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Stratigraphic Reassessment of the Mexican Chasmosaurine *Coahuilaceratops magnacuerna* as the First Diagnostic Dinosaur Remains from the Cerro Huerta Formation (Lower Maastrichtian) Supporting the Southern Origin of the Triceratopsini

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Abstract: Very few remains of ceratopsid dinosaurs have been recovered so far from the Difunta Group of Coahuila, Mexico. The enigmatic chasmosaurine *Coahuilaceratops magnacuerna* was previously described on the basis of two partial skulls purportedly derived from the Cerro del Pueblo Formation (~73–72.5 Ma?). On the basis of a new measured section and lithological identification of the host rock, we reassign *Coahuilaceratops* to the overlying Cerro Huerta Formation (~71.5–70.5 Ma?). Thus, we formally assign the first dinosaur taxon to the Cerro Huerta Formation. This reassignment is more consistent with the relatively derived phylogenetic position of *Coahuilaceratops*, with implications for the southern Laramidia hypothesis concerning the origin of the Triceratopsini.

Keywords: Ceratopsidae; Chasmosaurinae; Maastrichtian; Mexico

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1. Introduction

The Parras Basin in the southeastern part of Coahuila in northern Mexico has provided a substantial proportion of the known fossil record from the Late Cretaceous of Southern North America [1–12], with fossils having been reported from the area since the 1920s [13]. Within the Parras Basin, the Difunta Group (Figure 1) has produced a remarkable number of fossil discoveries, resulting in the description of several new taxa over the past two decades [14–18]. However, fundamental stratigraphic issues require resolution before the fossil assemblages of the Difunta Group can be properly compared and correlated within a global or North American stratigraphic framework. Although the basal Cerro del Pueblo Formation has been relatively well-sampled, the formations overlying it remain poorly understood. Due to its fossiliferous nature, some fossil discoveries have been preliminarily and erroneously attributed to the Cerro del Pueblo Formation.

Ceratopsid dinosaurs are a successful clade of megaherbivorous ornithischians known for their elaborate parietosquamosal frill structures and horned faces [19–23]. Latitudinal biogeographical vicariance has been suggested for North American dinosaur faunas, affecting chasmosaurine ceratopsid dinosaurs by creating a northern *Chasmosaurus* clade and a southern *Pentaceratops* clade during the early-late Campanian [19,20,22–27]. In the early

2000s, international collaborations prospecting within the Difunta Group yielded rare ceratopsid remains, among them the chasmosaurine ceratopsid *Coahuilaceratops magnacuerna*, known from two individuals consisting of fragmentary skull remains [19]. Since then, various other chasmosaurine taxa have been described from the southern portion of North America, among them *Navajoceratops sullivani* and *Terminocavus sealeyi* [22]; *Sierraceratops turneri* [28]; "*Bravoceratops polyphemus*" [22,27]; and *Bisticeratops froeseorum* [29]. These recent discoveries may prove to be important for our understanding of the evolution of the southern clade of ceratopsids through the late Campanian–early Maastrichtian.

