces almost directly at right angles to the base of the skull. This feature, in addition to the fact that the foramen magnum faces almost in the same direction, shows that the normal position of the skull was at right angles to the cervical vertebrae. Although none of the skeleton is known, this is conclusive evidence that *Pachycephalosaurus grangeri* probably was habitually bipedal.

The pterygoids are about like those of *Troödon validus*, as described by Gilmore (1924, pp. 21–22). The ventral portion, however, is folded back over the basisphenoid to a greater degree, the posterior ventrolateral wings are relatively more robust, and the anterior ventrolateral wings are less developed. Anteriorly, the pterygoids are incompletely preserved, and the sutures between them and the prevomers and palatines are not at all distinct. Only small portions of the ectopterygoids are present, and they show no features that would indicate they were essentially different from those of *T. validus*.

Only the posterolateral wing of the palatine is preserved. The anterior margin is above the fifth alveolus as in *Troödon validus*, but the wing is more robust and deeper than in that form. The prevomers are missing except the anterior ends which form a somewhat pear-shaped mass wedged firmly between the palatal portions of the maxillaries. The prevomers extend farther forward than in *Troödon validus*, but in that form the premaxillaries are large and the maxillary tooth

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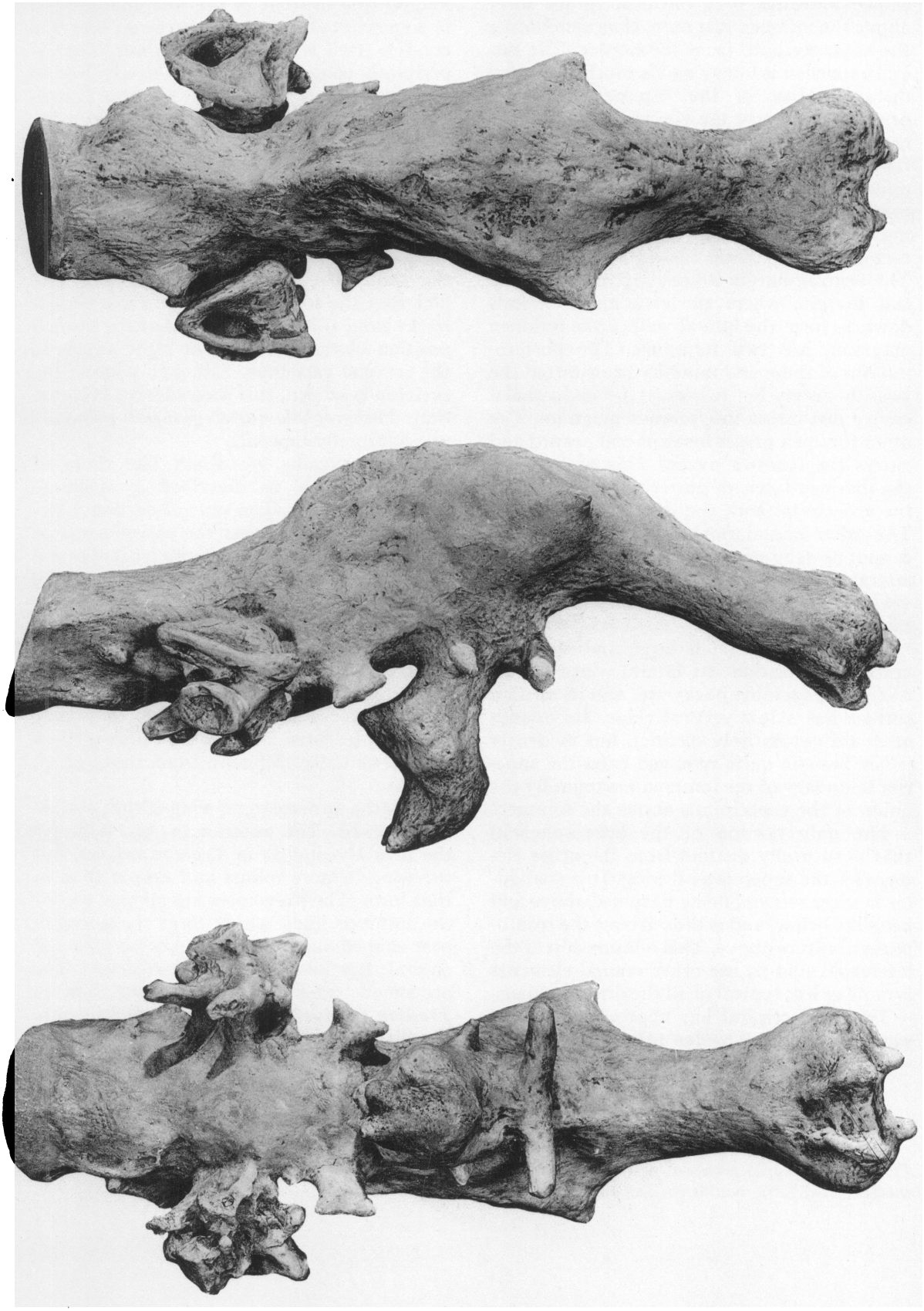
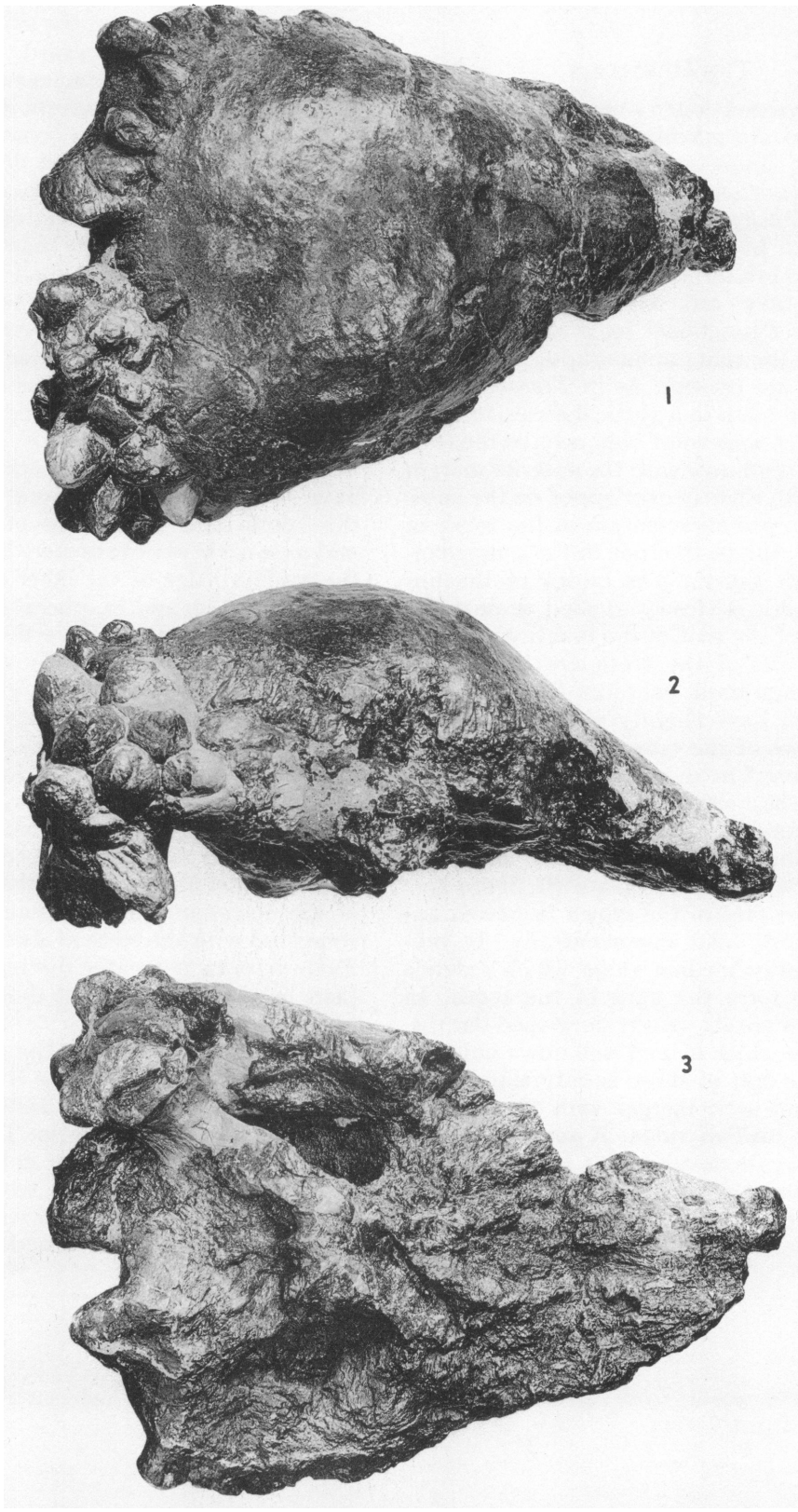
PLATE 41

