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THE VALIDITY OF THE LATE CRETACEOUS PACHYCEPHALOSAURID *STEGOCERAS NOVOMEXICANUM* (DINOSAURIA: PACHYCEPHALOSAURIDAE)

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Abstract—In light of a recent paper, we review, and reassess, the validity of the pachycephalosaurid dinosaur *Stegoceras novomexicanum* (Dinosauria: Ornithischia: Pachycephalosauridae). Specimens that are referred to *Stegoceras novomexicanum* are all late Campanian (early Kirtlandian) in age and are not only from a restricted stratigraphic horizon at the Fruitland/Kirtland transition, but also from a small geographic area of the San Juan Basin, New Mexico. While some of the characters initially used in diagnosing this taxon may be representative of an earlier (sub-adult) ontogenetic stage, such as the reduction of the size of the posteromedial extension of the parietal and the size of the supratemporal fenestrae, several other characters confirm its validity. These include the shape of the posteromedial extension of the parietal, the relative position of the supratemporal fenestrae, the shape and degree of inflation of the nasal boss, morphology of the prefrontal-frontal suture, curvature of the frontal-parietal suture, and its relative overall size and gracile form relative to the type (lectotype) of *Stegoceras validum* from the Judithian of Alberta, Canada. Although the holotype of *Stegoceras novomexicanum* may represent a sub-adult individual, it also possesses some diagnostic features that are indicative of an adult. This combination of features may indicate heterochrony for *Stegoceras novomexicanum* within the Pachycephalosauridae. Recently recovered small-bodied, high-domed pachycephalosaurid specimens from the Fruitland-Kirtland transition further support our interpretation that this taxon represents a distinct, small-bodied adult pachycephalosaurid in New Mexico. The previously described paratypes, and newly collected specimens, are conservatively assigned to cf. *Stegoceras novomexicanum*, as all this material comes from a very restricted stratigraphic interval and geographic area.

INTRODUCTION

Pachycephalosaurids (Ornithischia: Pachycephalosauridae) are an enigmatic and distinctive clade of small- to medium-sized, bipedal, herbivorous dinosaurs that inhabited North America and Asia during the Late Cretaceous. Most pachycephalosaurid taxa are known primarily from cranial material, usually consisting of a frontoparietal dome, sometimes with fused peripheral elements. The frontoparietal dome and adjacent peripheral bones can be distinctive, and they are the most common fossil elements known for these dinosaurs and one upon which their taxonomy primarily rests. However, the morphology of the frontoparietal can be quite variable within the same taxon depending on its ontogenetic stage (e.g., Williamson and Carr, 2002b; Horner and Goodwin, 2009; Schott et al., 2009, 2011; Evans et al., 2011; Schott and Evans, 2012; Goodwin and Evans, 2016; Williamson and Brusatte, 2016), although this morphology seems less variable in ontogenetically older individuals. The variation in frontoparietal dome morphology has caused problems in determining the relative individual age or ontogenetic stage of particular specimens and the assessment of some pachycephalosaurid taxa (e.g., Sullivan, 2003; Evans et al., 2016; Goodwin and Evans, 2016).

Jasinski and Sullivan (2011) named a new species of *Stegoceras*, *S. novomexicanum,* from the late Campanian (early Kirtlandian) of New Mexico and referred other individuals (paratypes) to this taxon. The holotype (NMMNH P-33898, Fig. 1) had previously been identified as an indeterminate pachycephalosaurid species (Williamson and Carr, 2002a), and in a subsequent paper (Sullivan and Lucas, 2006b) was considered to be a juvenile individual of *S. validum*. Jasinski and Sullivan (2011) also described two incomplete frontoparietal domes (SMP VP-2555 and SMP VP-2790), which were designated paratypes of *S. novomexicanum*.

In a recent paper, Williamson and Brusatte (2016) challenged the validity of *Stegoceras novomexicanum* based on issues concerning its inferred ontogenetic stage and presumed adult size. They reassessed *S. novomexicanum* using computed tomography scanning, morphometric and phylogenetic analyses, and compared it to the growth series of the better known sister taxon, *S. validum*. They concluded that: 1) the two paratypes (SMP VP-2555 and VP-2790) could not be confidently referred to *S. novomexicanum*; 2) most or all the specimens (NMMNH P-33898, SMP VP-2555, and SMP VP-2790) represented immature individuals; and 3) the original diagnosis of *S. novomexicanum* was problematic and that it could not be conclusively proven to be its own distinct species, or referred to *S. validum*, to *Sphaerotholus* ("*Prenocephale"*) *goodwini* or to any other known pachycephalosaurid. Below we address these issues and provide evidence that refutes key points of their arguments. In addition, we argue that chronostratigraphy, relative age, geographic distribution, and parsimony support the notion that not only is *Stegoceras novomexicanum* a valid and distinct species, but that the referred material should also be assignable to this taxon. Lastly, we also report on two new specimens that add further support our thesis that *S. novomexicanum* represents a distinct, small-bodied pachycephalosaurid.

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York City, New York; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SMP**, State Museum of Pennsylvania, Harrisburg, Pennsylvania; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta, Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; **Z. Pal**., Palaeontological Institute, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Pachycephalosauridae Sternberg, 1945
***Stegoceras* Lambe, 1902**
***Stegoceras novomexicanum* Jasinski and Sullivan, 2011**
(Figs. 1–4)

Pachycephalosauridae indet.: Williamson and Carr (2002a), p. 67.
Stegoceras validum: Sullivan and Lucas (2006b), fig. 1, p. 329.
Stegoceras novomexicanum Jasinski and Sullivan (2011), figs. 3A–C, 4, 5, 6, and 7, p. 202.

Revised Diagnosis—Differs from the holotype of *Stegoceras validum* (CMN 515), and all other known pachycephalosaurid taxa in possessing the following features: relatively low and shallowly transversely-convex shape of the frontal between and dorsal to the contacts with the nasals, prefrontals, and anterior supraorbitals; frontal flattens laterally near the contact for the anterior supraorbitals; prefrontal-frontal suture anteroposteriorly (or rostrocaudally) elongate between the anterior supraorbital and nasals, which tapers anteriorly (or rostrally) toward the nasal contacts; posteromedial extension of the parietal reduced and sub-rectangular; squamosal sutural surface contacts of the posteromedial extension of the parietal roughly parallel

