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Pachycephalosaurs (Dinosauria: Ornithischia) from the Upper Cretaceous (upper Campanian) of New Mexico: A reassessment of '*Stegoceras novomexicanum*'

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ABSTRACT

Pachycephalosaurs, a group of ornithischian dinosaurs with distinctive cranial ornamentation and skull domes, underwent dramatic changes in cranial morphology during ontogeny. This has caused debate about whether some specimens belong to juveniles or adults, which impacts studies of pachycephalosaur phylogeny and evolution. One such debate concerns a small skull roof specimen from the Campanian (Upper Cretaceous) of New Mexico, NMMNH P-33898, which was originally described as an indeterminate juvenile but later regarded as a mature adult and erected as the holotype of a new small-bodied species, *Stegoceras novomexicanum*. We restudied NMMNH P-33898 using computed tomography scanning, morphometric and phylogenetic analyses, and comparisons to growth series of other pachycephalosaurs (*Stegoceras validum*, *Pachycephalosaurus wyomingensis*). We conclude that two purported paratype specimens of *Stegoceras novomexicanum* cannot be referred to the same taxon as the holotype, that the holotype and controversial paratypes all belong to immature specimens and not aberrant small-bodied adults, but that current evidence cannot clearly determine whether NMMNH P-33898 is a juvenile belonging to its own diagnostic species (*S. novomexicanum*) or is a juvenile of *Stegoceras validum*, *Sphaerotholus goodwini*, or another known taxon. We review the pachycephalosaur record of New Mexico and demonstrate that pachycephalosaurs were important components of dinosaur faunas in the southern part of Western North America during the ~15 million years before the end-Cretaceous extinction, just as they were in roughly contemporaneous northern localities.

KEYWORDS

ontogeny, juvenile, frontoparietal, morphometric analysis, phylogeny, biogeography

1. Introduction

Pachycephalosaurs are a highly distinctive group of bipedal ornithischian dinosaurs that flourished during the latest Cretaceous (Maryańska et al., 2004). They are immediately recognized by their thickened skull roofs, which in some taxa are ornamented with nodes and horns and greatly expanded to form a rounded dome, which may have been used for display and intraspecific combat (Goodwin & Horner, 2004; Peterson et al., 2013; Snively & Theodor, 2011). Genera and species of pachycephalosaurs are primarily distinguished by differences in skull roof morphology. However, this is problematic because it is now known that pachycephalosaurs underwent extreme changes in cranial morphology during ontogeny, particularly in regards to the size, shape, fusion, and ornamentation of the skull dome (Horner & Goodwin, 2009; Schott & Evans, 2012; Schott et al., 2011; Williamson & Carr, 2002b). This has, in some cases, caused considerable disagreement about whether particular specimens are juveniles or adults, and what features can confidently diagnose species that undergo such radical changes during growth.

A prime example of such a disagreement concerns the interpretation and identification of a small pachycephalosaur specimen from the Campanian (Upper Cretaceous) of New Mexico. The specimen, NMMNH P-33898, consists of a portion of the skull roof, including the frontoparietal dome. When first described, the specimen was regarded as an immature individual of an indeterminate pachycephalosaur species, based on its small size and retention of classic juvenile pachycephalosaur features such as the relatively poor development of a dome, large size of the parietosquamosal shelf, and large size of the supratemporal fenestrae (Evans et al., 2011; Williamson & Carr, 2002a), traits that are plesiomorphic within Marginocephalia (Butler et al., 2011). It was later reinterpreted as a juvenile individual of the well-known taxon *Stegoceras valdium* (Sullivan & Lucas, 2006). Most recently, Jasinski & Sullivan (2011) came to a radically different interpretation, concluding that NMMNH P-33898 was a mature or near-mature individual. They established it as the holotype of a new small-bodied species, *Stegoceras novomexicanum*, to which they also referred two fragmentary paratype specimens from New Mexico (SMP VP-2555 and VP-2790). Resolving whether *Stegoceras novomexicanum* is valid or not is important, as this species has been included in phylogenetic analyses used to study pachycephalosaur evolution (e.g., Evans et al., 2013a; Watabe et al., 2011) and the number of pachycephalosaur taxa in latest Cretaceous North America has bearing on measures of taxonomic and morphological diversity used to study dinosaur diversification patterns during the run-up to their extinction at the end of the Cretaceous (e.g., Barrett et al., 2009; Brusatte et al., 2015; Brusatte et al., 2012; Campione & Evans, 2011; Upchurch et al., 2011).

Here we re-evaluate the maturity, taxonomic validity, and identification of *Stegoceras novomexicanum*, based on a restudy of the holotype specimen (NMMNH P-33898). This re-study includes a new high-resolution computed tomography (HRCT) scan, morphometric analyses of measurement data, a revised phylogenetic analysis, and comparison to recent work on the ontogeny of other pachycephalosaurs, including *Stegoceras validum* and *Pachycephalosaurus wyomingensis* (Horner & Goodwin, 2009; Schott et al., 2011). We come to the conclusion that the *S. novomexicanum* paratypes cannot be confidently referred to the same taxon as the holotype, that most or all purported specimens of *S. novomexicanum* belong to immature individuals, that the original diagnosis of *S. novomexicanum* is problematic, and that current evidence cannot conclusively determine whether the holotype belongs to its own valid species-level taxon (*S. novomexicanum*) or is a juvenile of *Stegoceras validum*, *Sphaerotholus goodwini*, or another known taxon.

Anatomical abbreviations: aso, contact surface for anterior supraorbital; f, frontal; f-f, frontal-frontal suture; f-p, frontoparietal suture; H:aso/pso, height of the sutural surface at the contact of the prefrontal and anterior supraorbital; H:n/n, height of the sutural surface at the contact of the nasals; H:prf/aso, height of the sutural surface at the contact of the prefrontal and anterior supraorbital; H:pso/po, height of the sutural surface at the contact of the posterior supraorbital and postorbital; L:aso, length of the anterior supraorbital suture; L:fp, length of the frontoparietal; n, contact surface for nasal; L:po, length of the postorbital suture; L:pso, length of the posterior supraorbital suture; p, parietal; pf, contact surface for prefrontal; pso, contact surface for posterior supraorbital; sq, contact surface for squamosal; T:fp, thickness of the frontoparietal; W:f/p, width of the frontoparietal dome at the contact between the frontal and parietal; W:prf/aso, width between the prefrontal and anterior supraorbital sutural contacts; W:aso/pso, width between anterior and posterior supraorbital sutural contacts; W:pso/po, width between the posterior supraorbital and postorbital sutural contacts; W:sq/sq, width between the squamosal suture just ventral to the node row; Z-1 to Z-3, histological Zones I to III.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; CMN, Canadian Museum of Nature, Ottawa; LACM, Los Angeles County Museum, Los Angeles; NMC, National Museum of Canada, Ottawa; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; ROM, Royal Ontario Museum, Toronto; SMP, State Museum of Pennsylvania, Harrisburg; TMP, Royal Tyrrell Museum of Paleontology, Drumheller; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta; UCMZ, Museum of Zoology, University of Calgary, Calgary; UWBM, University of Washington Burke Museum, Seattle.

2. Historical review of *Stegoceras novomexicanum*

In a short note, Williamson & Carr (Williamson & Carr, 2002a) described a small specimen of a pachycephalosaur from the Fruitland Formation (Fossil Forest Member, upper Campanian, Upper Cretaceous) of New Mexico. The specimen, NMMNH P-33898, consists of a nearly complete frontoparietal dome, a portion of the skull roof (Fig. 1A-E; note that NMMNH

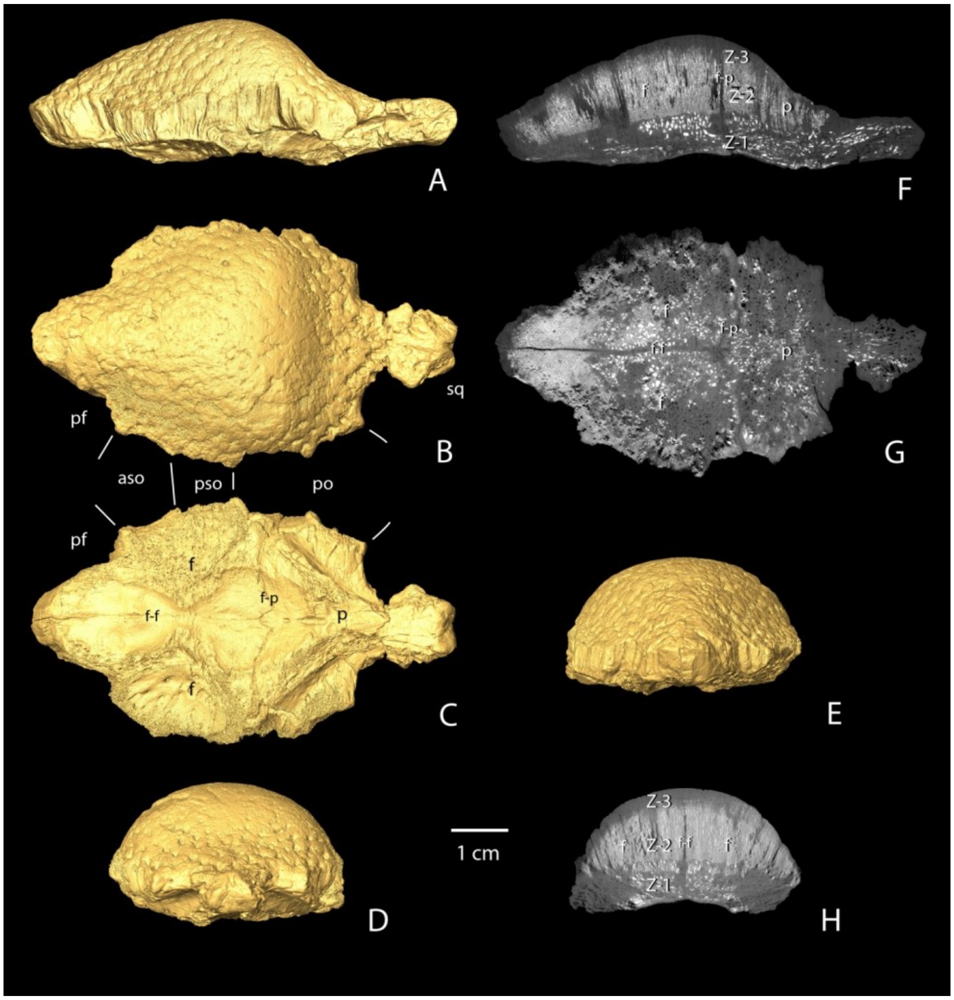

Figure 1. Surface model constructed from high-resolution CT (HRCT) images using Avizo v. 8.1

visualization software and selected CT slices of the frontoparietal NMMNH P-33898, holotype of Stegoceras novomexicanum. A, right lateral view (reversed); B, dorsal view; C, ventral view; D, posterior view; E, anterior view; F, sagittal section right of midline (reversed); G, horizontal section; H, coronal section at the contact of the posterior supraorbital and postorbital suture.