Endocranial cast taken from the type skull of *Pachycephalosaurus grangeri*, new genus and new species, A.M.N.H. No. 1696. Dorsal view above, right lateral view in middle, ventral view below, approximately ×1.




1
2
3

row is proportionately longer and extends farther forward.

The Dentition

For the reasons cited above, under the description of the maxillary-premaxillary relationship, it can be concluded with reasonable certainty that premaxillary teeth were not present in *Pachycephalosaurus grangeri*. There are 20 teeth in each maxillary, and, as is to be expected in a form whose skull is so heavily armored, they are relatively small. The crowns of 12 functional teeth are preserved, and either the roots or unerupted crowns of the others are present. As in *Troödon*, there are but two teeth in a vertical series, and the teeth are set somewhat obliquely to the long axis of the tooth row with the anterior margin of each tooth slightly overlapped on the outer side by the posterior margin of the tooth in front. Also, the teeth erupt in the same manner in both genera. The crown of the unerupted tooth is closely applied against the inner side of the root of the functional tooth.

The crowns of the teeth are low, transversely compressed, more or less vertically ribbed, and have slightly serrated margins. At the bases of the crowns they are oval in cross section. The detailed characters of the crowns are best shown by an unerupted tooth which is number fifteen in the series of the left side. The following is a description of this tooth which is shown in plate 40, figure 1.

The inner face of the crown is convex anteroposteriorly and dorsoventrally. It presents a heavy median ridge which extends upward to form the apex of the tooth. In front of this are six weakly developed but distinct ridges which extend well down onto the crown. The first of these is only slightly developed and soon merges with the apex of the heavy median ridge. A seventh is also present, but its development is slight and it merges into the node-like antero-internal corner of the tooth. Posterior to the heavy median ridge are four smaller ridges. The first of these is more weakly developed than the others and is located on the side of the main ridge. Extending downward and forward from the fourth is a prominent serrated cusp.

The outer face of the crown is slightly convex anteroposteriorly but concave dorsoventrally. There is only a slight development of the median ridge. Behind this are four ridges which correspond to the four on the postero-inner face of crown. At the base of, and posterior to, the fourth is a weakly developed cusp. There are seven ridges in front of the median ridge. The first three of these are oblique to the median ridge and terminate against it. The second and third of these and the other four correspond to the six ridges on the antero-inner face of the crown.