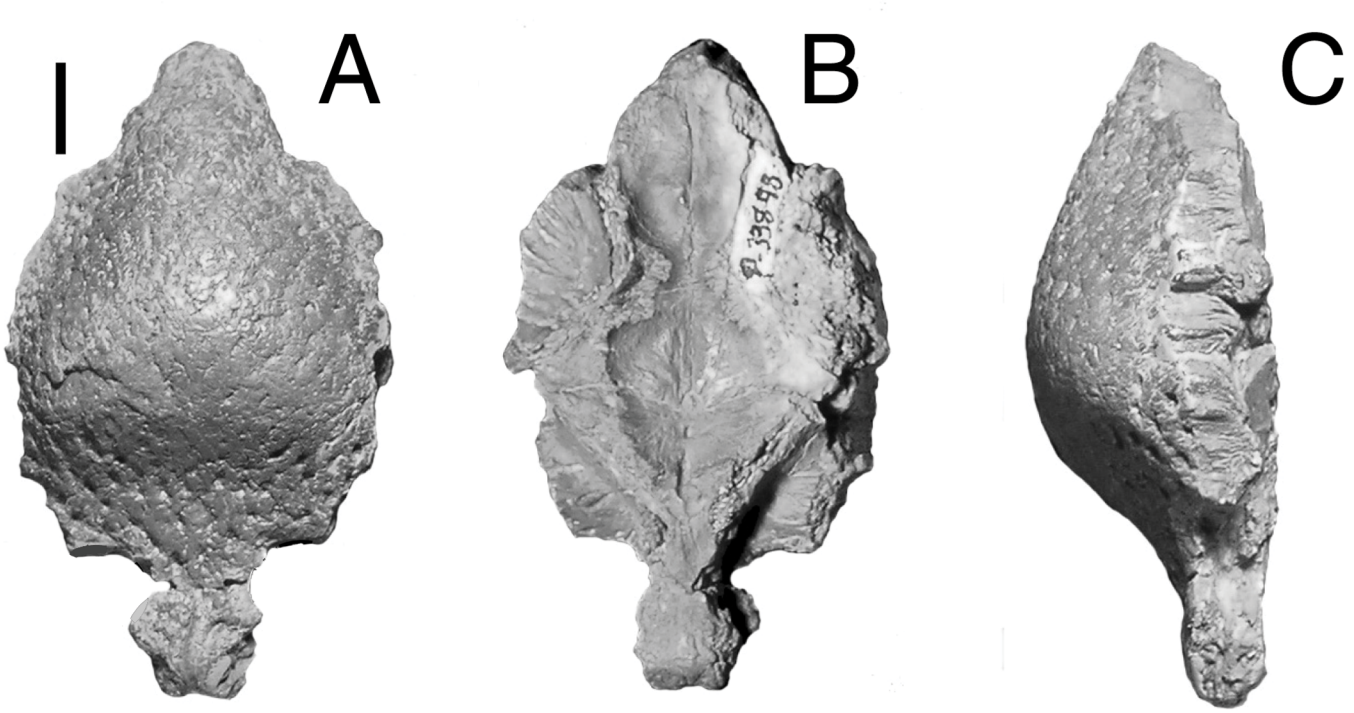

FIGURE 1. *Stegoceras novomexicanum* (NMMNH P-33983, holotype), nearly complete frontoparietal from the upper Fruitland Formation (Fossil Forest Member), San Juan Basin, New Mexico. **A**, dorsal view; **B**, ventral view; and **C**, right lateral view. Scale bar = 1 cm.

(11° from sagittal plane); supratemporal fenestrae positioned relatively medially; frontoparietal suture fused dorsally; gracile and relatively small body size.

Holotype—NMMNH P-33898, nearly complete frontoparietal (Fig. 1).

Paratypes—SMP VP-2555, greater posterior part of left frontal and anteriormost (or rostralmost) portions of left and right frontals; SMP VP-2790, incomplete parietal.

Holotype Locality—NMMNH locality L-4716, San Juan Basin, New Mexico. Precise coordinates are available at NMMNH to qualified researchers.

Formation/Age—Upper Fruitland Formation (Fossil Forest Member) to lower Kirtland Formation (Hunter Wash Member), late Campanian (early Kirtlandian).

Comments—Jasinski and Sullivan (2011) noted a number of characters that separated *Stegoceras novomexicanum* (NMMNH P-33898) from *S. validum* (CMN 515, the lectotype of the species, see Sullivan, 2003). The position of the enlarged supratemporal fenestrae lying more medial was considered a diagnostic feature of *S. novomexicanum* by Jasinski and Sullivan (2011). Schott et al. (2011) and Schott and Evans (2012) demonstrated that the size of the supratemporal fenestrae changes through ontogeny (and potentially among individuals) in a closely related pachycephalosaurid taxon (*S. validum*). The size of the supratemporal fenestrae may still have some taxonomic utility for the species, especially in concert with the other adult features, although more specimens are needed to further confirm this. Indeed, other features considered diagnostic of *S. novomexicanum*, including the shape of the posteromedial extension of the parietal and medial (including anteromedial or rostromedial) portions of the squamosal, do not seem to change through ontogeny, at least in *S. validum* (e.g., Schott et al., 2011; Schott and Evans, 2012) and presumably, by extension, in *S. novomexicanum*.

We concede that none of the referred specimens can be unequivocally referred to *S. novomexicanum* (see below). However, the fact that they are all small and high-domed suggests that these specimens represent small-bodied adult individuals and that they are most appropriately referable to this taxon.

Cf. *Stegoceras novomexicanum* Jasinski and Sullivan, 2011

New referred specimens—NMMNH P-70009 (Fig. 2), incomplete frontoparietal dome, NMMNH locality L-9128, lower Hunter Wash Member, Kirtland Formation; SMP VP-2555, greater caudal (or posterior) part of left frontal and rostral-most portions of left and right frontals (designated as a paratype by Jasinski and Sullivan, 2011), SMP locality 450, upper Fossil Forest Member, Fruitland Formation; SMP VP-2790, incomplete parietal (designated as a paratype by Jasinski and Sullivan, 2011), SMP locality 461, lower Hunter Wash Member, Kirtland Formation; and SMP VP-4370 (Fig. 3) incomplete right frontal fragment and sagittal section of incomplete frontoparietal dome, SMP locality 450, upper Fossil Forest Member, Fruitland Formation.

Descriptions of new referred specimens—NMMNH P-70009 (Fig. 2) is part of a frontoparietal consisting of the left side, with both frontal and parietal portions. The dome is broken along the sagittal plane. Seen in lateral view, the frontal slope is less steep than that of the parietal, and it is the slope of the frontal portion that is the primary criterion for the inferred orientation. The maximum depth is 5.0 cm, and the maximum (frontoparietal/sagittal) length is 6.7 cm. The frontal and parietal segments are separated by a near vertical crack that we infer corresponds to the frontoparietal suture. The dorsal surface of the frontoparietal is pitted, and the entire outer surface is eroded, exposing the internal cancellous bone. Only a small, fragmented portion of the external surface is preserved on the posterolateral (or caudolateral) left side. Here, incipient traces of tubercles are seen on portions of the external surface. Ventrally, the entire surface is broken, and no details of the ventral surface are preserved.

SMP VP-4370 (Fig. 3) consists of a small anterior (or rostral) fragment of the frontal and a sagittal section of an incomplete frontoparietal dome. The small frontal fragment (Fig. 3E) is approximately 1.9 cm long, and represents a portion of the rostral-most region of the frontal with a portion of the prefrontal sutural surface preserved. The maximum preserved length of the incomplete frontoparietal dome is 5.9 cm, while the maximum depth of the fragment is 3.5 cm. The ventral surface is thin, but a small portion of the cerebral impression and the smooth ventral surface of the caudal portion of the parietal can be discerned.

