

A TAXONOMIC REVIEW OF THE PACHYCEPHALOSAURIDAE (DINOSAURIA: ORNITHISCHIA)

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Abstract—The order “Pachycephalosauria” and the family Pachycephalosauridae are re-evaluated and determined to include the same taxa. They are thus of equal rank and redundant, so only the latter taxon is recognized, the former one being redundant. The family Pachycephalosauridae includes the so-called “flat-headed” and “dome-headed” morphotypes. *Stenopelix valdensis* is removed from the “Pachycephalosauria” and is considered to be an indeterminate ornithischian dinosaur. The North American taxa *Colepiocephale lambei*, *Stegoceras validum*, *Prenocephale brevis*, *P. goodwini*, *P. edmontonensis*, and *Hanssuesia sternbergi* are valid taxa. All species of the genus *Prenocephale* are distinguished by a single row of nodes on the lateral and posterior side of the squamosals. *Alaskacephale gangloffii*, n. gen. and sp., is a distinct taxon based on a squamosal characterized by two diverging row of nodes. The flat-headed Asian taxa *Goyocephale lattimorei*, *Tylocephale gilmorei* and *Homalocephale calathocercos* are considered valid pachycephalosaurids, although the validity of *G. lattimorei* is somewhat problematic. The node-based taxa *Goyocephalia*, *Homalocephaloidea* and *Tholocephalidae* are rejected as unsubstantiated typological conventions. *Wannanosaurus yangi* is considered Pachycephalosauridae *incertae sedis*. The distinctive corner node seen in such taxa as *Prenocephale* and *Homalocephale* is homologous with the large, hypertrophied central spike emanating from the squamosal in *Stygmoloch* and *Dracorex*. The holotype of *Tylosteus ornatus*, a small squamosal with broken spike-like nodes and low bulbous nodes, is not referable to *Pachycephalosaurus wyomingensis*, but rather is consistent with the ornamentation of *Dracorex hogwartsia*. The taxon *Ferganocephale adenticulatum* from the Middle Jurassic of Central Asia is not a “pachycephalosaur” and is considered to be a *nomen dubium*. A robust cladistic analysis of the Pachycephalosauridae is not presently possible due to uncertainty in the polarities of characters.

INTRODUCTION

Pachycephalosaurids are a group of ornithischian dinosaurs, commonly referred to as the “dome-headed dinosaurs,” which are known mostly from specimens found in western North America (including Alaska) and a few from Asia. Most pachycephalosaurid remains are incomplete, usually consisting of portions of the frontoparietal bone that forms the distinctive dome (in some taxa), often making taxonomic identification a challenging task. A few taxa are known from complete, or nearly complete, skulls, but only a handful of pachycephalosaurid taxa (e.g., *Stegoceras validum*, *Homalocephale calathocercos*, *Prenocephale prenes*) are associated with meager postcranial remains. The postcranial remains have not been fully utilized in the diagnoses of pachycephalosaurid taxa and will probably become more important as more detailed and comparative material becomes available. However, for the moment, the taxonomy of genera and species within the Pachycephalosauridae rests solely on the assessment of cranial characters. Over the years numerous pachycephalosaurid genera and species have been named on the basis of isolated and incomplete material, consequently the group has had a rather volatile and contentious taxonomic history. This has been further complicated by diverse interpretations of ontogenetic and sexual features. A number of new *Stygmoloch*-like specimens have been discovered within the last decade, some of which are in private collections and have yet to be described, but are known to display a mosaic of primitive and derived characters. The new pachycephalosaurid, *Dracorex hogwartsia* Bakker et al., 2006 lacks the distinctive dome, a feature that has long characterized the Pachycephalosauridae, and has well-developed supratemporal fenestrae and a heavily armored skull. Taking all these new specimens into consideration, it seems that a redefinition of the family is in order.

Recently there has been a number of critical papers dealing with “pachycephalosaur” and pachycephalosaurid dinosaurs, notably Averinov et al. (2005), Gangloff et al. (2005), Ryan and Evans (2005), Sereno (2000),

Sullivan (2000, 2003, 2005), and Williamson and Carr (2002). The most recent review of the group, presented by Maryańska et al. (2004) in the revised edition of *The Dinosauria*, is seriously flawed. A subsequent reassessment of some pachycephalosaurid genera and species by Ryan and Evans (2005), which is based on “conflicts” in phylogenetic analyses (i.e., Williamson and Carr, 2002 vs. Sullivan, 2003), does not provide a sufficient rationale for making taxonomic decisions. This latter contribution is typological in its approach and treats both competing phylogenetic analyses as equal, which they are not. Moreover, cladograms are hypotheses of relationships and are only as good as the data upon which they are based. They are not intended to be tools for establishing or synonymizing taxa. Lastly, there are some new contributions to the Pachycephalosauridae that are published in this volume (Bakker et al., 2006; Sullivan and Lucas, 2006a) that are assessed and commented on.

The purpose of this paper is to provide a brief review of the current state of the alpha taxonomic status of taxa previously attributed to the “Pachycephalosauria” and to briefly comment on problems dealing with aspects of various ontogenetic and phylogenetic analyses concerning taxa that comprise the Pachycephalosauridae.

In this paper, the institutional abbreviations are: ANSP = Academy of Natural Sciences, Philadelphia; CMN = Canadian Museum of Nature, Ottawa; GI SPS = Geological Institute, Section of Palaeontology and Stratigraphy, Academy of Sciences, Ulaanbaatar, Mongolian People’s Republic; GPI Gö = Geologisch-Paläontologisches Institute of the Georg-August-Universität, Göttingen; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology (Beijing); MPM = Milwaukee Public Museum (Milwaukee); BMNH = Natural History Museum (London); NMMNH = New Mexico Museum of Natural History and Science (Albuquerque); ROM = Royal Ontario Museum (Toronto); TMP = Royal Tyrrell Museum of Palaeontology, Drumheller; UALVP = University of Alberta, Laboratory of Vertebrate Paleontology, Edmonton; UAM = University of Alaska Museum - Earth Sciences Collections, Fairbanks; UCMP = University of Cali-

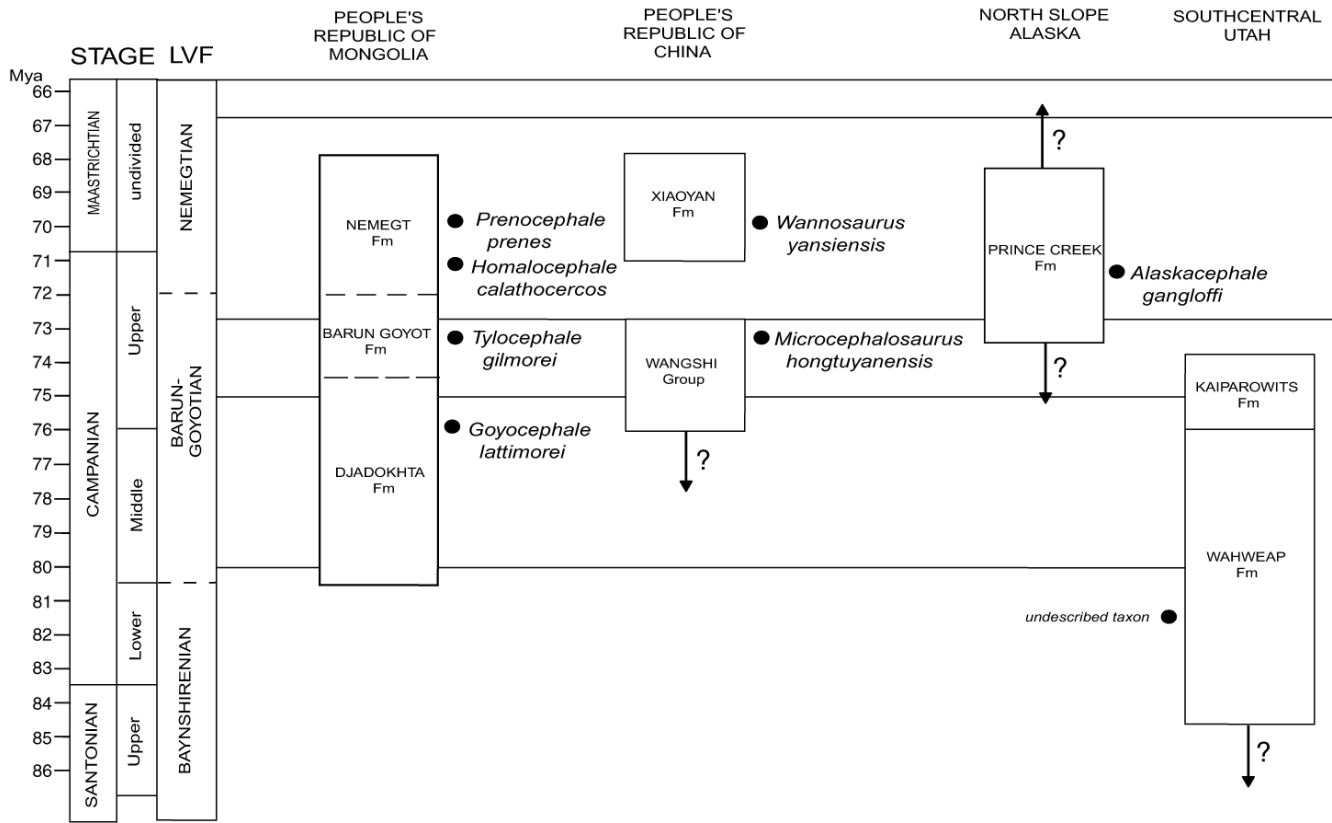


TABLE 13. Stratigraphic distribution of valid pachycephalosaurid taxa (including taxa regarded as *incertae sedis*, see text). Stratigraphic data compiled from Sullivan (2003) and Sullivan and Lucas (2006b).

ifornia, Museum of Paleontology, Berkeley; USNM = United States National Museum, Washington, D.C.; YPM = Peabody Museum of Natural History, Yale University, New Haven; Z. Pal = Palaeozoological Institute, Polish Academy of Sciences, Warsaw; and ZIN PH = Zoological Institute, Russian Academy of Sciences, Paleoherpological Collection, Saint Petersburg.

TAXONOMY

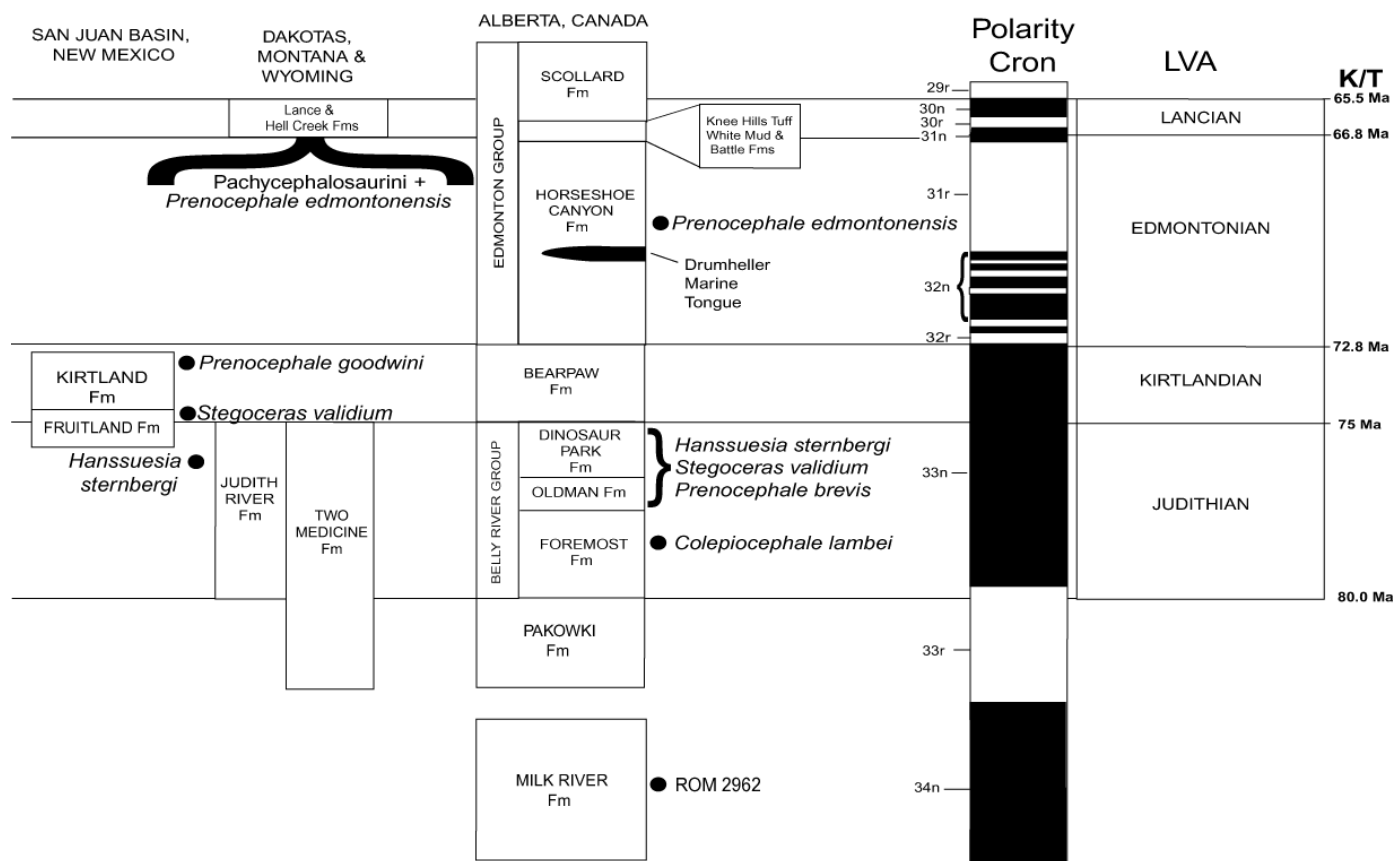
Status of the Taxon “Pachycephalosauria”