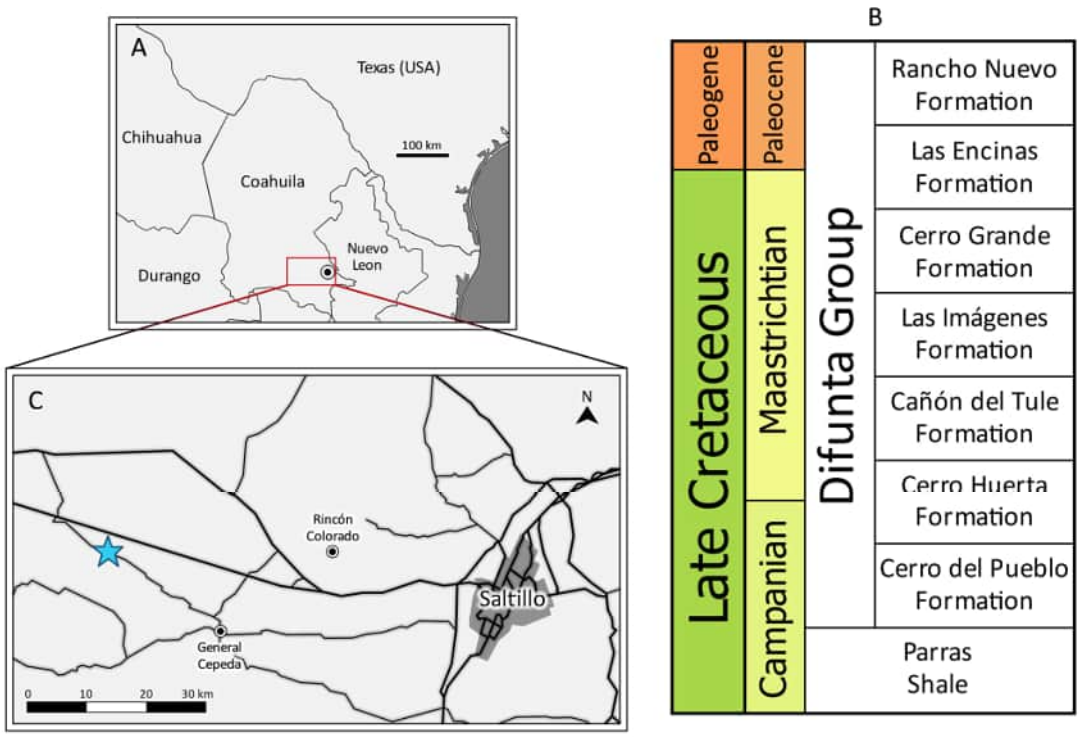

Figure 1. Geographic and stratigraphic setting. (**A**) Geographical setting, map of northern Mexico; (**B**) stratigraphic chart showing the formational divisions and age of the Parras Basin; and (**C**) location of the measured section marked with a blue star.

2. Geological Framework

The Parras Basin is an east–west oriented basin of ~27,000 km^2, located in southern Coahuila, Mexico. Several geological units outcrop here, with an estimated temporal range from the Campanian through the Paleocene. One of these units, the ~4000 m thick Difunta Group [30], comprises a number of formations, of which the basal-most is the Cerro del Pueblo Formation, which sits above the underlying marine strata of Parras Shale and below the overlying terrestrial strata of the Cerro Huerta Formation [2,31,32].

The Cerro del Pueblo Formation was deposited in a marginal marine setting, and it is characterized by abundant thick gray mudstones and sandstones, interpreted as coastal plain, lagoonal and deltaic depositional settings with brackish, shallow marine environments that were developed along the eastern shore of Laramidia [7,30,32]. It thickens westward, from 162 m at Saltillo, 499 m at Rincón Colorado (35 km west of Saltillo) and reaching 500+ m at Porvenir de Jalpa (70 km west of Saltillo) [30].

The Cerro del Pueblo is posited to be Late Campanian in age, based on biostratigraphy, magnetostratigraphy and isotopic analysis of strontium [5,7,30]. Working in the marine facies of the Cerro del Pueblo, Kirkland et al. (2000), described stratigraphic overlap of the ammonite *Sphenodiscus* with the bivalve *Inoceramus vanuxemi*, stating that this is correlative with the *Baculites reesidei* and *B. jenseni* ammonite zones of the Western Interior. This would place the age of the Cerro del Pueblo Formation as upper Campanian [33]. This is supported by analysis of the strontium isotopes of oysters from the Las Águilas tracksite giving an

absolute age of 73 ± 1 Ma [7]. Magnetostratigraphy shows the base of the Cerro del Pueblo Formation to occur just above the base of the 32n.3r magnetozone, and the upper boundary with the overlying Cerro Huerta to be coincident with the upper boundary of the 32n.2n magnetozone, stating a maximum age of 72.5 Ma [30].

The Cerro Huerta Formation (up to 978 m at the type locality, thickening southwest [1,2,30]) overlies the Cerro del Pueblo and is characterized by red and green siltstones, sandstones and mudstones, with occasional interbedded gray lithologies [2,5,30]. The Cerro del Pueblo–Cerro Huerta contact is marked by "the base of the first red or green bed" [2]. According to Eberth et al. (2004), the Cerro del Pueblo–Cerro Huerta Formation transition is not marked by a sudden transition to dominant red beds. Instead, a transitional zone tens of meters thick is recorded, consisting of gray–green and red sediments, which show a gradual increase in the thickness of the red beds. The Cerro Huerta Formation has been interpreted as a more inland environment than the underlying Cerro del Pueblo Formation, comprising lacustrine and continental depositional environments with occasional marine-to-brackish ingress [2,5,30–32]. The Cerro Huerta Formation is overlain by the gray siltstones of the Cañón del Tule Formation.

Currently, no age-diagnostic fossils have been recognized or described from the Cerro Huerta Formation, limiting the biostratigraphic correlation. However, magnetostratigraphic analysis shows that the base of the Cerro Huerta Formation spans the 32n.1r zone, while the overlaying Cañón del Tule Formation is correlated to near the boundary of the 31r.3r zone [30]. This would place the Cerro Huerta as ~2 million years younger than the underlying Cerro del Pueblo Formation and correlate the Cerro Huerta with the lower part of the Horseshoe Canyon Formation (Drumheller through Morrin Members) of Alberta, Canada [34].

3. Measured Section

The holotype *Coahuilaceratops* quarry was revisited with the original discoverer (C.L.D.) in order to compare its stratigraphy with newly discovered material within the Cerro del Pueblo Formation. It was then noticed by one of us (B.E.C.) that the *Coahuilaceratops* quarry in fact occurs within the Cerro Huerta Formation and not the Cerro del Pueblo. She then proceeded to measure a 1200 m thick section in the area immediately surrounding the site, ~70 km west of Saltillo (Figure 1), in order to ascertain this with greater precision. Although the overall thickness of individual beds was measured, structural deformation could not be accurately determined within the section, likely having some repeating sections, due to anticlines and synclines. Thus, although individual bed lithologies were reliably recorded, we advise caution regarding the total thickness of the units concerned and the precise stratigraphic position of formational boundaries and other sites of interest. Due to concerns over revealing the locations of fossiliferous horizons, GPS coordinates can be made available to qualified researchers for future reproducibility.