Comments—The two newly recovered specimens, NMMNH P-70009 and SMP VP-4370, have frontoparietal domes that are well-developed and similar to that of a previously documented specimen, SMP VP-2555 (Jasinski and Sullivan, 2011). The frontoparietal dome length of SMP VP-2555 cannot be determined with accuracy but it is estimated to be about 6 cm based on extrapolation of the frontal portion.

Despite its incompleteness the frontoparietal dome of NMMNH

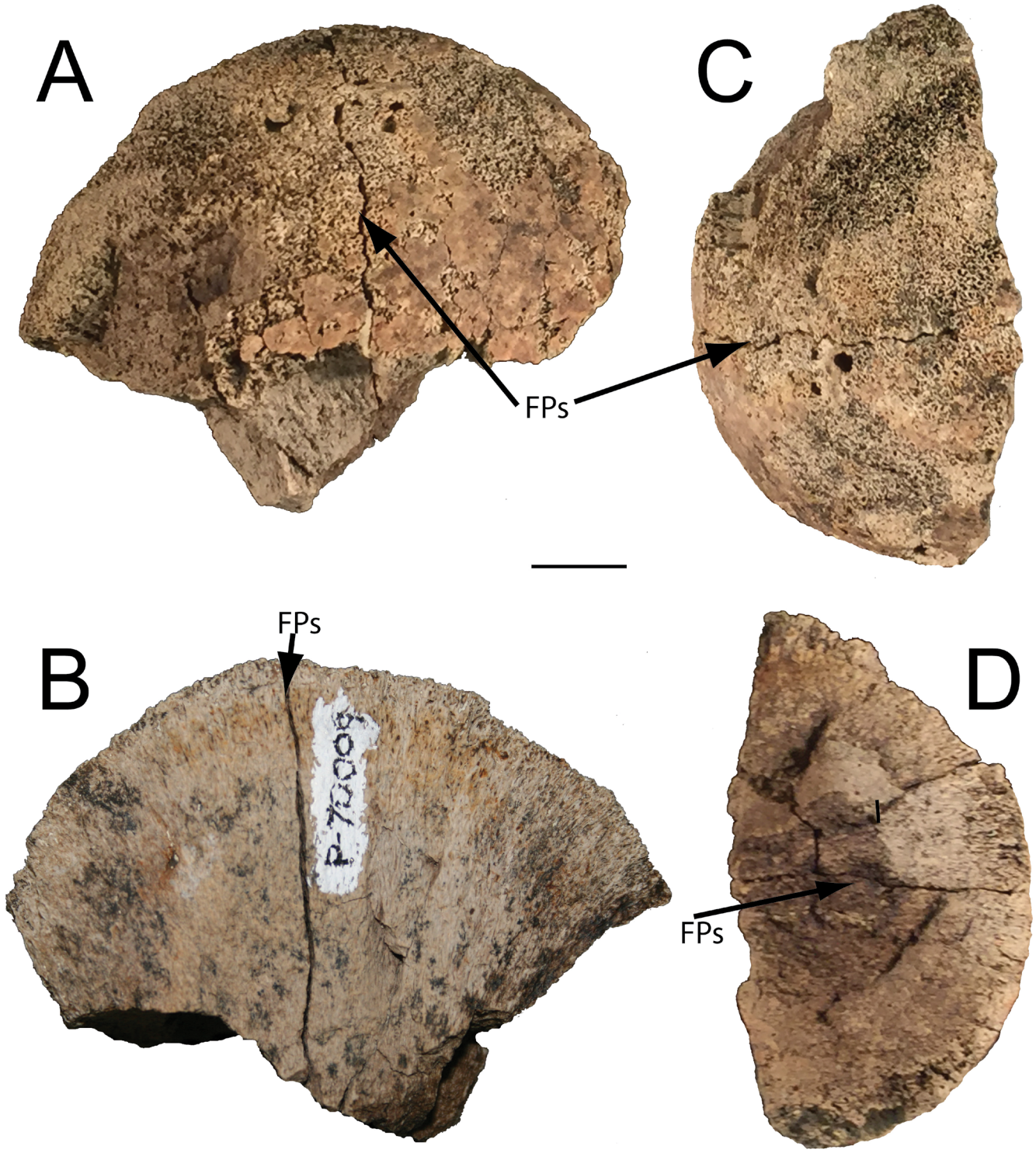

FIGURE 2. Cf. *Stegoceras novomexicanum* (NMMNH P-70009) left frontoparietal. **A**, sagittal view; **B**, left lateral view; **C**, dorsal view; and **D**, ventral view. Anterior (or rostral) to left for A and B; anterior (or rostral) top, for C and D. **Abbreviation**: **FPs**, frontoparietal suture. Scale bar = 1 cm.

P-70009 clearly represents a small individual with a highly inflated dome. It is slightly larger (6.7 cm) than the holotype (NMMNH P-33898), which measures 5.7 cm (frontoparietal dome length, not including the posterior [or caudal] extension of the parietal).

The frontoparietal dome of SMP VP-4370 is also quite similar to that of SMP VP-2555, indicating an individual of similar size based on its frontoparietal length. The posterior (or caudal) portion of the dome is preserved in SMP VP-4370, and rises steeply at an angle of approximately 66.7°. This indicates that the dome is nearly fully inflated, and suggests that SMP VP-4370 is slightly more mature relative to SMP VP-2555. Because the frontoparietal is a broken section of the sagittal region, the gross histology of the frontoparietal is clearly visible. The dense outer layer is relatively thick at approximately 12 mm, and the less densely packed inner layer (Zone II of Goodwin and Horner, 2004; Schott et al., 2011) is less porous than in SMP VP-2555. This specimen is similar to NMMNH P-70009 and SMP VP-2555 because the outer