The “Pachycephalosauria” was defined by Maryańska and Osmólska (1974, p. 50) as having the same diagnosis as the family Pachycephalosauridae. This dual taxonomic rank is considered to be redundant and thus has no phylogenetic value. However, recent cladistic analyses, notably that of Sereno (2000), have sought to validate the order by recognizing various “primitive” or “basal” sister taxa outside the Pachycephalosauridae. However, all the “primitive” or “basal” taxa (*Wannosaurus yansiensis*, *Goyocephale lattimorei*, *Homalocephale calathocercos*) are true pachycephalosaurids and cannot be distinguished by characters (such as flat skull and open supratemporal fenestrae) as being sister taxa to the Pachycephalosauridae. Indeed, all of these so-called “basal” taxa are problematic and, in my opinion, a reanalysis of characters (especially in the light of the new discoveries, discussed below), suggest these so-called “sister taxa” are nested within the clade Pachycephalosauridae. Therefore, a redefinition of the Pachycephalosauridae is

needed and is presented below based on new information and reanalysis of plesiomorphic versus synapomorphic characters. The previous abandonment of the “Homalocephalidae” of Dong (1978) by recent workers (e.g., Sereno, 2000), coupled with the recent suggestion that the so-called primitive characters seen in monotypic taxa such as *Wannosaurus*, *Goyocephale* and *Homalocephale*, suggests they may be secondarily derived or paedomorphic (Sullivan, 2005). Undoubtedly, redefining the family Pachycephalosauridae has profound implications and further undermines the concept of the Marginocephalia. Also, the subfamily “Pachycephalosaurinae,” defined by Sereno (2000) as being “fully-domed,” can no longer be supported in view of the new data presented below. Although the genera of pachycephalosaurids defined herein are certain, their respective positions to one another within the clade remain equivocal.

Status of *Stenopelix valdensis* Meyer, 1857

Comments—The holotype of *Stenopelix valdensis* is based on an incomplete postcranial skeleton from the Wealden (Lower Cretaceous) of northwestern Germany (Meyer, 1857; Sues and Galton, 1982). The taxon has had a rather tumultuous history with regard to its dinosaurian affinities (see Galton and Sues, 1982, for complete review). Suffice it to say, Maryańska and Osmólska (1974) were the first to consider it to be a member of the Pachycephalosauridae based on: (1) the exclusion of the pubis from the acetabulum and; (2) the presence of strong caudal ribs. Sues and Galton (1982) demonstrated that the “pubis” was part of the acetabulum and that the so-called “caudal ribs” were, in fact, sacral ribs. Moreover,



Sues and Galton (1982) showed that the curvature of the ischium, and the absence of an obturator foramen, were primitive features seen outside the Pachycephalosauridae. Based on the morphology of the ilium coupled with the reduction of the pubis, they considered *Stenopelix valdensis* to be a ceratopsian (i.e., the monophyletic clade of the Psittacosauridae + Protoceratopsidae + Ceratopsidae), and formally placed it in *Ceratopsia incertae sedis* (Galton and Sues, 1982).

Sereno's (2000) analysis placed *Stenopelix valdensis* as the most basal "pachycephalosaur" based on: (1) elongate posterior sacral ribs; (2) strap-shaped distal end of the scapular blade; and (3) distal expansion of the preacetabular process of the ilium. These features are not readily preserved in most pachycephalosaurid specimens, and their absence and/or presence in non-pachycephalosaurid taxa are not well-established. Therefore, I regard these as weak criteria for supporting "pachycephalosaur" affinities. Moreover, Sereno's (2000) comment regarding the potential "pachycephalosaur"-ankylosaur synapomorphy (exclusion of the pubis from the acetabulum) (Coombs, 1979), as not being present in the "most primitive pachycephalosaur" (i.e., *Stenopelix valdensis*) and absent in thyreophoran outgroups, is a circular argument predicated on the acceptance of *Stenopelix valdensis* as a "pachycephalosaur." I find Coombs (1979) analysis equally, if not more, compelling. Therefore, I consider *Stenopelix valdensis* Ornithischia *incertae sedis*.

Pachycephalosauridae

Revised diagnosis—Ornithischian dinosaurs with thickened, fully-flat or incipiently to fully-domed frontoparietals, broad and flattened postorbital-squamosal bar; supratemporal fenestrae absent to well-developed; broad exposure of the occiput; quadrate and ventral surface of squamosal (occipital plate) directed anteroventrally; squamosals developed into deep plates on the occiput with greatly enlarged upper-outer corners; two supraorbital elements lateral to the frontal; arched premaxillary-maxillary diastema; broad postorbital-jugal bar, plate-shaped basal tubera, variably developed nodes on the squamosal (either in rows or clusters), nasals and other parts of the skull.

Comments—The most recent definition for the Pachycephalosauridae was provided by Sereno (2000) and it was followed by Sullivan (2000, 2003) and Williamson and Carr (2002). Because the taxonomy has been predominantly based on features of the skull, I here restrict the revised diagnosis to only include cranial characters. Postcranial remains are rare and mostly incomplete where known. The defining character, doming of the frontoparietal, was considered to have occurred only once (Sereno, 2000), and it was the key synapomorphy that neatly clustered domed vs. non-domed "pachycephalosaurs." Sereno (2000) and Sullivan (2003) considered *Stegoceras* (i.e., *Stegoceras validum*) to be transitional between the fully-domed "Pachycephalosaurinae" and the "primitive," flat-headed taxa. However, because the appearance of "flat-headed" pachycephalosaurids occurs late in the stratigraphic record in both

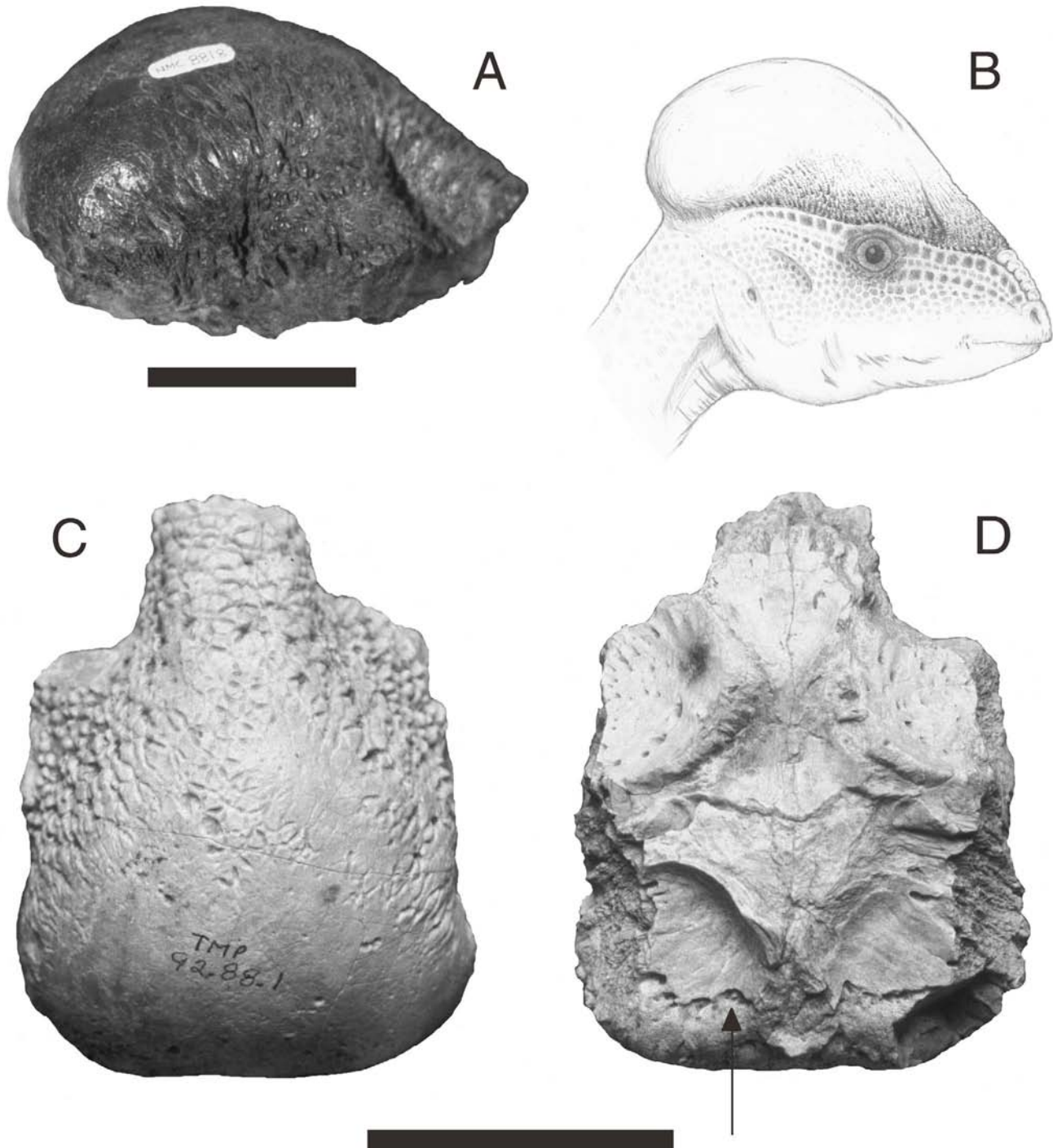


FIGURE 1. *Colepiocephale lambei* (Sternberg, 1945). **A**, CMN 8818 (holotype), nearly complete frontoparietal dome; **B**, artist restoration of *Colepiocephale lambei* by Denver Fowler; **C-D**, TMP 92.88.1, nearly complete frontoparietal dome. **C**, dorsal view; **D**, ventral view. Arrow indicates position of one of the vestigial nodes. Bar scale = 5 cm.

Asia and North America, a more critical assessment of the doming in these dinosaurs is warranted (see Table 1).

The recent recovery of the flat-headed *Dracorex hogwartsia* (Bakker et al., 2006), as well as the recent discoveries of additional, incipiently domed, *Stygimoloch* specimens from the late Maastrichtian of North America, suggests that being “domed” is no longer a viable character for this clade. This conclusion is reinforced by the fact that many of the so-called flat-headed types (*Wannanosaurus*, *Goyocephale*, *Tylocephale*) are also from

late Campanian-late Maastrichtian strata (see below). In fact, the original definition of the Pachycephalosauridae by Maryańska and Osmólska (1974, p. 50), “flat to dome-like” is more correct. Moreover, the typological assessment of Sereno (1986), recognizing the Goyocephalia (= Goyocephala of Maryańska et al., 2004), Homalocephaloidea and Tholocephalidae, and their variants (see Maryańska et al., 2004) is rejected because they are node-based taxa whose relationships have not been unequivocally substantiated. Moreover, they are considered to be taxa of the Pachycephalosauridae as

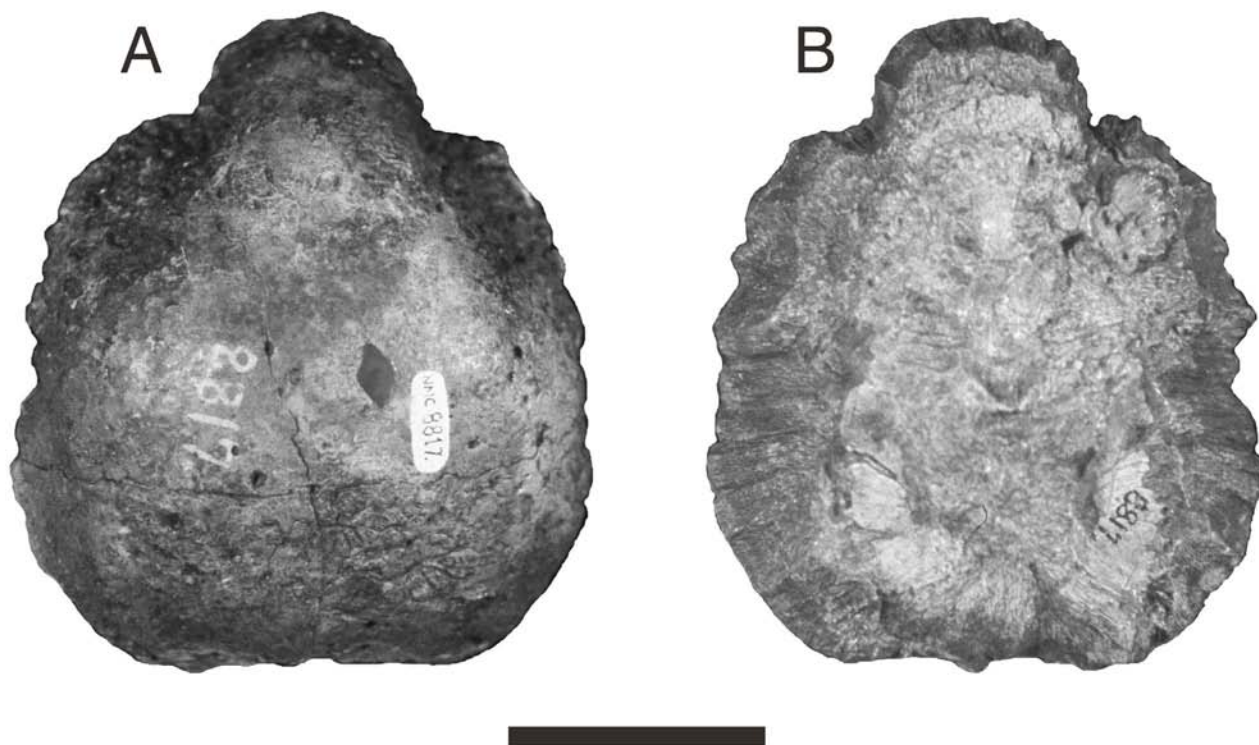


FIGURE 2. *Hanssuesia sternbergi* (Brown and Schlaikjer, 1943). CMN 8817 (holotype), frontoparietal dome. **A**, dorsal view; **B**, ventral view. Bar scale = 5 cm.

defined in this paper. Taxa such as *Ornatoholus browni*, included in the Homalocephaloidea by Maryañska et al., (2004), is considered a juvenile of *Stegoceras validum* (Sullivan, 2003, 2005; Sullivan and Lucas, 2006a).

