A NEW PACHYCEPHALOSAURID FROM THE BAYNSHIRE FORMATION (CENOMANIAN-LATE SANTONIAN), GOBI DESERT, MONGOLIA

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Abstract—A nearly complete pachycephalosaurid frontoparietal dome, from the Baynshire Formation at Amtgai, southern Gobi Desert, Mongolia, is identified as a new taxon. *Amtocephale gobiensis* n. gen., n. sp. differs from all other pachycephalosaurids in a combination of features that include: deep supratemporal fossae; broad (cranio-caudally) prefrontal sutureal surfaces with the nasal; prefrontal and anterior suprarorbitial sutureal surfaces lying in a single plane; short parietal (parietal length to the frontoparietal length is 2.44); the medial posterior extension the parietal sharply downturned and wide relative to the maximum width of the frontoparietal; and lacking supratemporal fenestrae. *Amtocephale gobiensis* may be the oldest known pachycephalosaurid as it comes from rocks that are no younger than late Santonian. While it may be the oldest known pachycephalosaurid, phylogenetic analysis *Amtocephale gobiensis* suggests relationship to the more derived pachycephalosaurids.

INTRODUCTION

Pachycephalosaurid dinosaurs are a group of bizarre ornithischian dinosaurus, distinguished by their unusual dome structures. They have been known for more than 100 years, but only recently has there been intense interest in the taxonomy, phylogenetic systematics, biostratigraphy and paleobiogeography of this unusual group of dinosaurs (Sereno, 2000; Sullivan, 2000, 2003, 2006; Ryan and Evans, 2005; Butler and Qi, 2009; Butler and Sullivan, 2009; Lehman, 2010; Longrich et al., 2010). Known mostly from North America and Asia (Sullivan, 2006; Butler and Sullivan, 2009; Lehman, 2010), pachycephalosaurids are typically represented in the fossil record by their ossified skull, especially the bones of the frontals and parietal that are often fused and commonly form a distinctive dome. Although the degree of doming among pachycephalosaurids is variable, this variation, in part, has been interpreted to be the result of various ontogenetic stages of development (Horner and Goodwin, 2009). Unfortunately, dome development has figured largely in the taxonomy and phylogenetic relationships of these dinosaurs. Consequently, some pachycephalosaurid taxa need to be reassessed, and the phylogenetic analyses presented by Sereno (2000), Sullivan (2003) and Schott et al. (2009) need to be scrutinized further because of the role that ontogeny may play in the morphological features of some taxa. Few specimens are included in the “Homalocephalidae,” in part, because doming may be an unreliable feature and not a synapomorphy of any particular clade (Butler and Sullivan, 2006). Sullivan (2006) revised the Pachycephalosauridae to include the “flat-headed” taxa previously included in the “Homalocephalidae,” in part, because doming may be an unreliable feature and not a synapomorphy of any particular clade (Sullivan, 2006), but mainly because the Pachycephalosauria and Pachycephalosauridae were originally diagnosed using the same characters (Maryańska and Osmólska, 1974).

A few pachycephalosaurids have been reported from Asia. These include: *Goyocephale lattimorei*, *Homaloccephale calathocercos*, *Prenocephalocephale prenes* and *Tylocephale gigomoi* (Maryańska and Osmólska, 1974; Perle et al., 1982) from Mongolia; and *Heishanosaurus pachycephalus* and “*Troodon*” *bexelli* (Bohlin, 1953), *Micro-pachycephalosaurus hongtuyanensis* (Dong, 1978) and *Wannanosaurus yansiensis* (Hou, 1977) from China. Butler and Qi (2009) considered *Micro-pachycephalosaurus hongtuyanensis* to be an indeterminate member of the Ceropoda because the holotype lacks the “unequivocal pachycephalosaur synapomorphies,” whereas Sullivan (2006) considered it to be a *nomen dubium*. *Wannanosaurus yansiensis* was considered to be a “pachycephalosaur” based on 10 synapomorphies (Butler and Qi, 2009), but Sullivan (2006) considered it to be Pachycephalosauridae incertae sedis. *Wannanosaurus yansiensis* was interpreted to be a juvenile (Sullivan, 2006; Butler and Qi, 2009) contra Perle et al. (1982). The holotype of *Micropachycephalosaurus hongtuyanensis*, which lacks skull material, was considered to be an adult by Perle et al. (1982), but recently has been reinterpreted as a juvenile (Butler and Qi, 2010). The problemata taxa *Heishanosaurus pachycephalus* and “*Stegoceras*” (= “*Troodon*”) *bexelli* were both regarded by Sullivan (2006) as *nomen dubia* because the former appears to be more like a non-descript ankylosaurid, and the latter is based on an incomplete and undiagnosable frontoparietal dome. Both holotype specimens are missing and are presumed lost (Sullivan, 2006). Sullivan (2006) revised the Pachycephalosauridae to include the “flat-headed” taxa previously included in the “Homalocephalidae,” in part, because doming may be an unreliable feature and not a synapomorphy of any particular clade (Sullivan, 2006), but mainly because the Pachycephalosauria and Pachycephalosauridae were originally diagnosed using the same characters (Maryańska and Osmólska, 1974).