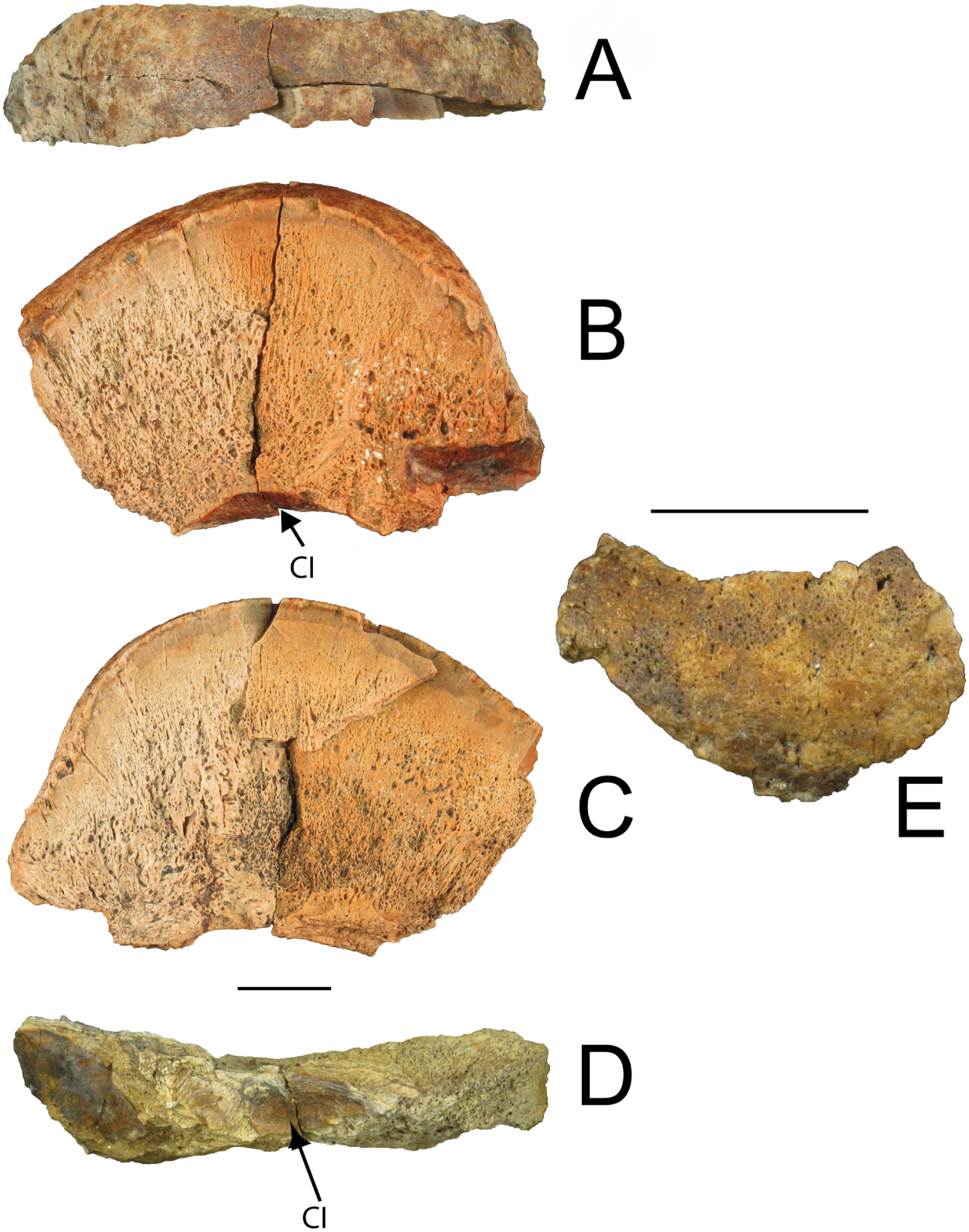

FIGURE 3. Cf. *Stegoceras novomexicanum* (SMP VP-4370) representing the sagittal section of an incomplete frontoparietal dome. **A**, dorsal view; **B**. right side of sagittal section; **C**, left side of sagittal section; **D**, ventral view; and **E**, anterior (or rostral) frontal fragment in dorsal view. Anterior (or rostral) to right for A, C and D; anterior (or rostral) left for B and E. **Abbreviation**: **CI**, cerebral impression. Scale bars = 1 cm, scale bar to left for A–D.

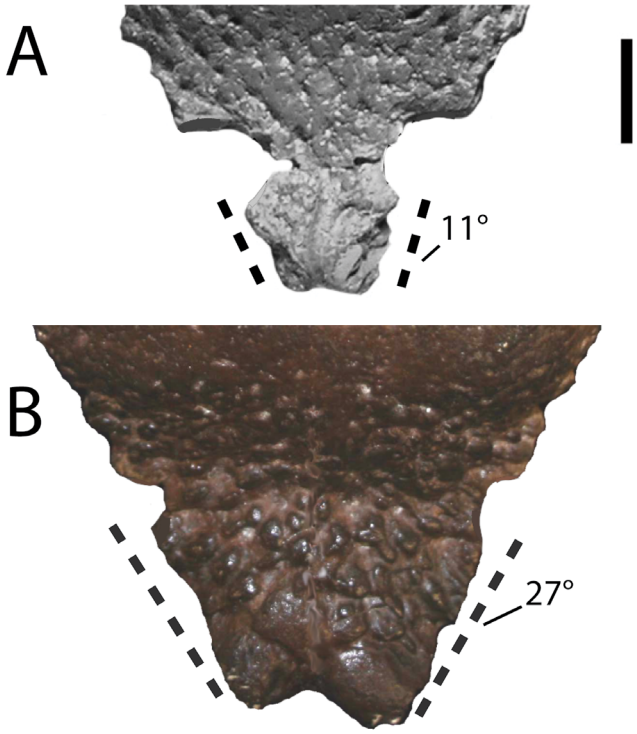

FIGURE 4. Posteromedial extension of the parietal in two species of *Stegoceras* (dorsal view). **A**, *Stegoceras novomexicanum* (NMMNH P-33983, holotype) and **B**, *Stegoceras validum* (CMN 515, holotype). Dark dashed lines highlight the posterolateral sutural contacts between the parietal and squamosal with those of *S. novomexicanum* making an angle of approximately 11° from the sagital plane, while those in *S. validum* make an angle of approximately 27°. Scale bar = 1 cm.

dorsal surface is smooth on top, particularly around the apex of the dome, while it is more rugose, with tubercles, toward the periphery.

The smallest-to-largest individuals, based on frontoparietal lengths and degree of doming are: NMMNH P-33898 (holotype of *Stegoceras novomexicanum*); SMP VP-2555; SMP VP-4370; and NMMNH P-70009. We suggest that these specimens represent a partial growth series for *S. novomexicanum*. Indeed, the holotype displays a few adult features similar to those of the more fully inflated frontoparietal domes, and this allows for the inference that the other specimens represent fully grown individuals. Moreover, because they all come from a restricted stratigraphic interval and geographic area, we contend that these pachycephalosaurid specimens are individuals of the same species (see below).

DISCUSSION

As previously noted, Williamson and Brusatte (2016) critically evaluated the the specimens we assigned to a new taxon, *Stegoceras novomexicanum*. Three main points formed the basis of their critique: 1) that the diagnosis of *S. novomexicanum* was problematic; 2) that most or all of the specimens we included in *S. novomexicanum* are immature specimens; and 3) that the two paratypes could not be confidently referred to the species *S. novomexicanum*. Here we address their points of contention and provide additional support for our interpretation that all these specimens are referrable to *S. novomexicanum*.