The alternative hypothesis, that these flat-headed taxa (*Homalocephale* or *Dracorex*) represent some primitive “ghost lineage,” can be dismissed on the grounds that these new forms co-existed with the incipiently domed *Stygimoloch*. Moreover, Sullivan (2003) pointed out that the oldest known bona-fide pachycephalosaurid (ROM 2962) is a small, fully-domed form. The broadening of the parietosquamosal shelf, opening of the supratemporal fenestrae, and loss of the well-developed dome, may be secondarily derived or may be paedomorphic (Sullivan, 2005). If so, then we are left with the situation that the family Pachycephalosauridae, and the order “Pachycephalosauria,” are one and the same. As pointed out by Sereno (2000), the establishment of the order “Pachycephalosauria” by Maryañska and Osmólska (1974) was an arbitrary “phenetic decision” not based on phylogenetic grounds. Moreover, the implications for the validity of the “Marginocephalia,” a group for which there has been weak support, would be profound: *the extension of the parietosquamosal shelf that obscures the occiput in dorsal view of the skull*, one of three, and arguably the most convincing, remaining synapomorphies, may be convergent and not homologous. Thus, the rationale for the group “Marginocephalia” is questionable. As suggested below, there is reason to believe that the development of the parietosquamosal shelf is secondarily derived in the Pachycephalosauridae and that it is not homologous with the condition seen in the Ceratopsia.

SYSTEMATIC PALEONTOLOGY

Pachycephalosauridae Sternberg, 1945

Alaskacephale, n. gen.

Type and only known species—*Alaskacephale gangloffii*, n. sp.

Diagnosis—Same as for species.

Age and Geographic Occurrence—late Campanian (?early Edmontonian), north slope of Alaska.

Etymology—The generic name is taken from the state of Alaska where the holotype is from; the term *cephale* is the common suffix used to denote members of the Pachycephalosauridae.

Alaskacephale gangloffii, n. sp.

Holotype—UAMAK-493-V-001, a nearly complete left squamosal.

Type Locality—North Slope Borough, Alaska.

Formation and Age—Prince Creek Formation, Colville Group; late Campanian (?early Edmontonian).

Diagnosis—A pachycephalosaur with two divergent rows of nodes on the squamosal, converging toward the midline of the skull; nodes with well-defined polygonal bases and prominent apices.

Etymology—The specific name honors Roland Gangloff who, in part, reported on the occurrence of the holotype and who has contributed significantly to our understanding of dinosaurs of the North American Arctic region.

Description—See Gangloff et al. (2005).

Comments—Gangloff et al. (2005) described the holotype, a nearly complete left squamosal, in detail and provided photographs and illustrations of the specimen. It is clear from both their description and figures that the specimen does not conform to any known genus or species of pachycephalosaurid, a fact noted by them. Among the key differences are: (1) the presence of two discrete divergent rows of nodes on the squamosal; and (2) the nodes have well-defined polygonal bases with prominent apices.

Gangloff et al. (2005) concluded that the quadrate appears to be sutured to the squamosal in a manner like that described by Galton and Sues (1983) for the genus *Pachycephalosaurius*. However, in all other pachycephalosaurids the proximal end of the quadrate is subtriangular, somewhat rounded, and lies in front the exoccipital where it joins with the

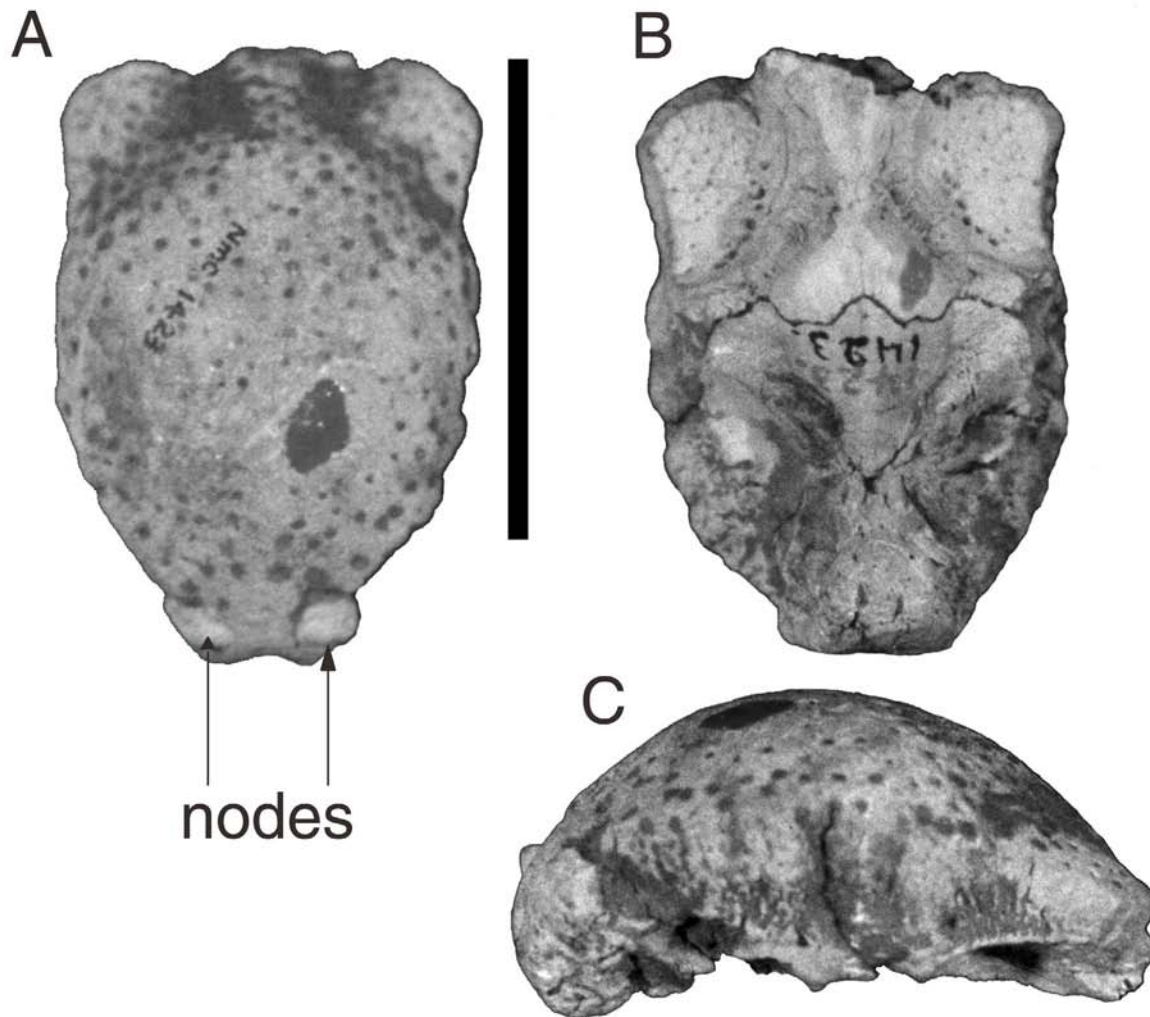


FIGURE 3. *Prenocephale brevis* (Lambe, 1918). CMN 1423 (holotype), frontoparietal. **A**, dorsal view; **B**, ventral view; **C**, right lateral view. Bar scale = 5 cm.

squamosal posterodorsally. The proximal end is surrounded by anteroventral and posteroventral projections of the squamosal, thus appearing to be firmly sutured. There is no evidence that this “suture” becomes interdigitated in any pachycephalosaurid and that it occurs far anterior to where it would normally join with the squamosal. This arrangement is seen in skulls of *Dracorex hogwartsia* (TCMI 2004-17-1), *Stegoceras validum* (UAVP-2), and the holotype skull (Z. Pal. MgD-1/104) of *Prenocephale prenes* (Fig. 4). It is unlikely, in my opinion, that the so-called “suture,” which is situated anteroventrally, reported in *Pachycephalosaurius wyomingensis* (Galton and Sues, 1983, fig. 1p), and in *Alaskacephale gangloffii* (Gangloff et al., 2005), is real. Rather, it represents a point of breakage along the lateral side of the quadrate, below where the proximal end of the quadrate articulates with the squamosal. Therefore, this condition is not a character that can be used to diagnose *Pachycephalosaurius* or any other pachycephalosaurid taxon.

***Colepiocephale lambei* (Sternberg, 1945)**

Synonyms—As per Sullivan (2003).

Holotype—CMN 8818, nearly complete frontoparietal (Fig. 1a).

Horizon/Stratum, Provenance and Age—Foremost Formation, Alberta; middle Campanian (early Judithian).

Comments—Sternberg (1945) named the species *Stegoceras lambei* based on CMN 8818, a nearly complete frontoparietal from the Foremost Formation (originally reported from the Oldman Formation) of

Alberta. Sullivan (2003) identified additional specimens of this species and noted that all the specimens of this taxon are from the Foremost Formation. The holotype and referred specimens are unique in the construction of the posterior parietosquamosal region and thus were referred to a new genus, *Colepiocephale* (Sullivan, 2003).

C. lambei is a nearly to fully-domed pachycephalosaurid characterized principally by the lack of a lateral and posteriosquamosal shelf, a strongly down-turned parietal, the absence of supratemporal fenestrae, and the presence of two incipient nodes tucked under the posterior-most margin of the parietosquamosal border as seen in TMP 92.88.1 (Fig. 1b). *Colepiocephale lambei* has the distinction of being the oldest known (middle Campanian) diagnosable pachycephalosaurid.

***Goyocephale lattimorei* Perle, Maryańska and Osmólska, 1982**

Holotype—GI SPS 100/1501, incomplete skull, mandibles with teeth and incomplete postcranial skeleton.

Horizon/Stratum, Provenance and Age—Upper Cretaceous (Boro Khovil), South Gobi Desert, Mongolia; middle to late Campanian (early-middle Barungoyotian).

Comments—Perle et al. (1982) named and described *Goyocephale lattimorei* based on an incomplete skull, mandibles with teeth and fragmentary postcranial material. The skull, which is nearly the same size as the holotype skulls of *Homalocephale calathocercos* and *Prenocephale prenes* (Perle et al., 1982), has many features in common with the former



FIGURE 4. *Prenocephale edmontonensis* (Brown and Schlaikjer, 1943). TMP 87.133.3 (holotype of *Sphaerolitholus buchholtzae* Williamson and Carr, 2002). Nearly complete frontoparietal dome with left squamosal and right postorbital. Bar scale = 5 cm.

(i.e., flat skull roof, well-developed supratemporal fenestrae, pattern of node ornamentation) but there are also differences in proportions and other aspects that support retention of separate taxa. Because of these differences, I tentatively retain *Goyocephale lattimorei* as a valid taxon. Perle et al. (1982) noted the occurrence of premaxillary and “mandibular” caniniform teeth, and an enlarged caniniform tooth that fit into the premax-maxillary diastema. Based on the occurrence of the diastema in *P. prenes* an enlarged caniniform tooth is believed to be present in this taxon (Perle et al., 1982).

Hanssuesia sternbergi (Brown and Schlaikjer, 1943)

Synonyms—As per Sullivan (2003).

Holotype—CMN 8817, frontoparietal dome (Fig. 2).

Horizon/Stratum, Provenance and Age—Oldman and Dinosaur Park formations, Alberta; Judith River Formation, Montana; late Campanian (late Judithian).

Comments—*Hanssuesia sternbergi* is distinguished from all other pachycephalosaurids in having a low, depressed parietal region, wide frontoparietal dome, broad nasal boss of on the frontal, reduced and more inflated prefrontal lobes and reduced parietosquamosal shelf (Sullivan, 2003). These features clearly distinguish it from *Stegoceras* and all other pachycephalosaurids.

Ryan and Evans (2005) resurrected the taxon *Stegoceras sternbergi* primarily based on what they perceived to be a conflict in cladistic analyses between those of Williamson and Carr (2002) and Sullivan (2003). However, there is no support for the inclusion of this species in the genus *Stegoceras* and none was given by Ryan and Evans (2005), so I reject their generic assignment and recognize *Hanssuesia sternbergi* as the proper name

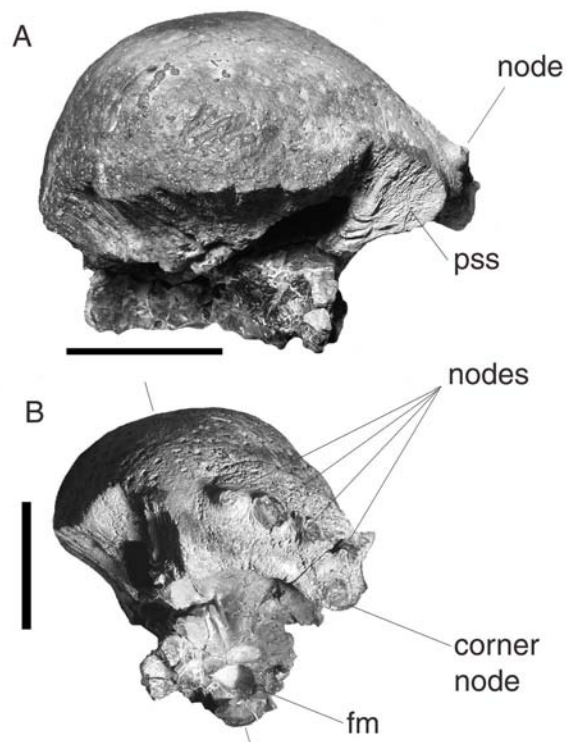


FIGURE 5. *Prenocephale goodwini* (Williamson and Carr, 2002). NMMNH P-27403 (holotype), incomplete skull, lacking facial and palatal bones. **A**, left lateral view showing medial-most right squamosal node; **B**, posterior view. Tick marks indicate orientation of the vertical axis. Abbreviations: fm = foramen magnum; pss = parietosquamosal suture surface of the parietal. Bar scale = 5 cm.

for this taxon.