At its base, the section is characterized by sandstones and gray mudstones indicative of the Cerro del Pueblo Formation, with a rich assemblage of fossils and depositional structures, including charophytes, ripple marks, invertebrate fossils and dinosaur remains (see Supplementary Information). The Las Águilas Tracksite (dated at 73 ± 1 Ma by strontium isotopic dating [7]) is located at the base of the measured section and 652 m below the Cerro del Pueblo–Cerro Huerta contact, well-nested within the Cerro del Pueblo Formation. The Cerro del Pueblo–Cerro Huerta formational contact occurs 652 m above the base of the measured section.

In the upper part of the measured section, the Cerro Huerta Formation is poorly exposed, faintly outcropping and revealing the variegated redbeds characteristic of its lower section. The *Coahuilaceratops* quarry is located approximately 503 m above the Cerro del Pueblo–Cerro Huerta contact, simultaneously 1155 m above the Las Águilas tracksite. Although no exact dates have been assigned to the outcrops of the Cerro Huerta Formation within the Porvenir de Jalpa area, magnetostratigraphic data from the La Escondida Formation reveal the Campanian–Maastrichtian boundary to occurs approximately 90 m

below the contact of the Cerro Huerta–Cañón del Tule formational contact [30]. It is then possible to assume a Latest Campanian or Maastrichtian age for the *Coahuilaceratops* quarry. Furthermore, the lithologies of the *Coahuilaceratops*' quarry—although poorly exposed—are characteristic of the Cerro Huerta Formation, with the quarry itself being nested in between red siltstone strata (Figure 2). It is of note to mention that within the measured section—although not well-exposed—the Cerro Huerta Formation appears to be more fossiliferous than previously thought, suggesting it may prove to be a formation potentially rich in the remains of dinosaurs and other early Maastrichtian fauna species found in the southern part of North America.