Diagnosis of *Stegoceras novomexicanum*

Williamson and Brusatte (2016) critiqued the characters used to diagnose *S. novomexicanum*. They disagreed that the shape of the posteromedial (or caudomedial) extension of the parietal is distinctive (Jasinski and Sullivan, 2011) and argued that it could not be readily distinguished from *S. validum* (CNM 515). However, we disagree with their assessment, especially with regards to the area that is caudal (or posterior) to the supratemporal fenestrae. While the parietosquamosal sutural surfaces are not perfectly parallel to each other, they diverge 11° from the sagittal plane, while those of CNM 515 diverge 27° (Fig. 4). This is a significant difference. The enlarged supratemporal fenestrae may be indicative of its relative ontogenetic stage as the size of the supratemporsl fenestrae would be expected to decrease in size and close in more mature individuals (such as in TMP 99.62.1; see Sullivan, 2003). While the size and basic shape of the supratemporal fenestrae change during ontogeny, their relative positions do not change during ontogeny. Indeed, Schott and Evans (2012) studied the variation of the squamosal through ontogeny for *S. validum*. They concluded that, while the size of the supratemporal fenestrae change, their positions relative to the squamosal (and the parietal) do not (see Schott and Evans, 2012, fig. 2). Based on these squamosals, and their morphology, the shape of the parietal and the position of the supratemporal fenestrae are consistent in *S. validum*, the closest known relative of *S. novomexicanum*. We infer, therefore, that the morphology of the parietal and the position (not the size) of the supratemporal fenestrae, in part, distinguish *S. novomexicanum*. Moreover, *S. validum* is far more robust than *S. novomexicanum* at a similar ontogenetic stage, further aiding in their distinction.

Williamson and Brusatte (2016) also critiqued additional characters that may be used to distinguish *Stegoceras novomexicanum* from *S. validum* and other pachycephalosaurids. They mentioned the "relatively low and more shallowly transversely convex shape of the frontals between the contacts with the nasals, prefrontals, and anterior supraorbitals," which means the nasal boss of *S. novomexicanum* is more strongly transversely convex than the same region of specimens of *S. validum* considered to be of a similar ontogenetic stage (e.g., CMN 138, CMN 8816, TMP 84.5.1). Williamson and Brusatte (2016, p. 36) also noted that the dome in NMMNH P-33898 "flattens laterally from the frontal portion of the dome as it nears the contact for the anterior supraorbitals." A groove or break in slope is present in this region of the dome in other pachycephalosaurids, including *S. validum*, *Colepiocephale*, *Hanssuesia*, and "*Prenocephale*" *brevis* (Williamson and Brusatte, 2016). Additionally, Williamson and Brusatte (2016, p. 36) noted that the contact of the frontal with 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 several other pachycephalosaurids, including *S. validum*, *Hanssuesia sternbergi*, and "*Prenocephale*" *brevis*. These characteristics, while not necessarily easy to quantify, distinguish *S. novomexicanum* from other known pachycephalosaurids, whereas the features listed by Schott et al. (2011) in their revised diagnosis of *S. validum* do not overlap in NMMNH P-33898. The features listed in the emended diagnosis for *S. novomexicanum* differentiates the two taxa.

The lack of a high and laterally convex nasal boss in *S. novomexicanum* (NMMNH P-33898) is another possible feature that separates it from NMMNH P-50900 and *S. validum* (CNM 515) as noted by Williamson and Brusatte (2016). They suggested the possibility that NMMNH P-33898 represents an immature individual of *Sphaerotholus* ("*Prenocephale*") *goodwini* (Williamson and Brusatte, 2016), which we believe is highly problematic, a fact reinforced by their recognition that *S. goodwini* does not possess a prominent parietosquamosal shelf. Rather, *S. goodwini* is of the *Prenocephale* type, characterized by a caudally-directed downward extension of the parietal. Sullivan (2000; 2003; 2006) and Sullivan and Lucas (2006b) believed *S. goodwini* was closely allied with *Prenocephale prenes* (and "*P.*" *brevis*) and that these taxa lacked prominent parietosquamosal shelves, regardless of their respective ontogenetic stage. It seems that a fully mature *Stegoceras novomexicanum* would probably be more similar to UALVP-2 (*Stegoceras validum*) than to *Sphaerotholus goodwini*. Regardless, without more specimens of *S. goodwini*, particularly throughout its growth series, it is impossible to refer NMMNH P-33898 to that species. It is more parsimonious to accept that NMMNH P-33898 represents a distinct taxon, *Stegoceras novomexicanum*.

Williamson and Brusatte (2016) incorporated *Stegoceras novomexicanum* into multiple principal component analyses (PCA) to aid in their determination of its validity. They incorporated NMMNH P-33898 into previous datasets by Evans et al. (2013a) and Mallon et al. (2015). The PCA from the modified Evans et al. (2013a) dataset (with measurements also taken from Evans et al. [2013b]), provided three main principal components based on 15 measurements. Williamson and Brusatte (2016, fig. 2A–B) interpreted PC1 (= principal component 1, accounted for 72.6° of total variance) as a body size component, while PC2 and PC3 (account for 18.4° of total variance together) were only weakly correlated with frontoparietal length (and therefore body size) and were potentially more phylogenetically informative. In their analysis, *Stegoceras novomexicanum* (NMMNH P-33898)

was closest to *S. validum*, but nevertheless was outside its convex hull in the plots comparing PC1, PC2, and PC3, supporting its distinct nature. Williamson and Brusatte (2016, fig. 2C–D) also incorporated *S. novomexicanum* into the dataset of Mallon et al. (2015), although it is noted that this dataset is based on only four measurements and is focused on morphology of and around the postorbital sutural surfaces. Based on the first two principal components, *S. novomexicanum* lies closest to *S. validum* in PC1 (60.9° of overall variance) vs. PC2 (30.1 of overall variance), approximately on the edge of its convex hull. Based on PC2 vs. PC3 (7.4° of overall variance), *S. novomexicanum* (NMMNH P-33898) lies close to the convex hulls of "*Prenocephale*" *brevis* and *S. validum*, and within the convex hull of *Sphaerotholus* ("*Prenocephale*") *buchholtzae*. The second set of PCAs (modified from Mallon et al. [2015]) implies that the postorbital sutural surface morphology is similar to that of several other pachycephalosaurids, including *Stegoceras validum*, "*P.*" *brevis*, and *Sphaerotholus buchholtzae*. On the other hand, the PCAs modified from the Evans et al. (2013a) dataset suggest *Stegoceras novomexicanum* may be distinct, and most closely related to *S. validum*. This is already assumed as those two are regarded as congeneric.

Indeed, Williamson and Brusatte (2016) came to a somewhat similar conclusion, believing that either the PCAs showed the distinctiveness of *S. novomexicanum* or that it may be related to, or a member of *S. validum*, with the former lying close to the latter in the PCAs. Evans et al. (2013a) partially used the position of the holotype specimen of *Acrotholus audeti* (TMP 2008.045.0001) within their PCA to help show its distinct nature among other studied pachycephalosaurid specimens, so this distinct nature of the holotype specimen of *S. novomexicanum* (NMMNH P-33898) may imply its validity as well. Additionally, they noted that few presumably immature specimens were included in the datasets other than some of *S. validum* (Williamson and Brusatte, 2016). This may have influenced the position of NMMNH P-33898 closer to *S. validum*, and they felt that more information and more specimens are needed to make a more complete determination (Williamson and Brusatte, 2016).