Homalocephale calathocercos Maryańska and Osmólska, 1974

Holotype—GI SPS 100/51, incomplete skull.

Horizon/Stratum, Age and Provenance—Nemegt Formation Gobi Desert, Mongolia; ?late Campanian to early Maastrichtian (Nemegtian).

Comments—Maryańska and Osmólska (1974) named the taxon *Homalocephale calathocercos* based on an incomplete skull and postcranial material (GI SPS 100/51) from the Nemegt Formation of the Gobi Desert, Mongolia. They characterized the taxon as having a flat skull with large supratemporal fenestrae, distinct frontoparietal suture, low and long infratemporal fenestrae, and a large, round orbit, as predominant features. They noted that the dorsal ornamentation (sculpturing) is very rough, with node-like ornamentation along the lateral and posterior sides of the squamosals. They concluded that the skull represents an adult, despite the fact that the sutures are discernable and that the skull is flat, not domed.

Homalocephale calathocercos is known only by the holotype (GI SPS 100/51), which was found in the same stratum as *Prenocephale prenes* (Maryańska and Osmólska, 1974). It is considered to be Nemegtian (?late Campanian to early Maastrichtian) age.

PRENOCEPHALE Maryańska and Osmólska, 1974

Synonyms—*Sphaerolitholus* Williamson and Carr, 2002, p. 779; *Stegoceras* Lambe, 1902; emend. Sues and Galton, 1987 (in part).

Type Species—*Prenocephale prenes* Maryańska and Osmólska, 1974, p. 53.

Revised diagnosis—*Prenocephale* is a fully-domed pachy-

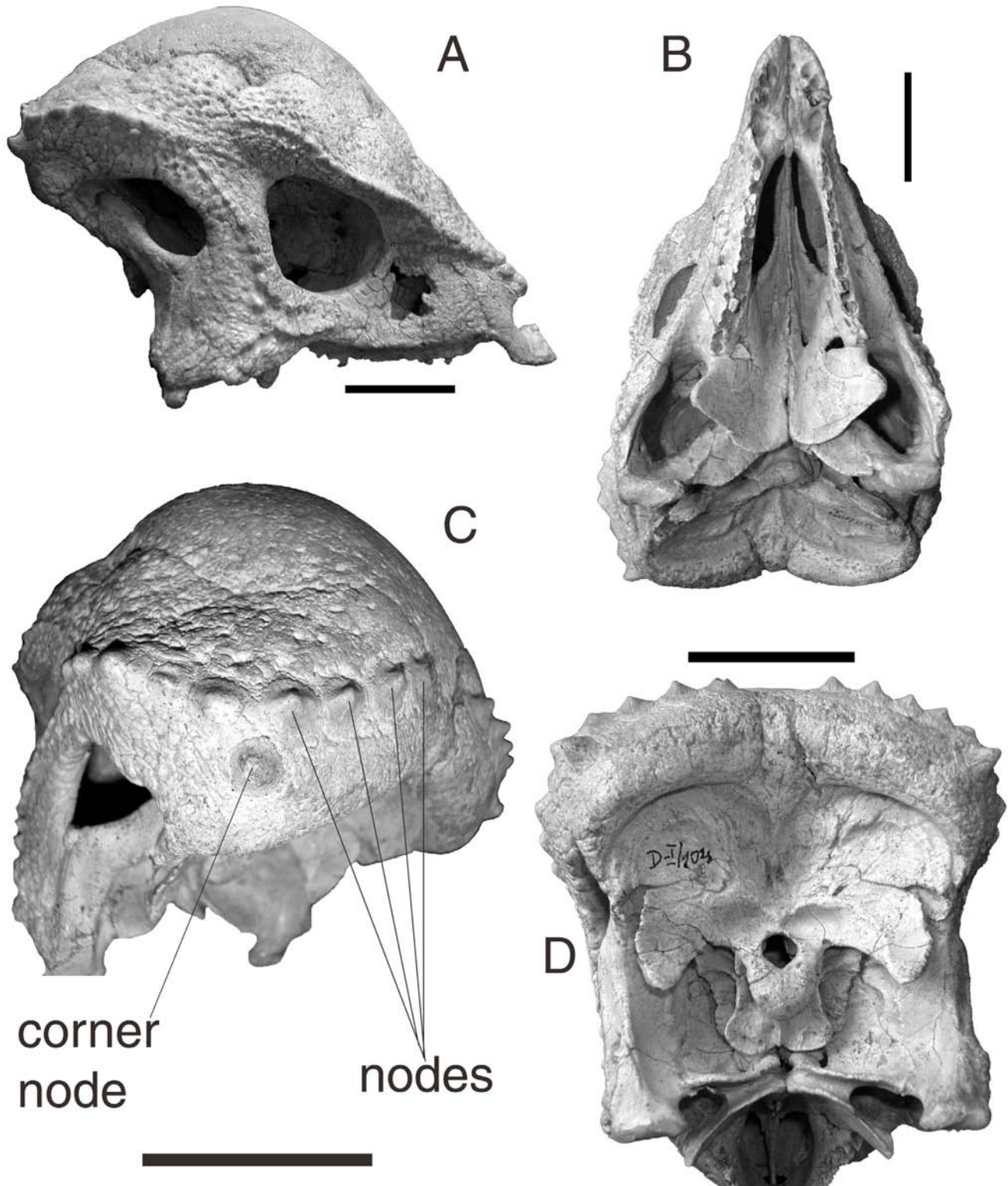


FIGURE 6. *Prenocephale prenes* Maryańska and Osmólska, 1974. Z. Pal. No. MgD-I/104 (holotype), nearly complete skull. **A**, right lateral view; **B**, palatal view; **C**, oblique posterolateral view of left squamosal showing distribution of posterior and corner nodes; and **D**, occipital (posterior) view. Bar scale = 5 cm.

cephalosaurid that is distinguished from all other pachycephalosaurids by having a single row of nodes located along the lateral and posterior portions of the squamosal, and a lower (lateroventral) corner node on each squamosal. Four species are recognized: *P. prenes*, *P. goodwini*, *P. brevis* and *P. edmontonensis*. In the latter two species the medial-most nodes

straddle the parietal-squamosal contacts of both sides. The nodes are restricted to the squamosals in the former two species. All lack a parietosquamosal shelf (a condition presumed in *P. brevis*) and supratemporal fenestrae.

Comments—*Prenocephale* is easily distinguished from *Stegoceras*

validum as it lacks the well-developed parietosquamosal shelf and open supratemporal fenestrae. In addition, all specimens of *Stegoceras* have numerous nodes, or clusters of nodes adorning the parietosquamosal. The taxon *Sphaerolitholus* has the same distribution and morphology (row of 5 nodes) and other features (see below) as does the type species of *Prenocephale prenes*, so it is a junior synonym (Sullivan, 2003). The genus ranges from late Campanian to late Maastrichtian.

***Prenocephale brevis* (Lambe, 1918)**

Synonyms—As per Sullivan (2003).

Holotype—CMN 1423, frontoparietal (Fig. 3).

Horizon/Stratum, Provenance and Age—Oldman and Dinosaur Park formations, Alberta; late Campanian (late Judithian).

Comments—Ryan and Evans (2005) resurrected *Stegoceras breve* despite the distinct nature of the strongly down-turned parietal and paired nodes that clearly indicate it is not *Stegoceras*. Contrary to their statement, there is no demonstrable growth series for this species, and primitive features (i.e., horizontal temporal chamber; frontal grooved anteriorly) do not support reference to a more “primitive” taxon (i.e., *Stegoceras sensu stricto*). The compelling feature is a single row of nodes, presumably on the squamosals, that lap onto the strongly downturned posterior part of the parietal. This character is not seen in *Stegoceras* but is also present in *Prenocephale edmontonensis*.

Sullivan (2000) transferred this species to the genus *Prenocephale* based on the fact that it has a single row of nodes along the posterior margin of the skull. Two distinct nodes on the downturned part of the parietal demonstrate affinities with *P. edmontonensis*. Unfortunately, no squamosals for this species have been identified, so the skull morphology of this pachycephalosaurid remains somewhat enigmatic. *P. brevis* is known from the Oldman and Dinosaur Park formations, so it is restricted to the late Judithian (Sullivan, 2000; 2003; 2005).

***Prenocephale edmontonensis* (Brown and Schlaikjer, 1943)**

Synonyms—As per Sullivan (2003).

Holotype—CMN 8830, nearly complete (water-worn) frontoparietal.

Horizon/Stratum, Provenance and Age—Horseshoe Canyon Formation (= “middle” Edmonton Formation [upper half]), Alberta; early Maastrichtian (late Edmontonian).

Comments—The holotype of *Prenocephale edmontonensis* (CMN 8830) consists of a less-than-perfect, water-worn frontal. Two additional specimens, CMN 8831 and 8832 (paratypes) are also known and were recovered from the same locality in the Horseshoe Canyon (=Edmonton) Formation (Brown and Schlaikjer, 1943), probably from an interval above the Drumheller Marine Tongue. Another, more complete and better preserved, specimen, TMP 87.113.3 (Fig. 4), from the Hell Creek Formation (Carter County, Montana) was collected and briefly reported by Giffin (1989), and later described in detail by Sullivan (2000), and it has served as the basis for characterizing this species. Williamson and Carr (2002) considered the holotype (CMN 8830) to be a *nomen dubium*, assigned the specimen to *Sphaerolitholus*, and established a new species *S. buchholtzae*. There is no doubt that the holotype specimen of *Prenocephale edmontonensis* (CMN 8830) and TMP 87.113.3 are the same taxon based on the morphology of the frontoparietal dome and the occurrence of the two nodes straddling the parietosquamosal contact. Sullivan (2003) synonymized *S. buchholtzae* with *P. edmontonensis*, rejecting their thesis that *P. edmontonensis* is a *nomen dubium*.

***Prenocephale goodwini* (Williamson and Carr, 2002)**

Synonyms—As per Sullivan (2003).

Holotype—NMMNH P-27403, incomplete skull lacking facial and palatal bones (Fig. 5).

Horizon/Stratum, Provenance and Age—Kirtland Formation (Dena-zin Member), San Juan Basin, New Mexico; late Campanian (late

Kirtlandian).

Comments—Williamson and Carr (2002) described an incomplete skull (NMMNH P-27403) as pertaining to a new genus *Sphaerolitholus goodwini*. They diagnosed it as differing from all other pachycephalosaurids, where known, in possessing a parietosquamosal bar that decreases in depth laterally (as seen in caudal view) and is bordered by a single row of nodes and one (lateroventral) corner node (on each squamosal) (Fig. 5b). Elsewhere, I synonymized *Sphaerolitholus goodwini* with the genus *Prenocephale* (Sullivan, 2003) as the overall morphology of *S. goodwini* is consistent with that of *Prenocephale prenes*. Indeed, the distinct, single row of 5 nodes (on each squamosal), lack of nodes on the medial extension of the parietal, presence of a distinct corner node (on each squamosal), and well-developed anterior and posterior supraorbitals, unequivocally demonstrate that it is the same genus. The second character cited by Williamson and Carr (2002), “decreasing in depth of the parietosquamosal bar,” is not present in *Prenocephale goodwini*, but is a feature seen in *P. edmontonensis* (see discussion below). The genus *Sphaerolitholus* cannot be distinguished from *Prenocephale*, so it is a subjective junior synonym (Sullivan, 2003, 2005).

Direct comparison of the holotype of *Prenocephale edmontonensis* to the holotype of *Sphaerolitholus buchholtzae* (TMP 87.113.3, Fig. 4) leaves no doubt that they are the same taxon (Sullivan 2000, 2003). Although the holotype (CMN 8830) is slightly smaller than TMP 87.113.3, it agrees in every respect. Posteriorly, the medial-most nodes straddle the parietal squamosal sutures. Laterally, the sutural surfaces that contact the anterior and posterior supraorbitals and postorbital are identical. Ventrally, the dorsal surface impressions of the cerebrum and cerebellar regions, dorsal surface impression of the olfactory bulbs and the dorsal surface of supratemporal regions of the parietal are also identical. TMP 87.133.3 differs from the holotype of *Sphaerolitholus goodwini* in: (1) reduction (5 to 4) in the number of nodes along the posterior border of the squamosal; (2) medial most nodes bisected by the parietal-squamosal suture; (3) loss of the corner (lateroventral) node; (4) apices of nodes directed up, not out or perpendicular to the surface of the skull; and (5) peripheral elements (squamosals, postorbitals, anterior and posterior supraorbitals) fully incorporated into the dome. TMP 87.133.3 does have a slight decrease in the depth of the squamosal laterally, giving the corner a more tapered appearance. However, this feature is not evident on the parietosquamosal shelf in the holotype of *Prenocephale* (= *Sphaerolitholus*) *goodwini* (NMMNH P-27403) as described by Williamson and Carr (2002). In *P. goodwini* the distance between the center of the nodes (apices where preserved) and the ventral margin of the posterior border of the parietal squamosal shelf is uniformly thick from the medial to lateral side as illustrated by Williamson and Carr (2002, fig. 12).