Here we describe a small frontoparietal dome from the Baynshire Formation at the Amtgai locality, southeastern Gobi Desert, Mongolia (Fig. 1), which we recognize as one of the oldest known pachycephalosaurids. Despite its incomplete nature, the specimen can be diagnosed based on a few features of the frontoparietal that set it apart from all known pachycephalosaurids. Our phylogenetic analysis of this taxon is considered here to be tentative due to the lack of characters and the need for a critical re-evaluation of some characters that have been used in previous studies (Sereno, 2000; Sullivan, 2003; Schott et al, 2009).

In this paper CMN = Canadian Museum of Nature, Ottawa; MPC = Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar; MPM = Milwaukee Public Museum, Milwaukee;
SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
PACHYCEPHALOSAURIDAE Sternberg, 1945
AMTOCEPHALE n. gen.

Etymology: The generic name is derived from the locality of Amtai from where the specimen was collected and from the Greek “cephalo” meaning head.

Type and only species: Amtocephale gobiensis n. gen., n. sp.

Diagnosis: As for the type species.

AMTOCEPHALE GOBIENSIS n. sp.

Figs. 2-3

Etymology: The species name “gobiensis,” is in reference to the Gobi Desert, Mongolia, the general region where the specimen was found.

Holotype: MPC-D 100/1203, nearly complete frontoparietal (Figs. 2-3).

Locality: Amtai, southern Gobi Desert, Mongolia.

Formation/Age: Bayshyn Suite (Formation)/early Late Cretaceous (Turonian-Santonian).

Diagnosis: A small pachycephalosaurid that differs from Prenocephale brevis and all other pachycephalosaurids in having the following combination of characters: deep supratemporal fossae; broad (craniocaudally) prefrontal sutural surfaces with the nasal prefrontal and anterior supraorbitals surfaces lying in a single plane; short parietal (parietal length to the frontoparietal length is 2.44); posterior medial extension of the parietal sharply downturned; posterior medial extension of the parietal wide relative to the maximum width of the frontoparietal; and supratemporal fenestrae absent.

Description: The holotype specimen (MPC-D 100/1203) consists of a nearly complete frontoparietal. The dorsal surface is badly weathered and pitted, with the pits and ridges irregularly arranged. By contrast, the ventral surface is very well-preserved, with most of the regions intact. The articular surfaces of the peripheral elements are visible, but they appear to be worn in places. There are a few fractures that run through the frontoparietal, and the frontoparietal suture is not visible. In lateral view, the frontoparietal is arched and has a maximum thickness of 19 mm (measured from the midline of the frontoparietal suture to a point perpendicular to it on the dorsal surface). The frontoparietal length (measured along the midline) is approximately 53.2 mm. The frontal length is 31.4 mm, and the parietal length is 21.8 mm, based on extrapolation of the frontoparietal midline juncture (Fig. 3A). The ratio of the parietal length to total length of the frontoparietal dome is 2.44, which is the highest for any known pachycephalosaurid taxon (Table 1).

Ventrally, the frontals are fused, and are united along a faint, discontinuous midline suture, that essentially forms a single (frontal) element. As noted above, the fused frontal is larger than the parietal. On the ventral surface, the frontal bears the impressions of the dorsal portions of the olfactory and cerebral lobes of the brain. Laterally, the superior margins of the orbital rims are preserved on each side, which in turn are bordered by the anterior and posterior supraorbital articular surfaces (Fig. 3A). Anteriorly, along the midline, the frontal is bordered by the articular surfaces of the paired nasals.

