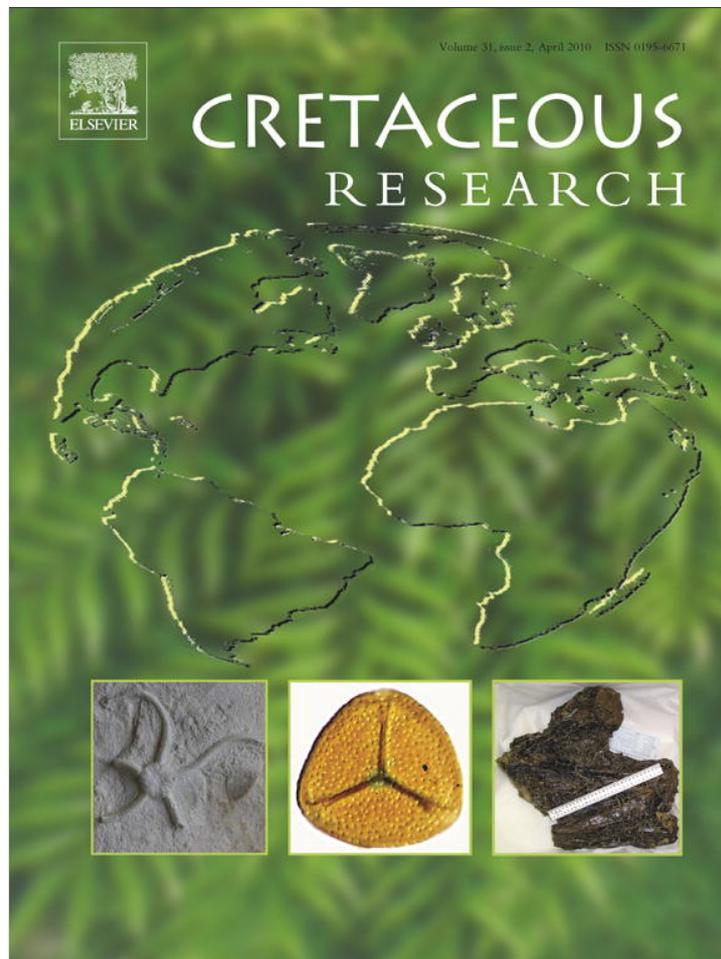


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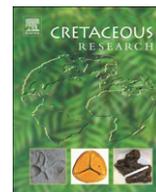
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Texacephale langstoni, a new genus of pachycephalosaurid (Dinosauria: Ornithischia) from the upper Campanian Aguja Formation, southern Texas, USA

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ABSTRACT

Recent work in the Campanian Aguja Formation of Big Bend, Texas, has resulted in the recovery of two frontoparietal domes from a new genus of pachycephalosaur. *Texacephale langstoni* gen. et sp. nov. is diagnosed by a tall, arched nasal boss, flange-like processes articulating the dome with the peripheral elements, and a low pedicel separating the cerebral fossa from the skull roof. The skull dome is composed largely of the fused frontals and parietals, with limited participation of the peripheral elements, and the supratemporal fenestrae remain open. Phylogenetic analysis indicates that *Texacephale langstoni* is a basal member of the Pachycephalosauria. The discovery of *Texacephale* supports previous suggestions that the dinosaur fauna of Texas was distinct from that of contemporary assemblages to the north. The phylogenetic analysis presented here indicates that the Asian pachycephalosaurs form a monophyletic group, deeply nested within the Pachycephalosauridae, and that the basal members of the group are all North American. This finding indicates that pachycephalosaurids originated in North America, rather than Asia, as previously believed. The high diversity of North American pachycephalosaurs and the late appearance of pachycephalosaurs in Asia are consistent with this hypothesis. The biology of *Texacephale* and other Pachycephalosauridae are also discussed. The morphology of the dome in *Texacephale* and other pachycephalosaurs supports the hypothesis that pachycephalosaurids engaged in intraspecific combat, while the occurrence of *Texacephale* and other pachycephalosaurs in nearshore deposits argues that the pachycephalosaurs were not restricted to inland habitats.

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1. Introduction

Big Bend National Park, Texas contains the southernmost Upper Cretaceous terrestrial deposits known from the United States. Although the region has been studied for many years, vertebrate fossils from these beds tend to be rare and poorly preserved, and as a result, comparatively little is known about the dinosaur fauna of the region. Pachycephalosaurs, a group of ornithischian dinosaurs characterized by a massive, domed skull roof (Maryańska et al., 2004), have been among the rarest and most poorly understood members of the dinosaur assemblage. Until now, only a single, highly fragmentary frontoparietal dome (TMM 42010–1) has been reported from the Aguja Formation of Big Bend, and three poorly preserved domes (TMM 42532–1,–2,–3) are known from the San Carlos Formation, a lateral equivalent to the Aguja that is exposed to the west of Big Bend (Lehman, 1985). The only other specimens

of Pachycephalosauridae that are known from Big Bend are isolated teeth (Sankey, 2001).

In January of 2008, the WPA (Works Progress Administrative) quarries near Talley Mountain were revisited as part of ongoing fieldwork in Big Bend National Park (Fig. 1). One of us (Tanke) discovered a frontoparietal dome (LSUMNS 20010) on a large ironstone concretionary mass exposed on the floor of WPA-1, a multitaxon bonebed dominated by *Agujaceratops*. Following another visit to the area in December of 2008, a second specimen was recovered from beds above WPA-1, again in association with *Agujaceratops*. Although initial studies suggested that the Aguja pachycephalosaur might be referable to *Stegoceras*, upon closer examination the Aguja skull was found to differ from any previously described pachycephalosaurid taxon. Despite the limited nature of the material, and despite the fact that the holotype and referred specimens exhibit predepositional wear, the material is sufficiently diagnostic to warrant the creation of a new taxon.

LSUMNS 20010 is significant because it represents the most complete pachycephalosaur specimen known from Texas, which allows for a detailed description and permits comparisons with

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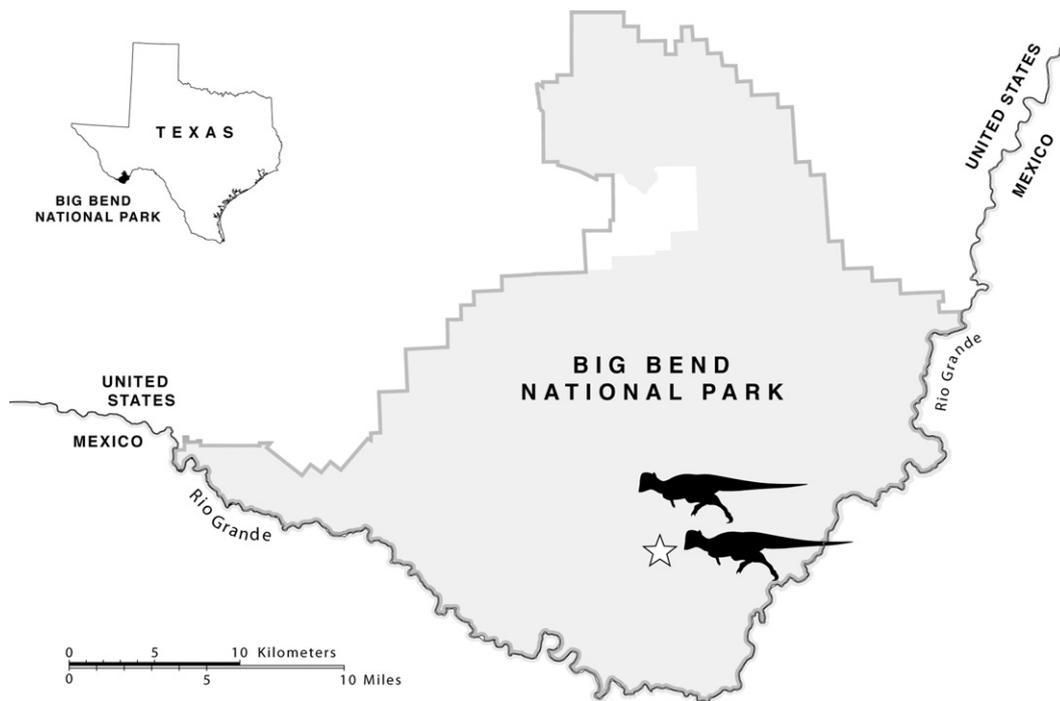


Fig. 1. Map showing Big Bend National Park and the location of the holotype LSUMNS 20010 and referred specimen LSUMNS 20012.

pachycephalosaurs found to the North. The second specimen, LSUMNS 20012, is fragmentary, but agrees well with LSUMNS 20010 in the preserved features, providing further evidence that the Texan specimens are distinct from previously known taxa. The systematics of the *Aguja* pachycephalosaur are of particular interest in light of the observation that the late Campanian of Big Bend supported dinosaur species that are not found to the north (Lehman, 1997; Sankey, 2001).