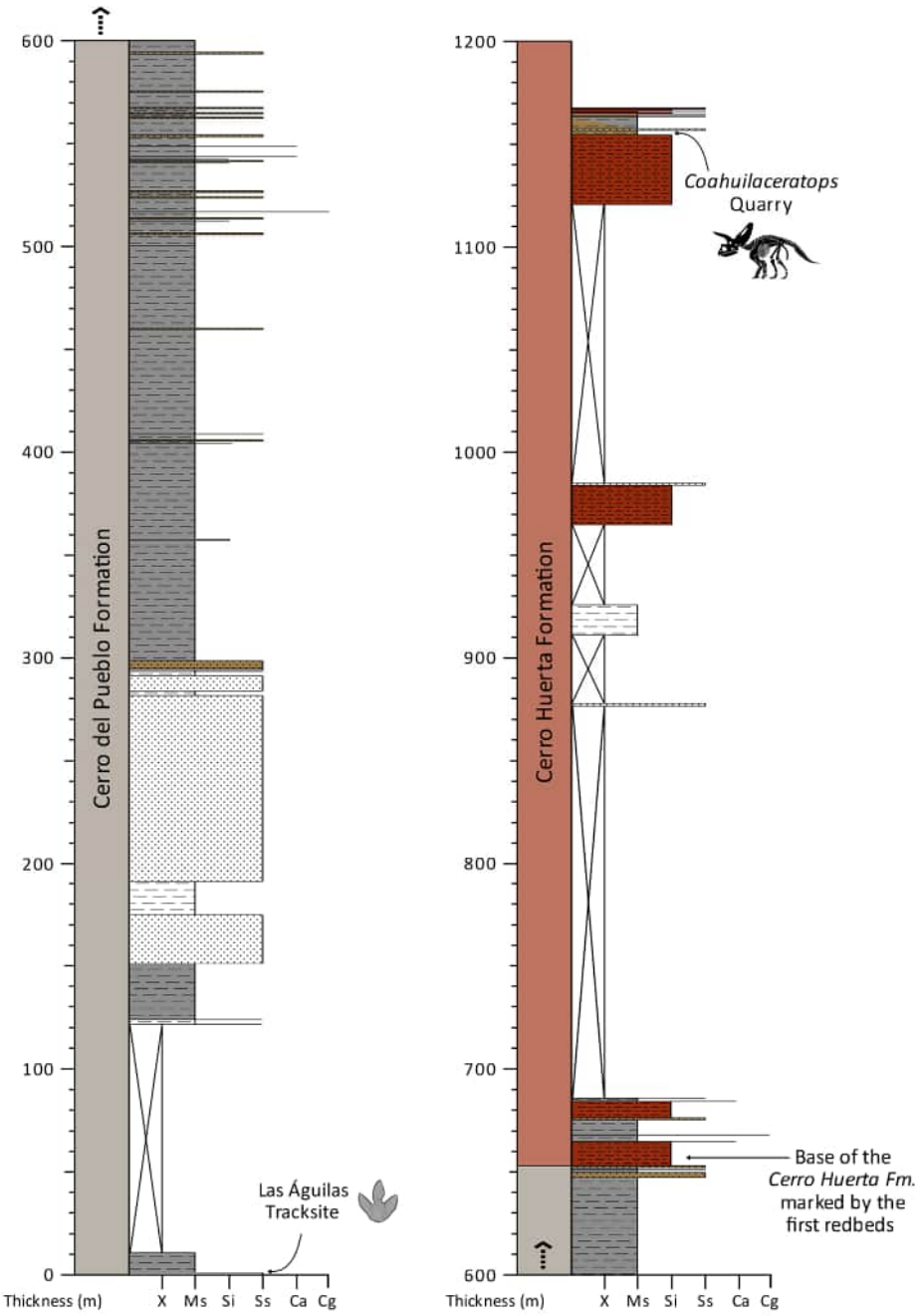

Figure 2. Stratigraphic column of the measured section. Abbreviations: X, unexposed; Ms, mudstone; Si, siltstone; Ss, sandstone; Ca, calcite; Cg, conglomerate. Note the shift to redbed intervals, marking the Cerro del Pueblo–Cerro Huerta contact, revealing the *Coahuilaceratops* quarry nested in between redbeds, belonging to the Cerro Huerta Formation.

The Cerro del Pueblo Formation is comprised of drab beige–brown interbedded sandstones and gray mudstones [2,5,7,30,32], which are not observable in the upper part of the measured section. However, the exposed sediments observed within the measured section, which contains the *Coahuilaceratops* quarry, consist mainly of thick red siltstones. The quarried horizon consists of beige–brown mudstone overlaying red siltstone strata and underlain by a thin drab sandstone, further overlain by more red sediments. The red beds that both underlie and overlie the *Coahuilaceratops* quarry are not characteristic of the Cerro del Pueblo Formation. Rather, they are typical of the overlying Cerro Huerta Formation. The Cerro Huerta Formation is poorly exposed within the Porvenir de Jalpa area, although these limited outcrops reveal the variegated redbeds characteristic of its lower part. This formational reassignment makes the specimen up to ~2 million years younger than previously thought, with notable implications for paleobiological interpretation.

4. Discussion

Fowler and Freedman Fowler (2020) hypothesized that in the Middle to Late Campanian, the North American subcontinent of Laramidia was inhabited by two chasmosaurine clades (a northern "*Chasmosaurus* lineage" and a southern "*Pentaceratops* lineage"). These were created by vicariance in the Early or Middle Campanian during a period of high sea level [35], which partitioned the Laramidian lowlands into northern and southern regions, separating ancestral subpopulations [22]. The *Chasmosaurus* lineage originated in northern Laramidia and later extended its range south as far as Utah, evolving into *Kosmoceratops* (Kaiparowits Formation [19]) in the Late Campanian, after which there is no further record [22]. The *Pentaceratops* lineage originated in southern Laramidia, but after regression of the Western Interior Seaway in the Middle Campanian [35], its descendants eventually moved north, evolving into *Anchiceratops* (Figure 3) [22].

Although this hypothesis well-explains the geographic occurrences and systematics of Campanian chasmosaurines, it does not explain the close relationship of the contemporaneous *Arrhinoceratops* and *Anchiceratops* [22]. Here, we hypothesize that a second vicariant event may have occurred within the *Pentaceratops* lineage in which a subpopulation stayed in southern Laramidia and evolved independently of the northern *Pentaceratops*–*Anchiceratops* lineage, giving rise to *Arrhinoceratops* and the Triceratopsini (Figure 4, which would later move northward after a marine regression reunited the Laramidian lowlands (Figure 3). *Coahuilaceratops* would therefore be an early representative of this southern lineage (Figure 4), which would be consistent with systematic analyses that place *Coahuilaceratops* as a relatively derived chasmosaurine exhibiting a number of characteristics also seen in the Triceratopsini (e.g., more anteriorly positioned nasal horn, relatively massive postorbital horns, Figure 5; retention later into ontogeny of raised bumps on the anterior end of the midline parietal bar, Figure 6), and may include other enigmatic taxa, including "*Bravoceratops*" [22,27], *Sierraceratops turneri* [28], and the Almond Formation chasmosaurine [36]. Unfortunately, *Coahuilaceratops* is missing the diagnostic posterior portion of the parietal, so it is difficult to address the absence or presence of a median embayment or to establish any further relationships until more complete material of this enigmatic taxon is recovered.

Others have reported *Coahuilaceratops* as belonging to a group of endemic southern Laramidian chasmosaurines, favoring a rapid regional radiation and high-diversity hypothesis for these occurrences rather than a biogeographic vicariance [28,29].