The parietal, as previously noted, is significantly shorter than the fused frontals. The ventral surface of the parietal bears the dorsal impression of the cerebellar region of the brain. Posterolaterally, on both sides, are the supratemporal fossae. In lateral view, they are short (craniocaudally) and deep. The walls of both the right and left fossae are made up of the parietal, which bears small supratemporal roof surfaces on both the right and left sides. The articulation surfaces of the parietal, which unite with the laterosphenoid + prootic, are complete. The posterior medial extension of the parietal is strongly downturned and relatively wide with respect to the maximum width of the frontoparietal. The ventral surface of the parietal forms an obtuse angle of 132° with the ventral surface of the frontal (Fig. 3B). There is slight damage along the caudal margin of the posterior extension of the parietal. The squamosals are absent.

The articular surfaces of the peripheral bones on the frontoparietal are preserved (Fig. 3). The nasal sutural surfaces are small and weakly developed, and their lateral extent is approximately 3 mm (measured along the inferior border), on both the right and left sides. The right nasal sutural surface is reduced do to weathering. The nasal sutural surfaces have a maximum height of 8 mm at the midline, and are followed by the rather well-developed prefrontal sutural surfaces, which extend laterally for 10 mm, flanking the anterolateral parts of both the right and left frontals, with a maximum height of 10 mm (measured parallel to the sutural ridges). Behind the prefrontal sutural surfaces are the anterior supraorbital sutural surfaces, which flank the anterior portions of the orbital roof region of the frontal, and extend posterolaterally for another 10 mm on both sides. The maximum height is 8 mm at the anterior ends, where they meet the prefrontal sutural surfaces, and gradually become shorter posteriorly, approximately 5 mm in height, on both sides. The nasal, prefrontal and anterior supraorbital sutural surfaces lie virtually in a single plane. The anterior supraorbital sutural surfaces are followed by the posterior supraorbital sutural surfaces, which extend 15 mm, on both the right and left side, along the inferior border of the frontals, to the frontoparietal suture. They have their shortest height anteriorly (5 mm) and become progressively taller posteriorly (13 mm), toward the juncture of the frontoparietal suture. From just in front of the frontoparietal suture contact, to just short of the postoriormost extent of the superior temporal fossa, is the postorbital sutural surface, measuring approximately 17 mm long on both sides. The height is 13 mm near the frontoparietal juncture where they meet the anterior-lying posterior supraorbital sutural surfaces on both sides. Posterolaterally the height is reduced to about 4 mm or less on both sides. The squamosal sutural surfaces have their greatest height where they meet the postorbital sutural surfaces (5 mm) and decrease in height caudally. The squamosal sutural surface on the right side appears to wedge-out where it meets the postoriormedial extension of the parietal. The supratemporal fossae may have led to very small supratemporal fenestrae on both sides of the parietal extension, based on the presence of small gaps near where the squamosal sutural surfaces terminate and where they meet the postoriormedial extension of the parietal. However, it is very difficult to demonstrate whether these paired features are indeed present on the holotype skull of Amtocephale gobiensis.

DISCUSSION

The pachycephalosaurid Amtocephale gobiensis (MPC-D 100/1203) is a small domed pachycephalosaurid, based on the fusion of the frontals and fused frontoparietal complex. The missing peripheral elements (supraorbitals, postorbitals, squamosals) are not fused, which suggests that it is probably a subadult individual. The deep supratemporal fossae are similar to those seen in an immature parietal (CMN 12351) tentatively identified as cf. Prenocephale sp., from the Dinosaur Park Formation of Alberta. As mentioned above, the nasal, prefrontal and anterior supraorbital sutural surfaces of Amtocephale gobiensis lie virtually in a single plane (Fig. 3A). This condition is unlike most other pachycephalosaurid taxa, with the exception of Prenocephale brevis, (based on ROM 31616) which is similar, but has a somewhat different angle towards the midline (45° versus 40°, respectively). The significance of this orientation, rather than the usual right angle that is formed at the juncture of the anterior supraorbital and the prefrontal + nasal sutural surfaces is unclear, and it may be an ontogenetic artifact.

