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Dental morphology in a juvenile mammal from the late Cretaceous of South America: tooth eruption and development.

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DENTAL MORPHOLOGY IN A JUVENILE MAMMAL FROM THE LATE CRETACEOUS OF SOUTH AMERICA: TOOTH ERUPTION AND DEVELOPMENT

By

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B.A., University of Mississippi, 2018

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DEDICATION

This thesis is dedicated to my parents, Rod and Vicki, for always encouraging me to explore the world and all it has to offer. You both never confined me to "fit the mold" and always challenged me to be authentic to myself. Thank you for always supporting my dreams and goals and providing me the opportunities to reach and achieve them. I am especially grateful to you both as well for supporting my choice to pursue a career in the sciences. Dad – always taking me to the natural history museum every time I asked. Mom – always helping me to learn about the human body and how to care for others. Without either of you, I would not be who or where I am today. Thank you.

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ABSTRACT

DENTAL MORPHOLOGY IN A JUVENILE MAMMAL FROM THE LATE CRETACEOUS OF SOUTH AMERICA: TOOTH ERUPTION AND DEVELOPMENT

Kayla E. Newton

April 26th, 2022

Meridiolestids are a diverse and distinct clade of Cretaceous–Miocene South American dryolestoid mammals ranging in size from small shrew-sized insectivores to large dog-sized omnivores. *Cronopio dentiacutus* from the Cenomanian La Buitrera locality, Rio Negro Province, Argentina (Candeleros Fm.) is the oldest and best known of them, represented by skull material and associated jaws. A juvenile skull as attributed to *Cronopio dentiacutus*, based on tooth size and morphology, was collected from the type locality. The specimen includes the skull and both articulated lower jaws. The fossil is poorly ossified and partially flattened; CT scanning reveals most of the dentition in place and few floating teeth. The juvenile proportions, poor ossification, and absolute lack of wear suggests that the specimen is still immature and likely not weaned. The developmental sequence does not conform to known therian patterns, and it is uncertain if it is generally viable as primitive for mammals.

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INTRODUCTION

Mammals, having a worldwide distribution, are diverse in appearance and habitat, and the study of fossil mammals has proved to contain valuable information into the class's evolutionary history (Kielan-Jaworowska et al., 2004; Rose, 2006). Such information comes in the form of partial or intact fossil specimens mainly comprised of teeth and associated jaw structures, skull fragments, or the rarer completely intact specimens. As more and better fossil mammals are uncovered and described, new evidence is brought to light allowing for the re-interpretation of previously collected and published data, when fortunate, enough is recovered to evaluate the evolution of soft character and produce a reconstruction of the major biological attributes of the extinct taxa. The new evidence can better diagnose individual taxa, refine phylogenetic hypotheses of relationships, and contribute to the overall body of knowledge for mammalian evolution.

Mammals are defined by the Encyclopedia Britannica as "any member of the group of vertebrate animals in which the young are nourished with milk from special mammary glands of the mother." This character based definition is functional in a popular or unspecialized environment, easily allowing to distinguish living mammals form any other major group of vertebrates (Dolly, 1999). However, with the advent of phylogenetic systematics in the nineteen eighties and nineties, a stricter criteria relying on a narrower concept of definition and diagnosis for Mammalia (Rowe, 1987; Rowe and Gautier, 1992) has become dominant in the natural sciences. The most common being

Mammalia divided into the three subclasses: marsupials, placentals, and monotremes. (Armstrong et al., 2021). Accordingly, Mammalia is defined as the last common ancestor of monotremes, marsupials and placentals plus all of its descendants (Rowe, 1998) or slightly similar formulation (Sereno, 1999). Each subclass having its distinct characteristics, fossil mammals can be categorized into one of these groups or can be found to fall outside the crown (living groups) sharing more similarities with the ancestors of one group more than another thus providing more information into their evolutionary histories, development, behavior, etc.

The study of the origin of mammals is of great importance, and in particular, the Mesozoic Era (252.5 – 66 million years ago) is of interest because it is during this distant past that the major feature we associate with mammals arose on the earlier member of the lineage and their forerunners (Luo, 2011; Rougier et al., 2011). The Mesozoic Era is colloquially referred to as the "Age of the Dinosaurs" making it a popular reference and topic of interest in modern society. However, what types of mammals lived alongside of and in the shadows of dinosaurs, and what do we know about them? The Mesozoic Era was transitional in nature both biologically and geologically including transformation of species following changes in the world landscape and mass extinctions. The Mesozoic Era is subdivided into three distinct time periods: Triassic (252 – 201 million years ago), Jurassic (201 – 145 million years ago), and Cretaceous (145 – 66 million years ago). The Cretaceous Period, spanning 79 million years, contains fossil remains of mammals that bridge primitive and modern mammalian forms.