The holotype and paratypes of *P. edmontonensis* are from the upper part of the Horseshoe Canyon Formation, which is early Maastrichtian in age (late Edmontonian), whereas TMP 87.133.3, from the Hell Creek Formation, is late Maastrichtian (Lancian). The range of *P. edmontonensis* is thus Maastrichtian.

***Prenocephale prenes* Maryańska and Osmólska, 1974**

Synonyms—As per Sullivan (2003).

Holotype—Z. Pal. MgD-I/104, nearly complete skull (Fig. 6) and various postcranial remains (see Maryańska and Osmólska, 1974).

Horizon/Stratum, Provenance and Age—Nemegt Formation, Gobi Desert, Mongolia; ?late Campanian to early Maastrichtian (Nemegtian).

Comments—*Prenocephale prenes* is based on a nearly complete skull and partial skeleton (Z. Pal. MgD-I/104) from the Nemegt Formation, Mongolia (Fig. 6). *Prenocephale prenes* was described in detail by Maryańska and Osmólska (1974) and was diagnosed, in part, as being highly domed, lacking a parietosquamosal shelf, lacking supratemporal fenestrae (fenestrae), frontal and prefrontal excluded from orbital margin, and strongly swollen (well-developed) squamosals with distinct row of nodes along the squamosals (see Maryańska and Osmólska, 1974 for the complete, original diagnosis). It can be easily distinguished from *Stegoceras validum* by

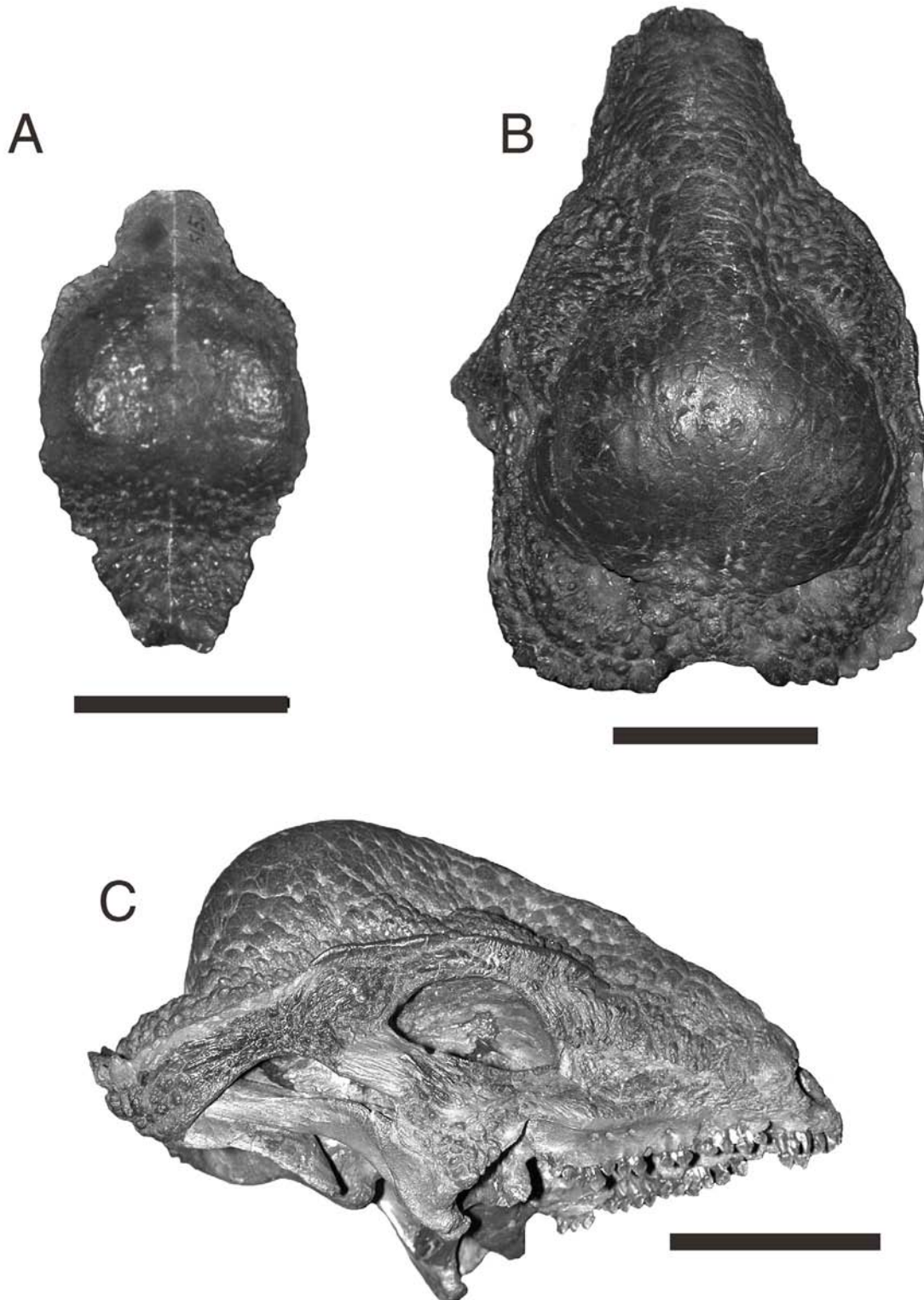


FIGURE 7. *Stegoceras validum* (Lambe, 1902); emend. Sues and Galton, 1987. A, CMN 515 (holotype), nearly complete frontoparietal; UALV 2, nearly complete skull. B, dorsal view; and C, oblique right lateral view. Bar scale = 5 cm.

the presence of a single row of nodes along the lateral and posterior margins of the squamosals, single lower corner node on each squamosal (Fig. 6b), and enlarged anterior and posterior supraorbitals. These features are also seen in all species of *Prenocephale* and to some degree in the holotype of *Tylocephale gilmorei* (PAL MgDI/105). Only one specimen of *Prenocephale prenes* is known.

***Stegoceras validum* (Lambe, 1902); emend. Sues and Galton, 1987**

Synonyms—As per Sullivan (2003).

Lectotype—CMN 515, nearly complete frontoparietal (Fig. 7).

Horizon/Stratum, Provenance and Age—Oldman and Dinosaur Park formations, Alberta and Fruitland Formation, New Mexico; late Campanian (late Judithian to early Kirtlandian).

Comments—In a recent study (Sullivan, 2003) I extensively reviewed this taxon. Suffice it to say, the assessment of Maryańska et al. (2004), who re-assign many of the species I recognized as distinct, is not acceptable. The monotypic taxon *Stegoceras validum* (*sensu stricto*) can be easily distinguished, in part, from other pachycephalosaurid taxa by having a near-flat to somewhat inflated frontoparietal dome, prominent parietosquamosal shelf, with incipient supratemporal fenestrae. These include all juvenile forms that are like the holotype of *Stegoceras* (= *Ornatolitholus browni* (Wall and Galton, 1979; Galton and Sues, 1983), a taxon considered by me to be a synonym of *Stegoceras validum* (Sullivan, 2003, p. 187) *contra* Maryańska et al. (2004). In all specimens, previously assigned to “*O.*” *browni*, the frontoparietal (or, if unfused, the frontals and parietals) is relatively flat, and have supratemporal fenestrae as indicated by the posterolateral portion of the parietal region. This morphology differs significantly from that of *Prenocephale*, a genus that is readily distinguished by a single row of nodes occupying the lateral and posterior margin of the squamosal (see below), fully-domed and lacking a frontoparietal shelf and supratemporal fenestrae.

In Alberta, *Stegoceras validum* is restricted to the Oldman and Dinosaur Park formations, and it is also known from the upper Fruitland Formation of New Mexico (Sullivan, 2005; Sullivan and Lucas, 2006a). Its stratigraphic range is limited; late Judithian to early Kirtlandian, approximately 77.5 to 74.5 Ma.

***Tylocephale gilmorei* Maryańska and Osmólska, 1974**

Holotype—Z. Pal. MgD-I/105, incomplete skull (Fig. 8).

Horizon/Stratum, Provenance and Age—Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; late Campanian (late Barungoyotian).

Comments—The genus *Tylocephale* is known by its sole species *T. gilmorei*. The holotype (Z. Pal. MgD-I/105) is rather small, poorly preserved and somewhat distorted (Fig. 8). It shares with *Prenocephale prenes* the same number of nodes on the squamosal (8) and a single large lower corner node on each squamosal; well-developed anterior and posterior supraorbitals; and it has a similar jugal morphology. The skull differs primarily in its high and narrow profile (Fig. 8a,c), but I attribute this, in part, to it being a subadult. The doming is not pronounced and appears to be transitional between the flat-headed (*Homalocephale*) and more fully-domed (*Prenocephale*) forms. It is difficult to assess this taxon due to the poor preservation of the holotype and the fact that there are no other specimens known.

Tylocephale gilmorei is known only from the Barun Goyot Formation, Khulsan, Mongolia. This unit has been considered to be late Campanian (Barungoyotian) to possibly early Maastrichtian, but is probably late Campanian (Lillegraven and McKenna, 1986; Jerzykiewicz and Russell, 1991; Lucas and Estep, 1998).

PACHYCEPHALOSAURINI

Stygomoloch spinifer and *Pachycephalosaurus wyomingensis* were united in the clade Pachycephalosaurini based on having hypertrophied nodes on the skull (Sullivan, 2003). Long considered a junior synonym of

Stygomoloch spinifer (Gabriel and Berghaus, 1988), *Stenotholus kohleri* was formally recognized as a junior synonym of *Stygomoloch spinifer* by Sullivan (2003). A re-evaluation of the holotype of *Stenotholus kohleri* (MPM 7111) and MPM 8111 confirms this. A third taxon, *Dracorex hogwartsia* (Bakker et al., 2006), is also a member of this group. These three pachycephalosaurins show a remarkable array of mosaic characters that makes dealing with these taxa challenging. They are restricted to the Hell Creek and Lance formations of the Western Interior and are all Lancian in age, an interval that ranges approximately from 66.8 Ma to 65.5 Ma (i.e., the base of the *Triceratops* zone as dated from the Kneehills Tuff to the K/T boundary) (Cifelli et al., 2004).

***Dracorex hogwartsia* Bakker, Larson, Porter, Salisbury, and Sullivan, 2006**

Holotype—TCMI 2004-17-1, nearly complete skull, plus four cervical vertebrae.

Horizon/Stratum, Age and Provenance—Hell Creek Formation, South Dakota; late Maastrichtian (Lancian).

Comments—Bakker et al. (2006) described this new flat-headed pachycephalosaurid as distinct from *Stygomoloch spinifer* and other taxa that comprise the Pachycephalosaurini (Sullivan, 2003). Although the taxon has squamosal spikes that are similar to those assigned to *S. spinifer*, the spike clusters are strikingly smaller than those of the holotype of *S. spinifer*. *Stygomoloch spinifer* has 3, greatly enlarged spikes, while *Dracorex hogwartsia* has 4 smaller spikes (Bakker et al., 2006). The former taxon is easily distinguished by its massive spike cluster, narrow dome and closed supratemporal fenestrae (Goodwin et al., 1998). The large, centrally-located spike seen in *Dracorex hogwartsia* and in the holotype of *S. spinifer* is without doubt the elongated corner node seen in such taxa as *Prenocephale* and *Homalocephale*.

Leidy (1872) named *Tylosteus ornatus* based on a worn, and very small, squamosal (ANSP 8568) bearing a cluster of nodes, many broken at their bases (Leidy, 1873; Baird, 1979). This taxon, however, was thoroughly documented by Baird (1979), who considered it to be *Pachycephalosaurus*, but rejected it as a *nomen oblitum*. This synonymy was accepted by Galton and Sues (1983). However, comparison of the holotype of *Tylosteus ornatus* (ANSP 8568) to the holotype of *Dracorex hogwartsia* (TCMI 2004-17-1) shows it to be closer to *D. hogwartsia* and the undescribed “Triebold specimen” than to *Pachycephalosaurus wyomingensis*, based on the size arrangement of node bases. It cannot be referred to *Stygomoloch spinifer* primarily based in its small size.

For reasons given below, and discussed elsewhere (Bakker et al., 2006), *Dracorex hogwartsia* cannot be considered a sub-adult, or sexual dimorph, of *Stygomoloch spinifer*. *Dracorex hogwartsia* is from the middle part of the Hell Creek Formation of South Dakota, so it is of late Maastrichtian age.

PACHYCEPHALOSAURUS BROWN AND SCHLAIKJER, 1943

Synonymy—*Troödon* Leidy, 1856 (in part).

Comments—Brown and Schlaikjer (1943) diagnosed the genus *Pachycephalosaurus* as having an extremely thick frontoparietal, strongly-developed node-like ornamentation, closed supratemporal fenestrae (fenestrae), and face narrow and shallow. They also suggested it lacked premaxillary teeth, although the evidence for this was lacking.

In their revised diagnosis of the genus, Galton and Sues (1983) noted the well-developed node ornamentation on the squamosals as well as a sutural contact between the squamosal and quadrate (discussed above). The generic diagnosis served as the diagnosis for *P. wyomingensis* as a separate diagnosis for the species was not given. *Pachycephalosaurus* is a monotypic taxon, with *P. wyomingensis* as the only known species.