2. Geological setting

The *Aguja* Formation (Fig. 2) is an eastward thinning deposit that ranges from 135 to 285 meters in thickness. The formation is composed of sandstones with interbedded shales. Marine, paralic, and floodplain depositional environments are present in the

formation (Lehman, 1985). The lower part of the upper shale member of the *Aguja* contains sandstones, carbonaceous mudstones, thin lignite beds, and occasional ironstone concretions. These sediments represent a range of depositional environments within a coastal floodplain environment, including distributary channels, levees, crevasse splays, marshes, and bays. The upper part of the upper shale member contains fluvial mudstones and sandstones with caliche lags, which were deposited in coastal plain and inland floodplain depositional environments (Lehman, 1985).

The age of the upper shale is not well-constrained, but the preponderance of evidence suggests that the upper shale member of the *Aguja* is late Campanian or early Maastrichtian in age, based on marine biostratigraphy (Lehman, 1985) and paleomagnetic data (Sankey and Gose, 2001). Two distinct volcanic deposits in the

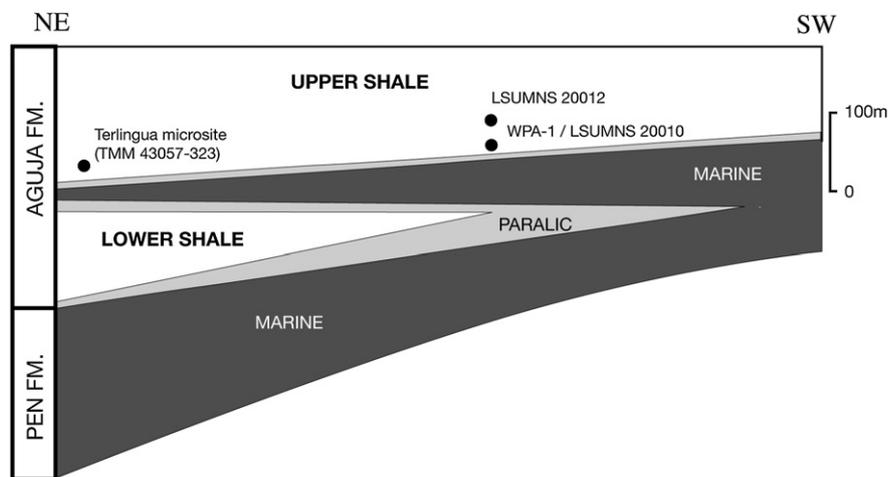


Fig. 2. Stratigraphy of the *Aguja* and *Pen* formations, showing the stratigraphic position of pachycephalosaurid specimens known from the *Aguja* Formation. Modified from Rowe et al., 1992.

upper Aguja have been dated to 72.6 Ma \pm 1.5 Ma and 76.9 Ma \pm 1.2 Ma (Breyer et al., 2007; Befus et al., 2008) using U-Pb SHRIMP-RG analyses of zircon grains.

The dinosaurian fauna of the Aguja Formation is not a rich one (Table 1). The assemblage is dominated by the hadrosaurine *Kritosaurus* sp., the chasmosaurine *Agujaceratops* (Lehman, 1989; Forster et al. 1993) and a nodosaur (AMNH 3072). Tyrannosauridae, Dromaeosauridae and *Richardoestesia* are known on the basis of teeth (Rowe et al. 1992; Sankey, 2001), and individual bones also document the presence of several other taxa of Coelurosauria. Nondinosaurian reptiles known from the Aguja include the giant crocodylian *Deinosuchus riograndensis* (Colbert and Bird, 1954), a pterosaur (Rowe et al., 1992), chelonians (Rowe et al., 1992; Tomlinson, 1997; Sankey, 2006) and lizards (Rowe et al., 1992). Mammals have also been recovered from the Aguja, including marsupials, multituberculates, and a possible eutherian (Rowe et al. 1992, Cifelli, 1995; Sankey and Gose, 2001). Amphibians found in the Aguja include urodeles, anurans, and albanerpetontids (Rowe et al., 1992); teleosts and chondrichthyes are also present in the formation (Rowe et al., 1992; Sankey, 1998, 2005, 2008).

3. Systematic palaeontology

Institutional abbreviations. AMNH, American Museum of Natural History, New York, New York; CCM, Carter County Museum, Ekalaka, Montana; LSUMNS, Louisiana State University Museum of Natural Science; Baton Rouge; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; NMC/CMN, National Museum of Canada (Canadian Museum of Nature), Ottawa; ROM, Royal Ontario Museum, Toronto; TMM, Texas Memorial Museum, Austin; UCMP, University of California Museum of Paleontology, Berkeley.

Dinosauria Owen, 1842
Ornithischia Seeley, 1888
Pachycephalosauria Maryańska and Osmólska, 1974
Pachycephalosauridae Brown and Schlaikjer, 1943
Texacephale new genus

Table 1

Aguja Formation dinosaurian faunal list, based on Rowe et al., 1992; Lehman 1985; 1989; Sankey, 2001; examination of TMM and LSUMNS collections.

Tyrannosauridae
Tyrannosauridae indet.
Ornithomimidae
Ornithomimid A
Ornithomimid B
Ornithomimid C
Oviraptorosauria
Caenagnathidae indet.
Dromaeosauridae
cf. <i>Saurornitholestes</i> sp.
Paraves incertae cedis
<i>Richardoestesia</i> sp.
Hadrosauridae
<i>Kritosaurus</i> sp.
Lambeosaurinae indet.
Ceratopsidae
<i>Agujaceratops mariscalensis</i>
Pachycephalosauridae
<i>Texacephale langstoni</i>
Nodosauridae
New genus and species

Type species. Texacephale langstoni new species.

Etymology. Derived from Texas, state of origin + Greek *cephale*, 'head'.

Diagnosis. As for species.

Texacephale langstoni, new species.

Etymology. in honor of Wann Langston, for his contributions to the vertebrate palaeontology of the Big Bend region.

Diagnosis. Medium-sized pachycephalosaurid characterized by the following autapomorphies: (1) parietal articulating with post-orbital via a series of flange-like processes, (2) tall, narrow nasal boss with a dorsal margin that is convex in lateral view, (3) skull roof elevated above the roof of the braincase by a low pedicel. These characters are unique to *Texacephale* among the Pachycephalosauridae and allow this animal to be distinguished from all previously described pachycephalosaurs.