The mammalian fossil record is far from complete – specimens have yet to be found across the globe or from each of the time periods. Recently, however, fossil specimen discoveries from South America have been valuable in filling in the knowledge gaps in published literature about mammals who thrived during the Mesozoic Era. In the Rio Negro Provence of Argentina, the La Buitrera locality (Leanza et al., 2004; Candia et al., 2018) has been found to be fossiliferous in nature. La Buitrera is located at the following coordinates: Latitude 39°36’54.11” S and Longitude 68°40’45.33” W (Figure 1). In particular, the Candeleros Formation – Cenomanian in Age (100.5 – 93.9 million years ago) – is home to diverse fauna of fossil specimens making it of particular interest (Figure 2). In recent years, this formation has produced substantial information and new discoveries for Mesozoic mammals including the famed dryolestoid, *Cronopio dentiacutus* (Rougier et al., 2011).

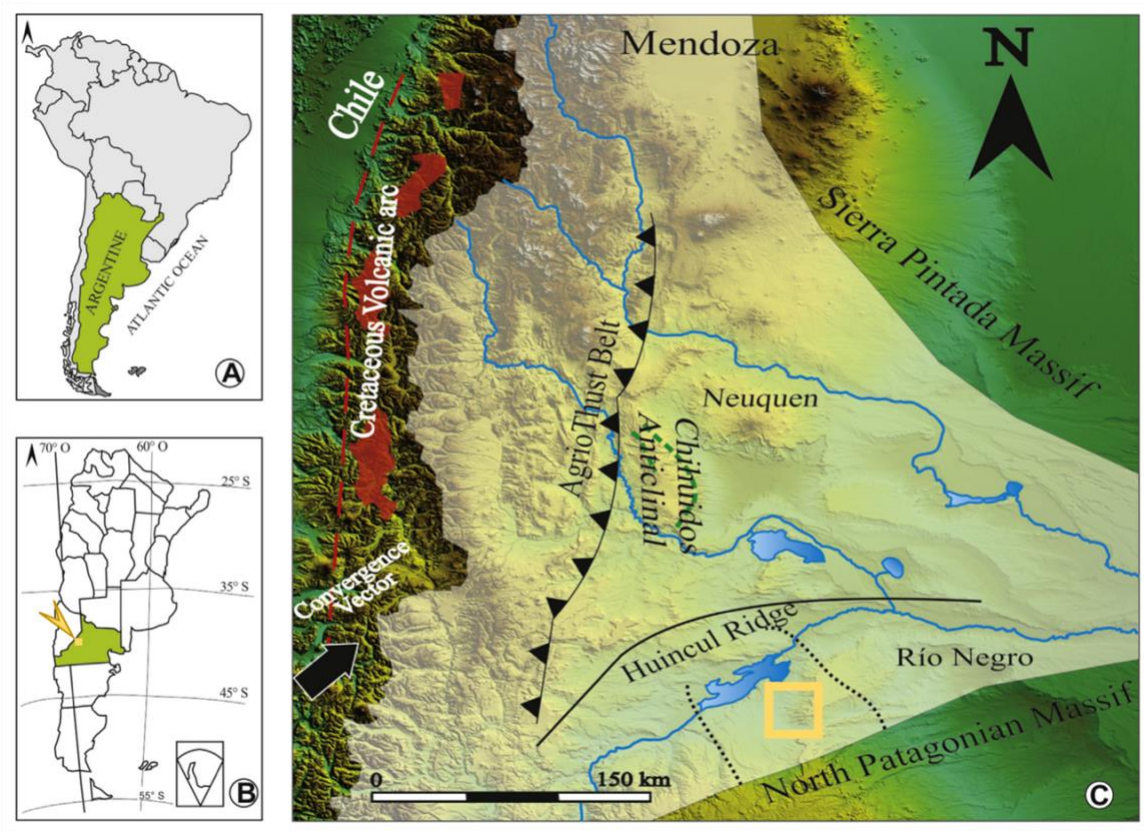

Figure 1. (Modified from Halupczok et al., 2018) Map of Rio Negro Provence, Argentina with La Buitrera Locality noted by a yellow square.