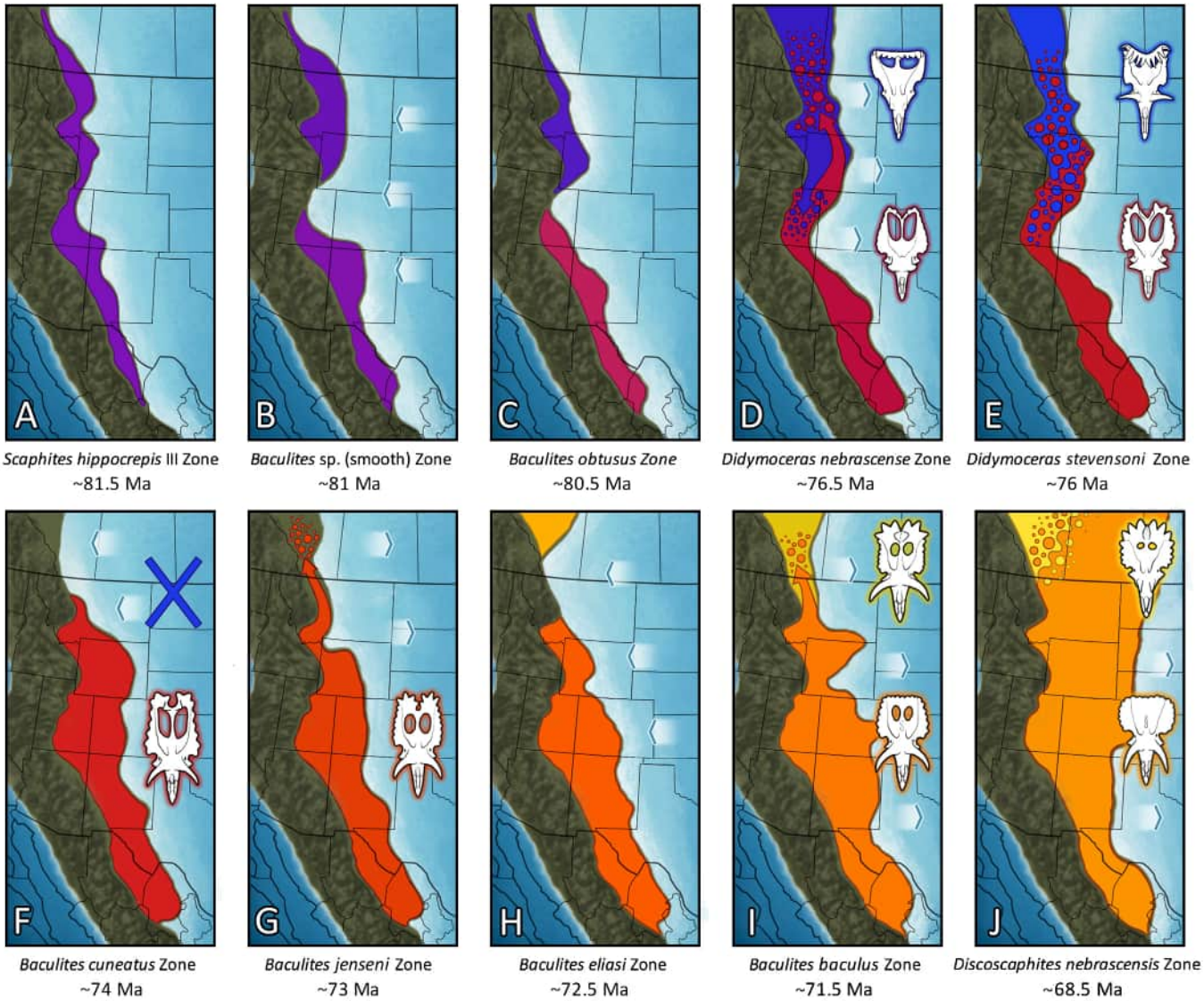

Figure 3. Latitudinal biogeographic vicariance hypothesis in chasmosaurines: maps based on [35]. (**A**) Ancestral population of basal chasmosaurines in Laramidia. (**B**) Marine transgression divides ancestral chasmosaurines. (**C**) Allopatric speciation occurs amongst chasmosaurines, evolving into a northern *Chasmosaurus* lineage (in blue) and a southern *Pentaceratops* lineage (in red). (**D**) Marine regression occurs, reuniting both lineages, resulting in faunal exchange. *Chasmosaurus* lineage, *Vagaceratops irvinensis*. *Pentaceratops* lineage, *Chasmosaurus russeli*, CMN 8800. (**E**) Lineages further evolve. *Chasmosaurus* lineage, *Kosmoceratops richardsoni*. *Pentaceratops* lineage, *Utahceratops gettyi*. (**F**) Marine transgression occurs, *Chasmosaurus* lineage becomes extinct, leaving no further record after *Kosmoceratops*. *Pentaceratops* lineage becomes cosmopolitan along Laramidian lowlands. (**G**) Marine regression occurs, a *Pentaceratops* lineage subpopulation moves north. (**H**) Marine transgression occurs, producing second latitudinal biogeographic vicariance event, resulting in allopatric speciation between the northern *Pentaceratops* lineage (in yellow) and southern *Pentaceratops* lineage (in orange). (**I**) Northern *Pentaceratops* lineage, *Anchiceratops ornatus*. Southern *Pentaceratops* lineage, *Arrhinoceratops brachyops*. Marine regression occurs, which reunites both lineages. (**J**) Further marine transgression expands the Laramidian lowlands. Lineages further evolve. Southern *Pentaceratops* lineage, *Triceratops*. This lineage becomes cosmopolitan along the subcontinent. Northern *Pentaceratops* lineage, *Regaliceratops peterhewsi*.