The articular surfaces for the squamosals are reduced caudally.
FIGURE 2. Amtocephale gobiensis (MPC-D 100/1203, holotype). A, dorsal, B, ventral, C, anterior, D, posterior and E, lateral views. Abbreviations: aSOSS = anterior superorbital sutural surface; Ppe = posteromedial extension of parietal; Nass = nasal sutural surface; olf = olfactory impression; or = orbital roof surface; PrFSS = prefrontal sutural surface; SQSS = squamosal sutural surface; stf = supratemporal fossa; and pSOSS = posterior superorbital sutural surface. Scale bar = 2 cm.
FIGURE 3. *Amtocephale gobiensis* (MPC-D 100/1203, holotype). Line drawing of A, ventral surface of the frontoparietal dome and B, left lateral view of same. Scale bar = 1 cm. **Abbreviations**: aSOss = anterior superorbital sutural surface; cbl = cerebellum impression; cer = cerebrum impression; Ppe = posteromedial extension of parietal; Nass = nasal sutural surface; olf = olfactory impression; or = orbital roof surface; PrFss = prefrontal sutural surface; SQss = squamosal sutural surface; stf = supratemporal fossa; and pSOss = posterior superorbital sutural surface.
The sharply downturned parietal of *Amtocephale gobiensis* is similar to that of *Prenocephale*, *Colepiocephale* and UALVP 8501. It lacks the dorsally-positioned supratemporal fenestrae seen in *Stegoceras validum* (*sensu stricto*). The roof of the supratemporal fossae is distinguished by incipient supratemporal surfaces on both the left and right sides. The posterolateral portions of the skull probably bore open supratemporal fenestrae. *A. gobiensis* is essentially the same size as UALVP 8501, identified tentatively as a water-worn specimen of *Prenocephale brevis*, and has a similar dome thickness (19 mm versus 21 mm in UALVP 8501). Although similar in size to UALVP 8501, *A. gobiensis* differs in a few features, namely: 1) deep supratemporal fossae; 2) wide posterior projection of the parietal; 3) sharply downturned postero medial extension of the parietal; and 4) wider posteriormost part of the postero medial extension of the parietal.

Unfortunately, there are not many characters, at present, to distinguish *Amtocephale gobiensis*, in a more robust way, from other Asian and North American taxa. We are confident that additional material from the Gobi Desert of Mongolia will eventually augment the characterization of this taxon.

### STRATIGRAPHY AND AGE

*Amtocephale gobiensis* is from the Bayn Shireh Formation at Amtgai, Gobi Desert, Mongolia. Hicks et al. (1999) correlated the Bayn Shireh Formation to the Cretaceous long normal chron 34 (121 to 83.5 Ma) and determined that this formation ranged from Cenomanian through Santonian time (98.5 to 83.5 Ma). This differs from the age reported earlier by Gradzinski et al. (1977) and by Jerzykiewicz and Russell (1991), who dated the Bayn Shireh Formation as late Cenomanian to early Santonian (95.0 to 85.0 Ma) and Turonian to lower Campanian (93.5 to 80.6 Ma), respectively (see Ogg et al., 2004).

Lucas and Estep (1998) reviewed the Mongolian land-vertebrate ages defined by Jerzykiewicz and Russell (1991) and concluded that some, including the “Baynshrienian,” were not distinctive. Lucas and Estep (1998) combined the “Baynshrienian” and the “Djadochtan” of Jerzykiewicz and Russell (1991) into a more inclusive Baynshrienian LVF. No correlation of the faunachron to the marine section was presented; nor was there any attempt to offer a precise age range for this revised faunachron. Lucas (2006) redefined the end of the Khukhtekian LVF by the beginning of the Baynshrienian LVF, with the Khukhtekian LVF spanning the late Aptian and all of the Alban (~125.0 to 99.6 Ma).

For the present, we accept that the age of the Bayn Shireh Formation at the Amtgai locality is no younger than 83.5 Ma (late Santonian). However, it may be older, but probably not by much based on what we know of the vertebrate faunas. We note that the age of the Milk River Formation in Alberta has been dated at 84.5 to 83.5 Ma (Payenberg et al., 2002), so the two formations may be essentially the same age.