Figure 2. Photographs at the La Buitrera camp taken by Sebastian Apesteguia. Exposures of the Candeleros Fm. Are visible as the red outcroppings beyond the camp (Bottom).

Dryolestoids are an assorted group of extinct mammals representing an ancestral lineage to modern therians – marsupials and placentals (Lillegraven et al., 1979; Kielan-Jaworowska et al., 2004; Rougier et al., 2021). Members of this distinct clade have been found to range in size from shrew-sized insectivores to relatively large dog-sized omnivores (Harper et al., 2022). Their representation today has been characterized in the fossil record by remaining isolated teeth, jaw fragments, and in some exceptional cases, complete skulls. Dryolestoids were prevalent in the Mesozoic Era (252 – 66 My), but they survived the extinction event of the late Cretaceous reaching at least the Miocene (Rougier et al., 2012; Wible and Rougier, 2017). They are known from the Jurassic through the Early Cretaceous in the Northern Hemisphere (North America, Eurasia, North Africa) (Kielan-Jaworowska et al., 2004). By the Late Cretaceous, dryolestoids are known in the Southern Hemisphere, more specifically South America (Bonaparte, 1986; 1990, 1994, Bonaparte and Migale, 2010). This radiation of South American dryolestoids is referred to as meridiolestidans (Rougier et al., 2011), and they are amongst the most copious group of mammals from the Cretaceous (Rougier et al., 2021) (Figure 3). Dryolestoids today are preserved in the fossil record in locations where they once flourished. Fossils from the Mesozoic Era are considered especially rare (Rougier et al., 2021), and these fossils are delicate and preserve important facts about mammalian life history. Each characteristic protected in this record provides information to corroborate phylogenetic associations to past and present taxa.