P-33898 has been erroneously listed under a variety of specimen numbers including NMMNH P-33983 [e.g., Lucas & Sullivan, 2006, Jasinski & Sullivan, 2011, Watabe et al., 2011] and NMMNH P-33893 [Lucas & Sullivan, 2006]). Williamson & Carr (2002a) regarded it as an immature pachycephalosaur based on its small size and retention of several characters that are present in the early ontogenetic stages of derived pachycephalosaurs, including large and open supratemporal fenestrae and a flattened posteromedial extension of the parietals, which indicates a prominent parietosquamosal shelf. These features are present in juveniles of *Stegoceras validum* and *Pachycephalosaurus wyomingensis* (Horner & Goodwin, 2009; Schott et al., 2011; Williamson & Carr, 2002b), taxa that develop high-domed skulls with small or closed supratemporal fenestrae and a reduced parietosquamosal shelf as adults. Because of its juvenile status and its lack of other portions of the skull that are highly diagnostic in pachycephalosaurs (particularly the squamosals), Williamson & Carr (2002a) could not confidently identify the specimen as belonging to a particular pachycephalosaur species. They tentatively suggested that it may be a juvenile representative of a new taxon from the Kirtland Formation of New Mexico, which they later named *Sphaerotholus goodwini* (Williamson & Carr 2002b), but they could not be certain. Therefore, the specimen was regarded as Pachycephalosauridae indet.

The specimen was later reexamined by Sullivan & Lucas (2006), who came to a different conclusion. They accepted that the specimen belonged to a juvenile, but concluded that it could be referred to *Stegoceras validum*, because it possessed a flattened posteromedial extension of the parietals (a pronounced parietosquamosal shelf) between the large and open supratemporal fenestrae, as is found in specimens interpreted to be subadult individuals of *Stegoceras validum* (Goodwin et al., 1998; Schott et al., 2011; Sullivan, 2003). *S. validum* is one of the best known pachycephalosaur taxa, as it is represented by numerous individuals (mostly from the Campanian of Alberta, Canada) that have allowed reconstruction of a growth series (Schott & Evans, 2012; Schott et al., 2011). However, it is now understood that the pronounced parietosquamosal shelf and large supratemporal fenestrae are general features of pachycephalosaur juveniles, not restricted to juveniles of *S. validum* (e.g., Horner & Goodwin, 2009; Schott & Evans, 2012; Schott et al., 2011; Williamson & Carr, 2002b).

More recently, Jasinski & Sullivan (2011) came to a radically different interpretation of NMMNH P-33898. Based in part on comparisons to two new fragmentary pacycephalosaur specimens from New Mexico (SMP VP-2555 and VP-2790), they concluded that NMMNH P-33898 was a “near fully-grown” individual (Jasinski & Sullivan, 2011:210). This determination was not based on study of NMMNH P-33898 itself, but rather on the similarity of the specimen to the two new fossils, which Jasinski & Sullivan (2011) argued were mature or near-mature based on: 1) the smoothness of the frontoparietal dome (in SMP VP-2555); 2) the interpretation of a ‘capping histological layer’ of bone on the top of the dome suggesting the specimens had finished growing (in SMP VP-2555 and VP-2790); and 3) partial fusion of the frontals on the midline and the frontals and parietals posteriorly (in SMP VP-2555). Because these specimens were identified as adults, but were much smaller than other pachycephalosaur adults (e.g., those of *Stegoceras validum*), Jasinski & Sullivan (2011) concluded that they must represent a new species of small-bodied pachycephalosaur. They named this species *Stegoceras novomexicanum*, and erected NMMNH P-33898 as the holotype and SMP VP-2555 and VP-2790 as paratypes.

In erecting *Stegoceras novomexicanum* as a new taxon, Jasinski & Sullivan (2011:202) provided a diagnosis that differentiated it only from *Stegoceras validum*. The following combination of features was held to distinguish *Stegoceras novomexicanum* from *Stegoceras validum*: "posteromedial extension of the parietal reduced and sub-rectangular; squamosal sutural surface contacts of the posteromedial extension of the parietal roughly parallel; supratemporal fenestrae more medial and enlarged; gracile and small adult size." The rationale for referring the two paratype specimens (SMP VP-2555 and VP-2790) to the same new taxon as the holotype (NMMNH P-33898) was only briefly articulated, and was based on overall similarity instead of possession of explicit synapomorphies.

Jasinski & Sullivan's (2011) arguments that *Stegoceras novomexicanum* is a valid taxon hinge on two things: 1) that the two referred specimens belong to the same diagnosable species as the holotype (NMMNH P-33898), as it was the referred specimens that were argued to belong to mature or near-mature adults; 2) that these specimens, particularly the holotype, are fully grown or nearly fully grown, and not juveniles.

3. Methods

We provide three new lines of evidence that help to interpret the maturity and taxonomic identity of the holotype of *Stegoceras novomexicanum* (NMMNH P-33898).

First, we subjected the holotype specimen of *Stegoceras novomexicanum*', NMMNH P-33898, to a high-resolution computerized tomographic (HRCT) scan at the University of Texas (Austin) High-Resolution X-ray Computed Tomography Facility. The following are the parameters of the scan: NSI scanner. Feinfocus source, high power, 220 kV, 0.28 mA, one brass filter, Perkin Elmer detector, 0.5 pF gain, 1 fps (999.911 ms integration time), no binning, no flip, source to object 128 mm, source to detector 1000 mm, continuous CT scan, no frames averaged, 0 skip frames, 1800 projections, 8 gain calibrations, 5 mm calibration phantom, data range [-4, 52] (rescaled from NSI default), beam-hardening correction = 0.15. Voxel size = 0.0405 mm. Total slices = 1847. The CT scan slices were then visualized and rendered into a 3D isosurface model in Avizo v. 8.1 data visualization software.

Second, we added NMMNH P-33898 to two morphometric datasets: one presented by Evans et al. (2013a), which includes 15 other pachycephalosaur specimens scored for several morphometric measurements of the frontoparietal, and another presented by Mallon et al. (2015), which includes 39 other pachycephalosaur specimens scored for four standard measurements relating to the dimensions of the postorbital sutural surfaces. The New Mexico taxon *Sphaerotholus goodwini* was added to the Mallon et al. (2015) dataset, and its measurements were revised in the Evans et al. (2013a) dataset, based on restudy of the original specimen. We measured the holotype specimen and obtained nearly identical values as Evans et al. (2013a), with the exception of two measurements; we found a different value for the H:n/n (height of the sutural contact at the contact of the nasals) 23.7 mm (estimated) versus 34.6 mm (Evans et al., 2011). This surface is damaged near the dorsal surface of the frontals and is incomplete (as indicated by italics, Table 1). Evans et al. (2011) did not indicate that their value is an estimate and we find that the Evans et al. (2011) measurement of this contact is too high, possibly because they misidentified the base of the n/n contact. They may have included a portion of the mineralized olfactory turbinates preserved in this specimen (see Bourke et al., 2014) in their measurement. There is also a small discrepancy in the values of L:pso (length of the contact for the posterior supraorbital; 39.5 mm versus 34.8 mm, respectively; Table 1).

Commented [S1]: Just because ‘significant’ to me (and maybe other readers) signifies statistical significance.

Both datasets were log-transformed and three missing values in the Mallon et al. (2015)

dataset were replaced with the mean value for that column across all other specimens (Appendix 1). The datasets were then individually subjected to Principal Components Analysis (PCA) in PAST v.2.17 (Hammer et al., 2001), using the correlation matrix for the Evans et al. (2013a) dataset and the variance-covariance matrix for the Mallon et al. (2015) dataset, following the original protocols of each analysis. For each dataset, PCA produces a multivariate morphospace. The position of NMMNH P-33898 in this morphospace can be used to test its systematic affinities, by determining whether it falls within the range of variation of another species (evidence that it belongs to that species) or is an extreme outlier (evidence that it is a distinct taxon).

Third, we updated the phylogenetic analysis of Evans et al. (2013a), which assessed the phylogenetic relationships within Pachycephalosauria with an analysis of 16 ingroup taxa, including *Stegoceras novomexicanum*, and 50 characters (see Evans et al., 2013a, supplementary table S4). We rescored a number of taxa as follows: *Prenocephale prenes* is scored as and "2" for character 29; ; *Stegoceras validum* is scored as polymorphic ("0/1") for character 28; *Pachycephalosaurus* is scored as "1" for character 7, *Alaskacephale* is scored as "?" for characters 18, 24, and 30; and *Stegoceras novomexicanum* is scored as "0" for character 42 (an updated version of the data matrix is available as supporting information; Appendix 2). We subjected the revised dataset to a parsimony analysis in TNT v. 1.1 (Goloboff et al., 2008) under the 'New Technology search' option, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was found in 10 replicates, with an aim to sample as many tree islands as possible. The recovered trees were then analyzed under traditional TBR branch swapping, a final step to more extensively explore each tree island.

4. Are the paratypes of *Stegoceras novomexicanum* referrable to the same taxon as the holotype?

Jasinski et al. (2011) referred two specimens to *Stegoceras novomexicanum* and designated them as paratypes. One specimen consists only of a portion of the frontal (SMP VP-2555 and the other (SMP VP-2790) consists of the anterior portion of a parietal, yet were referred to the same taxon as the holotype, NMMNH P-33898. The rationale for referring the two paratype specimens (SMP VP-2555 and VP-2790) to the same new taxon as the holotype (NMMNH P-33898) was that the diagnostic combination of characters distinguishing NMMNH P-33898 from *Stegoceras validum* were "either present or inferred to be present in the two paratype specimens" (Jasinski & Sullivan, 2011:203) and that, at least in the case of SMP VP-2555, it has "identical morphology of the ventral surfaces and similar size" to NMMNH P-38898 (Jasinski & Sullivan, 2011:207).