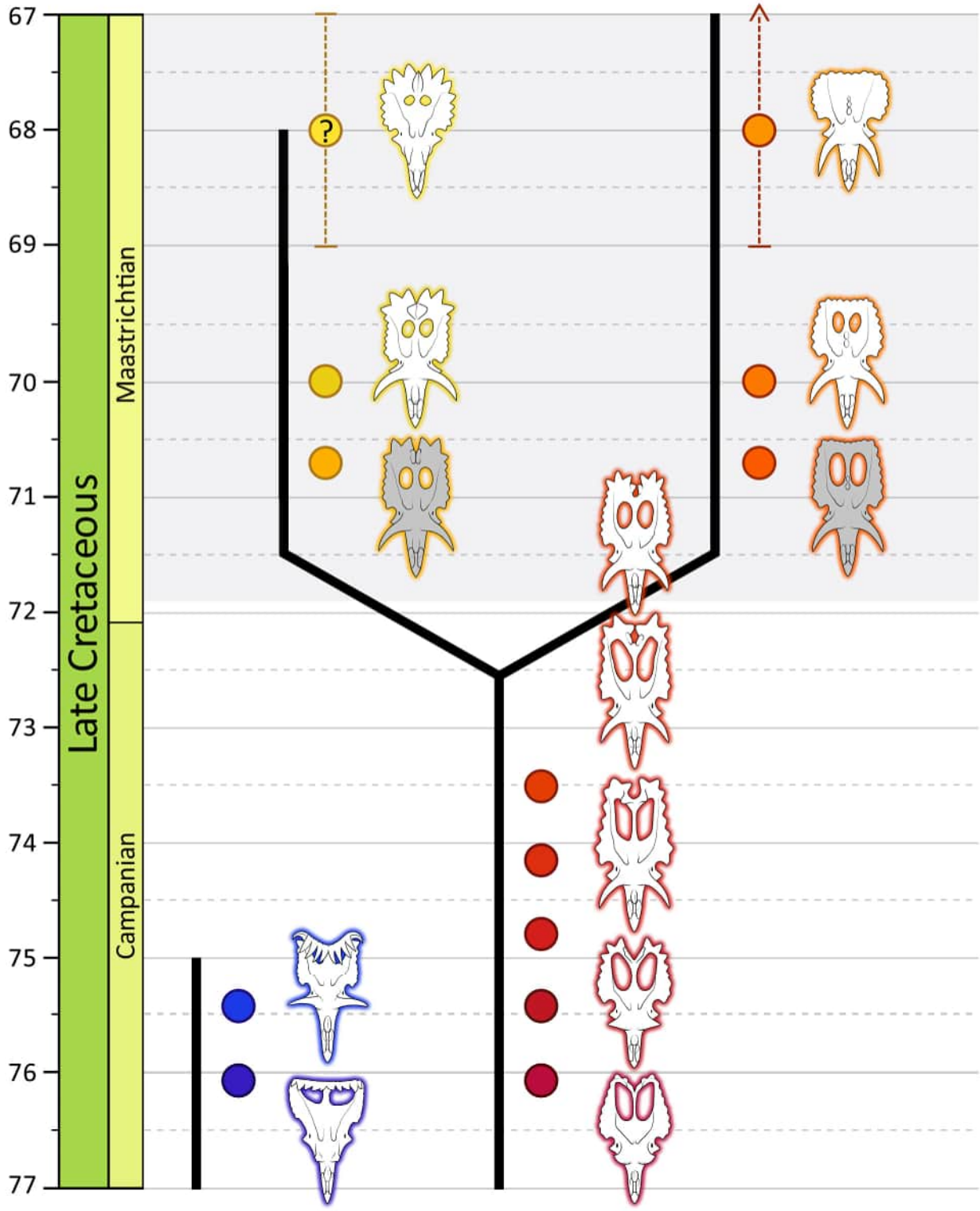

Figure 4. Hypothetical phylogenetic relationship of Upper Campanian and Maastrichtian chasmosaurines. Hypothetical skulls in gray. *Chasmosaurus* lineage in blue (skulls bottom to top: *Vagaceratops*, *Kosmoceratops*); *Pentaceratops* lineage in red (skulls bottom to top: CMN 8800, *Utahceratops*, *Pentaceratops*, *Navajoceratops*, *Terminocavus*); Northern *Pentaceratops* lineage in yellow (skulls bottom to top: *Anchiceratops* ancestor, *Anchiceratops*, *Regaliceratops*); Southern *Pentaceratops* lineage in orange (skulls bottom to top: *Coahuilaceratops*, *Arrhinoceratops*, *Triceratops*).