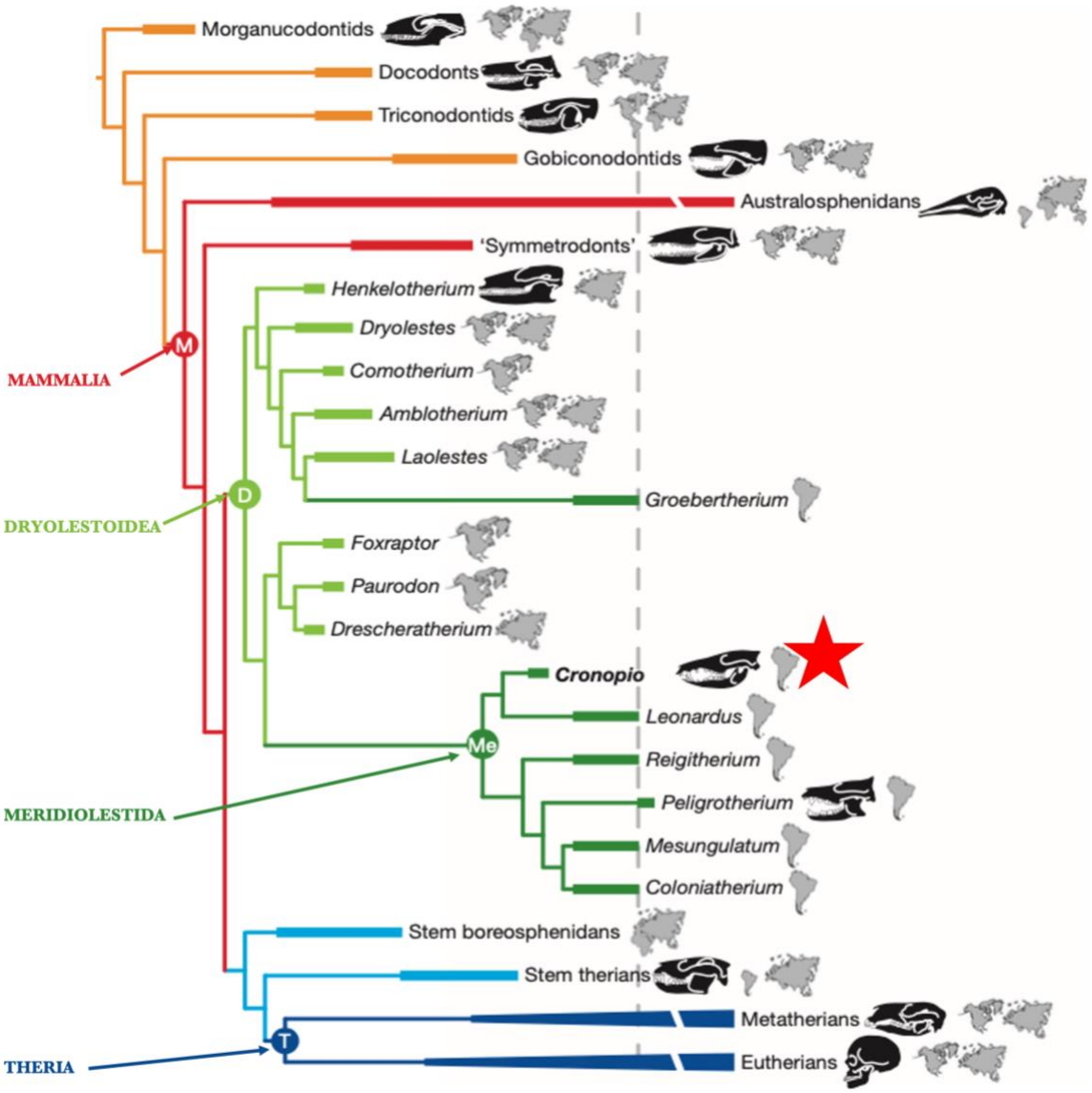

Figure 3. Phylogenetic tree (modified from Rougier et al., 2011), showing position of *Cronopio* (red star) within Meridiolestida. This clade is a monophyletic group endemic to South America, nested within Dryolestoidea.

Notably, the dentition of dryolestoids is easily distinguished and provides such data. The dentary is formed by a series of reversed triangles where the uppers are larger than the lowers (Rougier et al., 2021). Dryolestoids lack the presence of a protocone on the upper molars and have relatively small talonids (Butler, 1939; Patterson, 1956; Crompton, 1971; Davis, 2011) a characteristic present in both marsupials and placentals. The characteristics of the dentition including but not limited to the tooth formula, number of premolars – dryolestoids typically have five or more, type and size of cusps present, as well as eruption sequence all contribute to understanding the evolution of these mammals. Each character revealed by the dentition helps systematically associate this taxon and its relatives. The dentary of dryolestoids has been described in detail by Martin, 1999 and Kielan-Jaworowska et al., 2004. Because South American dryolestoids are described based on the remaining isolated tooth or jaw fragments, the features of their dentary may be incomplete in the record, in particular, traits that rely in the recovery of a specimen representing a short period of the development, such as deciduous dentition and eruption sequence. Unearthing fossils from this time period is rare, but to find a fossil specimen with little to no wear or defects to the morphology of its dentition or its anatomy is precious and an uncommon occurrence in the fossil record.

One of the best-known South American dryolestoids is *Cronopio dentiacutus* from the Cenomanian (100 My approximately) La Buitrera locality, Candeleros Fm., Argentina and is represented by skull material and associated jaws. The discovery of *Cronopio dentiacutus* represented the first-time cranial remains from the early Late Cretaceous of South America had been described (Rougier et al., 2011). The *Cronopio* specimens, MPCA 453 and 454, described by G.W. Rougier were adult specimens based

on size, proportions, and tooth morphology. The dentition was poorly preserved and showing extensive wear masking some of the main crown features. Here we have what we believe to be a juvenile *Cronopio* specimen, MPCA-PV 482, based on the same characteristics of size, proportions, tooth morphology as well as the degree of mineralization of hard tissues. This specimen is estimated to be from the Late Cretaceous (100 My), and the recovery of a juvenile mammalian specimen from this time period bearing a mostly intact dentition is remarkable. Not only are mammalian growth rates rapid – making juvenile stages transient, but also the specimens are small in size and extremely fragile (Chinsamy et al., 2006; O'Meara et al., 2016, 2018). For the first time, we can describe a nearly pristine dentition, lacking any wear, and get a glimpse of early tooth development and replacement in basal mammals.

Due to their ancestral ties to modern mammals – including humans, the study of dryolestoid fossils in important to the understanding of the conditions we see in living taxa today.