The first two or three teeth in the series have crowns which are more pointed than this tooth, and the crowns of the teeth in mid-area of the series are more blunt. In some the median ridge of the inner face is not so well developed, and in others the postero-internal cusp is weaker. Nevertheless, the pattern is essentially the same in all.

Since *Pachycephalosaurus grangeri* probably does not have premaxillary teeth, a comparison with the premaxillary teeth of *Troödon validus* is not possible. As far as the cheek teeth are concerned, however, the two are very close. They present a pattern which is distinctive for the family Troödontidae. This pattern is definitely not like that of the teeth of the stegosaurs and nodosaurs, and when compared with the teeth of *Ankylosaurus* and *Palaeoscincus*, a greater discrepancy is seen than between the teeth of those two genera and *Stegosaurus*.

Of all known dinosaurs, the pattern of the cheek teeth of the troödonts is closer to that of *Hypsilophodon* (Hulke, 1881, pl. 72, figs. 6–8) than to any other form. This in itself is not of too great value in determining the broad relationships of the troödonts. It is, however, one more character which favors an ornithopod rather than a nodosaur affinity.

PLATE 42

Pachycephalosaurus reinheimeri, new species, Colo. Mus. No. 469, type.

1–3. Dorsal, lateral, and ventral views of skull, approximately ×¼.

The Endocranial Cast

Again Mr. Otto Falkenbach has been successful in obtaining another fine endocranial cast of a dinosaur. The task in this instance was particularly difficult since the endocranial area of *Pachycephalosaurus grangeri* was filled with a very indurated matrix that was considerably more resistant than the bone with which it was in contact. This cast is unusually complete and without distortion. (See pl. 41.)

In its proportions and in the relative position of the nerves, the endocranial cast of *Pachycephalosaurus grangeri* is typically ornithischian, resembling that of the ornithopods and ceratopsians somewhat more closely than the stegosaurs and nodosaurs. In proportion to the size of skull, the endocranial cast is quite large for a dinosaur. Compared with the nodosaurs, it is similar only in one significant feature. In both, the olfactory lobes are completely surrounded by bone. This is accomplished by a downgrowth of marginal bone from the frontals, a forward growth of the laterosphenoids which enclose the lobes in front, and probably an upgrowth of the anterior portion of the basisphenoid, which is probably homologous with the parasphenoid. Sutures in this area in *Pachycephalosaurus grangeri* are not shown, but several of the *Troödon* crania show them very clearly. In front of the cavity for the olfactory lobes of *P. grangeri*, the bone is over 2 inches thick. Several foramina lead out from this cavity, two from the left lobe and three from the right. In the nodosaurs this wall of bone is much thinner. This unusual condition seems to be peculiar only to the troödonts and nodosaurs among the dinosaurs. In all the others the olfactory lobes were enclosed by a membranous structure more or less as in the modern crocodilians. Apparently it seems to be correlated in some way with the unusual thickening of the skull in both groups. As far as the rest of the endocranial cavity is concerned, the tröodonts and nodosaurs are quite dissimilar. In the nodosaurs the olfactory peduncles are very short, the whole brain is relatively very much shorter, and in all other significant features it is definitely unlike that of the troödonts. A detailed description of an endocranial cast of *Ankylosaurus* will be given by us in a subsequent paper.

Compared with the endocranial casts of trachodonts (Marsh, 1896, p. 77; Brown, 1914, pl. 37), that of *Pachycephalosaurus grangeri* is different mainly in that the cerebrum is neither so well developed nor so distinctly marked off from the cerebellum. Also the relatively large pituitary body extends downward, more as in *Protoceratops*, and tends to become separated distally. In the broad and elongated medulla oblongata and in the abrupt constriction between this area of the brain and the cerebellum, it is very similar to that of both the ornithopods and ceratopsians. It is definitely more ceratopsian, however, in the lack of clear demarcation between the cerebral and cerebellal areas. As in *Protoceratops* and *Anchiceratops*, there is a blunt projection on either side of the anterodorsal area of the cerebrum.

The second, or optic, nerves are relatively small and project directly outward from the front of the base of the pituitary body. The third cranial nerve is situated on the side of the base of the pituitary body. This body is proportionately very large and is directed backward and downward. The posterodorsal projection tends to become branched, as does the distal projection. The fourth nerve is not clearly shown. Presumably it was very small and probably was located just above, and slightly in front of, III where the endocranial cavity is fractured. The fifth nerve is small. It shows the usual anterior projection which probably represents V^1. The sixth is situated somewhat closer to the seventh than the fifth. The endocranial cavity shows the exit for the seventh nerve just in front of, and slightly below, the fenestra ovalis. They are so closely situated where they enter the cavity that they are reproduced as confluent in the plaster cast. Nerves IX–XI probably were all transmitted through the foramen lacerum posterius. The hypoglossal nerve was situated about halfway back on the medulla oblongata. The semicircular canals are fairly well preserved. The anterior canal is hardly recognizable. The horizontal canal is the longest, and the posterior one is very low.

The endocranial cast of *Pachycephalosaurus grangeri* definitely shows a closer affinity with the ornithopods than with the nodosaurs or stegosaurs.