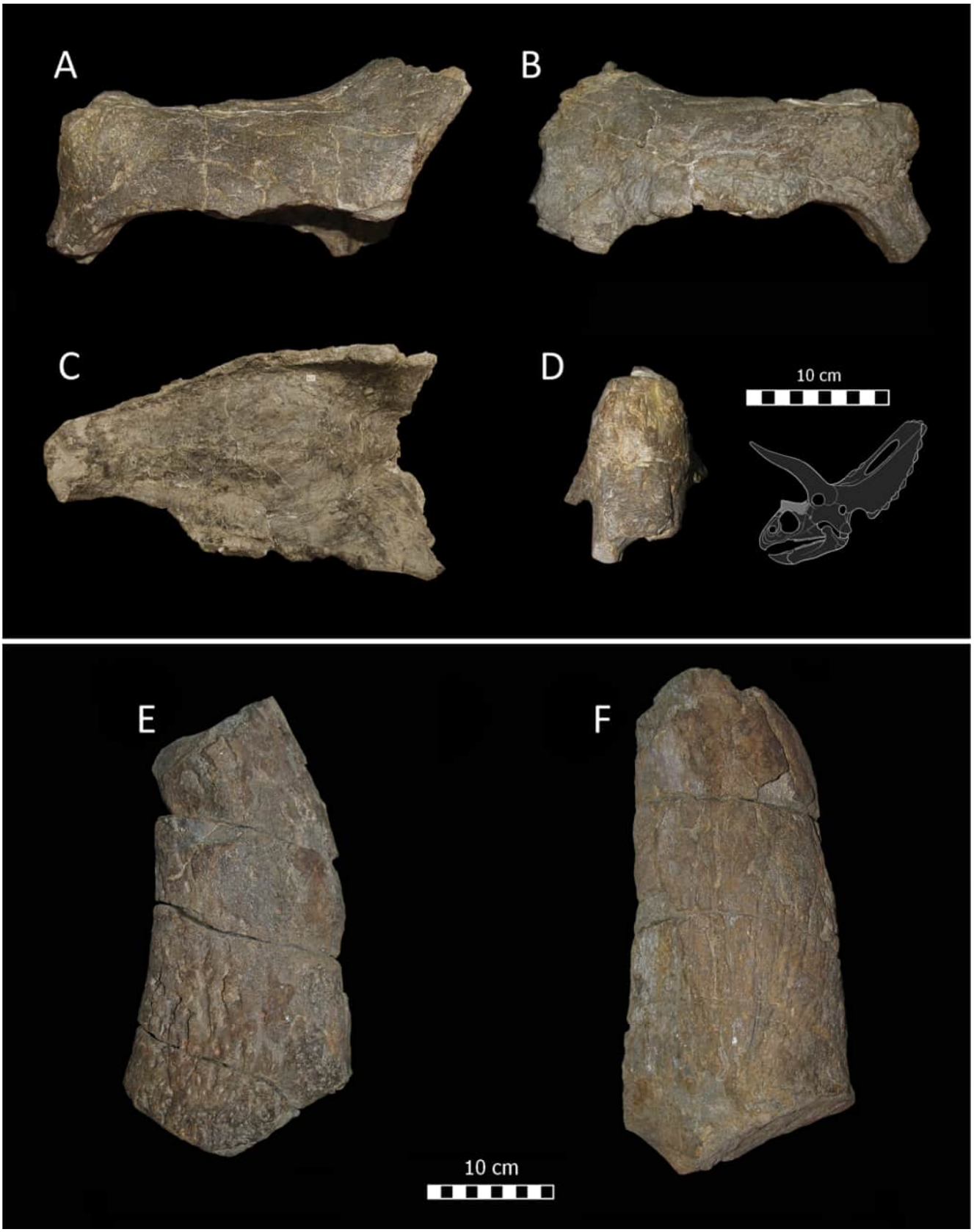

Figure 5. Horncore material of *Coahuilaceratops magnacuerna* (CPC 276). Fused nasals: (**A**) left lateral view; (**B**) ventral view; (**C**) right lateral view; and (**D**) anterior view. Supraorbital horncores: (**E**) left horncore; and (**F**) right horncore.