MATERIALS AND METHODS

A Computer Tomography (CT) Scan was taken of a presumably juvenile specimen, enclosed in sediment, measuring approximately 1.75 cm across (Figure 4). Specimen MPCA-PV 482 was collected from the Candeleros Formation (Cenomanian) in the La Buitrera locality of Patagonia, Argentina. The CT data was obtained using a Fein Focus High Power source, 120 kV, 0.19 mA, aluminum filter, Perkin Elmer detector, 0.25 pF gain, 1 fps, 1x1 binning, no flip, source to object 134.6 mm, source to detector 1316.831 mm, continuous CT scan, no frames averaged, 0 skip frames, 2875 projections, 5 gain calibrations, 0.762 mm calibration phantom, data range [-2.0, 200.0] (grayscales adjusted from NSI defaults), beam-hardening correction = 0.1. Voxel size = 9.8 μm. Total slices = 1830. Additional information was produced by direct observation under binocular microscopy. Comparative material of recent and fossil mammals was available during the study to help put the morphology into an evolutionary context. Measurements were taken directly form the renderings.

The scan revealed that the specimen consists of a skull and semi-articulated jaws that are compressed and displaced. The data slices were rendered by manipulating the CT images in Avizo – a visualization and analysis software. Using differences in the radiopacity of rock, enamel, and bone (via CT imaging) (Figure 5) the dentition and associated jaw structures were digitally extracted. The visualization between each of the material's radiopacities proved to be a challenge. Due to the specimen's juvenile stage,

the bone – not fully mineralized – was similar in radiopacity to the sediment encasing the specimen. The skull and associated cranial structures were not sectioned nor reconstructed for the scope of this project. Avizo was used to produce a 3D reconstruction and rendering of the specimen's dentition.

Reconstruction and rendering of the specimen revealed a nearly pristine dentition, and the morphology of each tooth present was described in detail. The specimen was compared with other potentially related taxa – Dryolestoids, meridiolestids and early therians in particular. The aim was to recognize primary versus secondary dentition using a variety of criteria ranging from enamel thickness to eruption phase and/or the presence of a dental lamina/developmental crypt. Crown morphology, tooth formula, and eruption pattern was analyzed in a phylogenetic context.

Figure 4. Photograph of entire, unprepared specimen, MPCA-PV 482. The specimen encased in rock measuring 1.75 cm across. The mandible is exposed.