COMPARATIVE MEASUREMENTS AND INDICES

	P. grangeri	*Troödon validus*
Greatest median length of skull	642.0 mm.	192 mm.
Greatest median length of skull to anterior of maxillaries	575.0	172
Greatest width of skull across squamosals	363.0	118
Greatest height of skull above bottom of occipital condyle	320.0	105
Basal length, occipital condyle to anterior of maxillaries	367.0	122
Greatest width of skull above center of orbits	238.0	105
Greatest length of frontoparietal area	377.0	130
Greatest width of frontoparietal area	264.0	88
Height of dome above endocranial cavity	222.0	—
Width of frontals where in contact with nasals	90.0	28
Median thickness of frontals where in contact with nasals	100.0	—
Depth of face halfway forward on nasals	135.0	65
Greatest width across distal ends of maxillaries on alveolar border	72.0	25
Distance from posterior border of orbit to posterior end of squamosal	252.0	73
Distance from anterior border of orbit to anterior end of maxillary	195.0	63
Median dorsal length of nasals	260.0	77
Width across posterior end of maxillary tooth rows on internal margin of last alveoli	130.0	51
Width across anterior of maxillary tooth rows on internal margin of first alveoli	53.0	21
Length of maxillary on alveolar border in front of teeth	25.0	3
Length of maxillary teeth row on alveoli	175.0	61
Antero-posterior length of crown of left maxillary tooth #15	8.5	—
Height of crown of left maxillary tooth #15	7.5	—
Thickness of crown of left maxillary tooth #15	5.0	—
Length of endocranial cast measured along median line on dorsal surface	162.0	—
Depth of endocranial cast above pituitary body	41.0	—
Depth of endocranial cast including the pituitary body	76.0	—
Greatest width of olfactory lobes	33.5	—
Greatest depth of olfactory lobes	19.0	—
Width across cerebral processes	44.5	—
Greatest width across cerebellum	29.0	—
Width of medulla oblongata at posterior base of hypoglossal nerves	28.0	—
Depth of medulla oblongata at posterior bases of hypoglossal nerves	25.0	—
Cubic capacity of endocranial cast without semicircular canals and nerve extensions	99 cubic cm.	—
$\frac{\text{Width across squamosals} \times 100}{\text{Median length of skull}}$	56.542	61.458
$\frac{\text{Height from bottom of occipital condyle} \times 100}{\text{Median length of skull}}$	49.844	54.687
$\frac{\text{Width across squamosals} \times 100}{\text{Basal length}}$	98.910	96.721
$\frac{\text{Height from bottom of occipital condyle} \times 100}{\text{Basal length}}$	87.193	86.065
$\frac{\text{Length of frontoparietal area} \times 100}{\text{Basal length}}$	102.724	106.557
$\frac{\text{Width of frontoparietal area} \times 100}{\text{Basal length}}$	71.934	72.131

COMPARATIVE MEASUREMENTS AND INDICES

	P. grangeri	*Troödon validus*
Height of dome above endocranial cavity / Basal length	60.490	—
Width of frontoparietal area / Length of frontoparietal area	70.026	67.692
Height of dome above endocranial cavity ×100 / Length of frontoparietal area	58.886	—
Height of dome above endocranial cavity ×100 / Width of frontoparietal area	84.091	—
Thickness of frontals where in contact with nasals ×100 / Width of frontals where in contact with nasals	111.111	—
Depth of face ×100 / Basal length	36.784	53.279
Postorbital length / Basal length	68.665	59.836
Antorbital length ×100 / Basal length	53.133	51.639
Length of endocranial cast ×100 / Basal length	44.141	—

Pachycephalosaurus wyomingensis
(Gilmore), 1931

Troödon wyomingensis, GILMORE, 1931, Proc. U. S. Natl. Mus., vol. 79, art. 9, pp. 1–6, pls. 1–5; GILMORE, 1936, Ann. Carnegie Mus., vol. 25, pp. 109–112, figs. 1–3.

TYPE: U.S.N.M. No. 12031, a well-preserved, fragmentary, frontoparietal area with squamosals and part of the occipital region. Collected by G. F. Sternberg, 1930.

HORIZON AND LOCALITY: Lance formation. Nine miles southwest of Warren P.O., Buck Creek, Niobrara County, Wyoming.