We find this rationale to be problematic. First, Jasinski & Sullivan (2011) did not list any features of ventral surface of the frontal in their diagnosis for *Stegoceras novomexicanum*, so it is unclear what exactly constitutes the "identical morphology" uniquely shared between SMP VP-2555 and the holotype. Second, skull and dome size is highly variable in pachycephalosaurs and clearly changes through ontogeny, so the similar size of SMP VP-2555 and the holotype is not a strong sign of taxonomic equivalency. Third and most problematic, all the features, other than size, explicitly listed in the diagnosis of *Stegoceras novomexicanum* concern the posterior part of the parietals, which is not preserved in either paratype. Moreover, at least one of the paratype specimens, SMP VP-2555, consists of a portion of the frontals that includes part of the articular surfaces for the anterior supraorbital, prefrontal, and nasal. This specimen preserves a highly transversely-convex frontal boss that is bordered laterally by a distinct groove, similar to what is seen in *S. validum* and some other pachycephalosaur taxa (e.g., "*Prenocephale*" *brevis*, *Colepiocephale lambei*, *Hanssuesia sternbergi*; Williamson and Carr, 2002b; Sullivan, 2003), but unlike the holotype of *Stegoceras novomexicanum* (NMMNH P-33898). This difference between SMP VP-2555 and NMMNH P-33898 may be evidence that these two specimens belong to different taxa. However, it is likely that the differences are due to ontogeny because the prominence of the frontonasal boss and the frontal grooves are variable within *S. validum*, and are generally more poorly developed in specimens of early ontogenetic stages (e.g., AMNH 5450, and CMN 515) (Schott et al., 2011).

In summary, there is no explicit character evidence that supports the referral of the paratypes SMP VP-2555 and VP-2790 to the same taxon as the *Stegoceras novomexicanum* holotype, NMMNH P-33898. Therefore, any arguments about the maturity of *Stegoceras novomexicanum* based on the paratype specimens are inconclusive.

5. Are the putative specimens of *Stegoceras novomexicanum* mature or near-mature?

The crux of Jasinski & Sullivan's (2011) argument that *Stegoceras novomexicanum* is a valid species is that all known material (the holotype and two controversial paratypes) belong to mature or near-mature individuals. If this is the case, then the small size of these specimens compared to other pachycephalosaur adults from the Late Cretaceous would indicate that the New Mexico specimens belong to a distinct small-bodied species.

When discussing pachycephalosaur ontogeny and identifying the maturity stage of individual specimens, there is a wealth of data to refer to. Understanding of pachycephalosaur ontogeny comes from the study of relatively large samples of specimens that are thought to represent a single taxon. These contain individuals that are from a variety of ontogenetic stages and can be used to reconstruct a growth series. Such a growth series has been reconstructed for *Stegoceras validum* based on large samples referred to that taxon from upper Campanian deposits of the Dinosaur Park Formation (Schott & Evans, 2012; Schott et al., 2011) and has been postulated for *Pachycephalosaurus wyomingensis* from the upper Maastrichtian of the Lance and Hell Creek formations of the northern Rocky Mountain region (Horner & Goodwin, 2009). These provide compelling evidence that these pachycephalosaurs underwent relatively extreme changes in cranial morphology during ontogeny.

Many authors, including Williamson & Carr (2002b), Goodwin & Horner (2004), Horner & Goodwin (2009), Schott et al. (2011), and Schott & Evans (2012) used a suite of characters to assess relative maturity in *Stegoceras validum* and/or *Pachycephalosaurus wyomingensis*. Changes that the pachycephalosaur skull underwent through ontogeny include an increase in the degree of sutural fusion between the paired frontals and between the frontals and parietal from widely open sutures in juvenile specimens to total fusion between these bones in adults; an increase in the overall size of the frontoparietal; an increase in the size and a change in shape of the frontoparietal dome as it expanded vertically and horizontally, resulting in reduction of the relative size of the parietosquamosal shelf and reduction or complete closure of the supratemporal fenestra; changes in surface texture of the dome from small, rounded tubercles, to larger, flat-topped platforms separated by sulci or depressions that develop as the underlying dome expanded; a change in the external cortical dome surface from one that presented exposed Sharpey's fibers to a blunt-shaped erosional or degraded surface; and a change in the internal bone texture of the skull roof from one that is highly vascularized with vascular spaces oriented primarily in a radial patter to one that is dense with a highly reduced vascularization.

With this information to draw from, along with new data from our HRCT analysis of

NMMNH P-38898, we comment on the maturity of the New Mexico specimens referred to *Stegoceras novomexicanum*. We individually discuss the features that Jasinski & Sullivan (2011) held to be indicators of maturity (or near maturity) in the New Mexico specimens. Importantly, we provide a clear assessment of the ontogenetic stage of the holotype (NMMNH P-38898), which Jasinski & Sullivan (2011) only briefly discussed. Instead, their ontogenetic argument was based on the referred paratypes, which is problematic because the holotype is the name-bearer of *Stegoceras novomexicanum* and because the paratypes cannot be reliably referred to the same taxon as the holotype (see Section 4 above).

5.1 Texture of the dorsal surface of the frontoparietal dome

Jasinski & Sullivan (2011:203) argued that the "smoothness of the frontoparietal dome" in the paratype specimen SMP VP-2555 supported its mature or near-mature status. However, the smoothness of the dome surface does not offer an effective way to clearly gauge relative maturity in pachycephalosaurs because it is related to the relative inflation of the underlying skull roof.

Nodal ornamentation changes ontogenetically in pachycephalosaurs, coinciding with inflation of the dome. In *S. validum*, the tubercular ornamentation on the domes typically exhibit low relief compared to those on the skull roof perimeter, a difference that is related to the local degree of dome inflation. This inflation is hypothesized to laterally expand surface tubercles that overly the dome, resulting in an increase in the diameter of individual tubercles, and a reduction in their vertical relief (Williamson & Carr, 2002b). Relatively unexpanded portions of the skull roof, usually found near the perimeter of the skull roof, typically retain relatively small and high tubercles. Indeed, the frontal fragment, SMP VP-2555 retains relatively small, high, and distinct tubercles lateral to the high and inflated nasal boss (Jasinski & Sullivan, 2011, fig. 4c).

The dorsal surface of NMMNH P-33898 does exhibit tuberculate ornamentation that is lower than typically observed in many immature specimens of *S. validum*. In particular, the tubercular ornamentation of NMMNH P-33898 is distinctly subdued transversely across the apex of the dome, over the approximate location of the frontoparietal sutures. However, it is unclear if this indicates a greater relative maturity than these *S. validum* specimens, for two reasons. First, the relative smoothness of the dome and subdued morphology of the tubercles may be due to postmortem abrasion of the specimen. Second, even if this morphology is genuine, domes in pachycephalosaurs typically show reduced tubercular ornamentation even in specimens that represent early ontogenetic stages (Schott et al., 2011; Williamson & Carr, 2002b) and so presence of a smooth surface over the domed portion of a frontoparietal does not necessarily indicate that maturity has been reached.

5.2 *Histology of the frontoparietal dome*

Jasinski & Sullivan (2011) argued that the histology of the frontoparietal dome of SMP VP-2555 and SMP VP-2790 indicated that the specimens belonged to mature adults that had stopped growing. Histological examination was based on gross observation of bone texture as revealed through a natural break in the specimen (Jasinski & Sullivan, 2011:fig. 6), not examination of thin sections or CT data. Jasinski & Sullivan (2011) regarded the more complete SMP VP-2555 as exhibiting four distinct histological regions (“histomorphs” in their terminology) that they interpreted to represent episodes of accelerated growth in the dome interrupted by episodes of slower growth, akin to lines of arrested growth (LAGs). In addition, they argued that the presence of “capping layer” composed of dense, avascular bone, near the dorsal surface of SMP VP-2555 and VP-2790 indicated that both specimens had essentially stopped growing.

There is a wealth of data on how frontoparietal histology changes during pachycephalosaur growth, based on examination of large samples of *Stegoceras* and *Pachycephalosaurus* (e.g., Goodwin & Horner, 2004; Schott et al., 2011). Goodwin & Horner (2004) recognized histological zones termed Zones I, II, and III within the frontoparietal domes of *Stegoceras validum* and *Pachycephalosaurus wyomingensis*. Zone I is a basal zone of “typical” bone of endochondral origin that remains constant through ontogeny. Zone II is a zone of vascular bone that decreases during ontogeny. Zone III is a zone of dense, sparsely vascularized bone below the periosteal surface of the dome. Jasinski & Sullivan (2011) regarded the dense outer h4 zone of SMP VP-2555 and VP-2790 to be equivalent to Zone III of Goodwin & Horner (2004), and we agree. We also interpret the histological zones 1 (h1) and 3 (h3) of Jasinski & Sullivan (2011) to represent histological Zones I and II, respectively, of Goodwin & Horner (2004), as their histological structure is nearly identical. We are not completely certain of the identification of the narrow zone of more cancellous bone that Jasinski & Sullivan (2011) identified as zone 2 (h2), which surrounds the tissue of zone 1. A similar zone has yet to be reported in other pachycephalosaurs that have been studied.

Jasinski & Sullivan (2011) used the histological structure of SMP VP-2555 and VP-2790 to make an argument about maturity, but this conclusion is at odds with the conclusions reached by other workers based on study of *Stegoceras* and *Pachycephalosaurus* (e.g., Goodwin & Horner, 2004; Horner & Goodwin, 2009; Schott, 2011). Jasinski & Sullivan (2011) argued that the presence of the dense, poorly vascularized outer layer of the dome (equivalent to Zone III of

Horner & Goodwin [2004]) indicates that the specimens had stopped growing. However, in *Pachycephalosaurus* and *Stegoceras*, Zone III appears early in ontogeny and its thickness increases as an individual grows. It is present as a thin layer even in very early ontogenetic stages of *S. validum* (UCMP 130049; Schott et al., 2011, fig. 5a). Therefore, the presence of this layer is not an indicator of maturity, contra Jasinski & Sullivan (2011).

The entirety of Jasinski & Sullivan's (2011) histology argument is based on the two referred specimens. Our restudy of the *Stegoceras novomexicanum* holotype (NMMNH P-33898) provides histological evidence that the specimen is immature. HRCT slices through the frontoparietal reveal details of the bone histology (Fig. 1F-H). In this specimen, many of the vascular spaces are filled with a relatively x-ray opaque mineral and these show up as white in the scans. The scans clearly reveal a distinct separation between a relatively thick and highly vascularized layer with approximately vertically-aligned bony struts separated by vascular spaces (Zone II, sensu Goodwin & Horner, 2004) sandwiched between an amorphous, but vascular, basal zone (Zone I) and dense dorsal zone (Zone III) below the surface of the skull roof (Fig. 1F-H).