Williamson and Brusatte (2016, fig. 3) also provided an updated phylogenetic analysis of *Stegoceras novomexicanum*. Previously, Watabe et al. (2011, fig. 4) incorporated *S. novomexicanum* into a cladistic analysis, although they did not find it to be sister to *S. validum*. Instead, it fell outside a large clade of derived pachycephalosaurids (including *S. validum*) in their strict consensus tree. Evans et al. (2013a) also incorporated *S. novomexicanum* into a dataset of 16 in-group taxa (18 total taxa) and 50 characters. Evans et al. (2013a, fig. 5) found *S. novomexicanum* to be sister to *S. validum* within a clade including *Hanssuesia sternbergi* and *Colepiocephale lambei*. Williamson and Brusatte (2016, fig. 3) also conducted a phylogenetic analysis using the same dataset as Evans et al. (2013a, 2013b). However, it is unclear why they did not find the same phylogenetic relationships, although they are similar to those of Evans et al. (2013a). These include an unresolved polytomy of *S. novomexicanum*, *S. validum*, *Colepiocephale lambei*, *Hanssuesia sternbergi*, and a clade of derived pachycephalosaurids (Williamson and Brusatte, 2016, fig. 3). While the phylogenetic relationships of *S. novomexicanum* remain somewhat unresolved, the analysis by Evans et al. (2013a) provides the greatest resolution, identifying a sister relationship between *S. novomexicanum* and *S. validum*. More specimens and further data are needed to better determine the phylogenetic relationships of *S. novomexicanum*.

Given these facts, we maintain that *Stegoceras novomexicanum* is distinct from *S. validum* and all other known pachycephalosaurid taxa.

Maturity and Ontogenetic Stages

Many of the arguments brought forth by Williamson and Brusatte (2016) hinged on the relative maturity and ontogenetic stages represented by the referred specimens and the holotype specimen (NMMNH P-33898) of *Stegoceras novomexicanum*. Jasinski and Sullivan (2011, p. 210) wrote "Although the dome of NMMNH P-33898 is not fully developed, we believe it represents a near fully grown individual and is the same ontogenetic stage as CMN 515 and CMN 138." Indeed, Schott et al. (2011, fig. 4), showed these two specimens in the middle of the growth series of *S. validum*. The frontoparietal dome in SMP VP-4370 is more inflated than that of SMP VP-2555 and NMMNH P-33898, but represents an individual of a similar body size. This implies that the overall size was not changing much at this point, and doming was nearly complete, although it was not yet as inflated as seen in UALVP-2 or ROM 53555, both identified as *Stegoceras validum* (Schott et al., 2011). The gross histology seen in the sagittal section of SMP VP-4370 also indicates a relatively mature individual, probably slightly more mature than SMP VP-2555, but, again, it is of similar body size.

At issue here is whether there are sufficient characters, and in common, among immature specimens, to allow for taxonomic identification. Critical too, is the ability to define and recognize various ontogenetic stages within pachycephalosaurid taxa. Schott et al. (2011, table 18) listed cranial features that change through ontogeny within the species *Stegoceras validum*. Of the features they listed, the holotype of *S. novomexicanum* has the following adult features: frontals and parietals (somewhat) thickened and domed; frontoparietal smooth (although pitted) with traces of tubercles along the periphery of the anterior (or rostral) frontal extension; frontals fused externally; and frontoparietals fused externally. Thus, it is noteworthy that these Fruitland/Kirtland pachycephalosaurids display adult features seen in end stages of growth as demonstrated for *S. validum* by Schott et al. (2011). Therefore, they are also considered adult features in *S. novomexicanum,* so they are useful in determining the approximate ontogenetic stages of specimens referred to it.

Hone et al. (2016) recently offered an assessment of ontogenetic stages in dinosaurs and noted that interpretations as to whether a dinosaur is a juvenile or adult can vary depending on the definition used. They noted that often there are "contradictions and overlap for various definitions of maturity" (Hone et al., 2016, p. 6). They redefined the ontogenetic stages of juvenile, sub-adult and adult and included the terms "hatchling," "neonate," and "nestling" within the descriptor "juvenile." NMMNH P-33898 has a more inflated dome relative to CMN 515, suggesting a slightly more advanced stage of ontogeny. Clearly, NMMNH P-33898 displays many of the features listed and cited above by Schott et al. (2011, table 18) for an adult individual of *Stegoceras validum*, Therefore, we maintain that the paratypes and newly referred specimens are most likely to be small-bodied, highly-domed adult (or sub-adult) individuals of the same taxon, *Stegoceras novomexicanum*.

Williamson and Brusatte (2016) declared that the smoothness on the dorsal surface of NMMNH P-33898 (and SMP VP-2555) may be due to postmortem abrasion and taphonomy as well. However, the outer dorsal surface of these specimens does not show any indications of abrasion; rather they appear like any other natural pachycephalosaurid frontoparietal surface. Indeed, abrasion would show irregularities and artifacts, such as grooves, striations, pitting, etc., which these specimens do not exhibit. The smoothness of the frontoparietal is considered an adult feature in *S. validum* (Schott et al., 2011). Williamson and Brusatte (2016) also noted that some individuals, believed to represent early ontogenetic stages (i.e., younger individuals, and probably referable to juveniles and/or sub-adults), can also possess smooth or relatively smooth dome surfaces. However, we infer, based on the study of Schott et al. (2011), that the smooth surface texture of these specimens is a condition seen in adults and more mature individuals. This indicates they are not juveniles, but rather should be considered more accurately as sub-adults based on the criteria and definitions of Schott et al. (2011) and Hone et al. (2016).

Williamson and Brusatte (2016) also examined the histology of the holotype specimen of *Stegoceras novomexicanum* (NMMNH P-33898) by computed tomography, and re-evaluated the histological interpretation of SMP VP-2555 to further support their interpretation. Jasinski and Sullivan (2011) noted the presence of a dense, poorly vascularized outer layer of bone in the frontoparietal dome that seemed to indicate that the paratype specimen (SMP VP-2555) had effectively stopped growing. Williamson and Brusatte (2016) correctly noted that this layer of bone is present in even early ontogenetic stages of *S. validum* (Schott et al., 2011), and does not indicate a specimen is fully mature or has stopped growing. We stated (see above) that the specimen was not fully developed (i.e., not fully grown) (Jasinski and Sullivan, 2011). Williamson and Brusatte (2016) noted a relatively thick Zone II (see Goodwin and Horner, 2004; Schott et al., 2011), which indicates immaturity. Indeed, this does indicate that NMMNH P-33898 is not fully "mature" and was still growing, as was previsouly noted (Jasinski and Sullivan, 2011). However, it displays various features of adult specimens listed by Schott et al. (2011, table 18) such as frontals and parietals thickened and domed, frontals fused externally, frontoparietal fused externally, and relatively smooth frontoparietal. Moreover, in comparison with specimens of *S. validum* (see Schott et al., 2011, fig. 4), the holotype of *S. novomexicanum* (NMMNH P-33898) compares well with the ontogenetic stage of the lectotype of *S. validum* (CMN 515). Again, this indicates the holotype of *S. novomexicanum* (NMMNH P-33898) is a sub-adult similar to the ontogenetic stage of the lectotype