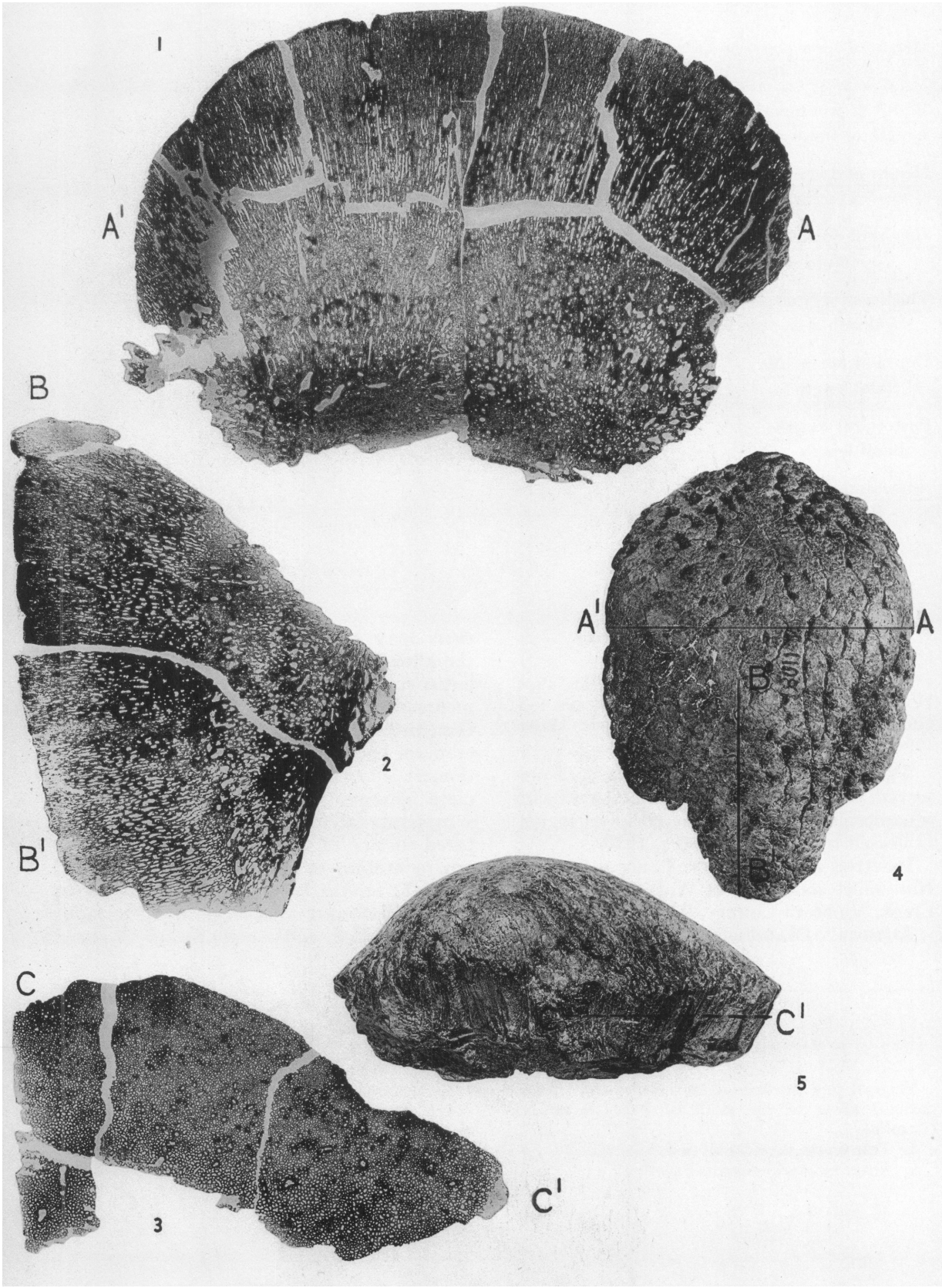
AUTHOR'S DIAGNOSIS: "*Troödon wyomingensis* may be at once distinguished from the known species of the genus by its much larger size. Judging by the few skull measurements obtainable, the type specimen is more than twice the size of the largest *T. validus* cranium known from the Belly River formation. It is further distinguished by the complete closure, by dermal bones, of the supratemporal fossae, the smooth unsculptured surface of the dome, and the simpler ornamentation of the cranium throughout. From *T. validus* Lambe it differs further in having a flattened supraoccipital area without a median ridge, and a more steeply inclined

PLATE 43

Vertical and horizontal sections of the frontoparietal areas of the skull of *Troödon validus* (Lambe).

1. Transverse vertical section.
2. Anteroposterior vertical section.
3. Anteroposterior horizontal section.

4–5. Dorsal and lateral views of frontoparietal region of a young skull, G.S.C. No. 1108, showing the locations of the sections illustrated in figures 1 to 3.


1
A'
A
B
2
B'
A'
A
B
B'
4
C
C'
5
3
C'


1
2

parietal region posterior to the dome, the latter making quite a difference in profile when viewed from the side" (Gilmore, 1931, p. 4).

REVISED DIAGNOSIS: Frontoparietal area low and only moderately thickened. A low parieto-squamosal shelf. Frontals low and fairly broad where in contact with the nasals. Distance from occipital condyle to posterior margin of skull short.

DISCUSSION: The type of this species represents a fully adult individual. Gilmore (1931) has described it thoroughly, and in addition has described (1936) the dome area of an immature individual (C.M. No. 3180) which he has rightfully referred to this species. A third specimen that consists of the major portion of the frontoparietal area of an adult in the Colorado Museum of Natural History (No. 470) is referable to this species. This specimen represents an adult and was collected from the Lance formation of Corson County, South Dakota.

Two other fragments which we also refer to this species are:

U.S.N.M. No. 7806. Two incomplete bone fragments collected from the Lance formation, Niobrara County, Wyoming.

U.S.N.M. No. 8295. A fragment of the posterior corner of the squamosal. Lance formation. Seven Mile Creek, Niobrara County, Wyoming.

In so far as it is known, *Pachycephalosaurus wyomingensis*, principally because of its less vaulted and relatively broader frontoparietal area and its low parieto-squamosal shelf, seems to represent a species that is somewhat less specialized than *P. grangeri*.

Pachycephalosaurus reinheimeri,[1] new species

TYPE: Colo. Mus. No. 469, frontoparietal area with parts of the squamosals and nasals preserved. Collected by Philip Reinheimer, 1922.

HORIZON AND LOCALITY: Lance formation. Near southwest corner of sec. 25, T. 20 N., R. 21 E., Corson County, South Dakota.

DIAGNOSIS: Frontoparietal area very low, broad, and shallow. Prominent parieto-squamosal shelf, with the posterior margin nodose and medially deeply notched. Frontals low and narrow where in contact with the nasals.

The type and only known specimen of this species represents a fully adult individual. In size it is approximately the same as *P. wyomingensis*. The dorsal surface of the frontoparietal area is smooth, as in all the known forms referable to *Pachycephalosaurus*. Of the diagnostic features given above the one that is unique is the nodose posterior margin of the skull with the deep median notch. This is in striking contrast to the condition in *P. grangeri*, in which the posterior margin of the skull curves posteriorly in the median area. In *P. wyomingensis* the posterior margin is slightly concave, and in both species this margin is smooth in the adult stage.

The postero-external corner of the squamosal has the usual welt-like nodes, but their arrangement is totally different than in the other species. There are seven subequal nodes. One occupies a central position with the other six arranged around it in circular fashion. (See pl. 42.)