Texacephale is further distinguished from *Colepiocephale* and *Gravitholus* by the absence of prominent lateral lobes of the parietal; from *Stegoceras* by the inflation of the supraorbital lobes of the frontal and by low postorbitals; and from *Hanssuesia* by the low postorbitals, low supraorbitals, open supratemporal fenestrae, and the tall nasal boss. *Texacephale* is distinguished from *Sphaerotholus*, *Prenocephale* and the Pachycephalosaurini by the following characters: open supratemporal fenestrae, limited contribution of the postorbitals to the dome, a large contact between supraorbital 1 and the frontal, and a tall nasal boss. Thus, even without considering the autapomorphies described above, the frontoparietal dome of *Texacephale* is distinct from any previously described pachycephalosaurid dome.

Holotype. LSUMNS 20010, fused frontoparietals (Fig. 3).

Referred material. LSUMNS 20012, incomplete frontoparietal dome.

Locality and horizon. The holotype, LSUMNS 20010, was recovered from site WPA-1, a site which lies low in the upper shale member of the Aguja Formation (Fig. 2). WPA-1 is a quarry in a multitaxon bonebed dominated by the ceratopsian *Agujaceratops mariscalensis* and hadrosaurs (Lehman, 1982; Davies and Lehman, 1989; Lehman, 2007); nodosaur remains are also present. The bonebed lies above the Terlingua Creek sandstone member, and within the lower part of the upper shale member of the Aguja (Lehman, 1989). This accumulation is located in a grey siltstone that is thought to represent an interdistributary marsh (Lehman, 1989). The referred specimen was recovered east of the bonebed, less than a kilometer away, and several tens of meters above WPA-1 (Fig. 2) in section. It was found as part of a deflation lag, along with numerous other dinosaur scraps that had weathered from an ironstone-cemented conglomerate. The only other diagnostic fossil recovered from this site is a parietal fragment from *Agujaceratops*.

4. Description

The holotype specimen LSUMNS 20010 consists of the fused frontals and parietals (Figs. 3,4) (except where noted, the description refers to the holotype). The holotype is comparable in size to *Stegoceras validum* (UA2), with the frontoparietal dome measuring 115 mm long in LSUMNS 20010, versus 125 mm in UA2. The referred specimen (Fig. 5) is slightly larger: while the holotype measures 69 mm across the orbital lobes, the referred specimen measures 81 mm here (Table 2). The frontoparietals are largely complete in the holotype, although the anterior tip of the nasal boss and the posterior margin of the parietal shelf are missing, and details of the ventral surface have been obscured by weathering. The dorsal surface of the frontoparietal is damaged in the holotype

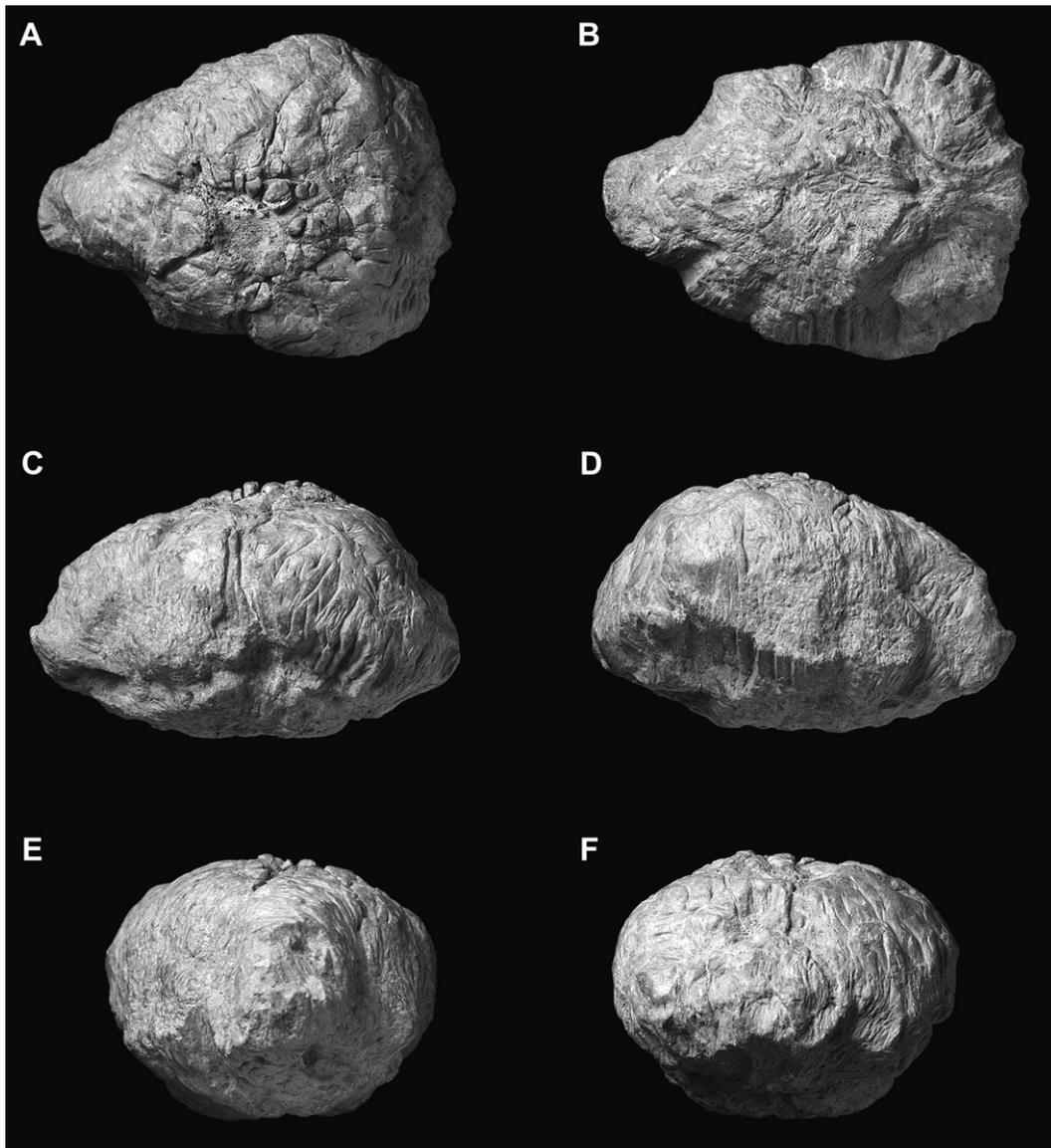


Fig. 3. Type specimen of *Texacephale langstoni*, frontoparietal dome LSUMNS 20010 in: A, dorsal view; B, ventral view; C, left lateral view; D, right lateral view; E, anterior view; F, posterior view.

(Figs. 3,4); although this may be exaggerated by weathering, the deep hole in the dorsal surface of the skull and the grooves extending from it do not appear to be an artifact. The referred specimen is missing much of the anterior and posterior portions of the frontoparietals.

The nasal boss of the frontals is tall, anteroposteriorly elongate, and covered with moderately large tubercles, as in *Stegoceras validum* (Gilmore, 1924; Sullivan, 2003) and *Colepiocephale lambei* (Sternberg, 1945, Sullivan, 2003). The nasal boss is broadest posteriorly and strongly tapers anteriorly. It is separated from the main body of the dome by pronounced sulci, as in *Stegoceras* and *Colepiocephale*. In lateral view, the dorsal margin of the nasal boss is convex, rather than straight or upturned, as seen in most other pachycephalosaurids.

The region of the frontal over the orbits is strongly expanded and contributes to the doming of the skull. In this respect, *Texacephale* is more derived than *Stegoceras validum*, and more closely resembles *Hanssuesia* (Brown and Schlaikjer, 1943; Sullivan, 2003), *Sphaerotholus* (Williamson and Carr 2002), *Prenocephale*

(Maryańska and Osmólska, 1974) and *Pachycephalosaurus* (Brown and Schlaikjer, 1943). The postorbital lobes are unusual in being strongly inflated and expanded laterally, giving the skull a mushroom-like appearance. The posterodorsal surface of the dome has a concave profile, indicating the presence of a prominent parietosquamosal shelf, as in *Stegoceras*.