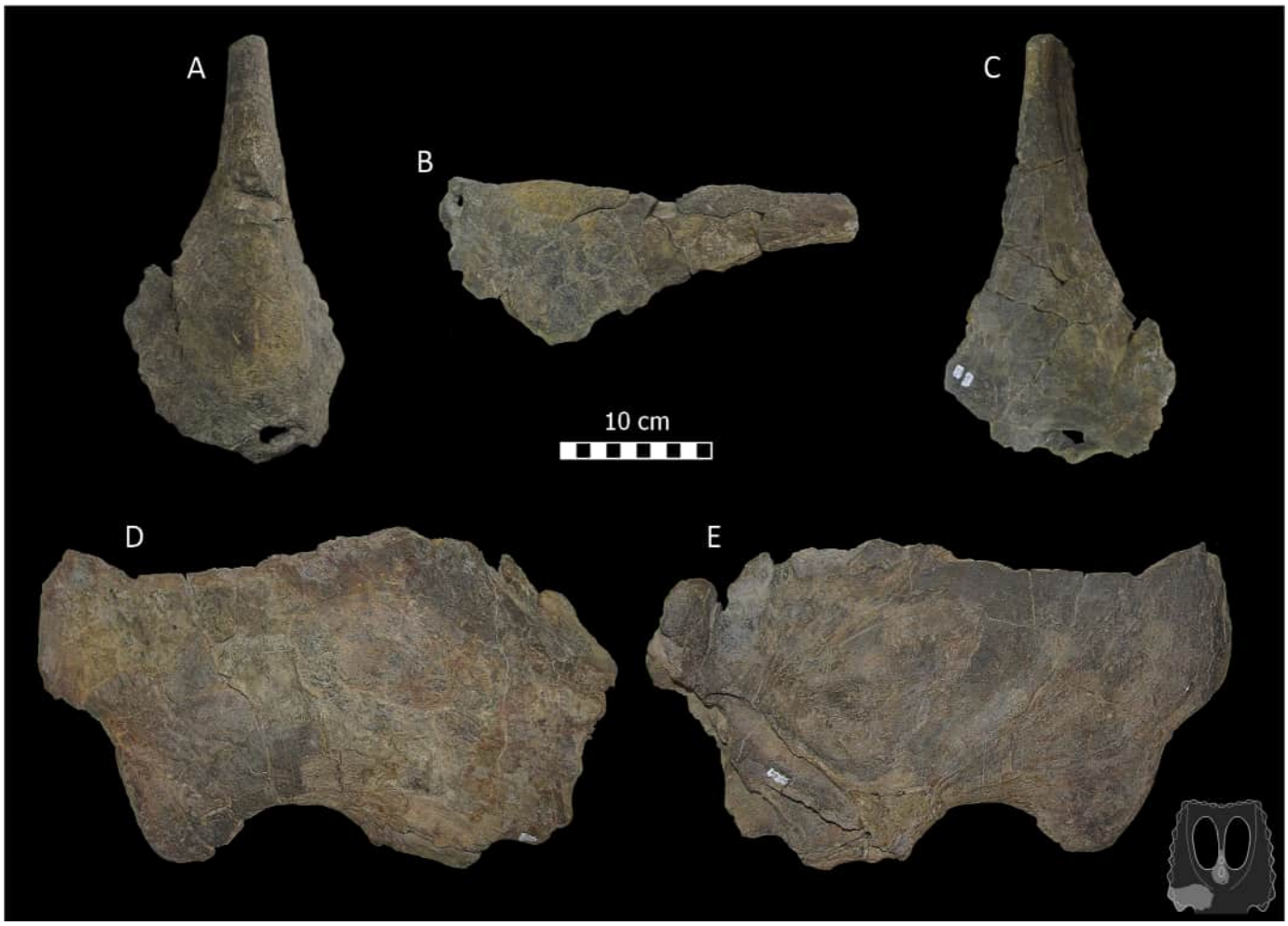

Figure 6. Parietosquamosal frill elements of *Coahuilaceratops magnacuerna* (CPC 276). Parietal in (**A**) dorsal view; (**B**) left lateral view; and (**C**) ventral view. Right squamosal in (**D**) dorsal view; and (**E**) ventral view.

5. Conclusions

Coahuilaceratops magnacuerna (Figure 7) is here reported to derive from the Cerro Huerta Formation rather than the previously reported underlying Cerro del Pueblo Formation. As a consequence, *Coahuilaceratops* is ~2 million years younger than previously stated and the first dinosaur taxon known from the Cerro Huerta Formation. Due to *Coahuilaceratops* exhibiting some craniofacial features also seen in the Triceratopsini (Figures 5 and 6), it is here hypothesized that it may represent the earliest member of this clade/lineage (Figure 4), lending credence to the southern Laramidia hypothesis concerning the origin of the Triceratopsini.

The recognition that *Coahuilaceratops* derives from the Cerro Huerta demonstrates the utility of accurate stratigraphic data in enhancing paleobiological analysis. We suggest that other fossil specimens purportedly from the Cerro del Pueblo Formation be reassessed in light of the complex stratigraphic relationships of the lower Difunta Group.

Finally, this demonstrates the great potential for further discoveries of important southern Laramidian dinosaur fossils in Mexico. Most notably, due to its probable early Maastrichtian age, the hitherto unknown Cerro Huerta fauna may prove to be of great importance in understanding the evolution of North America's final dinosaur fauna immediately preceding the K–Pg boundary mass extinction.

Figure 7. Skull reconstruction of *Coahuilaceratops magnacuerna* (**left**) and life reconstruction (**right**) courtesy of Gustavo Monroy.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d16070390/s1, Figure S1: Supp.Info Stratigraphy1; Figure S2: Supp.Info Stratigraphy2; Figure S3: Supp.Info Stratigraphy3.

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