Pachycephalosaurus reinheimeri is most closely related to *P. wyomingensis*, but presumably is an aberrant form that had digressed considerably from the main line of *Pachycephalosaurus* evolution.

MEASUREMENTS

Greatest width across squamosals	344 mm.
Greatest width of the frontoparietal area	270
Greatest length of the frontoparietal area	305
Height of the dome above the dorsal surface of the endocranial cavity	158

[1] Named for Mr. Philip Reinheimer, discoverer of the type.

PLATE 44

Troödon validus (Lambe), Univ. Alberta No. 2.
1. Skull, dorsal view.
2. Skull and jaw, lateral view of left side.
Both figures ×¾.

Pachycephalosaurus sp.

Triceratops, MARSH, 1896, 16th Ann. Rept. U. S. Geol. Surv., 1894–1895, pt. 1, p. 214, figs. 11–12, pl. 70.

Ceratopsian, HATCHER, MARSH, AND LULL, 1907, Monogr. U. S. Geol. Surv., vol. 49, p. 65, fig. 74.

THE SPECIMEN: Y.P.M. No. 335, the postero-external corner of the left squamosal of an immature individual.

HORIZON AND LOCALITY: Lance formation. Lance Creek, Niobrara County, Wyoming. Collected by J. B. Hatcher.

DISCUSSION: This specimen was described and figured by Marsh (1896, p. 214, figs. 11–12, pl. 70) who considered it as dermal ossification of *Triceratops*. Hatcher (1907, p. 65) was not so definite about its determination but favored assignment to the Ceratopsia.

The specimen possesses the expectable nodes characteristic of the *Pachycephalosaurus* squamosal. It is unique, however, in having the central node, around which ten other nodes are clustered, developed into a short horn-like structure. This "horn," as preserved, stands 2½ inches above its base, and at least ½ inch more is broken away from its tip. The specimen represents an immature individual which means that in the adult stage the "horn" would probably be at least 5 or 6 inches long. In all the known species of *Pachycephalosaurus* the main cluster of nodes on the squamosal are always subequal in size and are never more than 1½ inches long in the adult stage. (Pl. 40, fig. 2.)

This specimen may well represent a new species of *Pachycephalosaurus*, but we feel that a new species should not be founded on such fragmentary material.

THE ORIGIN OF THE DOME OF THE TROÖDONT DINOSAUR SKULL

The problem of the composition of the bone which forms the dome-like mass of the troödont skull has received considerable attention in the literature on troödonts. Hatcher (1907, p. 98) believed that " . . . the different bones of this region have been greatly reinforced from above by the coalescence of dermal ossifications which rise in a dome-shaped mass above the brain case, completely enveloping the cranial elements of this region and thus giving great additional strength to the cranium." Gilmore (1924, p. 12) at first thought that this dome-like mass was " . . . brought about by a great thickening of the parietal and frontal bones." Later, however (1931, p. 3), he felt that " . . . the dome, after all, may not be a thickening of the parietal and frontal bones, as formerly thought, but is a concentration of a series of dermal ossifications that have become fused, not only to one another but to the underlying skull elements." In a cursory comparison of the *Troödon* cranium with that of *Ankylosaurus*, Russell (1932, p. 336) says, "*Troödon*, however, appears to have the cranial bones themselves greatly thickened and still forming the dorsal surface of the skull, as can be seen in the fractured edges of the rather common fronto-parietal masses." To this, Sternberg (1933, p. 232) adds, "The thick parieto-frontal mass seems unquestionably to be the result of a thickening of the cranial bones, and not the addition of dermal ossification as is the case with the nodosaurs."

It was our feeling that thin sections of the frontoparietal area for a microscopic investigation would be valuable in considering the origin of this unique dome-like structure of the skull. We selected, therefore, a very well-preserved frontoparietal area of an immature individual of *Troödon validus* (G.S.C. No. 1108) which is shown in plate 43, figures 4, 5. With the permission of the Geological Survey of Canada we had three thin sections made from the specimen. One is a transverse vertical section made just in front of the frontoparietal suture, another is a longitudinal vertical section through the right frontal, and the third is a horizontal section made through the left frontal. Enlarged photographs of these sections are reproduced in plate 43, figures 1 to 3. The purpose of making these sections was three-fold: first, to determine if the frontoparietal suture and the suture between the frontals extend up through the dome mass; second, to determine the struc-

ture of the bone; and third, to ascertain whether or not there was a distinct lower zone of bone, representing the frontals and parietals, on which the overlying bony substance forming the dome was built.

This specimen shows beyond question that the frontoparietal suture and the suture between the frontals extend up through to the very surface of the dome. This is also substantiated in three other specimens of *Troödon validus* (G.S.C. Nos. 2369 and 2379, and specimen No. 684 in the collection of Mr. Roy L. Fowler of Aldersyde, Alberta, Canada). In all three the sutures are clearly shown extending up through the dome.

The horizontal section through the left frontal (pl. 43, fig. 3, C) shows numerous nutrient canals and the typical cellular structure of the bone. There is not the slightest bit of evidence that this bone is composed of the " . . . concentration of a series of dermal ossifications that have become fused . . . ," as Gilmore suggested. The transverse vertical section shows the radiating structure of the outer area of the dome that is so clearly shown in all the specimens. Because of this radiating structure, the bone is somewhat denser about halfway down in the dome where the many small columns of bone merge. This section and the anteroposterior vertical section through the right frontal (see pl. 43, fig. 2, A and B) show that the lower area is more vascular than the upper area. These sections show no evidence whatsoever of a ventral layer of bone representing the frontals to which an overlying bony substance has been fused.

The structure of the dome of *Troödon validus* is homologous with that of all the troodonts, and because of the evidence cited above it is clear that the dome of the troodont skull has resulted simply as an upgrowth of the roof bones of the skull, principally the frontals and parietals.