The margins of the dome bear large sutural surfaces to receive the peripheral elements of the skull. The articular surfaces for the prefrontals and supraorbital ossifications are low, as in *Stegoceras*. The articular surface for the prefrontal is strongly notched, a feature shared with *Hanssuesia*. An extensive contact between supraorbital I and the frontal is indicated by the articular surface. This contrasts with the condition in *Sphaerotholus*, *Prenocephale*, and *Pachycephalosaurus*, where the articulation between the two bones is reduced. The articular surfaces of the right side are distinctly taller than those of the left, corresponding to the overall greater degree of expansion of the dome on this side.

The articulation for the postorbital indicates that the postorbital's contribution to the dome is relatively modest. In contrast,

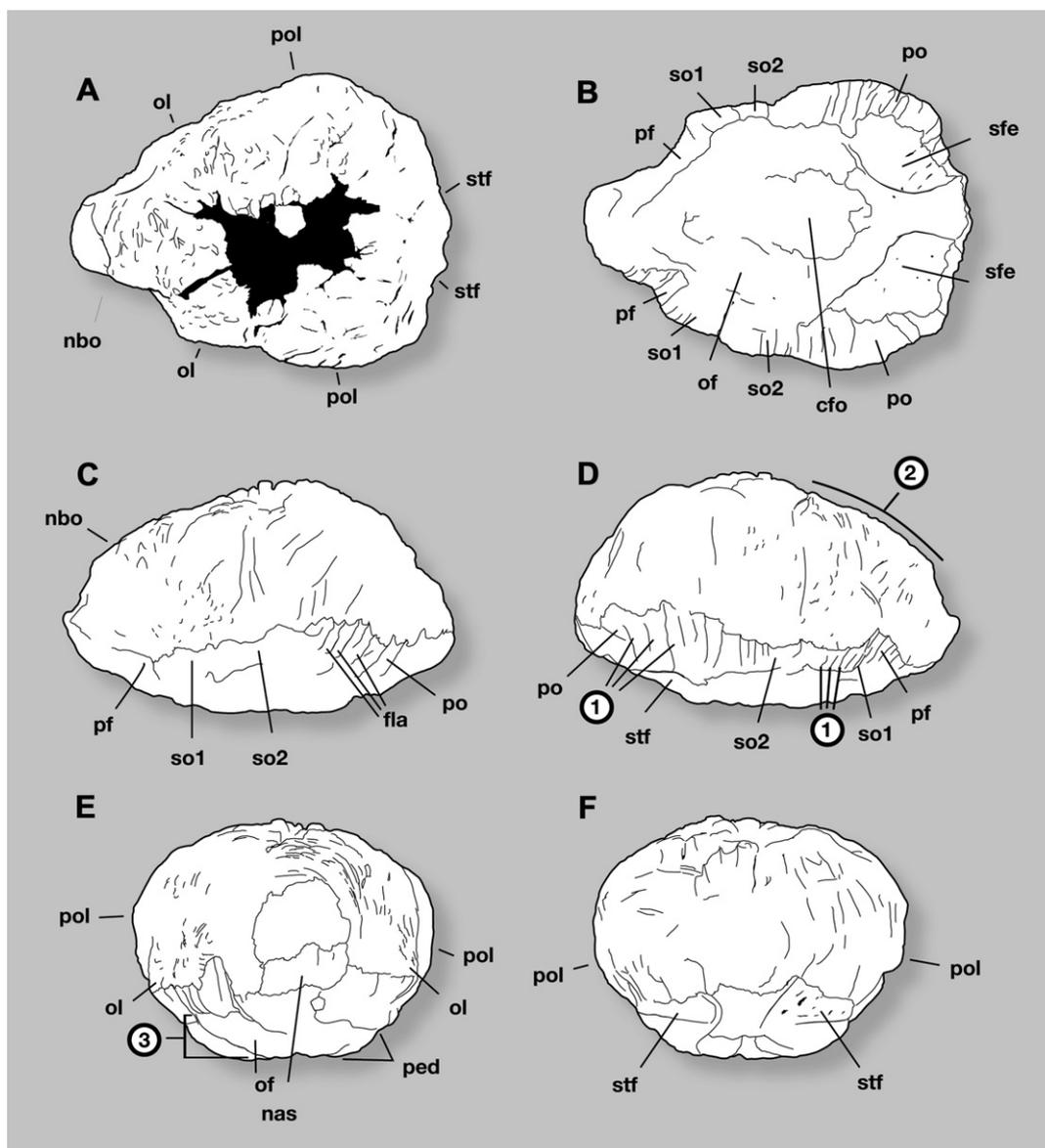


Fig. 4. Schematic drawing of *Texacephale langstoni*, frontoparietal dome LSUMNS 20010 in: A, dorsal view; B, ventral view; C, left lateral view; D, right lateral view; E, anterior view; F, posterior view. Abbreviations: cfo, cerebral fossa; fla, articular flanges; nas, nasal articular surface; nbo, nasal boss; of, orbital fossa; ol, orbital lobe of frontoparietal dome; pat, pathology; pf, prefrontal articular surface; pol, postorbital lobe of frontoparietal dome; sfe, supratemporal fenestra; sfo, supratemporal fossa; so1, supraorbital 1 articular surface; so2, supraorbital 2 articular surface. Autapomorphies of *Texacephale* are indicated by numbers: (1) flanges articulating the dome to peripheral skull elements, (2) tall, arched nasal boss, and (3) low pedicel separating orbital fossa from peripheral skull elements (and resulting in a ventrolateral inclination of the orbital fossae).

the postorbitals are tall and make an extensive contribution to the dome in *Stegoceras*, *Hanssuesia*, and *Pachycephalosaurinae* (see, e.g., Brown and Schlaikjer, 1943; Maryańska and Osmólska, 1974; Williamson and Carr, 2002; Sullivan, 2003).

The postorbital articular surface is unusual in bearing a series of 5–6 vertical flanges, which give the bone a corrugated appearance. Presumably, the postorbital would have had a series of corresponding grooves to receive these flanges; as a result the parietals and postorbitals would have had a tightly interlocking suture, meshing together almost like a pair of gears. Other *Pachycephalosauridae* do have interdigitating sutures between the dome and peripheral elements, but the ridges are lower, narrower, and more numerous. Thus, the series of large articular flanges seems to be unique to *Texacephale*. Posteriorly, two shallow notches in the back of the dome appear to represent the margins of the supratemporal fenestrae. The back of the dome is damaged, however there appears

to have been a short parietosquamosal shelf, as in *Stegoceras*, but unlike *Hanssuesia*.

Ventrally, the frontoparietal bears a small depression, the cerebral fossa, where the brain would have rested against the skull roof. The cerebral fossa is located below the level of the supraorbital elements of the skull, being separated by a sort of low pedicel or platform of bone. As a result, the orbital fossae are directed ventrolaterally (Fig. 4E). In contrast, the cerebral fossa sits at the level of the supraorbital elements in other *pachycephalosaurids*, such as *Stegoceras*, and the orbital fossae are more or less horizontal.