Schott et al. (2011) assessed relative maturity of specimens of *Stegoceras validum* based upon the relative amount of void space within the frontoparietal. In their study, they calculated the percentage of void space from thresholded coronal CT slices of the skull roof at the postorbital-squamosal contact. Void space is found primarily within Zone II and is reduced through ontogeny as Zones I and III increase in relative thickness at the expense of Zone II (see Schott et al., 2011, fig. 10). Unfortunately, the presence of relatively opaque minerals within the void spaces of NMMNH P-33898 prevents us from obtaining a useful thresholded image of the specimen. Nevertheless, the relative thickness of Zone II compared to Zones I and III can be readily compared in CT slices (Fig. 1) and reveal a highly vascularized Zone II that is significantly thicker than either Zone I or Zone III. The relative amount of void space within the dome and relative thickness of Zone II is strongly similar to that in immature specimens of *Stegoceras validum*, and is much thicker than in adult or near-mature specimens (see Schott et al., 2011) and is a clear indication that NMMNH P-33898 represents a juvenile specimen.

5.3 Suture closure on the dorsal surface of the frontoparietal dome

Jasinski & Sullivan (2011:203) held that the “partial fusion” of the left and right frontals and the frontals and parietals in SMP VP-2555 was a sign of maturity. Their concept of “partial fusion” was the lack of visible sutural contacts between the frontals and the frontals and parietals on the external surface of the specimen.

Stegoceras and *Pachycephalosaurus* close sutural contacts between the paired frontals and between the frontals and parietals, as well as between other skull roof bones, during ontogeny. In specimens that represent early ontogenetic stages, the frontoparietals remain completely unfused, with sutures that are visible on the external surface of the specimens. However as ontogeny ensues, the sutures between the frontals and parietals often become indistinguishable on the dorsal surface even in subadult specimens, while remaining open internally (Horner & Goodwin, 2009; Schott et al., 2011).

Jasinski & Sullivan (2011) focused most of their attention on the sutural morphology of SMP VP-2555 and did not discuss the condition in NMMNH P-33898 in much detail. In this specimen, the frontal-frontal and frontoparietal sutures are not visible near the midline of the external (dorsal) surface of the dome but remain distinct on the ventral surface. Moreover, the frontal-parietal sutures are clearly visible on the lateral surfaces of the specimen and on the dorsolateral surfaces of the dome. HRCT scans of NMMNH P-33898 (Fig. 1F-H) show frontal-frontal and frontoparietal sutures as dark lines with little, or no, mineralization. These indicate that the sutures between the frontals and between the frontals and parietals were open through most of the skull height, closing only very close to the dorsal surface near the midline of the skull. This is a strong indication that the specimen represents an immature individual, because early in pachycephalosaur ontogeny the suture trace disappears from the external surface while remaining open internally (Horner & Goodwin, 2009; Schott et al., 2011).

5.4 Additional features of the anatomy

In addition to the three explicit features that they used to argue for the maturity or near-maturity of *Stegoceras novomexicanum* specimens, Jasinski & Sullivan (2011) also mentioned some other characters that purportedly supported their assessment. They argued that NMMNH P-33898 exhibits a degree of development of the dome, frontoparietal shelf, and supratemporal fenestrae similar to the condition in specimens of *Stegoceras validum* that they held to be mature or nearly mature, particularly CMN 515, the holotype of *S. validum*, and CMN 138, another specimen that they regarded as approximately the same ontogenetic stage (although they acknowledged that some features suggested it was not fully mature). These CMN specimens possess a partially expanded dome with an extensive frontoparietal shelf and large, open supratemporal fenestrae. In this regard, we agree that they are similar to NMMNH P-33898. However, we note that Schott et al.'s (2011) comprehensive study of *S. validum* growth came to a much different conclusion on the ontogenetic maturity of CMN 515 and 138. Unlike Jasinski &

Sullivan (2011), who considered these specimens to be mature, Schott et al. (2011) found both to be in the middle portion of the *S. validum* growth series, approximately midway between the earliest ontogenetic stage and the latest (see Schott et al., 2011, fig. 4). If Schott et al. (2011) are correct, then the similarity between NMMNH P-33898 and the two CMN species would be evidence that NMMNH P-33898 is also an immature individual far from being fully grown or osteologically mature.

5.5 Summary

The suite of morphological features that are typically used to assess ontogeny in *Stegoceras validum* and other pachycephalosaurs indicate that NMMNH P-33898 represents a relatively early ontogenetic stage rather than a mature or nearly mature individual. Furthermore, none of the features that Jasinski & Sullivan (2011) considered as supporting the maturity of NMMNH P-33898 and the two controversial paratypes hold up to scrutiny. Therefore, all evidence indicates that the specimens of *Stegoceras novomexicanum* are immature, and there are no grounds to consider this pachycephalosaur to be an unusual small-bodied taxon.

6. Is *Stegoceras novomexicanum* a valid taxon?

The holotype and controversial paratype specimens of *Stegoceras novomexicanum* belong to immature individuals, but of which species? It is possible that *Stegoceras novomexicanum* may still be a valid taxon, albeit represented only by juvenile material. Alternatively, there may be evidence that the *Stegoceras novomexicanum* specimens belong to another pachycephalosaurid taxon, such as *Stegoceras validum* (as hypothesized by Sullivan & Lucas 2006) or *Sphaerotholus goodwini* (which was raised as a possibility by Williamson & Carr 2002a), which is found in strata of similar age in the San Juan Basin of New Mexico. We review several lines of evidence bearing on this issue.

6.1 Original diagnosis

The starting point for this discussion is the original diagnosis of *Stegoceras novomexicanum* from Jasinski & Sullivan (2011:202). They regarded the following characters as diagnostic for *Stegoceras novomexicanum* relative to only one other taxon, *S. validum*: a reduced posteromedial extension of the parietal that is sub-rectangular in shape, squamosal sutural surfaces on the parietal that is roughly parallel (a result of the sub-rectangular shape of the posteromedial extension of the parietal), supratemporal fenestrae that are large and medially positioned, and small adult size.

We have issues with all of these characters. We discounted the latter two characters (above), demonstrating that the enlarge fenestrae and small body size are juvenile features. The other features considered diagnostic by Jasinski & Sullivan (2011) deserve further comment.

Jasinski & Sullivan (2011:210) made a distinction between the reduced and sub-rectangular posteromedial parietal extension of *Stegoceras novomexicanum* with the relatively wider, “more robust and trapezoidal” posterior process of the parietal in *S. validum*, which results in more laterally positioned supratemporal fenestrae and “splayed” sutural surfaces for the squamosal. Based in part on this description, the shape of the posteromedial (intrasquamosal) process of the parietal has been incorporated into phylogenetic analyses, with two states, ‘nonrectangular' and 'rectangular' (Watabe et al., 2011: ch. 47). However, we feel that the distinction between these two conditions is not clear-cut, particularly as it has not been quantified in any way. We argue that the posteromedial projection of the *Stegoceras novomexicanum* holotype (NMMNH P-33898) is more trapezoidal than rectangular in shape when seen in dorsal view, as it is wider transversely at the posterior margin of the supratemporal fenestra than at the anterior sutural surface for the squamosal. In addition, the contact surfaces for the squamosals are not parallel, but they converge posteriorly. These sutural surfaces are separated on the midline by the subcutaneous surface of the parietal, which forms a narrow dorsoventrally aligned and ventrally-widening groove on the posterior surface of the parietal (Fig. 1D). The parietosquamosal contact surfaces, therefore, resemble those of *S. validum*, with the minor different that in NMMNH P-33898 they faces dorsolaterally and posteriorly rather than posterolaterally as in *S. validum* (see, for example, Schott et al., 2011, fig. 7). Therefore, we see no clear, easy-to-define distinction between *Stegoceras novomexicanum* and *S. validum* in these features.

6.2 Other discrete characters

Based on our restudy of NMMNH P-33898, we have identified some additional characters that may have bearing on the taxonomic status of the specimen. One feature that may set NMMNH P-33898 apart from *Stegoceras validum*, and a number of other pachycephalosuar taxa (e.g., *Colepiocephale, Hanssuesia, "Prenocephale" brevis*) is the relatively low and more shallowly transversely convex shape of the frontals between the contacts with the nasals, prefrontals, and anterior supraorbitals (Fig. 1A-E). This frontal boss is much more strongly transversely convex on specimens of *Stegoceras validum* that probably represent a similar ontogenetic stage (see below; e.g., CMN 138, 8816, TMP 84.5.1; see Sullivan, 2003: fig. 2). Moreover, in NMMNH P-33898, the dome flattens laterally from the frontal portion of the dome as it nears the contact for the anterior supraorbitals. There is no indication of an abrupt break in slope or grooving that is typically found in *Stegoceras validum*, and several other taxa (e.g., *Colepiocephale, Hanssuesia, "Prenocephale" brevis*) which have strongly vaulted doming of the frontal dome between the prefrontals and a separate inflation of the dome laterally adjacent to the anterior supraorbitals (the "lateral frontal lobes" of some workers). The frontal boss of CMN 128, and TMP 84.5.1, specimens that have approximately the same degree of dome development as NMMN P-33898, have a more inflated frontal boss with distinct sulci, or break in slope, separating the frontal boss from the laterally adjacent parts of the frontoparietal which have undergone some inflation. In addition, the contact for the prefrontal in NMMNH P-33898 is anteroposteriorly elongate between the anterior supraorbital and nasals, and more gently tapers anteriorly toward the nasal contacts, than in *S. validum*, *Hanssuesia*, and "*Prenocephale" brevis*. The frontals are elongate, but nearly parallel-sided between the prefrontals in *Colepiocephale*.

Schott et al. (2011) revised the diagnosis of S. validum, one one of the most likely taxa that NMMNH P-33898 may belong to. Schott et al. (2011) noted that a number of features that Sullivan (2003) considered to be diagnostic for *S. validum*, such as the extent of doming of the skull roof, degree of closure of the supratemporal fenestrae, and degree of development of the parietosquamosal shelf, were highly ontogenetically variable. In their emended diagnosis, Schott et al. (2011:8) distinguished *S. validum* from all other pacycephalosaurs by the distinct ornamentation of the parietosquamosal shelf (*S. validum* differs from all other pachycephalosaurs in the presence of minute tubercles on the lateral and posterior sides of the squamosals, and in having a single prominent row of five-to-eight dorsally projecting nodes on each side of the parietosquamosal bar and a row of small, keel-shaped nodes on the dorsolateral margins of the squamosal); by the less developed incorporation of peripheral elements, particularly the supraorbitals, into the dome than in *Prenocephale*, *Sphaerotholus*, and *Pachycephalsoaurus*; the absence of nasal ornamentation; a greatly reduced diastema in the upper tooth row; and a pubic peduncle that is mediolaterally compressed and plate-like.