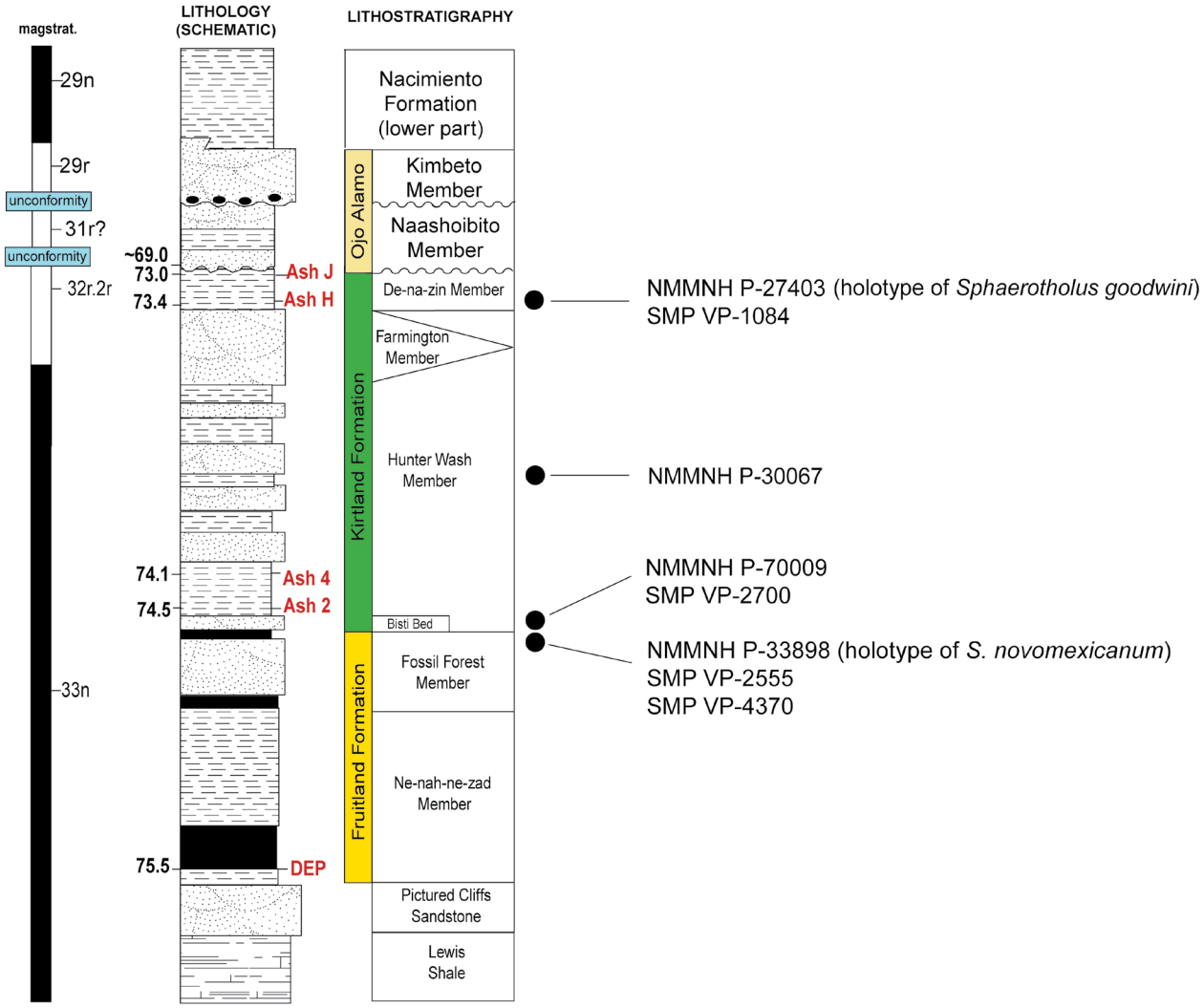

FIGURE 5. Stratigraphic distribution of pachycephalosaurid frontoparietal specimens from the San Juan Basin. (modified from Jasinski and Sullivan [2011] and Sullivan and Lucas [2014]).

of *S. validum* (CMN 515).

Williamson and Brusatte (2016) agreed that NMMNH P-33898 represents an individual at a similar ontogenetic stage as exemplified by CMN 515. CMN 515 is located just beyond midway through the growth series for *Stegoceras validum* presented by Schott et al. (2011, fig. 4). It is apparent that CMN 515 represents a sub-adult individual, not a juvenile, and it can then be inferred that NMMNH P-33898 is a sub-adult as well. Other characters considered to change through ontogeny in pachycephalosaurids, such as the size of the supratemporal fenestrae (and whether they are still open or not), size (and degree of inflation) of the frontoparietal dome, and size of the parietosquamosal shelf, indicate that NMMNH P-33898 is not a fully mature adult. If SMP VP-2790 does represent *S. novomexicanum*, then the size of this pachycephalosaurid would not have been significantly different from that predicted by the holotype (NMMNH P-33898). Indeed, in SMP VP-2790, the caudal edge of the parietal (and therefore the posteromedial edge of the skull and dome), is preserved and does not indicate a much larger individual. However, it is still possible that SMP VP-2790 represents a different pachycephalosaurid taxon, but there is no evidence for this. Regardless, NMMNH P-33898 represents an individual of comparable ontogenetic stage to CMN 515, and suggests that *S. novomexicanum* was smaller than *S. validum*, making it at least a relatively small pachycephalosaurid.

Referral of the Paratypes and Other Specimens to *S. novomexicanum*

Williamson and Brusatte (2016) challenged the referral of the paratype specimens (SMP VP-2555 and SMP VP-2790) to *S. novomexicanum*. Jasinski and Sullivan (2011, p. 207) referred SMP VP-2555 to *S. novomexicanum* based on "identical morphology of the ventral surfaces and similar size." They noted that no distinct features were identified and that this line of evidence was not backed up. Previously no features were identified as distinct on the ventral surface of the frontoparietal dome between *S. novomexicanum* and *S. validum*. However, we note here that the contact between the frontal and parietal exhibits a slight sigmoidal curve in the holotype (NMMNH P-33898) of *S. novomexicanum,* ventrally, versus an essentially straight contact with no sigmoidal curve in *S. validum*. SMP VP-2555 also exhibits a slight sigmoidal curve (see Jasinski and Sullivan, 2011, fig. 5B), although the degree to which this contact morphology may vary is not known and is probably due to individual variation. SMP VP-2790 possesses similar texture to NMMNH P-33898 and represents a pachycephalosaurid of a similar size.

Williamson and Brusatte (2016) also stated that, as dome size varies throughout ontogeny, it is not a good indicator for taxonomic identification. We agree, although Jasinski and Sullivan (2011) used size as more of a secondary indicator for the referral of specimens to *Stegoceras novomexicanum*.