***Pachycephalosaurus wyomingensis* (Gilmore, 1931)**

Synonyms—*Troödon wyomingensis* Gilmore, 1931, p. 1.;

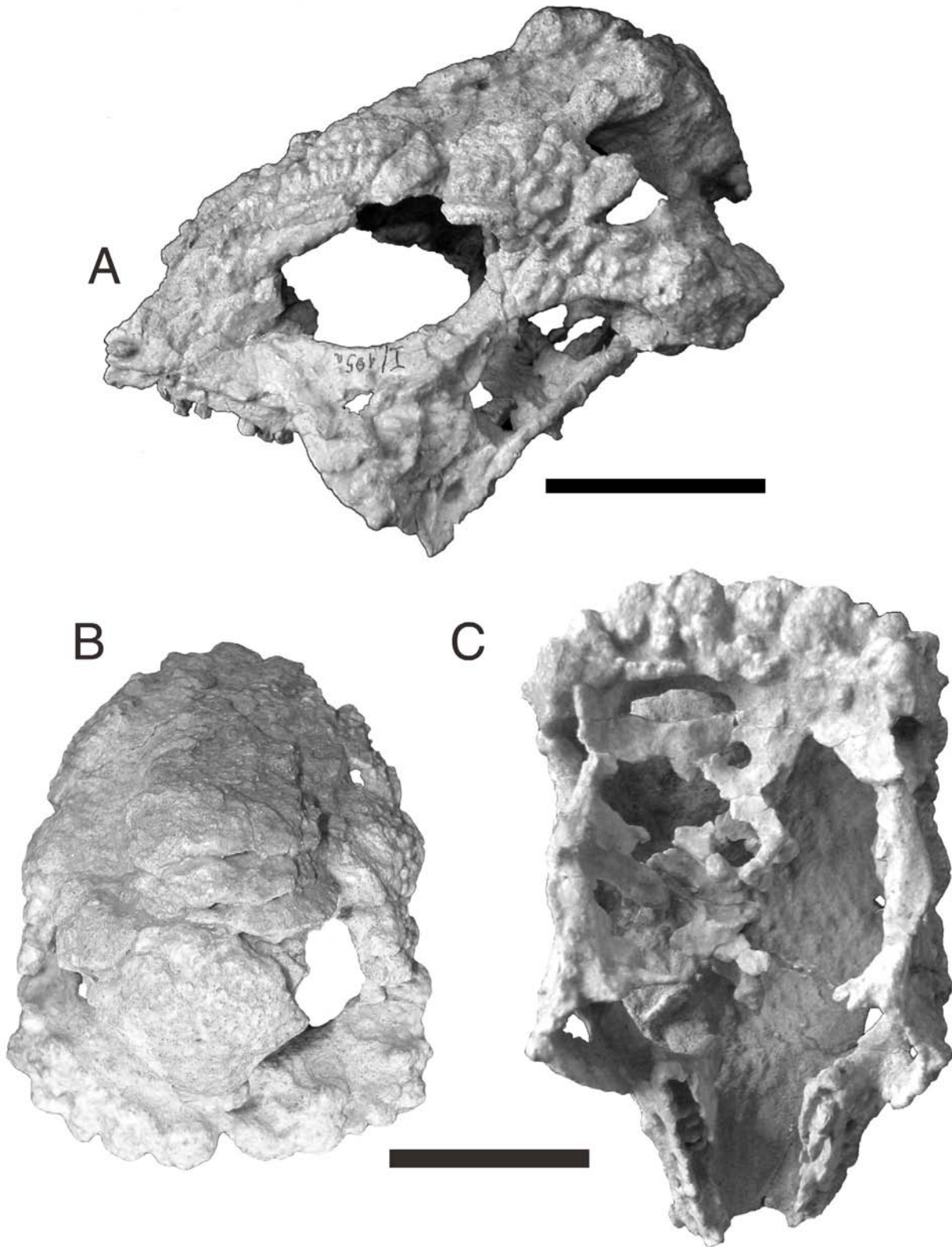


FIGURE 8. *Tylocephale gilmorei* Maryańska and Osmólska, 1974. Z. Pal. No. MgD-I/105, incomplete skull. A, left lateral view; B, dorsal view; and C, occipital (posterior) view. Bar scale = 5 cm.

Pachycephalosaurus grangeri Brown and Schlaikjer, 1943, p. 133; *Pachycephalosaurus wyomingensis* (Gilmore, 1931), p. 1.; *Pachycephalosaurus reinheimeri* Brown and Schlaikjer, 1943, p. 143.

Holotype—USNM 12031, incomplete skull consisting mostly of the frontoparietal and squamosals (Fig. 9a-d).

Horizon/Stratum, Age and Provenance—Lance Formation, Montana and Wyoming; Hell Creek Formation, South Dakota; late Maastrichtian (Lancian).

Comments—Gilmore (1931) named *Troödon wyomingensis* based on an incomplete frontoparietal dome USNM 12031 (Fig. 9a-d), and Gilmore (1936) published on a second, more complete specimen (CM 3180, Fig. 10a-c). Brown and Schlaikjer (1943) established the genus *Pachycephalosaurus* and transferred “*T.*” *wyomingensis* to it and named two additional species, *P. grangeri* and *P. reinheimeri*, which were later formally synonymized with *P. wyomingensis* (Galton, 1971).

Sues and Galton (1987) noted that *P. wyomingensis* lacks a parietosquamosal shelf, the quadrate is inclined further forward compared to other pachycephalosaurids, the basicranial region is foreshortened, and the occipital condyles are perpendicular to the basicranial axis. However, these observations were largely based on AMNH 1696 (holotype of *P. grangeri*), an extensively restored skull, so their reliability is somewhat problematic. They synonymized the species *P. grangeri* and *P. reinheimeri* with *P. wyomingensis* (Sues and Galton, 1987).

Few specimens of this taxon are known; most consist of frontoparietal domes, in various states of completeness, bearing clusters of prominent knobby nodes on the squamosal regions. Only one reasonably complete specimen exists: AMNH 1696.

P. wyomingensis has been mostly characterized as a large pachycephalosaurid, with a well-formed (expanded) dome and lacking a parietosquamosal shelf. All specimens are from the Lance and Hell Creek formations (or equivalents), although one specimen (NHM R8648), in the collection of the Natural History Museum (London), has been reported as derived from the Oldman Formation (Wall and Galton, 1979). However, Sullivan (2003, 2005) believes the provenance of this to be in error, so all are late Maastrichtian age (Lancian).

***Stygimoloch spinifer* Galton and Sues, 1983**

Synonyms—*Stenotholus kohleri* Giffin, Gabriel and Johnson, 1987, p. 399.

Holotype—UCMP 119433, nearly complete left squamosal.

Horizon/Stratum, Age and Provenance—Hell Creek Formation, Montana, North and South Dakota; Lance Formation, Wyoming; late Maastrichtian (Lancian).

Formation/Age—late Maastrichtian (Lancian).

Comments—Galton and Sues (1983) named and described an isolated left squamosal (UCMP 119433) characterized by distinctive hypertrophied, spike-like nodes. They diagnosed the taxon as having three or four massive horn-cores (spikes) developed on a prominent squamosal shelf, and noted that the supratemporal fenestrae are open in juveniles. This latter observation was based on a smaller, four-spiked specimen (YPM 335) that clearly preserves the posterior margin of the right supratemporal fenestra (Galton and Sues, 1983). It should be noted that open supratemporal fenestrae do not necessarily indicate the ontogenetic state of the pachycephalosaurid skull. *Homalocephale*, *Goyocephale* and other flat-headed taxa have been characterized, in part, by having this condition. Comparison of YPM 335 to TCMI 2004-17-1, the holotype of *Dracorex hogwartsia*, suggest that this is not a juvenile character. This specimen has been referred to *Dracorex hogwartsia* (Bakker et al., 2006).

An unnumbered specimen from the Hell Creek Formation of South Dakota, reported by Triebold (1997) and informally attributed to both *Stygimoloch* and *Pachycephalosaurus*, remains unstudied. The “Triebold specimen” has squamosal spikes similar to those of the holotype of *Dracorex hogwartsia* (Bakker et al., 2006), but this undescribed specimen appears to have been fully-domed based on the peripheral remnants of the fronto-

parietal. A critical assessment of this specimen has yet to be made.

The taxon *Stenotholus kohleri* was based on a nearly complete subadult frontoparietal (Giffin et al., 1987). The holotype (MPM 7111) is distinctive, with a well-developed narrow dome and steeply-dipping parietal region. Gabriel and Berghaus (1988) considered *S. kohleri* to be *Stygimoloch spinifer*, a synonymy formalized by Sullivan (2003). Based on a re-evaluation of the holotype (squamosal spike cluster) of *S. spinifer* (UCMP 119433) and referred material (MPM 8111), it is certain that *Stenotholus kohleri* is a junior synonym of *Stygimoloch spinifer*. The domes are nearly the same in MPM 7111 and MPM 8111 (Fig. 11). The primary difference is that there appears to be a posterior extension of the parietal separating the two squamosals in MPM 7111, whereas in MPM 8111 the parietal is excluded from the shelf. The supratemporal fenestrae are closed and the massive spike cluster consists of only three spikes and this spike covered squamosal is indistinguishable from the holotype of *Stygimoloch spinifer*.

The skulls of all pachycephalosaurids are rather long and somewhat narrow, including *Pachycephalosaurus wyomingensis* (based on the nearly complete skull AMNH 1696). In *P. wyomingensis*, there is a broad participation of the parietal extension (80 mm) separating the left and right squamosals, based on the holotype skull (USNM 12031) (Fig. 9). The narrow dome seen in MPM 7111 and MPM 8111 appears to be a distinctive feature of *Stygimoloch spinifer*, coupled with the occurrence of the massive squamosal spike cluster and open supratemporal fenestrae.

Another specimen, briefly described and figured by Galiano and Mehling (2001), is similar to the holotype of *Dracorex hogwartsia* (TCMI 2004-17-1), except that it has a wider posterior parietal bar, hence it has smaller supratemporal fenestrae, slight doming of the anterior part of the parietal, and less ornamentation on the parietal (Fig. 12). While the skull is nearly the same size as the skulls of *Stygimoloch*, *Dracorex*, and the “Triebold specimen,” it lacks the sharp elongate spikes seen in these taxa and the “Triebold specimen.” All the nodes appear to be roughly the same size and are rather blunt in morphology. This specimen has yet to be studied in detail.

Recently, additional *Stygimoloch* specimens have come to light, but unfortunately these are in the hands of private collectors and are not yet available for study. They all have the distinct narrow, incipient dome, lack supratemporal fenestrae, and have massive spike clusters on the squamosals.

PACHYCEPHALOSAURIDAE INCERTAE SEDIS

***Wannanosaurus yansiensis* Hou, 1977**

Holotype—IVPP V4447, partial skull (right frontal, ?right posterior supraorbital, right postorbital), left mandible and postcranial elements.

Horizon/Stratum, Provenance and Age—Xiaoyan Formation, Anhui Province, People’s Republic of China; ?early Maastrichtian (Nemegtian).

Comments—Hou (1977) named the enigmatic *Wannanosaurus yansiensis* based on the remains from two immature individuals, so its phylogenetic position as a “basal pachycephalosaur” was considered tenuous by Sereno (2000). The holotype is small and characteristically “primitive” with a flat skull roof and well-developed supratemporal fenestrae. This taxon is not unlike *Homalocephale calathoceros* and *Goyocephale lattimorei* (discussed above). Its small size suggests that it is probably a juvenile. Because this “primitive” pachycephalosaur may be of Nemegtian (early Maastrichtian) age (Lucas and Estep, 1998) it may be synonymous with *Homalocephale calathoceros* (also of Nemegtian age) based on the structure of the skull roofing bones (i.e., parietal, frontal, postorbital and squamosal). I tentatively retain *Wannanosaurus yansiensis* as valid, but consider it Pachycephalosauridae incertae sedis.