THE TROÖDONT DINOSAUR SKELETON

The only recorded troödont skeletal remains were found with the nearly perfectly preserved skull and jaws of *Troödon validus* (Univ. of Alberta No. 2) frequently referred to above. They consist of eight caudal and two dorsal vertebrae; a large number of ribs; many abdominal ribs; a scapula and coracoid; a humerus, ulna, and radius; an excellently preserved ilium and ischium; a femur, tibia, and fibula; and a considerable portion of the hind foot. This material has been thoroughly described and figured by Gilmore (1924).

General features of the *Troödon validus* skeleton indicate that it was quite a primitive ornithischian. This fact has caused some, notably Nopcsa (1929 and 1931), to doubt that the skeletal remains belong with the rather highly specialized skull. Both Russell (1932) and Gilmore (1936) have replied to Nopcsa quite adequately on this point. Indeed, it is not unusual in vertebrates that the skull becomes more specialized than the postcranial skeleton. In *Protoceratops*, for example, the postcranial skeleton is predominantly that of a primitive ornithischian, while the skull is equally as specialized along certain lines as is that of *Troödon*. Many other such examples could be cited.

Perhaps the most noteworthy feature of the *Troödon* skeleton, as known, is the close resemblance to that of the primitive Ceratopsia. This is reflected particularly in the vertebrae and in the pectoral girdle. An unusual feature of the dorsal vertebrae, as Gilmore (1924) has shown, is the tongue and groove articulation of the zygapophyses. It is interesting to note that there is also an indication of this in some of the *Protoceratops* dorsals. The compressed neural spines and the general form of the dorsals and caudals are also suggestive of *Protoceratops*. A greater similarity, however, is shown in the pelvis, of which only the ilium and the ischium are known in *Troödon*. The only real difference between the ilium of *Troödon* and that of the Protoceratopsidae is that the dorsal margin is somewhat broadened and possesses a slight inward projection at the front of the postacetabular portion. It is identical in all other features. The ischium of *Troödon* is decidedly protoceratopsian throughout. This is especially true in its relatively great length, its

downwardly curved form, its slenderness, and its somewhat expanded distal end. All these similarities, and the camptosaurid characters pointed out by Gilmore (1924), displayed in the limbs, suggest a closer relationship to the Ceratopsia-Ornithopoda line than to the Stegosauria-Nodosauria group.

AFFINITIES OF THE TROÖDONT DINOSAURS

As a result of his study of *Troödon validus*, Gilmore (1924) concluded that the troödonts were more closely related to the Ornithopoda than to any of the other known dinosaurs. Several workers on the troödonts, such as Russell (1932) and Sternberg (1933), agree with Gilmore's conclusion, while others favor an assignment of the Troödontidae to the Nodosauria. Gregory (*in* Osborn, 1924, p. 10) states that "*Troödon* of the Lance (Upper Cretaceous) is far more primitive than the ankylosaurs of older formations," but gives no reasons for this inferred relationship. Romer (1927, p. 228) places the family Troodontidae under the Ankylosauria [=Nodosauria] and on the basis of characters shown in the ilium and ischium concludes (p. 272): "The writer has provisionally associated *Troödon* with the ankylosaurs. It is still a biped, and thus seems an anomaly in a group of heavy quadrupeds. But the structure of the pelvic girdle seems suggestive, at least, of the conditions to be expected in a primitive ankylosaur . . . ." Nopcsa (1929, 1931) is very firm in his opinion that the specimen described by Gilmore in 1924 is a composite, consisting of a nodosaur skull, the postcranial skeletal parts of an unnamed ornithopod, and some fish bones which Gilmore considered as parts of the abdominal cuirass. These conjectures have been answered quite adequately by Russell (1932).

A careful analysis of all the troödonts shows that nearly all the nodosaur resemblances they possess are superficial. The thickening of the skull roof and the development of excrescences on the skull are nodosaur-like in general appearance only. In the troödonts, as shown above, these are accomplished by thickening of the skull bones, while in the nodosaurs numerous separate scute-like dermal elements become adhered to the underlying skull bones.

As stated previously, the one character which is common to both the troödonts and nodosaurs is that the olfactory lobes are enclosed by a thick wall of bone. This feature seems to be correlated in some way with the unusual skull thickening in both groups and is of no special taxonomic significance, since the endocranial casts of the two groups are so very dissimilar. The endocranial cast of *Pachycephalosaurus* is definitely closer to that of the ceratopsians and ornithopods.

As far as the teeth are concerned, there is no record of premaxillary teeth in any nodosaur, and the tendency in that group is for tooth reduction. The early troödonts have premaxillary teeth, and the tendency is for the maxillary teeth to increase in number in the later forms. Furthermore, the tooth pattern of the troödonts is distinct, and the closest approximation to it is found among the early ornithopods.

Although no postcranial elements are known in *Pachycephalosaurus* from the uppermost Cretaceous, evidence shown in the basicranial area of the skull indicates that this form was even more adapted to a bipedal habit than *Troödon*. The occipital region is even more steeply inclined, and the foramen magnum and occipital condyle are directed ventrally even more than in the earlier forms. As pointed out earlier, all the characters in the known portions of the *Troödon* postcranial skeleton definitely show an ornithopod-ceratopsian, rather than a stegosaur-nodosaur relationship.

Because the evidence in the known troodont material overwhelmingly favors an assignment of this group to the ornithopods, we, therefore, place the family Troödontidae in the suborder Ornithopoda.