### PHYLLOGENETIC ANALYSIS

A critical re-evaluation of the characters used in previous analyses of pachycephalosaurid phylogeny by Sereno (2000), Sullivan (2003) and Schott et al. (2009) is necessary in light of recent papers by Butler and Sullivan (2009) and Goodwin and Horner (2009). We do not accept the characters utilized by Longrich et al. (2010) and regard *Taxacephale langstoni* as a nomen dubium (Jasinski and Sullivan, 2011). We used *Yintong* (Xu et al., 2006) and rescored *Stenopelix*, based on Butler and Sullivan’s (2009) paper; together they served as our out group. We added one character (postero medial extension of parietal: non-rectangular = 0; rectangular = 1) based on the study by Jasinski and Sullivan (2011), and another (parietal/frontoparietal length ratio: > 2.25 = 0; < 2.25 = 1) from our analysis of *Amtocephale* in this paper. We corrected the scoring presented by Sullivan (2003) for *Colepiocephale* using Schott et al. (2009), giving them the benefit of the doubt that their scoring is more accurate, although we have some reservations with respect to the revised scoring implemented by them. However, we have retained the remaining scoring included by Sullivan (2003), except for a few characters. Character 3 of Sereno (2000) (preacetabular process, shape of distal end: tapered = 0; expanded = 1) is eliminated because Butler and Sullivan (2009) demonstrated that this character is highly homoplastic and occurs in many ornithischians. Character 4 of Sereno (2000) (frontal and parietal thickness: thin = 0; thick = 1) is also eliminated because it is redundant with regard to doming of the skull (Sereno’s character 33). Doming of the skull is most certainly widespread among pachycephalosaurid dinosaurs and the fact that doming is probably ontogenetic in most, if not all, pachycephalosaurids (Horner and Goodwin, 2009), means all pachycephalosaurids by default have thick skulls. The fact that doming probably occurs late in ontogeny also reinforces the observation of Sullivan (2006, p. 350) that doming may no longer be a viable character that can be used to separate the non-domed “pachycephalosaurs” from the fully-domed taxa, and that the clade Pachycephalosauridae includes both morphs (and stages in between). Therefore, character 36 of Sereno (2000) (frontoparietal doming, extent incomplete = 0; complete =1, posteriorly and laterally) is also eliminated. We have retained Sereno’s character 33 (frontoparietal doming: absent = 0; present = 1) which is considered a synapomorphy for the entire clade. Lastly, we scored character 33 for *Wannanosaurus*, *Goyocephale* and *Homalocephale* in the traditional way (Sereno, 2000), where these taxa retain their flat heads as adults. We note, however, that there is a strong possibility that these taxa developed domes as adults, late in ontogeny, as all three are considered to be based

### Table 1. Frontoparietal ratios for selected pachycephalosaurids.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen No.</th>
<th>parietal length</th>
<th>frontal length</th>
<th>total p + f length</th>
<th>parietal to total length</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Colepiocephale lambi</em></td>
<td>TMP 92.88.1</td>
<td>31.3</td>
<td>31.3</td>
<td>31.3</td>
<td>31.3</td>
</tr>
<tr>
<td><em>Stegoceras validum</em></td>
<td>CMN 515</td>
<td>52.23</td>
<td>52.23</td>
<td>52.23</td>
<td>52.23</td>
</tr>
<tr>
<td><em>Stegoceras validum</em></td>
<td>NNMMNH P-33983</td>
<td>34.45</td>
<td>34.45</td>
<td>34.45</td>
<td>34.45</td>
</tr>
<tr>
<td><em>Prenocephale brevis</em></td>
<td>ROM 31616</td>
<td>40</td>
<td>25</td>
<td>65</td>
<td>1.62*</td>
</tr>
<tr>
<td><em>Prenocephale goodwini</em></td>
<td>SMP VP-1218</td>
<td>79.3</td>
<td>79.3</td>
<td>79.3</td>
<td>79.3</td>
</tr>
<tr>
<td><em>Prenocephale edmontonensis</em></td>
<td>CMN 8830</td>
<td>47.18</td>
<td>47.18</td>
<td>47.18</td>
<td>47.18</td>
</tr>
<tr>
<td><em>Prenocephale edmontonensis</em></td>
<td>TMP 87.113.3</td>
<td>58.79</td>
<td>58.79</td>
<td>58.79</td>
<td>58.79</td>
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<tr>
<td><em>Hanssuesia sternbergi</em></td>
<td>CMN 8817</td>
<td>67.54</td>
<td>67.54</td>
<td>67.54</td>
<td>67.54</td>
</tr>
<tr>
<td><em>Homalocephale calathoceros</em></td>
<td>MPC-D 100/1201</td>
<td>64***</td>
<td>64***</td>
<td>64***</td>
<td>64***</td>
</tr>
<tr>
<td><em>Dracorex hogwartsia</em></td>
<td>TCMI 2004.17.1</td>
<td>130**</td>
<td>130**</td>
<td>130**</td>
<td>130**</td>
</tr>
</tbody>
</table>