This feature seems to be unique to *Texacephale*. The ventral surface of the skull is damaged, but it appears that *Texacephale* would have resembled other *pachycephalosaurs* in having large sutural surfaces for the prootic, laterosphenoid, and accessory orbital ossifications. The frontals broadly roof the orbits. Posteriorly, the parietals roof over the supratemporal fenestrae, with large

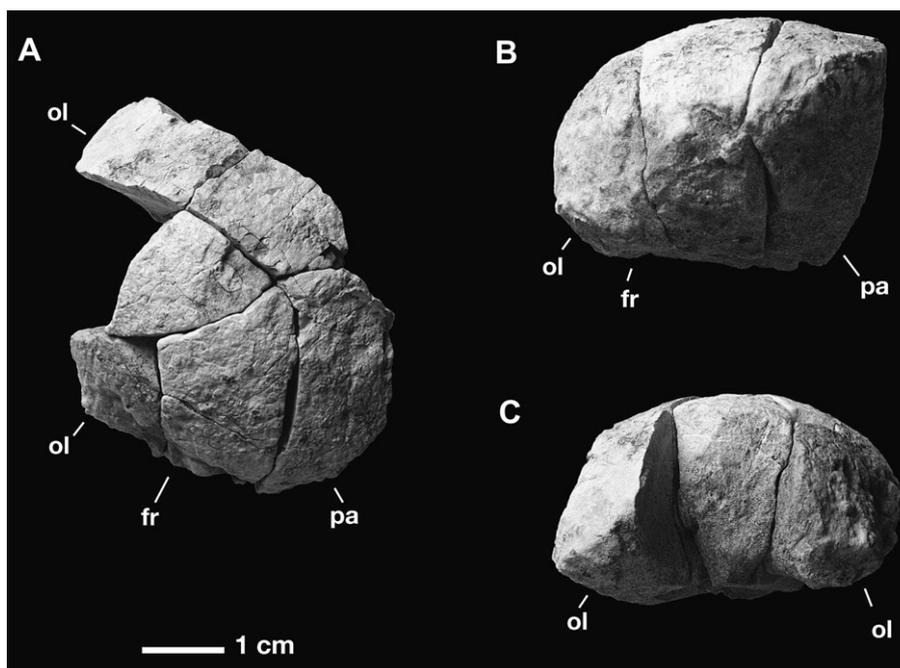


Fig. 5. Referred specimen of *Texacephale langstoni*, partial frontoparietal dome LSUMNS 20012 in: A, dorsal view; B, lateral view; C, anterior view. Abbreviations: fr, frontal; ol, orbital lobe, pa, parietal.

supratemporal fossae delimiting the dorsal wall of the chamber that housed the adductor muscles of the jaw. The supratemporal fossae are shallow, as in *Stegoceras*, *Hanssuesia*, and *Colepiocephale* (Brown and Schlaikjer, 1943; Sternberg, 1945; Sullivan, 2003). In contrast, the supratemporal fossae deeply excavate the parietal in *Sphaerotholus* (TMP 87.113.1), *Pachycephalosaurus* (CCM 87–1), and *Stygimoloch* (Giffin et al., 1987; Goodwin et al., 1998). The roof of the adductor chamber also differs from that seen in *Stegoceras* and in *Hanssuesia* in that the roof is nearly horizontal.

5. Phylogenetic analysis

Phylogenetic analysis was conducted using a matrix of 90 characters and 20 taxa. Following first-hand examination of the fossils and study of the literature, it was found that the data matrix presented by Sereno (2000) has a relatively large number of miscoded characters: e.g. in this matrix, *Stegoceras* is miscoded for characters 5, 22, 30, and 37 (NRL, pers. obs. of UA2); 24 appears to be miscoded for *Goyocephale* (Perle et al., 1982) and cannot be coded for *Wannanosaurus* (Butler and Zhao, 2008). Other codings are difficult to verify; e.g., characters 14 and 16 in *Wannanosaurus*). For this reason, a new character–taxon matrix was created. Characters include those taken from Sereno (2000), Williamson and Carr (2002), and Sullivan (2003) as well as new characters. Codings were made directly from specimens and casts, but where specimens or casts were not readily available, the literature was employed (Perle et al., 1982; Gangloff et al., 2005; Sullivan, 2006;

Butler and Zhao, 2008). Analysis was performed using PAUP* 4.0b10. The analysis follows previous studies (Sereno, 2000; Williamson and Carr, 2002; Sullivan, 2003) in using *Psittacosaurus* spp. as an outgroup; however because *Stenopelix* is fragmentary and its affinities are uncertain (Butler and Sullivan, 2009), the well-known *Thescelosaurus neglectus* was used as an outgroup in its place.

The issue of selecting taxa for analysis is complicated by the fact that several taxa referred to the Pachycephalosauria are now considered to either lie outside of this clade or to be of questionable validity. *Yaverlandia bitholus* and *Micropachycephalosaurus hongtuyensis* are no longer believed to represent pachycephalosaurids (Sullivan, 2003; Butler and Zhao, 2008) and were therefore excluded from this analysis. *Ornatolithus browni* (Wall and Galton, 1979) is now considered to represent a juvenile of *Stegoceras* (Williamson and Carr, 2002; Sullivan, 2003) and was excluded on this basis. *Gravitholus albertae* (Wall and Galton, 1979) has recently been referred to *Stegoceras* (Williamson and Carr, 2002; Sullivan, 2003). However, *Gravitholus* exhibits characters that are not seen in *Stegoceras*. These include the absence of large nodes on the parietoquamosal shelf and an extremely broad, flat nasal boss; and therefore *Gravitholus* is treated as a valid taxon for this analysis. *Sphaerotholus edmontonense* has been considered a nomen dubium (Williamson and Carr, 2002) but the holotype NMC 8830 differs from *S. goodwini* in that the parietals are broad posteriorly and bear a pair of nodes, and *S. edmontonense* can be distinguished from *S. buchholtzi* by the longer parietals. Accordingly, *Sphaerotholus edmontonense* is treated as a valid taxon in this analysis.

The status of the flat-headed forms *Dracorex*, *Homalocephale*, *Goyocephale*, and *Wannanosaurus* is problematic, because it is thought that these animals may represent juveniles of domed forms (Sullivan, 2007). In particular, *Dracorex hogwartsi* may represent a juvenile of the co-occurring *Stygimoloch spinifer* while *Homalocephale* may represent a juvenile of the co-occurring *Pre-nocephale prenes*; *Goyocephale* and *Wannanosaurus* appear to represent valid taxa but could represent juvenile morphs of domed species. However, because the ontogeny of pachycephalosaurs is poorly understood, these forms were included. To test for the

Table 2
Measurements of the the frontoparietals of *Texacephale langstoni*.

	LSUMNS 20010	LSUMNS 20012
Frontoparietal dome, maximum length	115 mm	–
Orbital lobes, maximum width	69 mm	81
Frontoparietal dome, maximum width	88	–
Frontoparietal dome, maximum height	76 mm	–
Frontoparietals, width across ventral surface	55 mm	–
Frontals, width across nasal lobes	24 mm	–

possibility that these forms are juveniles, an attempt was made to identify derived characters in these forms that are unrelated to the doming of the skull, and include them in the analysis.

Analysis was conducted using the branch-and-bound search algorithm of PAUP* 4.0b10 (Swofford, 2002). The analysis resulted in 45 most parsimonious trees of 127 steps. 11 characters were found to be parsimony-uninformative. When excluded, the resulting trees have a consistency index (CI) of 0.7500, a retention index (RI) of 0.8204, and a rescaled consistency index of 0.6281. The strict consensus of 180 trees (Fig. 5) reveals four distinct clades.

One clade contains four forms from the Maastrichtian of North America: *Pachycephalosaurus wyomingensis*, *Stygimoloch spinifer*, and *Alaskacephale gangloffii*. *Dracorex hogwartsii* is found to cluster with *Stygimoloch spinifer*.

The sister taxon to this clade is a clade containing all Asian pachycephalosaurs. These include the domed *Prenocephale prenes* and *Tylocephale gilmorei*. This clade also includes the domeless pachycephalosaurs *Homalocephale calathocercos*, *Goyocephale latimorei*, and *Wannanosaurus yansiensis*.

The third clade contains three species of *Sphaerotholus*: the late Maastrichtian *Sphaerotholus buchholtzae*, the early Maastrichtian/late Campanian *Sphaerotholus edmontonensis*, and the late Campanian *Sphaerotholus goodwini*. The position of *Sphaerotholus? brevis* is unresolved.