A detailed comparison of *Troödon validus* and *Pachycephalosaurus grangeri* is given in one of the earlier sections of this paper. An analysis of this comparison shows that the following main evolutionary changes have taken place in the troödont skull:

1. There is an increase in linear size of more than three times.
2. The frontoparietal area shows a mod-

erate to extreme thickening, which has changed considerably the form of the surrounding bones.

3. There is a strong development of the node-like ornamentations of the skull.

4. The face becomes narrow and shallow.

5. The supratemporal fenestrae are always completely obliterated in the adult.

6. The premaxillary teeth are probably lost, and there is an increase in number of maxillary teeth. The general tooth pattern, however, remains virtually the same.

7. The foramen magnum becomes rounded and relatively smaller, and it, together with the occipital condyle, becomes more ventrally directed.

8. The basicranial area becomes relatively shorter.

Using these changes and other characters shown in the various forms as criteria, the relationship of the troödont species may be summarized as follows:

1. *Troödon validus* is an ideal forerunner for all the later forms. It possesses not a single character which would eliminate it from such a position. *T. formosus* is so slightly known that its position in the scheme of troödont evolution cannot be determined. It certainly seems closer to *T. validus* than to any of the others.

2. *T. edmontonensis* is an archaic form that has persisted into uppermost Cretaceous time. It has stayed primitive mainly in such features as its small size, the low, gently arched frontoparietal area, and in the lack of sharp demarcation of the position of the frontals that are in contact with the nasals. It has digressed, however, from the primitive stage in such features as the oval form of the frontoparietal area, the relative increase in size and form of the endocranial cavity, and in the straightness of the base of the parietals behind the endocranial cavity.

3. *T. sternbergi* represents an ideal intermediate stage between *T. validus* and *Pachycephalosaurus*, although it is definitely closer to *T. validus*. This species has remained primitive in its relatively small size, although it has progressed in this respect, as it is larger than any other known species of *Troödon*. The low frontoparietal area is also primitive. Broadening in this area, however, and the proportionate increase in width between the orbits on the base of the frontals are progressive characters.

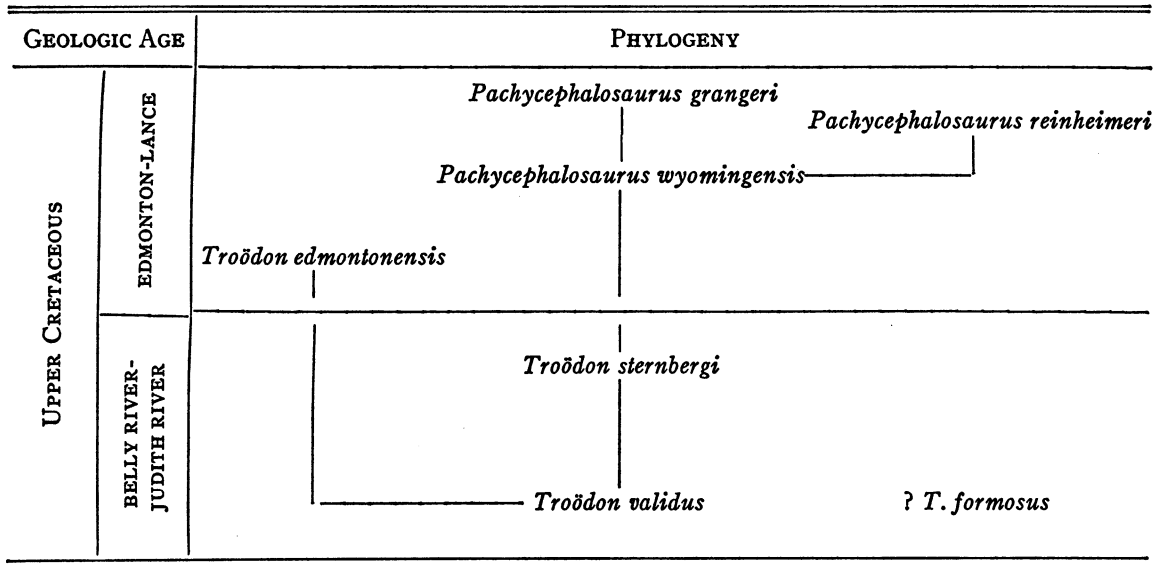
4. *Pachycephalosaurus* shows a marked advance beyond the *Troödon* stage. This is especially shown in the striking increase in size, the extreme thickening in the frontoparietal area, the strong development of the node-like ornamentations, the complete obliteration of the supratemporal openings, the development of a narrow and shallow face, and in the probable loss of premaxillary teeth.

5. *P. grangeri*, on the basis of our present information, represents the climax in troodont evolution. This species has progressed beyond the other known forms in such features as the high-arched and extremely thickened frontoparietal area, the lack of any trace of the parieto-squamosal shelf, the great increase in depth and narrowness of the frontals where they are in contact with the nasals, and the increase in the extent of the skull behind the occipital condyle.

6. *P. wyomingensis* is definitely less specialized than *P. grangeri*. This is shown principally by the less vaulted and relatively broader frontoparietal area and the presence of a low parieto-squamosal shelf. This species forms an excellent structural ancestral stage for *P. grangeri*.

7. *P. reinheimeri* is primitive in its low, broad, and shallow frontoparietal area. The parieto-squamosal shelf is not so prominent as in *P. wyomingensis*, in which feature it is somewhat more specialized. On the other hand, *P. reinheimeri* is much more specialized in the nodose posterior margin of the skull with the very deep median notch. An evaluation of these characters seems to indicate that *P. reinheimeri* is, structurally at least, an aberrant form derived from the *P. wyomingensis* stock.

The above conclusions on the phylogeny of the troödont species are graphically shown in the accompanying diagram.



Phylogeny of the troödont dinosaur species.

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