Williamson and Brusatte (2016, p. 32) observed that SMP VP-2555 possesses a "highly transversely-convex frontal boss that is bordered laterally by a distinct groove." They noted that this feature is not present in NMMNH P-33898 but is present in several other pachycephalosaurid taxa (e.g., *Stegoceras validum*, "*Prenocephale*" *brevis*, *Colepiocephale lambei*, *Hanssuesia sternbergi*; Williamson and Carr, 2002b; Sullivan, 2003). However, they also conceded that the prominence of the frontonasal boss and frontal grooves are variable in

S. validum, and seem to vary through ontogeny and among individuals (Schott et al., 2011; Williamson and Brusatte, 2016). This variation indicates that this feature should not be used for diagnostic purposes, but does not preclude the specimens from representing the same taxon.

We assert, for reasons presented here (see above and below), that the paratypes SMP VP-2555 and VP-2790 can be referred to *Stegoceras novomexicanum*, although we conservatively identify them as cf. *S. novomexicanum*.

Other Considerations

Parsimony: Chronostratigraphy, Age, Geographic Distribution

All the specimens of *Stegoceras novomexicanum* come from a highly confined temporal range and geographic area. This fact, together with the morphological evidence presented above, further supports reference to *S. novomexicanum.* Although one can argue that stratigraphic and geographic provenance are relatively weak lines of evidence for a referral, as they are not morphological features, parsimony would suggest otherwise. Indeed, stratigraphic provenance has been used as supporting evidence in suggesting referrals for some pachycephalosaurids such as *Colepiocephale*, *Acrotholus* and *Pachycephalosaurus* (Sullivan, 2003; Evans et al., 2016; Goodwin and Evans, 2016). It is a well-known fact that most genera and species of dinosaurs come from very restricted stratigraphic intervals within a small geographic area (see Lucas et al., 2016). Indeed, small body size also implies small home range. The fact that additional, small-bodied pachycephalosaurid specimens continue to be found (see newly referred material, above) within the same stratigraphic horizon and geographic region, further supports the interpretation that these are, in fact, representatives of the same taxon. Moreover, no medium- to large-sized specimens (size of *Stegoceras validum* [UALVP-2] or *Prenocephale prenes* [Z. Pal. MgD-1/104] to *Pachycephalosaurus wyomingensis* [AMNH 1696]) have been found from this stratigraphic horizon, yet small-bodied pachycephalosaurids continue to be discovered. All four specimens are known from the Fruitland-Kirtland transition: two are from the upper Fossil Forest (Fruitland Formation) and two are from lower Hunter Wash (Kirtland Formation) members within a little over 0.8 km of each other. The holotype is from the uppermost part of the Fruitland Formation within 6 meters of the Fruitland/Kirtland boundary as mapped by Scott et al. (1979b). Thus, all the specimens are from a restricted interval near the Fruitland/Kirtland boundary (Fig. 5) as Jasinski and Sullivan (2011) stated.

Williamson and Brusatte (2016) commented on several other pachycephalosaurid specimens from the Fruitland and Kirtland formations in New Mexico. They mentioned an undescribed specimen (NMMNH P-50900) collected from the Hunter Wash Member (lower Kirtland Formation) that resembles *S. validum* and possesses a high and laterally convex frontal boss (Williamson and Brusatte, 2016, p. 40). This specimen is currently under study by Williamson and co-authors and it may represent a new taxon.

In addition, Williamson and Brusatte (2016) stated that NMMNH P-30068 (and NMMNH P-25049, a specimen referred to *Bistahieversor sealeyi*, see Carr and Williamson, 2002b), is from NMMNH locality 3097, and that this locality is in the younger Farmington Member and not the underlying Hunter Wash Member. However, based on the mapping of Scott et al. (1979a), it is clear that this locality is in the Hunter Wash Member and not the Farmington Member. Thus these two specimens are from the former member. We note here, too, that while NMMNH P-30068 (and NMMNH P-25049) were initially collected illegally by a third party, Jasinski and Sullivan (2011) did not mean to imply that Williamson and Carr (2002b), or any other researcher, were the one(s) who collected it illegally. The specimens were confiscated and are held in the collections of the NMMNH. Regardless, NMMNH P-30068 cannot be confidently referred to *Stegoceras novomexicanum*, or any known pachycephalosaurid taxon at the moment, and so this does not change the known stratigraphic range of *S. novomexicanum*.

Additionally, Williamson and Brusatte (2016) discussed the New Mexico pachycephalosaurids in a regional context. They noted that multiple formations are known from more northern localities with at least three pachycephalosaurid taxa, including the Dinosaur Park and Judith River formations. However, Evans et al. (2013a) noted that the diversity of pachycephalosaurids is probably vastly underestimated, even in well sampled units. Although it seems there are at least two, and potentially three (including NMMNH P-50900), pachycephalosaurid taxa known from the upper Campanian of New Mexico, even this diversity may be underestimated.

Finally, the lectotype of *Stegoceras validum* (CMN 515) and all other specimens of this species, are from the older Judithian age Dinosaur Park and Oldman formations of Alberta, Canada (see Sullivan, 2003), while *S. novomexicanum* is from the younger Kirtlandian age upper Fruitland/lower Kirtland transition. Not only is there a substantial age difference (approximately 0.5–1.0 million years), but the geographic separation between the two taxa is also significant.

Ontogeny and Phylogeny

The combination of adult and non-adult characters and their respective timing in their appearance needs to be considered. The near fully-formed frontoparietal dome in *Stegoceras novomexicanum* may indicate a shift in the timing of the expression of this feature, compared to other pachycephalosaurids such as the late Maastrichtian taxon *Pachycephalosaurus wyomingensis* (Goodwin and Evans, 2016). Indeed, while some features are indicative of more mature individuals, others suggest less mature or sub-adult individuals. Heterochronic development of a fully formed frontoparietal dome earlier on suggests changes in the timing or rate of developmental events relative to the same events in an ancestor or related species (e.g., Gould, 1977; Alberch et al., 1979; McKinney and McNamara, 1991; McNamara, 1986, 2012). The early doming in small pachycephalosaurids suggests heterochrony within *S. novomexicanum* relative to other pachycephalosaurids, particularly with progenesis. This may explain why *S. novomexicanum* is smaller than the lectotype of *S. validum* and other pachycephalosaurids, while maintaining some mature features. However, more complete series of fully mature and ontogenetically older specimens are needed to evaluate this hypothesis.

CONCLUSIONS

Stegoceras novomexicanum is a valid taxon that represents a small-bodied pachycephalosaurid. The type specimen (NMMNH P-33898) represents a sub-adult individual but is distinguishable from other known pachycephalosaurid taxa. Additional specimens, including the previously designated paratypes, are more highly-domed than the holotype and are small-bodied as well, are referable to cf. *S. novomexicanum*. The fact that these small, highly-domed pachycephalosaurids come from a restricted stratigraphic Fruitland/Kirtland interval (upper Fossil Forest/lower Hunter Wash members) and restricted geographic area, further suggests they probably are representative of the same taxon.

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