Hanssuesia sternbergi and *Texacephale langstoni* occupy a basal position in the tree, along with a clade containing *Stegoceras validum*, *Colepiocephale lambei*, and *Gravitholus albertae*. Owing to the high percentage of missing data and character conflict, this part of the tree is poorly resolved and future studies are bound to change the topology recovered here.

6. Discussion

6.1. Biogeography and biodiversity

As the southernmost known pachycephalosaurid, *Texacephale* is important for understanding Late Cretaceous dinosaur biogeography. Previously, it has been argued that the paleocommunity of the Aguja is distinct from the assemblages found in more northern locales such as Alberta and Montana (Rowe et al., 1992; Lehman, 1997; Sankey, 2001). Vertebrates found in the Aguja, but not in contemporary northern assemblages include the dinosaurs *Agujaceratops mariscalensis* (Lehman, 1989; Forster et al. 1993), *Kritosaurus* sp. (Lehman, 1989), and now, *Texacephale langstoni*. The Aguja also contains a number of non-dinosaurian vertebrates that are not found in contemporary strata to the north, including the crocodylians *Deinosuchus* (Colbert and Bird, 1954) and *Goniopholis* (Rowe et al., 1992), the turtle *Helopanoplia* (Sankey, 2006), the giant amiid *Melivius*, stingrays (Dasyatidae), and sawfish (Sclerorhynchidae) (Rowe et al., 1992). In addition, the vegetation of the Aguja Formation differs from that of the Dinosaur Park Formation. Arboreal angiosperms are known from fossilized wood in the Aguja, along with podocarp (Podocarpaceae) and araucarian (Araucariaceae) conifers (Wheeler and Lehman, 2005); these taxa are not known from the fossil wood assemblages found in the Campanian of Alberta (Koppelhus, 2005).

Because the age of the upper shale member of the Aguja Formation is not known with precision, the faunal differences could conceivably be explained by slight differences in the age of the Aguja and the assemblages found to the north (Lehman, 1997). Faunal differences between the top and bottom of the Dinosaur Park Formation are likely to result from evolution and extinction of species over time (Ryan and Evans, 2005) and the faunal differences seen in the Gobi redbeds are likewise thought to reflect differences in the ages of the deposits (Makovicky, 2008; Longrich et al., in

press). However, interpreting the distinct fauna of the Aguja as resulting from faunal succession is problematic, given that the Belly River and Edmonton groups of Alberta preserve a relatively continuous record of the vertebrate community, and none of the assemblages known from Alberta resemble the Aguja assemblage. Instead, we follow Lehman (1997) in interpreting differences between the Aguja and northern formations as resulting from regional differences in the paleocommunity structure. Such differences could result from geographic isolation, the differing climates of the regions, the differing vegetation structure of the various regions (Lehman, 1997) or some combination of these factors.

Admittedly, it is not unexpected to find different animals inhabiting different environments. What is perhaps unexpected is the high degree to which medium sized and large dinosaurs were able to segregate themselves compared to contemporary mammalian faunas (Lehman, 2001), and their ability to do so within the confines of the relatively small area of Western North America. In general, there is a positive correlation between the body size of animals and their geographic range (Gaston and Blackburn, 1996), and body mass of the largest tetrapods on a land mass is positively correlated with the area of that land mass (Burness et al., 2001). Dinosaur species inhabiting the Late Cretaceous of Western North America would have had their potential ranges greatly reduced by the presence of the Western Interior Seaway, which divided North America into two separate landmasses. Yet, remarkably, non-avian dinosaurs were able not only to persist within the confines of the western land mass, they appear to have been able to segregate themselves such that certain taxa inhabited only a restricted portion of this land mass. Despite their limited geographic ranges, some of these taxa weighed many tons (Paul, 1997). It remains unknown how so many species of large dinosaur were able to coexist in such limited areas.

These patterns have important implications for understanding dinosaur diversity. Much of what we know about dinosaur diversity in the final 10 million years of the Cretaceous comes from a relatively small area of the Western Interior that encompasses Alberta, Saskatchewan, Montana, Wyoming, and the Dakotas. It has been suggested that dinosaur diversity was in decline in the late Maastrichtian (Archibald, 1996; Sarjeant and Currie, 2001; Archibald and Fastovsky, 2004), however this supposed trend is based almost entirely on the low diversity in the Maastrichtian of the Hell Creek and Lance Formations, versus the higher diversity in the Campanian beds of Alberta. The diversity patterns seen in the Western Interior of North America are then generalized to the rest of North America and to the rest of the globe.

Texacephale and the other dinosaurs of the Aguja, however, illustrate the difficulties in trying to extrapolate from the biodiversity of a limited geographic area to larger areas. The taxa found in the south, such as *Texacephale*, *Agujaceratops*, and *Kritosaurus*, are distinct from those known from the North. The community structure differs as well. Chasmosaurine ceratopsids and hadrosaurine hadrosaurs dominate in the Aguja (Lehman, 1997), whereas centrosaurine ceratopsids and lambeosaurine hadrosaurs are more common in the Belly River Group (Currie and Russell, 2005). Furthermore, the assemblage appears to have been characterized by relatively low species richness. Relatively few dinosaur taxa are known from the interval (Table 1), whether the fauna is examined in terms of large dinosaur remains (Lehman, 1989) or microfossils (Rowe et al., 1992; Sankey, 2001), and the assemblage is dominated by just a few taxa, primarily *Agujaceratops* and cf. *Kritosaurus*. Although the low diversity is almost certainly exaggerated by the limited number of skeletons available from the Aguja, this does suggest that the exceptionally high diversity that is seen in the Campanian of Alberta may not have characterized North America as a whole. Dinosaur diversity is very much a local phenomenon;

community composition and community structure can differ radically from one region to another. This is perhaps expected, but it does illustrate the difficulties in attempting to reconstruct large-scale patterns in dinosaur diversity from a relatively limited geographic area.

6.2. Systematics

In the trees recovered here (Fig 7), *Texacephale* is found to be a basal member of the Pachycephalosauria. The basic topology of these trees agrees with several previous analyses (Sereno, 2000; Williamson and Carr, 2002; Sullivan, 2003) in recovering a topology where *Stygimoloch* and *Pachycephalosaur* form a clade (Pachycephalosaurini), and *Prenocephale* and *Stegoceras* are successive outgroups to the Pachycephalosaurini. The various species of *Sphaerotholus* are found to occupy a more basal position than *Prenocephale*, contradicting Sullivan's (2003) referral of this taxon to *Prenocephale*.