Unfortunately, NMMNH P-33898 does not preserve many of the features listed in this diagnosis. NMMNH P-33898 lacks the squamosals and is a juvenile, and so it does not preserve features of the parietosquamosal bar or other cranial ornamentation considered diagnostic for *S. validum*. Because it is a juvenile, it retains a prominent parietosquamosal shelf and did not incorporate peripheral skull elements into the dome, as presumably did the juveniles of all domed taxa that have poorly developed peripheral elements into the dome as adults. Other bones relevant to the diagnosis of Schott et al. (2011), such as the nasals, premaxillae and maxillae, and ilium, are unknown in NMMNH P-33898. Therefore, it is currently difficult to assess whether NMMNH P-33898 could belong to *S. validum* using the diagnosis of Schott et al. (2011).

6.3 Principal component analyses

The PCA of the updated Evans et al. (2013) dataset (Tables 1 and 2; Appendix 1) returned 14 principal components, the first three of which account for 91% of the total variance. PC1, which accounts for 72.6% of total variance, is strongly correlated with frontoparietal length, a proxy for body size (r^2=0.86). PCs 2 and 3 are very weakly correlated with frontoparietal length (r^2<0.026 in both cases), and therefore reflect variation that may be more phylogenetically informative than that the mostly size-related variation encapsulated on PC1. The plot of PC1 versus PC2 (Fig. 2A) shows that the *Stegoceras*

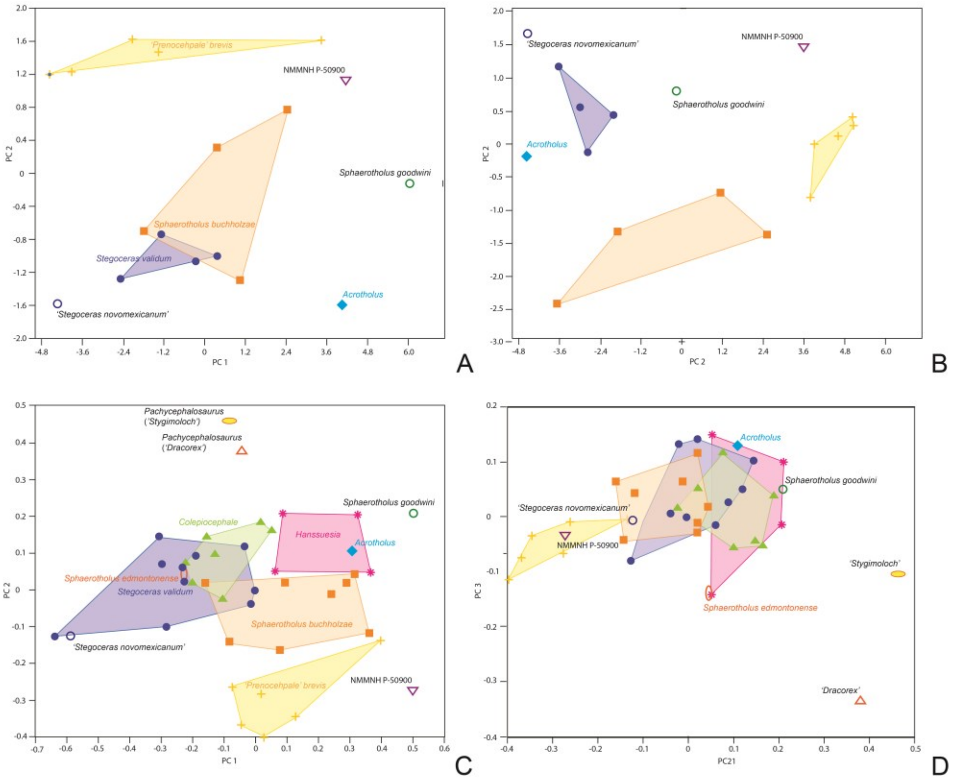

Figure 2. Selected results of morphometric analysis of pachycephalosaur frontoparietal domes (based on measurements from Evans et al. 2013, supplementary table s1) and postorbitals (based on measurements from Mallon et al., 2015, appendix a) including measurements of NMMNH P-33898 (holotype of Stegoceras novomexicanum) and revised measurements of NMMNH P-27403 (holotype of Sphaerotholus goodwini). Plots of PC1 versus PC2 (A) and PC2 versus PC3 (B) from frontoparietal measurements and PC1 versus PC2 (C) and PC2 versus PC3 (D) from postorbital measurements showing the placement of Stegoceras novomexicanum in morphospace

relative to other pachycephalosaur taxa.

novomexicanum holotype (NMMNH P-33898) is something of an outlier, as it does not fall within the convex hulls of the three other taxa represented by multiple specimens in the analysis, *Stegoceras validum*, *Sphaerotholus buchholtzae*, and '*Prenocephale' brevis*. However, NMMNH P-33898 does plot within the 95% confidence ellipses of both *S. validum* and *S. buchholtzae*. A similar pattern is seen in the plot of PC2 versus PC3 (Fig. 2B), as NMMNH P-33898 is not placed within the convex hulls of the three other pachycephalosaurs, but does fall within the confidence interval of *S. validum*, but in this case not *S. buchholtzae*.

The PCA of the updated Mallon et al. (2015) dataset returned four principal components, the first three of which account for 98% of the total variance. PC1 accounts for 60.9% of the overall variance, while PC2 accounts for 30.1% and PC3 7.4%. The plot of PC1 versus PC2 (Fig. 2C) shows that the *Stegoceras novomexicanum* holotype (NMMNH P-33898) is something of an outlier, although it is immediately adjacent in morphospace to UCMZ (VP) 2008.001, a very young individual of *Stegoceras validum*. Because of the close proximity of these two specimens, NMMNH P-33898 falls within the convex hull of *S. validum*. Furthermore, it is within the 95% confidence envelopes of *S. validum*, *Sphaerotholus buchholtzae*, and *Hanssuesia sternbergi*. On the plot of PC2 versus PC3 (Fig. 2D), NMMNH P-33898 is positioned within a dense cloud of specimens, and is plotted particularly close to specimen of *S. validum* (CMN 1108A) and '*Prenocephale' brevis* (TMP 1987.050.0029). It falls within the convex hull of *Sphaerotholus buchholtzae* and immediately outside the convex hulls of *S. validum* and '*P.*' *brevis*, and is within the 95% confidence intervals of all taxa known from more than one specimen.

The large taxon sample in the Mallon et al. (2015) dataset allows us to conduct a discriminant analysis in PAST v3.0 (Hammer et al. 2001). This analysis uses pre-determined groups (in this case, pachycephalosaur species) to create a morphospace in which these groups are maximally separated. Specimens whose identities are uncertain, such as NMMNH P-33898, can then be classified according to which group they are most similar to in this discriminant morphospace. In total, 70% of other pachycephalosaurs are classified correctly when they are treated as having uncertain affinities and their measurements are used to classify them in discriminant space, indicating that this exercise returns reasonable results. Our analysis classifies NMMNH P-33898 as *Stegoceras validum*, and places it within the 95% confidence envelopes of both *S. validum* and *Hanssuesia*.

PCA and discriminant analysis are tools that can help determine the most likely affinities of specimens, but they require some interpretation. Our interpretation of the above results is that *Stegoceras novomexicanum* may potentially be a distinctive taxon, given the outlier position of its holotype in the morphospace generated from the Evans et al. (2013) dataset. A similar rationale was used by Evans et al. (2013) as one line of evidence to support the taxonomic distinctiveness of *Acrotholus*, a new species of pacycephalosaur they were describing. However, the *Stegoceras novomexicanum* holotype does plot within the 95% confidence intervals of other taxa in the Evans et al. (2013) morphospace, and within both the convex hulls and 95% confidence intervals of other taxa in the Mallon et al. (2015) morphospace. In total, the strongest and most consistent similarities are between NMMNH P-33898 and *S. validum*. The *Stegoceras novomexicanum* holotype falls within the 95% confidence intervals of *S. validum* in plots of PC1 versus PC2 and PC2 versus PC3 of both datasets (Fig. 2). Furthermore, in the plot of PC1 versus PC2 of the Mallon et al. (2015) dataset (Fig. 2A), NMMNH P-33898 nearly overlaps with a specimen of juvenile *S. validum*. In total, these findings suggest that if *Stegoceras novomexicanum* can be referred to another known taxon of pachycephalosaur, that species is most likely *S. validum*. Additionally, the close correspondence in morphospace between NMMNH P-33898 and the juvenile *S. validum* specimen is further evidence that the *Stegoceras novomexicanum* holotype is immature.

However, there is a caveat. Because NMMNH P-33898 is a juvenile specimen, it may be expected to plot in morphospace with a taxon that is relatively plesiomorphic, and/or one that is represented by some juvenile specimens in the dataset. *S. validum* fulfils both of these criteria It is a relatively plesiomorphic taxon, closer to the root of pachycephalosaur phylogeny than other potential candidates that NMMNH P-33898 could be referred to, such as '*Prenocephale' brevis*, *Sphaerotholus buchholtzae*, and *Sphaerotholus goodwini*. Additionally, some of the *S. validum* specimens in the datasets are juveniles. Other taxa based on, or probably based on, juvenile specimens, such as *Wannanosaurus* and *Homalocephale* (Evans et al., 2011), are not included in either dataset. For these reasons, we are hesitant to interpret the PCA and discriminant analysis results as explicitly supporting the referral of NMMNH P-33898 to *Stegoceras validum*.

6.4 Phylogenetic analysis

A phylogenetic analysis of the revised Evans et al. (2013) dataset (Appendix 2) recovered 12 most parsimonious trees of 77 steps (Fig. 3; consistency index = 0.753, retention index = 0.796).