NOMINA DUBIA

***Gravitholus albertae* Wall and Galton, 1979**

Comments—*Gravitholus albertae* (holotype TMP 72.27.1) from

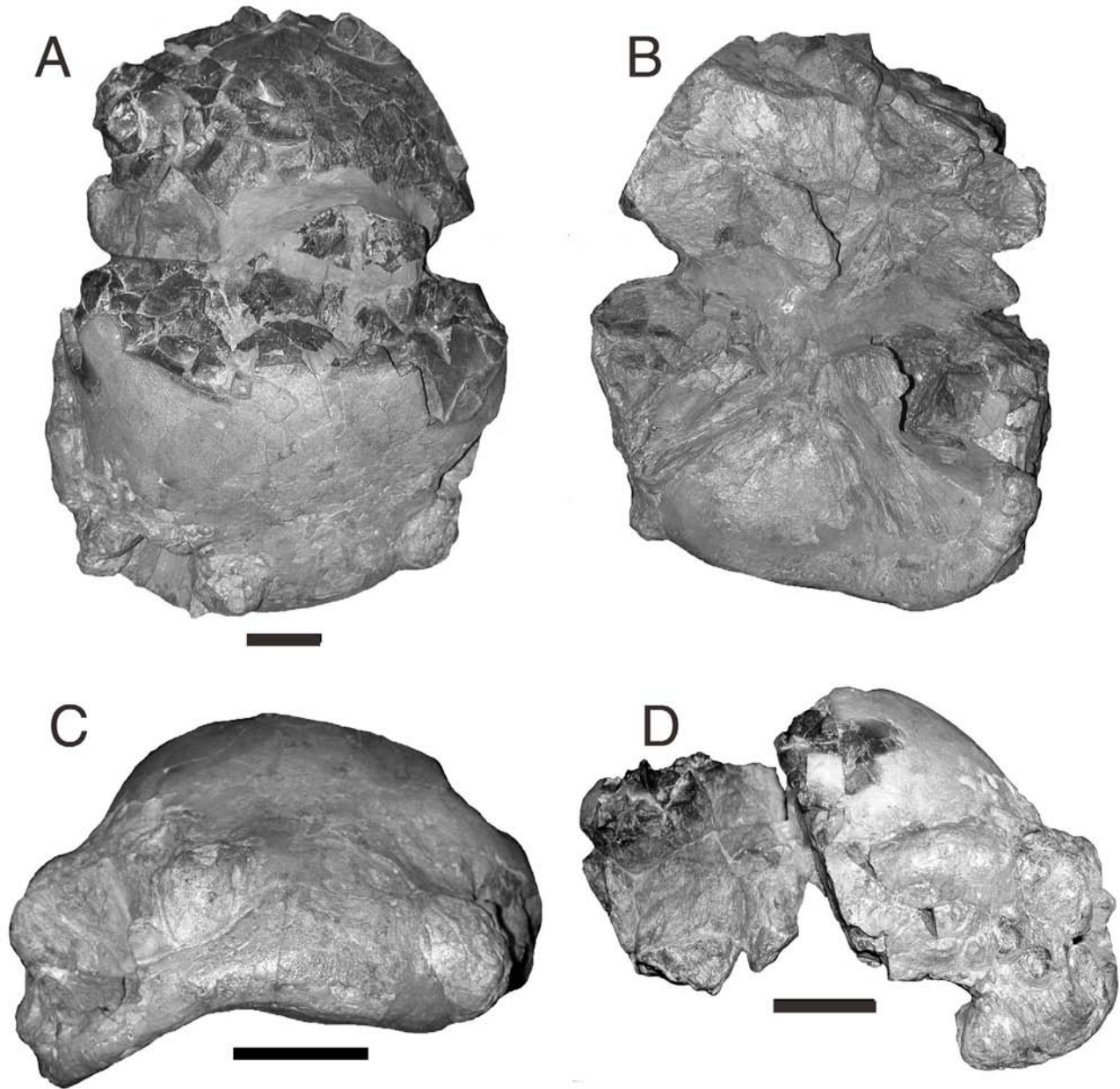


FIGURE 9. *Pachycephalosaurus wyomingensis* (Gilmore, 1931). USNM 12031 (holotype), incomplete skull consisting mostly of the frontoparietal and squamosals. A, dorsal view; B, ventral view; C, posterior view; and D, left lateral view. Bar scale = 5 cm.

the Oldman Formation, has been problematic since its original description (Sullivan, 2000, 2003). It is not referable to any of the other taxa with certainty due to distortion and erosion of the type specimen. It most closely resembles *Hanssuesia sternbergi*, but the holotype is too incomplete for any definitive diagnosis (Sullivan, 2003, 2005), so I considered it to be a *nomen dubium*.

***Ferganocephale adenticulatum* Averianov, Martin and Bakirov, 2005**

Comments—Averianov et al. (2005) named *Ferganocephale adenticulatum* based on isolated teeth (holotype: ZIN PH 34/42, unworn adult tooth) from the Middle Jurassic Balabansai Svita of Kyrgyzstan (Central Asia). Despite their detailed diagnosis, few of the features (characters) are diagnostic of pachycephalosaur teeth.

“Pachycephalosaur,” or more appropriately, pachycephalosaurid,

teeth are known to have different morphologies depending on where they are positioned in the premaxilla, dentary and maxilla (Brinkman, 2005; and pers. observation). The holotype tooth of *Ferganocephale adenticulatum* bears little resemblance to typical pachycephalosaurid teeth which are, in part, characterized by well-developed serrations along the carina on both sides of the crown. The crown of the unworn holotype of *F. adenticulatum* (ZIN PH 34/42) bears no serrations and thus departs from most pachycephalosaurid teeth. The referred material, consisting mostly of worn teeth, is too incomplete for identification, despite one tooth having a well-developed cingulum. The cingulum is not a character unique to pachycephalosaurids. Regardless, the teeth, which may represent an indeterminate non-pachycephalosaurid ornithischian dinosaur, are insufficient for establishing a taxon at the generic and specific levels. I consider *Ferganocephale adenticulatum* to be a *nomen dubium*.

Heishansaurus pachycephalus Bohlin, 1953

Comments—Bohlin (1953) named *Heishansaurus pachycephalus* based on a crushed and incomplete skull, including parts of the basicranium, along with four teeth, incomplete vertebrae, ribs and osteoderms (“dermal plates”). The material, which was believed to be from a single individual (field no. 60), is now lost. Bohlin (1953) noted that he originally believed *Heishansaurus pachycephalus* to be an ankylosaur (*Pinacosaurus*), and that there were enough differences to warrant the recognition of a new genus and species. Later, in the same article, he contrasted the similarities and differences between “*Troödon*” *bexelli* and *Heishansaurus pachycephalus*, casting doubt on the phylogenetic affinities of the latter. He believed the two taxa to be similar based on the thickness of the skull (~7-8 cm). I note that skulls of ankylosaurids are robust, and that the skull element illustrated by Bohlin (1953, pl. 1, fig. 6) does not bear any resemblance to that of a pachycephalosaurid. The basicranium and occipital condyle, as figured by Bohlin (1953, fig 25a,c), are consistent with the morphology in ankylosaurids, and are not like the short, constricted basicrania typical of pachycephalosaurids. Bohlin (1953) stated that the teeth of *Heishansaurus* differed from those of *Pinacosaurus* (they are unknown for “*Troödon*” *bexelli*). However, the teeth he illustrated, which are very large for most pachycephalosaurids, have morphology that is more like ankylosaurid teeth. Bohlin (1953) was convinced that some of dermal ossifications bore resemblance to nodes of the North American taxon *Pachycephalosaurus*. However, a number of the ossifications he figured do not look like they are *Pachycephalosaurus*, or for that matter *Stygomoloch*-like, nodes, rather they are more consistent with osteoderms from an ankylosaurid. Based on Bohlin’s (1953) description, I conclude that *Heishansaurus pachycephalus* is an indeterminate ankylosaurid, not pachycephalosaurid (*contra* Maryańska et al., 2004). Regardless, I consider the taxon a *nomen dubium*.

Micropachycephalosaurus hongtuyanensis Dong, 1978

Comments—Dong (1978) described a small, flat-headed pachycephalosaurid based on an incomplete skull, ilium and sacrum (IVPP V5542), from the Campanian Wangshi Group (Shandong) of the People’s Republic of China, which is considered to be late Campanian (late Barungoyotian) age (Lucas and Estep, 1998). The sutures of the holotype skull are reportedly not evident, but this taxon, along with the holotype of *Wannanosaurus yansiensis* (discussed above) were considered by Perle et al. (1982) to represent adult individuals. *Micropachycephalosaurus hongtuyanensis* is considered to be a *nomen dubium* by Sereno (2000), a designation that is followed here.

“*Stegoceras*” *bexelli* (Bohlin, 1953)

Synonymy—*Troödon bexelli* Bohlin, 1953, p. 32.

Comments—Bohlin (1953) named *Troödon bexelli* based on an unnumbered and incomplete parietal from the Minhe Formation (Nei Mongol Zizhiqu), People’s Republic of China. The Minhe Formation is correlative to either the Bayshirenian or Barungoyotian based on the co-occurrence of *Microceratops* (Lucas and Estep, 1998). Based on Bohlin’s (1953) illustrations and photographs (fig. 11a-f and pl. 1, figs. 1-2), it is apparent that the specimen, in part, has a domed parietal with incipient supratemporal fenestra (on the right). The frontoparietal surface appears to be thick, attesting to the doming of the frontoparietal. Unfortunately, the holotype specimen appears to be too incomplete for diagnostic purposes, and its whereabouts is presently unknown. Reference to the North American genus *Stegoceras* cannot be supported as it lacks any characters that would unequivocally allow reference to that, or any other recognized, pachycephalosaurid taxon. Its relationships, if any, to *Heishansaurus pachycephalus*, cannot be corroborated. I consider “*Stegoceras*” *bexelli* to be a *nomen dubium*.

TAXA REMOVED FROM THE “PACHYCEPHALOSAURIA”

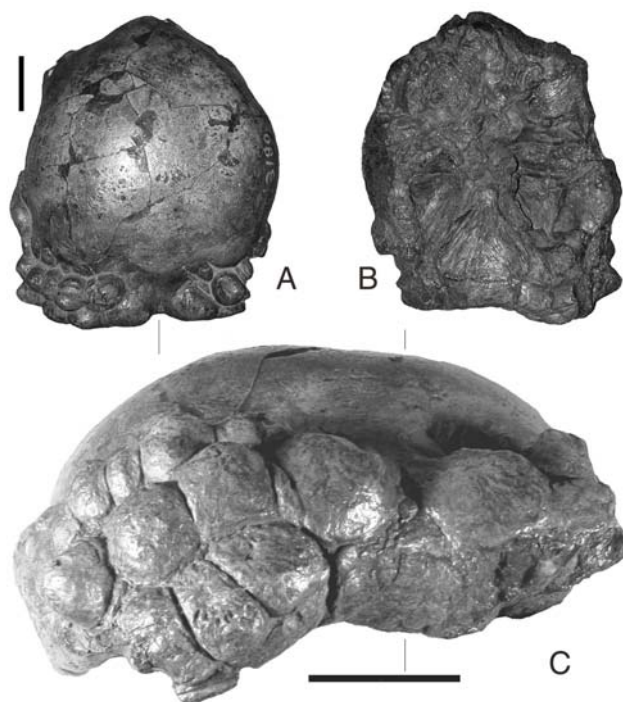


FIGURE 10. *Pachycephalosaurus wyomingensis* (Gilmore, 1931). CM 3180, incomplete skull consisting mostly of the frontoparietal and squamosals. A, dorsal view; B, ventral view; C, oblique posterior view. Tick marks denote midline of skull. Bar scale = 5 cm.

Majungatholus atopus Sues and Taquet, 1979

Comments—*Majungatholus atopus* was named by Sues and Taquet (1979), based on frontals, incomplete parietals and braincase from the Maevarano Formation, Mahajana Basin, northwestern Madagascar. Subsequent, and more complete, material demonstrated that *Majungatholus atopus* is an abelisaurid theropod (Sampson et al., 1998). This determination has resulted in restricting pachycephalosaurids to the northern hemisphere.

Yaverlandia bitholus Galton, 1971

Comments—*Yaverlandia bitholus* was named by Galton (1971) based on a incomplete coalesced frontal (MIWG 1530) from the Isle of Wight (UK), and was determined by him to be a primitive pachycephalosaurid. Sullivan (2000) removed it from the Pachycephalosauria (Pachycephalosauridae of this paper) because it lacks characters that permit inclusion with this group. This reassessment was reiterated by Sullivan (2003) and more recently by Sullivan (2005), who noted that the frontal bore a thin dermal (granular) covering (sculpturing), unlike anything in members of the Pachycephalosauridae. Maryańska and Osmólska (1974) described the “pitted ornamentation” of *Homocephale calathocercos* as similar to that in *Yaverlandia bitholus*, but it is not.

Presently, *Yaverlandia bitholus* is being restudied by Darren Naish, who believes it to be a theropod, based on a number of characters seen in the holotype, including: (1) bilobed cerebral concavity; (2) narrow olfactory tract; (3) ventral concave orbital margins; (4) small, closely appressed olfactory bulbs, among other features (D. Naish, pers. communication, 2004).

It is worth noting that the “pachycephalosaurs” *Majungatholus*, and *Yaverlandia*, now regarded as theropods, and with the removal of *Stenopelix* from the “Pachycephalosauria,” establishes the distribution of the Pachycephalosauridae as restricted to the Holarctic of Asia and North America.

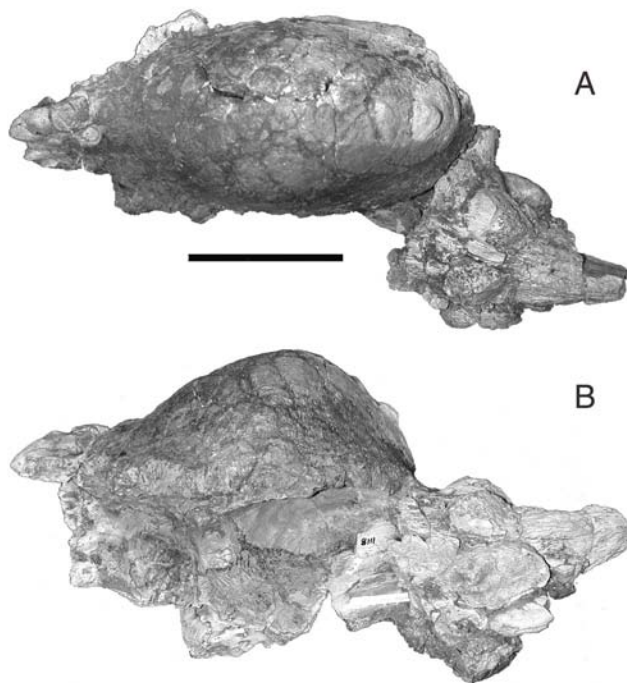


FIGURE 11. *Stygimoloch spinifer* Galton and Sues, 1983. MPM 8111, incomplete skull consisting primarily of the frontoparietal dome and left squamosal (spike-cluster). A, dorsal view; B, left lateral view. Anterior direction is left. Bar scale = 5 cm.