The principle difference between this analysis and all previous analyses concerns the position of the domeless Asian forms. Previous studies have found that the domeless Asian pachycephalosaurs *Homalocephale calathocercos* (Maryańska and Osmólska, 1974), *Goyocephale laticornis* (Perle et al., 1982), and *Wannanosaurus yansiensis* (Hou, 1977; Butler and Zhao, 2008) represent basal members of the Pachycephalosauria (Sereno, 2000; Williamson and Carr, 2002; Sullivan, 2003; Maryańska et al., 2004). In this study, they are found to form a monophyletic assemblage, along with *Prenocephale prenes* and *Tylocephale gilmorei*, that is deeply nested within the Pachycephalosaurinae. This group is not well supported, with the clade being diagnosed by a single unambiguous synapomorphy (quadrate head articulating low on squamosal descending ramus; see Butler and Zhao 2009: Fig 6E). However, numerous derived characters are shared by the domeless taxa and advanced pachycephalosaurines to the exclusion of *Stegoceras*. These include prominent nodes on the postorbitals (*Goyocephale*, *Homalocephale*, *Wannanosaurus*) enlarged nodes on the nasals (*Goyocephale*, unknown for *Homalocephale* and *Wannanosaurus*) and a reduced articulation between the frontal and supra-orbital 1 (*Goyocephale*, unknown for *Homalocephale* and *Wannanosaurus*). *Homalocephale* and *Goyocephale* also exhibit a laterally deflected and paddle-shaped preacetabular process of the ilium, and a 'crown' formed by the lateral expansion of the squamosal and postorbital; these features are shared with *Prenocephale* (Maryańska and Osmólska, 1974) but are absent from *Stegoceras* (Gilmore, 1924). Given this, and that *Homalocephale* and *Prenocephale* are remarkably similar in the construction of the palate, occiput, and pelvis, it seems almost certain that *Homalocephale* is a juvenile or a female of *Prenocephale*, which occurs in the same formation. *Goyocephale* can be distinguished from *Prenocephale* by the morphology of the ilium (Perle et al., 1982) but given that it is deeply nested in the Pachycephalosaurinae, it seems likely that it represents the juvenile or female of a fully-domed, *Prenocephale*-like form. *Wannanosaurus* may represent a valid taxon (Butler and Zhao, 2008) but again, it seems probable that it is a juvenile of a fully-domed form.

The hypothesis presented here is tentative, and it must be tested by the discovery of more complete pachycephalosaur specimens. However, it is worth exploring some of the implications of this unusual topology. One interesting implication is that if this topology is correct, then the long ghost lineages that are created by placing the flat-headed forms in a basal position would disappear. Another significant result of such an arrangement concerns the biogeography of the Pachycephalosauria. Placing the domeless Asian forms in a basal position would suggest an Asian origin of the clade (Maryańska et al., 2004). In the arrangement presented here,

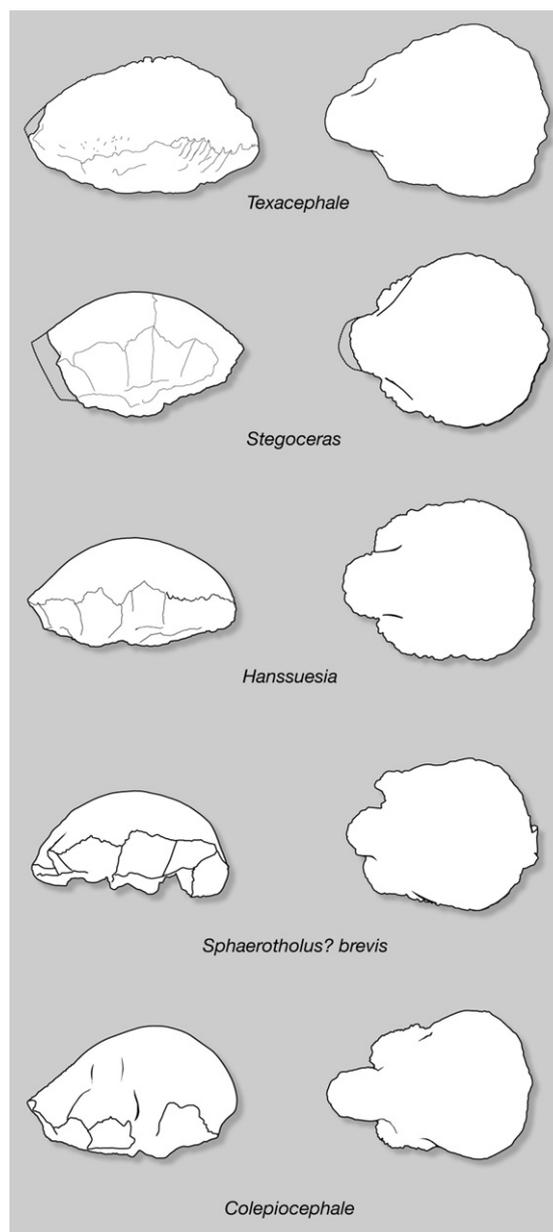


Fig. 6. Comparison of *Texacephale langstoni* and other late Campanian pachycephalosaurs in lateral (left) and dorsal (right) view.

the most basal pachycephalosaurians, including *Stegoceras*, *Texacephale*, and *Hanssuesia*, are all North American (Fig 7); the Asian pachycephalosaurs are most parsimoniously accounted for by a single dispersal from North America to Asia. The hypothesis of a North American origin for the group is consistent with the observations that (1) the earliest definitive pachycephalosaur is currently known from North America, rather than Asia (Sullivan, 2003), and (2) the group appears to have had a much higher diversity in North America than in Asia.

Finally, the analysis recovers *Dracorex hogwartsii* as the sister taxon of *Stygimoloch spinifer*. This topology is interesting, given the controversy over the validity of *Dracorex* (Bakker et al., 2006; Sullivan, 2007; Horner et al., 2007). Bakker et al. (2006) distinguished *Dracorex* from *Stygimoloch* on the basis of three characters: (1) absence of the dome, (2) presence of the supratemporal fenestrae, and (3) four short hornlets on the squamosal (versus three long hornlets in *Stygimoloch*). Characters (1) and (2) are thought to be

ontogenetic (Williamson and Carr, 2002) and therefore their utility for diagnosing *Dracorex* is questionable. Character (3) could conceivably represent a diagnostic feature of this taxon, however the precise number of nodes on the squamosal can vary; e.g. the holotype of *Prenocephale prenes* has 5 nodes on the caudodorsal margin of the right squamosal, and four on the left. What is perhaps more striking are the derived characters shared by *Stygimoloch* and *Dracorex*. These include a rosette of spike-like nodes centered around a single central, horn-like node, posterolateral elongation of the squamosals to form pedicels for the squamosal nodes, and midline contact of the squamosals (Goodwin et al., 1998; Bakker et al., 2006). Given this, the evidence for separating *Dracorex* from *Stygimoloch* is weak. However, the possibility that they represent distinct taxa cannot be ruled out entirely. More fossils are required to determine whether the differences between the two forms are discrete (as would be expected for two separate species), or simply extremes in a continuous range of variation, with the differences reflecting ontogenetic and/or intraspecific variation.

6.3. Habitat of *Texacephale*

Conventional wisdom holds that pachycephalosaurids were inland animals, and are primarily represented by domes because these are one of the few elements that could survive transport from their inland habitat (Dodson, 1971; Maryańska et al., 2004; Ryan and Evans, 2005; Butler and Barrett, 2008). However, the Aguja pachycephalosaur specimens come from coastal floodplain deposits, and the paleoenvironment has been interpreted as a densely vegetated coastal marsh (Lehman, 2007). Both domes are worn, raising the possibility of transport (although weathering on the surface could also explain this damage). However, the pachycephalosaur teeth recovered from the Terlingua and Talley Mountain sites (Rowe, et al., 1992; Sankey, 2001) have more limited potential for transport, and show little evidence of wear. This suggests that pachycephalosaurs did inhabit the coastal lowlands of Cretaceous Texas. Surprisingly, no pachycephalosaurs have been reported from the more inland deposits of the Javelina Formation of Big Bend, despite the relatively high preservation potential of pachycephalosaur frontoparietals.