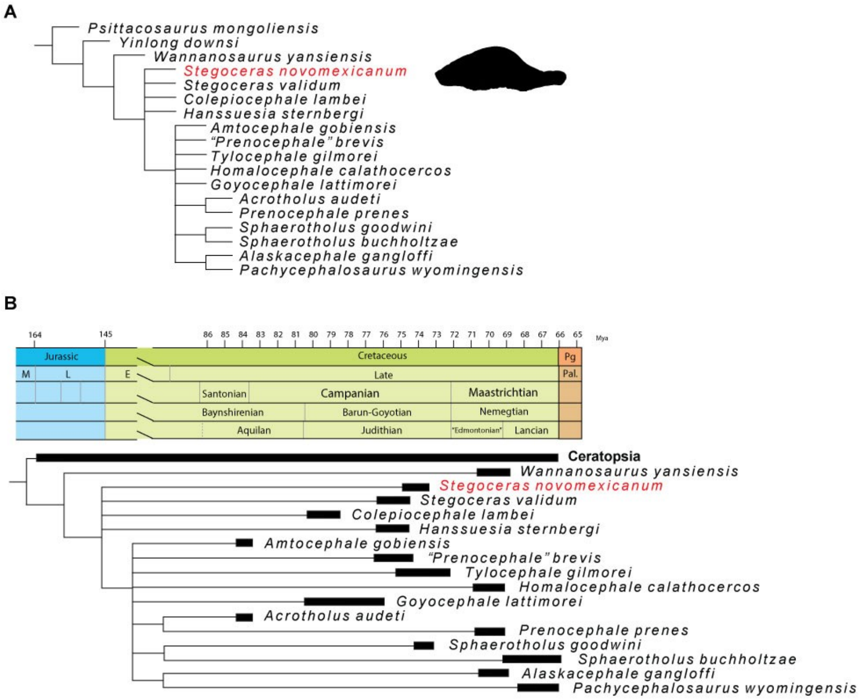

Figure 3. Phylogeny of Pachycephalosauria. (A), Strict consensus of 12 most parsimonious trees with a shortest length of 77 steps resulting from a phylogenetic analysis consisting of 18 pachycephalosaur taxa and two successive outgroups; Yinlong and Psittacosaurus and 50 characters, after Evans et al. (2013). Analysis was run in TNT v. 1.1 (Goloboff et al., 2008); consistency index = 0.753, retention index = 0.796). (B), Temporally-calibrated phylgeny of Pachycephalosauria including NMMNH P-33898 (Stegoceras novomexicanum) showing approximate ranges of each taxon. Time scale is after Huang (2012) and ranges of pachycephalosaur taxa follow Evans et al. (2013).

Wannanosaurus was found to be the basal-most pachycephalosaur, followed by a polytomy consisting of *Stegoceras novomexicanum*, *Stegoceras validum*, *Colepiocephale*, *Hanssuesia*, and the lineage leading to all of the remaining pachycephalosaurs. This lineage collapses into another large polytomy, the only resolution being the sister-taxon pairs of *Acrotholus* and *Prenocephale prenes*, *Sphaerotholus goodwini* and *Sphaerotholus buccholtzae*, and *Alaskacephale* and *Pachycephalosaurus*. These results are more poorly resolved than those of Evans et al. (2013, supplementary fig. s8). Evans et al. (2013) placed *Stegoceras novomexicanum*, *Stegoceras validum*, *Colepiocephale*, and *Hanssuesia* in their own clade of basal pachycephalosaurs, and then recovered complete resolution among the more derived taxa.

The most important result of our re-analysis is that there is no longer a restricted subclade that includes both *Stegoceras novomexicanum* and *S. validum* on the strict consensus tree (Fig. 3). This on its own does not say much about the taxonomic affinities of *Stegoceras novomexicanum*, as the analysis can only speak to the relationships between OTUs and not the diagnosability of the OTUs themselves. However, since *Stegoceras novomexicanum* and *S. validum* no longer occupy a restricted subgroup on the phylogeny and our dataset returns less resolution than previous analyses, we interpret this as a decrease in support for the hypothesis that *Stegoceras novomexicanum* can be referred to *S. validum*.

6.5 Summary

The taxonomic affinities of NMMNH P-33898 are still unclear on the generic and specific level. The original features that Jasinski & Sullivan (2011) used to diagnose the specimen as a distinct taxon, *Stegoceras novomexicanum*, are problematic, but we have identified additional features that could potentially support its taxonomic distinctiveness. The PCAs and discriminant analysis suggest that, if NMMNH P-33898 belongs to a known taxon, that taxon is most likely *Stegoceras validum*, but there are caveats regarding the data sampling of these analyses that make this uncertain. The phylogenetic analysis also provides decreased support for a close relationship between NMMNH P-33898 and *S. validum*. In sum, based on our current state of knowledge, we are not certain whether *Stegoceras novomexicanum* is a valid taxon or not, and if not, whether it is a juvenile of *S. validum* or perhaps another taxon like *Sphaerotholus goodwini*. The only way to resolve this conundrum is with a larger comparative sample of specimens of the same approximate ontogenetic stage as NMMNH P-33898. In particular, unequivocal immature specimens of *Sphaerotholus goodwini* may be the critical missing piece of the puzzle.

7. Discussion

7.1 The New Mexico pachycephalosaur record

All pachycephalosaur specimens recovered from the Campanian of New Mexico come from the Fruitland and Kirtland formations of the San Juan Basin. The Fruitland and Kirtland formations (exclusive of Naashoibito Member; Fig. 4) span only about two million years (from

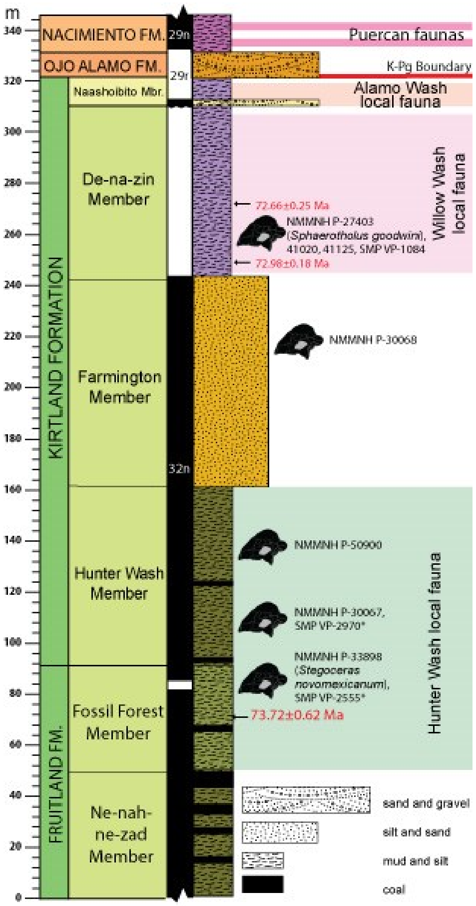

Figure 4. Generalized stratigraphic section for upper Campanian, Upper Cretaceous strata of the Bisti/De-na-zin Wilderness area, San Juan Basin, New Mexico modified after Fasset amd Steiner (1997) and Fassett (2009) showing the approximate stratigraphic position of all Fruitland and Kirtland Formation pachycephalosaur specimens. Absolute dates are based on 40Ar/39AR dates from volcanic ashes

(Fasset and Steiner, 1997) as recalibrated by Roberts et al. (2013). Magnetic polarity and reversal boundaries are placed after Fassett (2009).

All pachycephalosaur specimens recovered from the Campanian of New Mexico come from the Fruitland and Kirtland formations of the San Juan Basin. *The Fruitland and Kirtland formations span about 75 Ma to 73.0 Ma; Fassett and Steiner, 1997; Roberts et al., 2013). Nearly all pachycephalosaur specimens from these units are from two local faunas: the Hunter Wash (Clemens, 1973) and Willow Wash (Williamson & Sullivan, 1998) local faunas, comprised of localities in the Fossil Forest Member of the upper Fruitland Formation and the Hunter Wash Member of the Kirtland Formation, and from the De-na-zin Member of Kirtland Formation, respectively (Fig. 4).*

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There are at least two pachycephalosaur taxa in the Hunter Wash and Willow Wash local faunas, including an undescribed specimen that may represent a new taxon (NMMNH P-50900; Hunter Wash local fauna) and *Sphaerotholus goodwini* (Carr & Williamson, 2002b; Willow Wash local fauna). The specimen NMMNH P-50900 is currently under study by Williamson and co-authors and will be described elsewhere, but it resembles *S. validum*, and several other pachycephalosaur taxa, in having a high and laterally convex frontal boss.

Does '*Stegoceras novomexicanum*' represent a subadult of either of these taxa, or is it a third distinct species? There is the possibility that NMMNH P-33898 represents an early ontogenetic stage of *Sphaerotholus goodwini*, a prospect entertained by Williamson & Carr (2002a), but dismissed by Sullivan & Lucas (2006) because NMMNH P-33898 possesses a prominent parietosquamosal shelf, which is not present in known specimens of *Sphaerotholus goodwini*. However, as discussed above, the strength of the parietosquamosal shelf is ontogenetically variable and retention of a prominent shelf may be expected in domed pachycephalosaurs of an early ontogenetic stage (e.g., Evans et al., 2011). Unfortunately, early ontogenetic stages are not known for *Sphaerotholus*, or for a number of other pachycephalosaur taxa for that matter. NMMNH P-33898 also lacks a high and laterally convex nasal boss found in NMMNH P-50900 and specimens of *Stegoceras validum* that are of a similar ontogenetic stage.

A similar problem concerns the identities of the Asian flat-headed pachycephalosaurs *Goyocephale latttimorei* and *Homalocephale calathocercos*, as the known specimens may represent juvenile stages of domed taxa (Evans et al., 2011; Longrich et al., 2010) or adults that possibly exhibit pedomorphosis in dome development (Bakker et al., 2006; Sullivan, 2007). *Homalocephale* is found in the Nemegt Formation of Mongolia, in strata that have also yielded the highly-domed *Prenocephale prenes*, and it has been suggested that it may be a subadult or sexual dimorph of that taxon (Butler & Sullivan, 2009; Longrich et al., 2010). Evans et al. (2011) considered that question and concluded that although *Homalocephale* likely was based on an immature specimen, it is taxonomically distinct from *Prenocephale* based on its large size and unique pattern of parietosquamosal ornamentation, features that appear not to change significantly through ontogeny in *Stegoceras validum* (Evans et al., 2011; Schott and Evans, 2012; Schott et al., 2011). *Homalocephale* also differs from *Prenocephale* in other features such as the pattern of tooth wear, shape of the maxillary tooth row, and tooth morphology (Evans et al., 2011; Maryańska and Osmólska, 1974). If Evans et al. (2011) are correct; this is an example of how a juvenile specimen may still be diagnostic and taxonomically distinct from a co-existing taxon based on adult material.