*estimated
**measurement of dorsal side
***from Evans et al. (2010)
on immature specimens (Sullivan, 2003; Butler and Qi, 2009; Horner and Goodwin, 2009; Evans et al., 2010). A revised list of characters and their scoring is presented in Appendix 1. The data matrix used in this analysis is presented in Appendix 2.

Forty-eight characters were used in our analysis. The best tree had a tree length of 40, with a Consistency index (CI) of 0.8500, Rescaled Consistency index (RC) of 0.7459, and a Retention index (RI) of 0.8776. The strict consensus tree of 1716 trees is presented in Figure 4.

It is notable that *Amtocephale gobiensis* is nested within the *Prenocephale* clade (including *Tyrlocephale*) rather than with the more “primitive” taxa (*Wannanosaurus*, *Goyocephale*, and *Homalocephale*). Thus, despite its early occurrence (at least late Santonian), *A. gobiensis* seems, on the face of it, to be a more derived pachycephalosaurid. This assumes that doming is derived feature and that the flat-headed taxa (*Wannanosaurus*, *Goyocephale*, and *Homalocephale*) are expressing the adult frontoparietal morphology (non-domed), rather than retaining the primitive flat-frontoparietal morphology in the adult, which would be regarded as paedomorphic (Sullivan, 2005, 2006). However, given the nature of the holotype, and recognizing the fact that the amount of information that can be gleaned from this specimen is little, we do not put much faith in this phylogenetic analysis. Moreover, we realize that some of the characters used by past workers need additional scrutiny. Only with more complete and better preserved specimens can we hope to come to a more complete understanding and a more accurate hypothesis of pachycephalosaurid relationships.

**CONCLUSIONS**

*Amtocephale gobiensis* n. gen., n. sp., is a new pachycephalosaurid dinosaur from the Amtgai locality of the Gobi Desert, Mongolia. The holotype specimen (MPC-D 100/1203) consists of a small, nearly complete, frontoparietal dome that is badly damaged by erosion of the dorsal surface. Despite the poor nature of the holotype, the specimen is clearly distinguished from other Asian and North American pachycephalosaurs, based on a combination of features pertaining to the frontal and parietal elements. Our phylogenetic analysis places *A. gobiensis* among the more derived pachycephalosaurs, but we recognize the limitations of this analysis, due not only to the incomplete nature of the holotype specimen, but also to the questionable validity of some of the characters used previously (Sereno, 2000; Sullivan, 2003; Schott et al., 2009) in assessing the phylogenetic relationships of these unusual ornithischian dinosaurs.

**ACKNOWLEDGMENTS**

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RMS also thanks Steven E. Jasinski (State Museum of Pennsylvania) for his help in rescoring and running the preliminary data matrices. Thanks are extended to David Evans (Royal Ontario Museum) and Ryan Schott (University of Toronto) for discussions concerning pachycephalosaurid phylogenetic systematics and analyses.

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**FIGURE 4.** Strict consensus tree generated from 1726 trees. Some characters were rescored (see Appendices 1 and 2) and others eliminated based on works of Butler and Sullivan (2009) and Jasinski and Sullivan (2011) (see text for discussion).
REFERENCES


APPENDIX 1.

List of characters. Revised pachycephalosaurid characters (compiled and modified from Sereno, 2000; Butler and Sullivan, 2009; Schott et al., 2009; Jasinski and Sullivan, 2011; and this study). Characters in parentheses (bold face) are the ones used in this study and are followed by the number used by originating author.Italicized characters are not used in this analysis (see text for discussion).