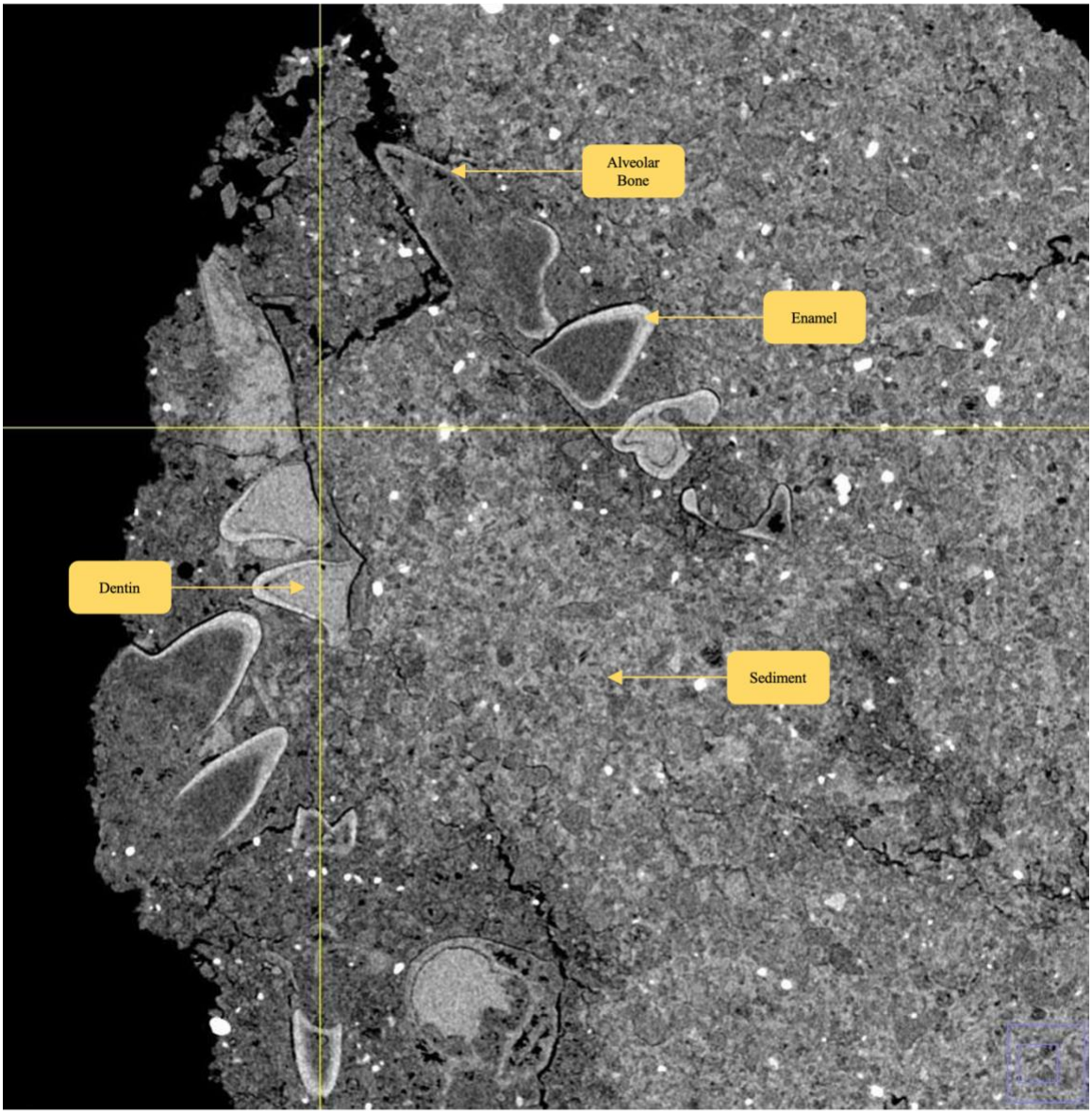

Figure 5. Computer Tomography (CT) data slice of Specimen MPCA-PV 482 encased in rock. The differences in the radiopacity of enamel, dentin, alveolar bone, and sandstone can be seen.

DESCRIPTIONS

General Description

The specimen is a juvenile preserving most of the skull with the jaws articulated, but they are not in natural occlusal position. The bones are poorly ossified in general, and the CT contrast in the individual slices is poor making the exact morphology of the maxilla and mandible unable to be fully determined. The specimen MPCA-PV 482 has been flattened dorso-ventrally during the process of fossilization and likely has compressed the erupting teeth into the jaw. The jaws retain their articulation throughout the incompletely preserved symphysis, and they are deviated to the right from the main axis of the skull. They appear to preserve – at least on the right side – the approximate natural antero-posterior position. The upper and lower molars are roughly in an expected, functional relationship (Figures 6, 7, 8 and 9). The deviation to the right of the jaws makes the premolars out of natural alignment. The specimen was collected by surface picking, and it had been exposed to the elements for an unknown length of time. The inclusion of the skull and jaws in a little concretion preserved the bulk of the teeth and craniomandibular elements. However, erosion and breakage are evident affecting mostly the mesial elements of the specimen and the upper left ante-molar positions, most of which have been lost prior to collection. Given the remarkable state of preservation of the fossil, it is likely that at one time the full dentition was present. However, we have no evidence of the upper incisors, canines, or anterior premolars, and we are missing most of the inferior incisors with the exception of the last right incisor.

Based on comparisons with recent mammals, we believe this represents a very early stage of development with an animal in which the dentition is not yet fully functional. Similar to the situation that we see in young opossums of an approximate age of Dental Class 3-5 or roughly 7-11 months old (Diaz et al,. 2008; Tyndale-Biscoe et al., 1976). This fact is supported not only by the position of the teeth deeply nested inside the jaw and not fully erupted, but also by the combined fact that no roots are fully developed in the specimen. In most cases, the crown is being completed or is close to its final morphology as such the overall mineralization of the enamel and dentin appears to be less mature than in a fully adult tooth which diminishes the contrast in CT images. This is also true of the known non-dental materials which appears as thin sheets of bone and presents a challenge in establishing the continuity of the structures. Traditionally, early ossified elements like petrosals and mandibles are precociously ossified in modern mammals (Goswami et al., 2009; Koyabu et al., 2014; Rager et al., 2014; Sánchez et al., 2017). This is seen in the specimen reflecting a commonality of ossification with modern mammals. Although none of the dental elements at this stage are fully functional, the relative position to each other appear similar to what has been observed in adults of *Cronopio* indicating that the pre-eruptive phase mirrors the adult morphology. That is the molars are erect and appear to show no rotation in the process of eruption. This is the condition for at least the first two molars and the last two premolars. The only last molar preserved approximately in place is the right lower m3 which preserves its general orientation for the anterior teeth, but it is tilted mesially giving the crown a generally proclive orientation that is not seen in the anterior molars. This is also the condition that we see in marsupials in the process of eruption of the last molar (Rougier et al., 1998).