Another pertinent case involves *Dracorex hogwartia* and *Stigymoloch spinifer*, which wereregarded as a juveniles of *Pachycephalosaurus wyomingensis* by Horner and Goodwin (2009), a conclusion tentatively accepted here. *Dracorex* has a flat skull roof and large

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supratemporal fenestrae as in juvenile stages of other domed taxa. *Stygimoloch* has a relatively small and narrow dome and the supratemporal fenestrae are closed, but it retains a distinct parietosquamosal shelf and is posited to represent an ontogenetic stage intermediate between that of *Dracorex* and the large-domed *Pachycephalosaurus* (Horner & Goodwin, 2009). All three taxa are relatively large with relatively elongate skulls, possess similar distinctive nodal ornamentation (e.g., clusters of nodes on the posterolateral corners of the squamosals and pyramidal nodes over the rostrum) supporting their recognition as a single, ontogenetically highly variable taxon. However, if this is correct, then the squamosal nodes are hypothesized to first increase in size to form medium to large pointed horns (e.g., from the *Dracorex* to the *Stygimoloch* stages of ontogeny), before shrinking through bone erosion to relatively shorter and blunted structures in more mature stages (Horner & Goodwin, 2009), a somewhat extreme change in cranial ornamentation not observed in other pachycephalosaur taxa.

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7.2 Discussion of a problematic specimen from New Mexico

One New Mexican pachycephalosaur specimen, a partial dentary associated with some skull fragments (NMMNH P-30068), was discovered from the Farmington Member near the head of Pinabete Arroyo at NMMNH locality L-3097, which is approximately contemporaneous with the Hunter Wash or Willow Wash local faunas (Fig. 4). There has been some inaccurate information in the literature regarding this specimen and the Upper Cretaceous stratigraphy of the San Juan Basin, which we wish to correct.

First, Jasinski & Sullivan (2011, fig. 1) misplotted the location of L-3097. Precise locality information is available to qualified researchers from the NMMNH. It is located between

Brimhall Wash and Pinabete Arroyo (“Pina Veta China Arroyo” of literature prior to 1966).

Second, to correct any misconceptions, the skull fragments and partial dentary of NMMNH P-30068 were collected from NMMNH locality L-3097 along with NMMNH P-25049, a specimen that was referred by Carr & Williamson (2010) to the tyrannosauroid theropod *Bistahieversor sealeyi*. These specimens were indeed collected illegally, as stated by Jasinski & Sullivan (2011), but we want to be clear that the illegal collection was not by Williamson. Contra Jasinski & Sullivan (2011), the pachycephalosaur specimens were not found with the holotype of *B. sealeyi* (NMMNH P-27469), which is from the Hunter Wash Member of the Kirtland Formation within the Bisti/De-na-zin Wilderness Area.

Third, Jasinski & Sullivan (2011) stated (p. 207) that the pachycephalosaur specimen, NMMNH P-30068, is “almost certainly from the Hunter Wash Member” and (p. 210) that “exposures of the Farmington Member…crop out only in the eastern parts of the Bisti/De-na-zin Wilderness area”. However, this is incorrect. Bauer (1916) gave the name ‘Farmington Sandstone Member’ to a series of sandstone lenses that form a prominent bluff, “455 feet thick” (about 140 m), on the San Juan River (Bauer, 1916, fig. 27; Plate LXVIIIA). Bauer (1916, Plate LXV) shows in a series of stratigraphic sections along the Chaco Valley that the Farmington Member thins, from over 400 feet in its type area, to a thickness of 87 feet in the area of the Bisti/De-na-zin Wilderness. Jasinski & Sullivan (2011) argued that the area from where NMMNH P-30068 was collected was mapped by Brown (1983) as Hunter Wash Member, Kirtland Formation. However, L-3097 does not fall within the area covered by Brown’s geologic map. NMMNH locality L-3097 is located about 10 km from the northwest corner of Brown’s map and is close to the type section of the Farmington Sandstone Member. Therefore, this specimen clearly comes from the Farmington Member, not the Hunter Wash Member (Fig. 4).

7.3 The New Mexico pachycephalosaur record in a regional context

Western North America contains some of the richest terrestrial Upper Cretaceous deposits in the world. A number of remarkably fossiliferous units were deposited along the western margin of the Cretaceous Western Interior Seaway within a narrow interval of time between about 80 and 73 Ma. The Dinosaur Park, Two Medicine, and Judith River formations to the north and the Kaiparowits, Kirtland, Fruitland, and Aguja formations to the South all fall, at least partially, within this interval and provide an exceptional window into late Campanian terrestrial ecosystems (Gates et al., 2010; Roberts et al., 2013). They have provided a wealth of data for analyzing large-scale biogeographic patterns of late Cretaceous dinosaur faunas of the western interior (e.g., Gates et al., 2012; Gates et al., 2010; Loewen et al., 2013), and also give insight into how dinosaurs were evolving during the run-up to the end-Cretaceous mass extinction (e.g., Brusatte et al. 2015).

Northern upper Campanian units, particularly the Dinosaur Park Formation, have yielded a large number of late Campanian pachycephalosaur specimens. These constitute, by far, the most abundant small-bodied ornithischian dinosaur fossils from Campanian faunas of North America which is undoubtedly due to preservational biases that favor the fossilization of the thick and durable skull roof (Evans et al., 2013a). At least three pachycephalosaur taxa (*Stegoceras validum*, “*Prenocephale*” *brevis*, and *Hanssuesia sternbergi*) are recognized in the upper Campanian Dinosaur Park Formation (Evans et al., 2013a; Ryan & Evans, 2005) and three or more taxa (e.g., *Stegoceras validum*, *Colepiocephale lambei*, and “*Prenocephale*” *brevis*) are known from the Judith River Formation of Montana (Goodwin, 1990; Schott et al., 2009).

Southern late Campanian faunas have not yet yielded anywhere as many specimens as the northern units, but growing discoveries hint at a considerable diversity of pachycephalosaurs. At least one taxon is known from the Aguja Formation of west Texas, (Lehman, 2010; Longrich et al., 2010). A new pachycephalosaur taxon, *Texacephale langstoni* was named based on a frontoparietal from the Aguja Formation (Longrich et al., 2010), although Jasinski & Sullivan (2011) concluded that it is a nomen dubium, a decision that we agree with and is followed here. Pachycephalosaurs are known from the upper Campanian Kaiparowits Formation of southcentral Utah, but described specimens are too incomplete for generic identification (Evans et al., 2013b).

The Campanian faunas of the Fruitland and Kirtland formations of the San Juan Basin are slightly younger than faunas from the northern Rocky Mountain area (Roberts et al., 2013), but provide the only generically diagnostic pachycephalosaur specimens from the upper Campanian of the southern part of the western interior. Specimens recovered from these units reveal the presence of at least two pachycephalosaur taxa (see 7.1 above). All four pachycephaosuar specimens from the De-na-zin Member of the Kirtland Formation of the San Juan Basin (Fig. 4; Sullivan, 2000; Williamson and Carr, 2002b; Williamson and Carr, 2005) are probably referable to *Sphaerotholus goodwini*, and no certainly referable specimens of *Sphaerotholus* have been recovered from stratigraphically lower strata of the San Juan Basin (i.e., Fruitland Formation and Hunter Wash and Farmington members, Kirtland Formation). Therefore it is possible that *Sphaerotholus* is the sole pachycephalosaur present in the De-na-zin Member, Willow Wash local fauna (Fig. 4).

Sphaerotholus is elsewhere found in the lower Maastrichtian Horseshoe Canyon Formation of southern Alberta (*S. edmontonense*), a taxon that is tentatively considered valid following Mallon et al. (2015), and the upper Maastrichtian Hell Creek and Frenchman formations (*S. buchholtzae*) of Montana and Saskatchewan, respectively (Mallon et al., 2015; Williamson & Carr, 2002b). The stratigraphic distribution of *Sphaerotholus* may indicate that it arrived relatively late in the upper Campanian of the Western Interior compared to other pachycephalosaur taxa such as *Stegoceras*, *Hannsuesia*, and "*Prenocephale*" *brevis*. However, we urge caution in accepting this interpretation considering the small number of pachycephalosaur specimens represented in many areas. Indeed, Evans et al. (2013a) suggested that ghost lineages inferred from their phylogeny of pachycephalosaurs shows that the diversity of pachycephalosaurs is seriously underestimated even in well sampled intervals of the middle and upper Campanian of North America.

Our reassessment of NMMNH P-33898 as a juvenile that may be referable to one of a number of existing taxa, as well as our reassessment of other taxa, allows us to conclude that late Campanian pachycephalosaurs from the San Juan Basin of New Mexico are morphologically similar, in terms of body size and skull roof shape, to those reported from approximately coeval faunas throughout the Western Interior. Clearly, pachycephalosaurs were an important component of the diverse terrestrial faunas in western North America during the penultimate stage of dinosaur evolution, before the non-avian species disappeared at the end of the Cretaceous.

Conclusion

Our reassessment of the described specimens of '*Stegoceras novomexicanum*' leads to the following conclusions: 1) the two fragmentary paratype specimens (SMP VP-2555 and VP-2790) cannot be referred to the holotype (NMMNH P-33898) based on explicit synapomorphies or other detailed character similarities; 2) the holotype and controversial paratypes belong to juvenile individuals, not mature or near-mature adults as argued by Jasinski & Sullivan (2011); 3) there is therefore no evidence that '*Stegoceras novomexicanum*' was a peculiar small-bodied pachycephalosaur species; 4) the original diagnosis of '*Stegoceras novomexicanum*' by Jasinski & Sullivan (2011) is problematic, but it is currently unclear whether the holotype specimen does belong to its own valid species-level taxon (*Stegoceras novomexicanum*) or is a juvenile of *Stegoceras validum*, *Sphaerotholus goodwini*, or another taxon; 5) at least two valid diagnostic pachycephalosaur species are known from the Campanian of New Mexico, indicating that pachycephalosaurs were an integral component of latest Cretaceous dinosaur faunas in the southern part of Western North America just as they were in roughly contemporaneous northern localities.

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Figures

Figure 1. Surface model constructed from high-resolution CT (HRCT) images using Avizo v. 8.1 visualization software and selected CT slices of the frontoparietal NMMNH P-33898, holotype of *Stegoceras novomexicanum*. A, right lateral view (reversed); B, dorsal view; C, ventral view; D, posterior view; E, anterior view; F, sagittal section right of midline (reversed); G, horizontal section; H, coronal section at the contact of the posterior supraorbital and postorbital suture.