A similar pattern is seen in other formations. The uppermost Foremost Formation, which was deposited in a coastal lowland environment, preserves an exceptional number of pachycephalosaur domes, even though other dinosaur remains are relatively rare here (NRL, pers. obs.). Likewise, the coastal plain environment of the late Maastrichtian Hell Creek and Lance Formation contains a diverse pachycephalosaur assemblage, including *Pachycephalosaurius*, *Stygimoloch*, *Sphaerotherolus* and perhaps *Dracorex* (Sullivan, 2006). In contrast, upper Maastrichtian deposits from the inland Scollard Formation of Alberta have produced only two fragments of pachycephalosaur skulls, and no pachycephalosaurs are known from the inland, seasonally arid Frenchman Formation of Saskatchewan (NRL, unpublished data). Some pachycephalosaurs obviously were able to exploit inland environments (e.g., *Tylocephale* and *Prenocephale* in Asia) (Maryańska and Osmólska, 1974) but pachycephalosaurids are neither particularly diverse nor particularly common in these assemblages, and so there is little evidence to support the generalization that the Pachycephalosauridae as a whole favored inland habitats. The rarity of articulated skeletons of pachycephalosaurids compared to the dome probably does not reflect transport over long distances, instead it reflects two facts: (1) there are strong taphonomic biases against the preservation of small vertebrates as articulated skeletons in fluvial deposits, and (2) taphonomic biases favor the preservation of elements that are large, dense, and durable, e.g., pachycephalosaurid domes.

6.4. Function of the dome in *Texacephale* and other pachycephalosaurs

The function of the dome seen in *Texacephale* and other members of the Pachycephalosauridae has proven an almost inexhaustible source of speculation and debate. It has been proposed that the head served as a weapon (Colbert, 1955), and in particular that the head may have been used in head butting of the kind practiced by extant bighorn sheep (Galton, 1970; Sues, 1978). However, it has also been argued that the rounded domes would have tended to glance off of each other, making head-butting difficult or impossible; for this reason it has been suggested that the dome may instead have been employed in flank butting (Sues and Galton, 1987; Carpenter, 1997) or species recognition (Goodwin and Horner, 2004).

However, the shape of the pachycephalosaur dome is not necessarily inconsistent with head-butting behavior. Although the apex of the dome may be narrow, the posterodorsal surface of the dome in *Texacephale* is broad and rounded. This broad posterodorsal surface is also seen in *Stegoceras*, *Colepiocephale*, *Prenocephale* and especially in *Gravitholus*; indeed this morphology appears to characterize all pachycephalosaurs with the exception of *Stygimoloch* (Goodwin et al., 1998) where the dome is laterally compressed. Furthermore, several bovids have evolved a horn morphology which grossly resembles the pachycephalosaurid dome. In the musk ox (*Ovibos moschatus*) and African buffalo (*Syncerus caffer*) the bases of the horns are extended medially and flattened so as to create a broadly domed, helmet-like boss (Nowak, 1991). In both species this domelike structure is used in head-butting and head-to-head shoving matches (Lent, 1988; Lundrigan, 1996). This does not necessarily prove that pachycephalosaurs did use their domes in the same fashion, but it does argue that the highly domed morphology of the pachycephalosaur skull does not preclude such a function.

Goodwin and Horner (2004) have recently argued against the hypothesis that the dome functioned as a weapon; instead they argue that the dome functioned for species recognition. It was argued that the radial bone texture seen in the pachycephalosaur skull was a transitory feature, and that therefore this structure could not have been an adaptation for intraspecific combat. This may be, but it does not logically follow that if a particular feature is not an adaptation for intraspecific combat, then the dome cannot have functioned for combat. Species recognition also seems a rather unlikely function for the dome, given that it does not vary markedly between species. Although the details of the dome's construction vary between taxa, the domed shape of the skull is conserved across a wide range of taxa. For this reason, at first glance, *Texacephale* is easily mistaken for *Stegoceras* or *Colepiocephale*, for instance, and the differences between the various North American genera are sufficiently subtle that almost all North American pachycephalosaurs were referred to *Stegoceras* until recently. Indeed, the fact that the dome's general form is relatively conservative (when compared to the wildly varying crests of hadrosaurs and frills of ceratopsids) would have made it relatively useless for species discrimination, and instead argues for a set of mechanical constraints on its design, such as those imposed by intraspecific combat. Furthermore, the closure of the frontoparietal and frontal-frontal sutures, and the elaborate sutural flanges found in *Texacephale*, suggest that the elements of the dome had to be kept from dislocating under sizeable loads. Finally, it simply seems improbable that natural selection would favor the investment of such a large amount of material and energy in building, maintaining, and carrying several pounds of bone unless it had a strong effect on the animal's fitness that went beyond species recognition. Given that most animals can and do recognize other members of

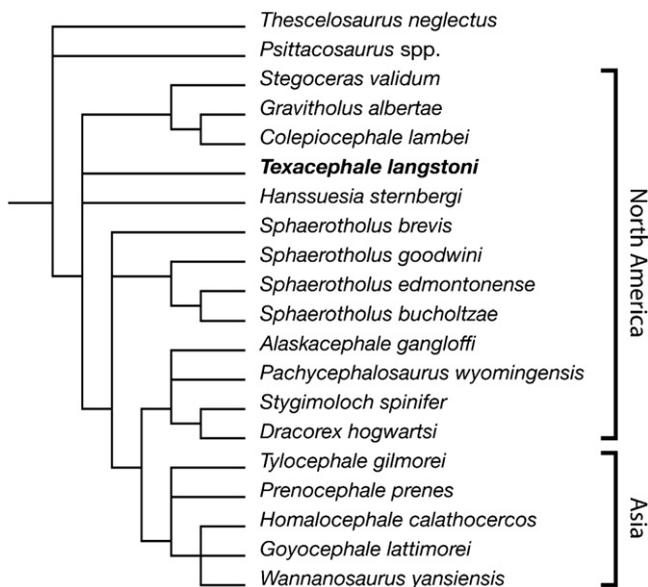


Fig. 7. Strict consensus of 46 most parsimonious trees, showing the phylogenetic position of *Texacephale langstoni*. 20 taxa and 88 characters were analyzed using PAUP 4.0b10, with *Thescelosaurus* and *Psittacosaurus* used as outgroups. The Asian forms form a monophyletic clade deeply nested in the Pachycephalosauridae and the remaining taxa are known from North America, suggesting that the group may have originated in North America.

their species perfectly well without employing such elaborate and costly structures, this hypothesis does a poor job of explaining why the pachycephalosaurs would invest such an extraordinary amount of energy and resources into the cranial dome.

It seems possible if not probable that the dome was employed as a signaling device. The handicap of investing one's finite resources into such a large and expensive structure can make it an honest signal of fitness (Iwasa et al., 1991). Expensive structures are therefore an effective tool for intimidating rivals in disputes, or courting members of the opposite sex. However, compared to a display structure such as a peacock's tail or a chameleon's frill, the structure requires a remarkable amount of material for what would be only a moderately impressive display. For this reason, it seems unlikely that display was the primary selective pressure behind the evolution of the dome.

Some of the unusual features of the dome described above may have bearing on the issue of the dome's function. As described above, the skull of *Texacephale* is highly asymmetrical. The right side of the skull is distinctly more inflated than the left, and has taller sutural surfaces, indicating that the peripheral elements were larger as well. Although one might assume that this kind of asymmetry represents a serious pathology, examination of other pachycephalosaurid skulls reveals that this kind of asymmetry is common. Examples include *Hanssuesia sternbergi* (NMC 8817 and NMC 192) *Stegoceras validum* (NMC 38079, UALVP 2) and *Prenocephale prenes* (ZPAL MgD-I/104). Given this, it seems likely that the asymmetry seen in *Texacephale* and other pachycephalosaurids represents fluctuating asymmetry—random deviations from perfect, bilateral symmetry. Fluctuating asymmetry tends to be particularly well-developed in structures that are under strong sexual selection, either as weapons used in intraspecific combat (Moller, 1992) or display structures (Moller and Hoglund, 1991); for example, the antlers of deer frequently differ in their length, diameter, and number of the tines on each side (Ditchkoff et al., 2001). The asymmetry seen in the pachycephalosaurs is therefore consistent with the hypothesis that these are sexually selected

features, used either for display to potential mates, in combat for mates/territory, or both.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi: [10.1016/j.cretres.2009.12.002](https://doi.org/10.1016/j.cretres.2009.12.002)

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