The left lower m3 is not in place and none of the last upper molars are preserved in place. The upper M3s are not fully mineralized and are represented by the paracone and most of its crests leading to the buccal margin of the tooth which is yet to ossify. These teeth, the upper M3s, have fallen out of the maxilla and are floating in the matrix and are far from their natural position

Figure 6. Buccal View – 3D reconstruction of the entire dentition and associated jaw structures present for specimen MPCA-PV 482.

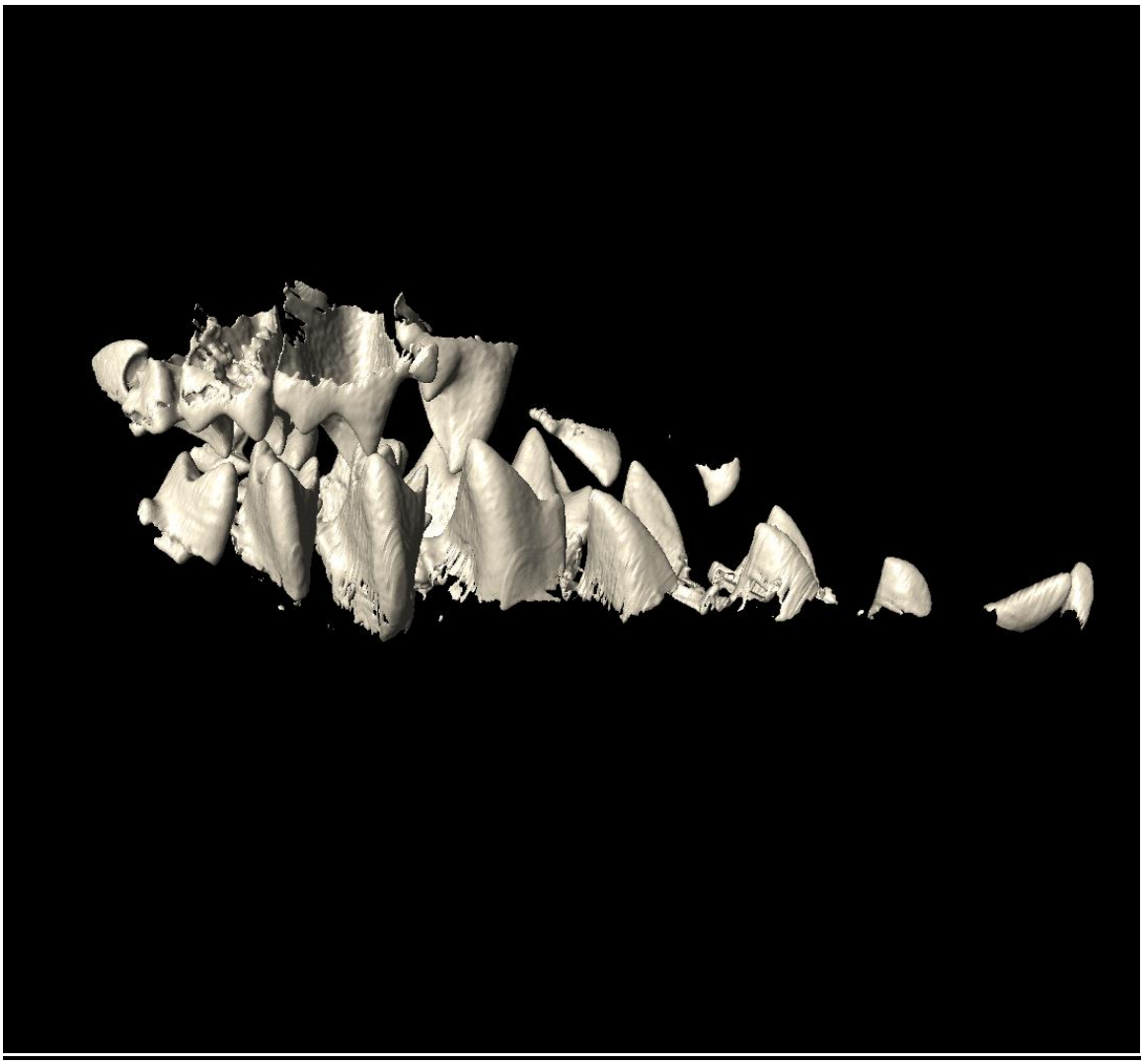

Figure 7. Buccal View – 3D reconstruction of the entire dentition without associated jaw structures present for specimen MPCA-PV 482. Root formation can be seen on the m1.