Figure 2. Selected results of morphometric analysis of pachycephalosaur frontoparietal domes (A-B; based on measurements from Evans et al. 2013, supplementary table s1) and postorbitals (C-D; based on measurements from Mallon et al., 2015, appendix a) including measurements of NMMNH P-33898 (holotype of *Stegoceras novomexicanum*), revised measurements of NMMNH P-27403 (holotype of *Sphaerotholus goodwini*), and 50900. Plots of PC1 versus PC2 (A) and PC2 versus PC3 (B) from frontoparietal measurements and PC1 versus PC2 (C) and PC2 versus PC3 (D) from postorbital measurements showing the placement of *Stegoceras novomexicanum* in morphospace relative to other pachycephalosaur taxa.

Figure 3. Phylogeny of Pachycephalosauria. (A), Strict consensus of 12 most parsimonious trees with a shortest length of 77 steps resulting from a phylogenetic analysis consisting of 18 pachycephalosaur taxa and two successive outgroups; *Yinlong* and *Psittacosaurus* and 50 characters, after Evans et al. (2013)(Appendix 2). Analysis was run in TNT v. 1.1 (Goloboff et al., 2008); consistency index = 0.753, retention index = 0.796). (B), Temporally-calibrated phylgeny of Pachycephalosauria including NMMNH P-33898 (*Stegoceras novomexicanum*) showing approximate ranges of each taxon. Time scale is after Huang (2012) and ranges of pachycephalosaur taxa follow Evans et al. (2013).

Figure 4. Generalized stratigraphic section for upper Campanian, Upper Cretaceous strata of the Bisti/De-na-zin Wilderness area, San Juan Basin, New Mexico modified after Fasset amd Steiner (1997) and Fassett (2009) showing the approximate stratigraphic position of all Fruitland and Kirtland Formation pachycephalosaur specimens. The names *Sphaerotholus goodwini* and *Stegoceras novomexicanum* are placed in parentheses below the holotype specimens. Specimens referred to *S. novomexicanum* are followed by an asterisk. Absolute dates are based on 40Ar/39AR dates from volcanic ashes (Fasset and Steiner, 1997) as recalibrated by Roberts et al. (2013). Magnetic polarity and reversal boundaries are placed after Fassett (2009).

Tables

Table 1. Measurements of pachycephalosaur frontoparietals from Evans et al. (2013) with measurements of NMMNH P-33898, revised measurements of NMMNH P-27403 and including measurements of NMMNH P-50900. All measurements are in mm.

Table 1

Taxon	**Specimen**	**H:n/n**	**H:pfr/aso**	**H:aso/pso**	**H:pso/po**	**W:n/pfr**	**W:pfr/aso**	**W:aso/pso**	**W:pso/po**
Stegoceras validum	CMN 515	16.5	15.4	10.2	14.7	26.5	41.9	51.8	58.5
Stegoceras validum	AMNH 5450	9.9	11.7	11.4	14.3	18.4	30.7	43.8	45.4
Stegoceras validum	CMN 138	15.2	11.2	8.9	14.3	25.8	39.4	55.1	56.6
Stegoceras validum	TMP 1984.005.0001	13.6	11.7	7.8	12.6	21.2	36.3	48.6	56.3
Prenocephale brevis	TMP 1987.050.0029	22.5	22.4	16.9	27.8	26.5	42.8	69.9	82.4
Prenocephale brevis	TMP 1991.036.0265	2.1	4.8	4.8	11	15.8	30.7	37.7	38.5
Prenocephale brevis	TMP 1985.036.0292	6.8	8.5	7.4	17.2	16.9	27.6	47.7	50.4
Prenocephale brevis	TMP 1999.055.0122	4.3	6	5.5	12.8	15.4	26.3	39.7	45.2
Prenocephale brevis	UALVP 8508	7.7	10.6	8.2	17.4	17.5	*28.7*	48.7	55.3
Sphaerotholus buchholtzae	CMN 8830	10.9	11.3	10.4	18.7	*19.5*	38.7	*53.7*	*64*
Sphaerotholus buchholtzae	TMP 1987.113.0003	19.8	15.7	12.1	28.9	22.2	50.6	60.3	77.6
Sphaerotholus buchholtzae	UCMP 186026	10	10.5	8	15	18	37.2	43.8	48.4
Sphaerotholus buchholtzae	LACM 64000	15.5	14.9	13	20.1	23.7	52	57	61.5
Sphaerotholus goodwini	NMMNH P-27403	*23.7*	27.3	23.3	41.4	*35.6*	56.2	79.5	101.25
Acrotholus audeti	TMP 2008.045.0001	28.2	28	25.6	37	28.5	63.2	70	76.3
Stegoceras novomexicanum	**NMMNH P-33898**	**7.7**	**7.1**	**9.7**	**8.2**	**13.3**	**30**	**40**	**43.2**
X	NMMNH P-50900	29.7	*28.6*	*26.3*	*31.4*	*27.9*	*52*	*75.4*	*78*

Taxon	**Specimen**	**W:f/p**	**W:Sq/Sq**	**L:aso**	**L:pso**	**L:po**	**L:fp**	**T:f/p**
Stegoceras validum	CMN 515	57.5	8.4	9.4	20.2	35.8	93.5	35
Stegoceras validum	AMNH 5450	39.2	4.3	10.1	15.5	24.5	82.3	20
Stegoceras validum	CMN 138	53.1	6.2	12.1	16	33.9	84.2	34
Stegoceras validum	TMP 1984.005.0001	52.7	7.3	11.8	14.9	29.2	85.7	25
Prenocephale brevis	TMP 1987.050.0029	84.1	20.5	17.6	33.7	28.3	95.1	53
Prenocephale brevis	TMP 1991.036.0265	39.4	12.8	8.9	17.6	17.3	57.1	27
Prenocephale brevis	TMP 1985.036.0292	49.3	13.9	12.8	22.7	18.3	66.8	26
Prenocephale brevis	TMP 1999.055.0122	44	10.7	10.5	18	16.2	61.1	24
Prenocephale brevis	UALVP 8508	56.4	*14*	12.3	22.8	20.3	70.3	31.6
Sphaerotholus buchholtzae	CMN 8830	*66*	16.4	*11.6*	18.2	*40.4*	93	41
Sphaerotholus buchholtzae	TMP 1987.113.0003	83.5	23.4	9.7	25.4	33.8	106.7	49
Sphaerotholus buchholtzae	UCMP 186026	52.7	11.3	6.2	14.8	28	73.2	30.7
Sphaerotholus buchholtzae	LACM 64000	*62.7*	17.5	4.6	17	41.1	84.4	40.9
Sphaerotholus goodwini	NMMNH P-27403	101	7.4	16	39.5	62.4	133.4	75
Acrotholus audeti	TMP 2008.045.0001	70.1	7.4	8.6	25.1	44.2	104.7	59

Stegoceras novomexicanum	**NMMNH P-33898**	**26.8**	**3**	**10.6**	**14.1**	**22.1**	**70.7**	**21.4**
X	NMMNH P-50900	*81.8*	*15.7*	*27.1*	*23.4*	*25.5*	111.8	63.2

Table 2. Measurements of pachycephalosaur postorbitals from Mallon et al. (2015, appendix a) with those of NMMNH P-27403 (holotype of *Sphaerotholus goodwini*), 33898 (holotype of *Stegoceras novomexicanum*), and 50900. All measurements are in mm.

Table 2

Taxon	**Specimen**	**length dorsal**	**length ventral**	**anterior height**	**posterior height**
Hanssuesia	CMN 9148	47	27	25	10
Hanssuesia	CMN 8817	46	39	22	25
Hanssuesia	CMN 8945	55	48	27	18
Hanssuesia	CMN 38079	46	46	25	10
Prenocephale' brevis	CMN 121	21	17	14	14
Prenocephale' brevis	CMN 8819	22	16	14	17
Prenocephale' brevis	TMP 1985.036.292	20	23	15.8	11.4
Prenocephale' brevis	ROM 31616	19.6	21	19.3	18
Prenocephale' brevis	TMP 2000.12.0001	21	23	16	14.7
Prenocephale' brevis	TMP 1987.050.0029	29.1	32	29.8	25.2
Stegoceras	CMN 515	34	34	13	7
Stegoceras	CMN 2369	30	32	NA	NA
Stegoceras	CMN 138	34	37	15	7
Stegoceras	CMN 38428	41	37	19	9
Stegoceras	CMN 1074	32	34	18	11
Stegoceras	ROM 803	35	38	15	5
Stegoceras	CMN 8816	28	33	NA	6
Stegoceras	ROM 64183 (cast)	29.8	26	15	5.2
Stegoceras	UCMZ (VP) 2008.001	21.3	24	6.7	4
Stegoceras	CMN 1108A	27	25	12	7
Sphaerotholus buchholzae	UWBM 89701	30.8	32	18.3	7
Sphaerotholus buchholzae	LACM 64000	36.5	34.8	19.9	13.1
Sphaerotholus buchholzae	UCMP 186026	28.1	24.6	14.4	10.8
Sphaerotholus buchholzae	ROM 53667	38.8	37.4	24.7	19.2
Sphaerotholus buchholzae	ROM 53584	38.7	39.7	28.2	18.8

Sphaerotholus buchholzae	TMP 87.113.03	33	36	28	16
Sphaerotholus buchholzae	ROM 65563 (cast)	28.7	32.6	31.3	21.9
Colepiocephale	CMN 8818	33	34	17	6
Colepiocephale	TMP 1992.088.001	30.3	32.8	15.4	7
Colepiocephale	TMP 1986.146.0001	40.4	48.3	17.9	11.6
Colepiocephale	ROM *Colepiocephale*	35.3	40.3	13.9	8.7
Colepiocephale	ROM 59044 (TMP cast)	29.8	31.7	16.2	9
Colepiocephale	TMP 1987.046.0001	42.8	45.5	20.3	9.6
Colepiocephale	TMP 2009.37.0001	39.1	41.4	13.8	7.9
Dracorex	ROM Dracorex	57.9	74	9.5	12
Stygimoloch	ROM 61045	64	74	14	8
Sphaerotholus edmontonensis	CMN 8830	36	33	10	8
Sphaerotholus buchholzae	CMN 56510	27	25	22	13
Acrotholus	TMP 2008.045.0001	44.9	39.2	34.4	15.6
Sphaerotholus goodwini	**NMMNH P-27403**	**62.4**	**46.3**	**38.1**	**23.1**
Stegoceras novomexicanum	**NMMNH P-33898**	**22.1**	**23.2**	**8.2**	**4.0**
	NMMNH P-50900	**25.5**	**25.9**	**31.5**	**34.3**

Appendices

Appendix 1. Dataset used in PCA analyses and results of PCA analyses. Estimated measurements are in italics.

Appendix 2. Nexus file of taxon-character matrix used in the phylogenetic analysis.