ONTOGENY AND PHYLOGENY

Deciphering the morphological diversity among pachycephalosaurids, whether it be individual, sexual and/or taxonomic variation, is critical. Only when we have a handle on what this variation and diversity means can we reach conclusions about their phylogeny. To that end, I here point out some critical facts that go against previous thinking regarding characterization of some pachycephalosaurid species and the phylogeny of the group most recently summarized by Sereno (2000). Since what I am about to present here undermines, in part, what has been widely accepted regarding pachycephalosaurid phylogeny, it is my opinion that we are only now beginning to “tease-out” the salient features that would allow for a robust cladistic analysis. Therefore, I do not present any phylogenetic hypothesis (cladogram) here, rather I establish the phylogenetic parameters by reassessing the characters, and their polarities, that have been previously used in establishing pachycephalosaurid relationships.

One key, and arguably the most distinctive, trait of pachycephalosaurids is the presence of the dome. The relative development of the dome has been used as a phylogenetic marker, separating a crown clade (“Pachycephalosaurinae”) from all the rest (Sereno, 2000). However, the recent recovery of the flat-headed *Dracorex* and other pachycephalosaurins, demonstrate that having a dome cannot be used for uniting all the taxa into this clade. Thus, the “Pachycephalosaurinae,” as presently accepted, is paraphyletic. Preliminary evidence also seems to suggest that the flat-headed morphs are not sexual dimorphs of the domed forms, nor are they ontogenetic variants of the domed forms. Nor can flat-headed pachycephalosaurids be considered as remnants of some “ghost” lineage.

Although flat frontals and parietals are without doubt primitive, it has been noted that fully-domed pachycephalosaurids incongruently appear first in the fossil record during late Santonian time (Sullivan, 2003, 2005). The oldest pachycephalosaurid (ROM 2962), although not diagnosable because of its incomplete condition, is fully-domed. The oldest

diagnosable pachycephalosaurid is *Colepiocephale lambei*, from the Foremost Formation of Alberta, which is middle Campanian age (Sullivan, 2003, 2005). It is, in part, characterized by a well-developed frontoparietal dome, with the squamosals tucked under the posterior margins of the skull. There are a handful of *Colepiocephale* specimens known, representing different sizes and thus different ontogenetic stages, all show the same morphology irrespective size. As noted above, one specimen (TMP 92.88.1) bears two vestigial nodes, visible ventrally, lying between the ventral margin of the parietosquamosal border and the occiput (Sullivan, 2003). This condition is of extreme importance as it offers a clue to the origin and development of the parietosquamosal shelf in pachycephalosaurids.

I suggest that the development of the parietosquamosal shelf is secondarily derived in all pachycephalosaurids. It has been suggested by me (Sullivan, 2005) that it may be a paedomorphic feature, with the primitive condition retained in the adult. The primitive, flat-headed taxa with well-developed supratemporal fenestrae are therefore all derived. This is consistent with their appearance in the fossil record and negates the necessity for separate ghost lineages to explain their stratigraphic provenance.

The “crown” taxa considered to be members of the clade Pachycephalosaurini also present some interesting problems. Here, we have what appear to be three closely related monospecific taxa (*Dracorex*, *Pachycephalosaurius*, *Stygimoloch*), simultaneously appearing in a short interval of time 66.8 Ma to 65.5 Ma (Lancian). Two of these taxa (*Pachycephalosaurius*, *Stygimoloch*) are domed whereas the other (*Dracorex*) has a flat-skull with large supratemporal fenestrae (fenestrae). Also, in *Dracorex* the adductor origin has expanded forward onto the skull table unlike any other pachycephalosaurid and most ornithischians (Bakker et al., 2006). One is characterized by large, rounded nodes (*Pachycephalosaurius*) whereas the other two (*Dracorex*, *Stygimoloch*) have elongated spikes emanating from the squamosals. *Stygimoloch* has three massive spikes on the squamosal; *Dracorex* has four smaller spikes on the squamosal. Parenthetically, there is no indication, based on the available evidence, that the nodes of *Pachycephalosaurius* are worn down spikes. All three taxa share a near identical arrangement of nasal nodes consisting of two half-rings of prominent nodes, with only minor differences that I attribute to individual variation. Thus, I consider the node arrangement to be homologous among *Dracorex*, *Pachycephalosaurius* and *Stygimoloch*.

Some questions remain to be answered. What ontogenetic stages are represented by the specimens? Are there any unequivocal examples of sexual dimorphism among these morphotypes? Also, what features can be attributed to individual variation within this group? These are clearly important questions that need thorough investigation, the resolution of which are beyond the scope of this paper.

BIOSTRATIGRAPHIC DISTRIBUTION

Although pachycephalosaurids are known from Asia and North America (USA and Canada), the majority of specimens are from Alberta, Canada. Their biostratigraphic distribution is of extreme importance in understanding the timing of migrations/paleogeographic distributions and recognizing ontogenetic trends and establishing character polarities. A summary of the stratigraphic distribution of valid pachycephalosaurid taxa is presented in Table 13.

An unnamed taxon, consisting of an incomplete, and indeterminate, fully-domed skull from the upper part of the Milk River Formation (upper Santonian), has the distinction of being the oldest known North American pachycephalosaurid (Sullivan, 2003). This taxon, although not diagnosable, demonstrates that fully-domed pachycephalosaurids were present early on and, for the most part, are older than all of the flat-headed genera (*Wannanosaurus*, *Goyocephale*, *Tylocephale*, *Homalocephale*) from Asia. Another old and domed pachycephalosaurid is represented by the specimen recently reported from the Wahweap Formation of Utah (Kirkland and Deblieux, 2005). Unfortunately, the precise age of this material has yet to be firmly established but it appears to be lower Campanian in age. *Colepiocephale lambei* is known solely from the Foremost Formation and is the oldest diagnostic pachycephalosaurid from North America

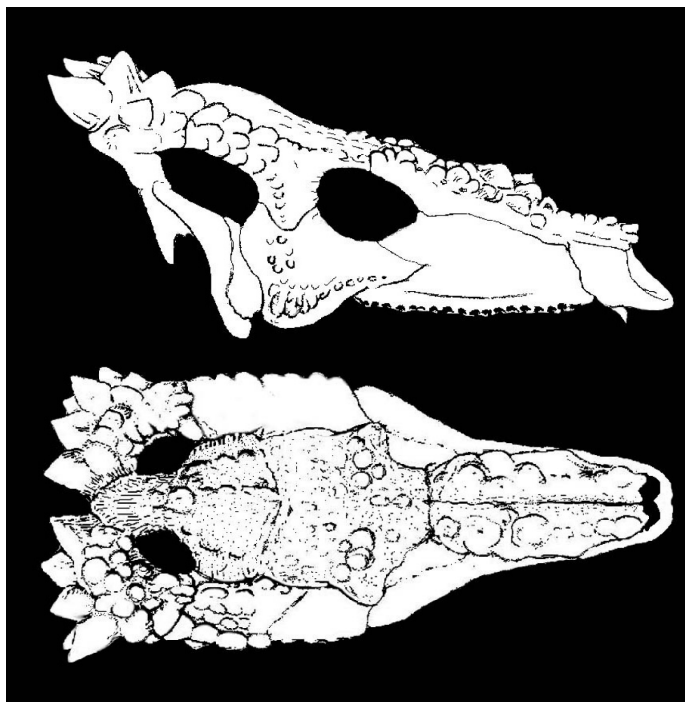


FIGURE 12. Right lateral and dorsal views of undescribed pachycephalosaurid reported by Galiano and Mehling (2001). Illustration courtesy Henry Galiano.

(Sullivan, 2003). The flat-headed taxon *Goyocephale lattimorei* is present in the Djadokhta Formation of Mongolia and is considered to be of middle Barungoyotian age. Its occurrence is coeval with the appearance of the intermediate North American taxon *Stegoceras validum* which is, in part, characterized by a greatly expanded parietosquamosal shelf with open supratemporal fenestrae (in some individuals). In North America, the Oldman and Dinosaur Park formations both yield specimens of *Stegoceras validum*, *Hanssuesia sternbergi* and *Prenocephale brevis*. *Prenocephale brevis* and the holotype and paratypes of *Hanssuesia sternbergi* are known from the Horseshoe Canyon Formation, below the Drumheller Marine Tongue. One specimen of *H. sternbergi* (UCMP 130051) has been noted to come from the Judith River Formation of Montana (Goodwin, 1990; Sullivan, 2003). *Stegoceras validum* is also present in the upper Fruitland Formation of New Mexico (Sullivan and Lucas, 2006a).

In 1916, Charles H. Sternberg collected a specimen of the advanced pachycephalosaurin *Pachycephalosaurus wyomingensis* (BMNH R8648) that allegedly came from the Oldman Formation (Wall and Galton, 1979). Sullivan (2003) concluded that the stratigraphic data associated with this specimen are probably incorrect because *P. wyomingensis* is known from a number of specimens, all of which are of late Maastrichtian age. Surely if this taxon is present in the strata of Dinosaur Provincial Park (Oldman and/or Dinosaur Park formations), then other specimens would have been discovered by now (over 90 years later). The fact is that among the hundreds of pachycephalosaurid specimens that have been recovered from these strata, none of them are *P. wyomingensis*. It is known almost exclusively from the Hell Creek and Lance formations of the United States, and presumably this is where Sternberg collected it.

The pachycephalosaurids *Homalocephale calathocercos*, *Prenocephale prenes*, *Wannosaurus yansiensis* (Nemegtian) and the new taxon *Alsakacephale gangloffii* are from strata that are probably equivalent to the early Edmontonian age (72.8 Ma to 70 Ma). *Prenocephale edmontonensis* spans strata from the late Edmontonian to Lancian age (70 Ma to 65.5 Ma). The taxa of the Pachycephalosaurini (*Dracorex hogwartsia*, *Pachycephalosaurus wyomingensis*, *Stygomoloch spinifer*) are restricted to the Lancian (66.8 Ma to 65.5 Ma).

FUTURE WORK

Although remains pachycephalosaurids have been known for over a century, our knowledge of the origin of the Pachycephalosauridae, their relationships to other ornithischian dinosaurs, the alpha taxonomy of some genera and species, and hence the phylogenetic relationships among pachycephalosaurids, remain equivocal. More complete specimens from Asia and North America are needed. New material, such as that recently discovered in China by Phil Currie and his crew, may significantly add to our knowledge of these enigmatic dinosaurs and provide additional useful characters that will help to resolve issues of morphological variation and phylogeny. Characters that have been used in the past to define subgroups (such as doming vs. flat-headed taxa) need further critical re-evaluation. The apparent taxonomic explosion of pachycephalosaurin genera (*Dracorex*, *Pachycephalosaurus*, *Stenotholus*, *Stygomoloch*) in a very short period of time (66.8–65.5 Ma) needs a thorough, more complete assessment. A consensus of the morphologic variation among taxa must be met. To this end, this contribution is a call for continued work along these paths.

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This contribution was also made possible through the help of many individuals, in various capacities, over the past few years. These include: Robert Bakker, Paul Barrett, Don Brinkman, Michael Caldwell, Thomas Carr, Phil Currie, Ted Daeschler, David Eberth, David Evans, Anthony Fiorillo, Denver Fowler, Peter Galton, Henry Galiano, Roland Gangloff, James Gardner, Mark Goodwin, Jack Horner, Spencer G. Lucas, Sam McLeod, Darren Naish, Kieran Shepherd, Kevin Seymour, Solweig Stuenes, Hans-Dieter Sues, Mary Ann Turner and Thomas E. Williamson.

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NOTE ADDED IN PROOF

Williamson and Carr (2006) report on a specimen (TMP 81.27.24) that they have tentatively identified as the pachycephalosaurin cf. *Stygomoloch*. Unfortunately, they have misidentified this specimen, as they have done previously with so many others (Williamson and Carr, 2002) (see above).

TMP 81.27.24 has all the features that are consistent with young individuals of *Stegoceras* (i.e., small “dorsal” supratemporal fenestra, posterior medial parietal extension with lateral attachment for the squamosal, etc.). Also, the posterior extension of the parietal divides the left and right squamosals, as indicated in their illustrations. Comparison of this specimen to those of *Stegoceras validum* I have previously illustrated (Sullivan, 2003, figs. 2d–g), indicates that the TMP specimen is virtually the same—the squamosals almost meet medially, converging in a V-shape toward the midline. The articular surfaces on TMP 81.27.24 are on both sides of the parietal extension, resulting in a left-squamosal-parietal-right squamosal contact. In MPM 8711 this is also the case; in MPM 8111 the squamosals are co-joined (therefore, this character is variable). Moreover, the parietal conforms in shape and size to specimens of *Stegoceras*, not *Stygomoloch*. Contrary to their assertions, Williamson and Carr (2006) do not take into

serious consideration variation due to ontogenetic stage, individual variation and sexual dimorphism (the latter is problematic). This is especially true as *Stygimoloch* is not, and cannot be, diagnosed on the basis the squamosal contact, as we know this also to occur in *Dracorex* (Bakker et al., 2006).

Lastly, I find it most curious that among all the hundreds of pachycephalosaur specimens in the Royal Tyrrell Museum of Palaeontology, only one is a putative "*Stygimoloch*." Parsimony alone casts doubt on the occurrence of "*Stygimoloch*" in the Dinosaur Park Formation. I can only conclude that Williamson and Carr are selective typologists, who choose to embrace, or "cherry pick," certain morphological features, while disregarding the significant ones. The fact that they are unable to discern the mor-

phological differences between *Stegoceras* and *Colepiocephale*, for example (the latter taxon is clearly distinguishable from *Stegoceras*), yet, at the same time, identify insignificant features that are without doubt within the realm of individual variation of *Stegoceras*, as being somehow unique and proof of alternative taxon is difficult to understand.

In summary, Williamson and Carr continue to misidentify pachycephalosaurid taxa based on a typological approach, which is a consistent pattern of these two authors. Their most recent contribution (Williamson and Carr, 2006) only further muddies the scientific literature, not only from a taxonomic and phylogenetic standpoint, but also a biostratigraphic one as well.

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