(1) 1. Sacral rib length: subrectangular (0); strap-shaped (1)

(2) 2. Scapular blade, distal width: (0) broad; narrow (1)

3. Preacetabular process, shape of distal end: tapered (0); expanded (1)

4. Frontal and parietal thickness: thin (0); thick (1)

5. Arched premaxilla-maxilla diastema, dentary canine: absent (0); present (1)

6. Postorbital-squamosal bar, form: bar-shaped (0); broad, flattened (1)

7. Squamosal exposure on occiput: restricted (0); broad (1)

8. Anterior and posterior supraorbitals bones: absent (0); present (1)

9. Postorbital-squamosal tubercle row: absent (0); present (1)

10. Humeral length: more (0), or less than (1), 50% of the femoral length

11. Humeral shaft form: straight (0); bowed (1)

12. Deltopectoral crest development strong (0); rudimentary (1)

13. Fibular mid-shaft diameter: 1/4 or more (0); or 1/5 or less (1), mid-shaft diameter of tibia

14. Postorbital-parietal contact: absent (0); present (1)

15. Postorbital-jugal bar, shape: narrow (0); broad (1)

16. Squamosal tubercle row (5 to 7): absent (0); present (1)

17. Angular tubercle row: absent (0); present (1)

18. Zygopophyseal articulations, form: flat (0); grooved (1)

19. Ossified interwoven tendons: absent (0); present (1)

20. Iliac blade, position of medial tab: above acetabulum (0); on postacetabular process

21. Iliac blade, medial flange on postacetabular process: absent (0); present (1) (collapsed into one character (28) by Sullivan [2003])

22. Iliac blade. Lateral deflection of preacetabular process: weak (0); marked (1)

23. Iliac blade, medial tab: absent (0); present (1)

24. Parietal septum form: narrow and smooth (0); broad and rugose (1)

25. Quadratojugal ventral margin, length: moderate (0); very short (1)

26. Pterygoid quadrates rami, posterior projection of ventral margin: weak (0); pronounced (1)

27. Prootic-basisphenoid plate: absent (0); present (1)

28. Iliac blade, position of medial tab: above acetabulum (0); on postacetabular process

29. Iliac blade, medial flange on postacetabular process: absent (0); present (1) (collapsed into one character (28) by Sullivan [2003])

30. Ischial pubic peduncle, shape: transversely (0); dorsoventrally (1) flattened

31. Pubic body: substantial (0); reduced (1)

32. Interfrontal and frontoparietal sutures open (0); closed (1)

33. Frontoparietal doming: absent (0); present (1)

34. Parietal-squamosal position relative to occiput: dorsal (0); posterodorsal (1)

35. Supratemporal opening: open (0); closed (1)

36. Frontoparietal doming, extent: incomplete (0), or complete (1), posteriorly and laterally

37. Jugal-quadrate contact: absent (0); present (1)

38. Quadratojugal fossa: absent (0); present (1)

39. Preorbital skull length: much less than (0), or subequal to (1), length from anterior orbital margin to posterior aspect of quadrate head

40. Squamosal node cluster: absent (0); present (1)

41. Anterior snout nodes: absent (1) present


41. Nodes on squamosal and lateral sides of the skull: minute node clusters (0); large nodes in a linear row (1)

42. Number of nodes on squamosal: four or less (0); more than 4 (1)

43. Three or less distinct nodes on squamosal with medial node straddling the squamosal/parietal: absent (0); present (1)

44. Medial-most nodes partly or wholly on medial posterior extension of parietal: present (0); absent (1)

45. Posterior medial extension of parietal: not strongly downturned (0); strongly downturned (1)

46. Lateral peripheral elements of the dome: discrete (0); indistinguishably fused

47. Squamosals present on: lateral side (0); posteriorly (1)

48. Prominent nasal boss of the frontoparietal flanked by incipient recessed lobes: absent (0); present (1)

49. Parietosquamosal shelf reduced posteriorly with minute nodes: absent (0); present (1)

Jasinski and Sullivan (2011)

47. Shape of the posterior extension of the parietal: non-rectangular (0); rectangular (1) (new)

This study

48. Frontoparietal length ratio: < 2.25 (0); > 2.25 (1) (new)
APPENDIX 2.

Data matrix. Data matrix scoring *Wannanosaurus*, *Goyocephale* and *Homalocephale* in the traditional way as flat-headed taxa (see text for discussion).

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