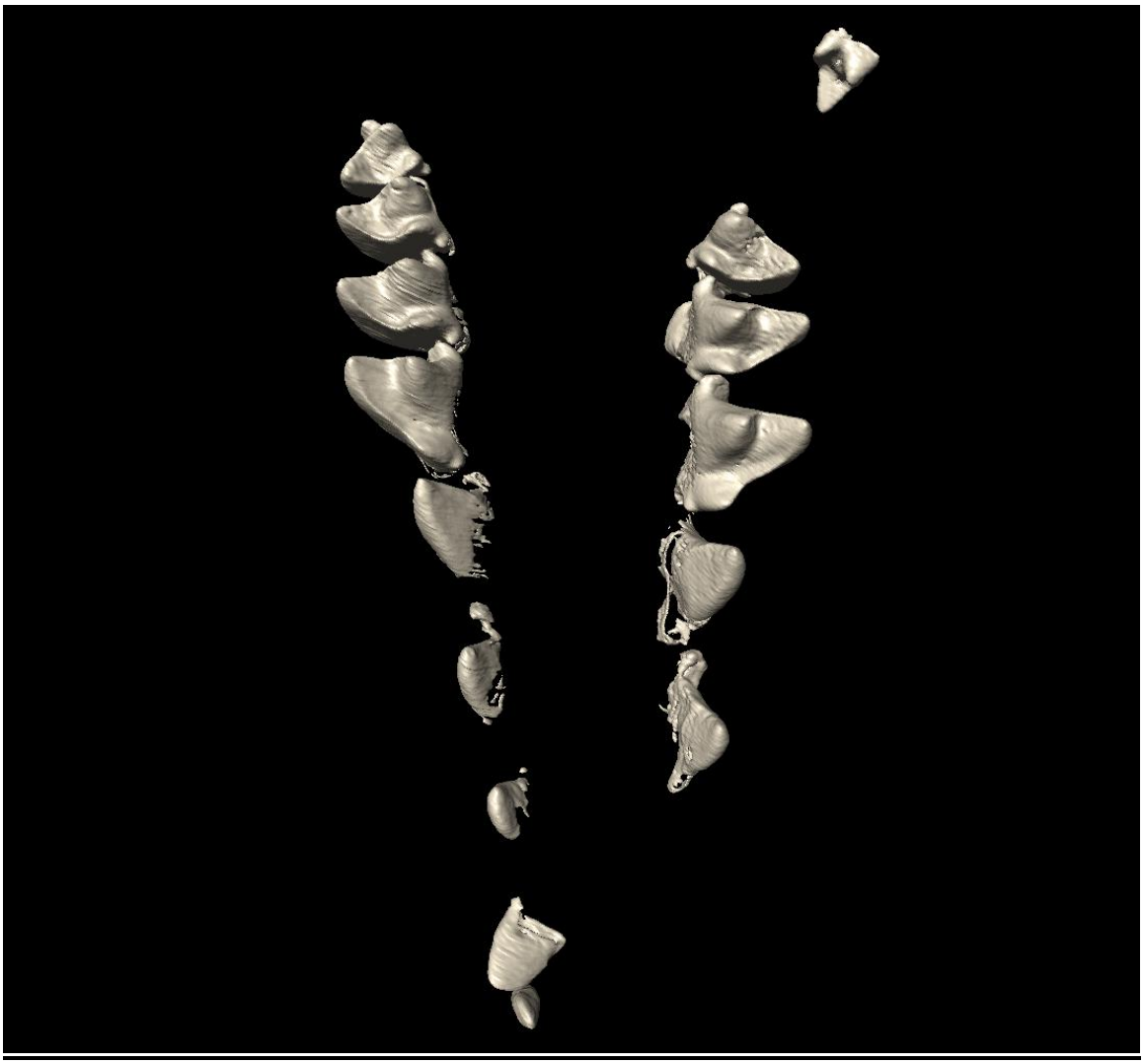

Figure 8. Occlusal View – 3D reconstruction of the present mandibular dentition for specimen MPCA-PV 482.

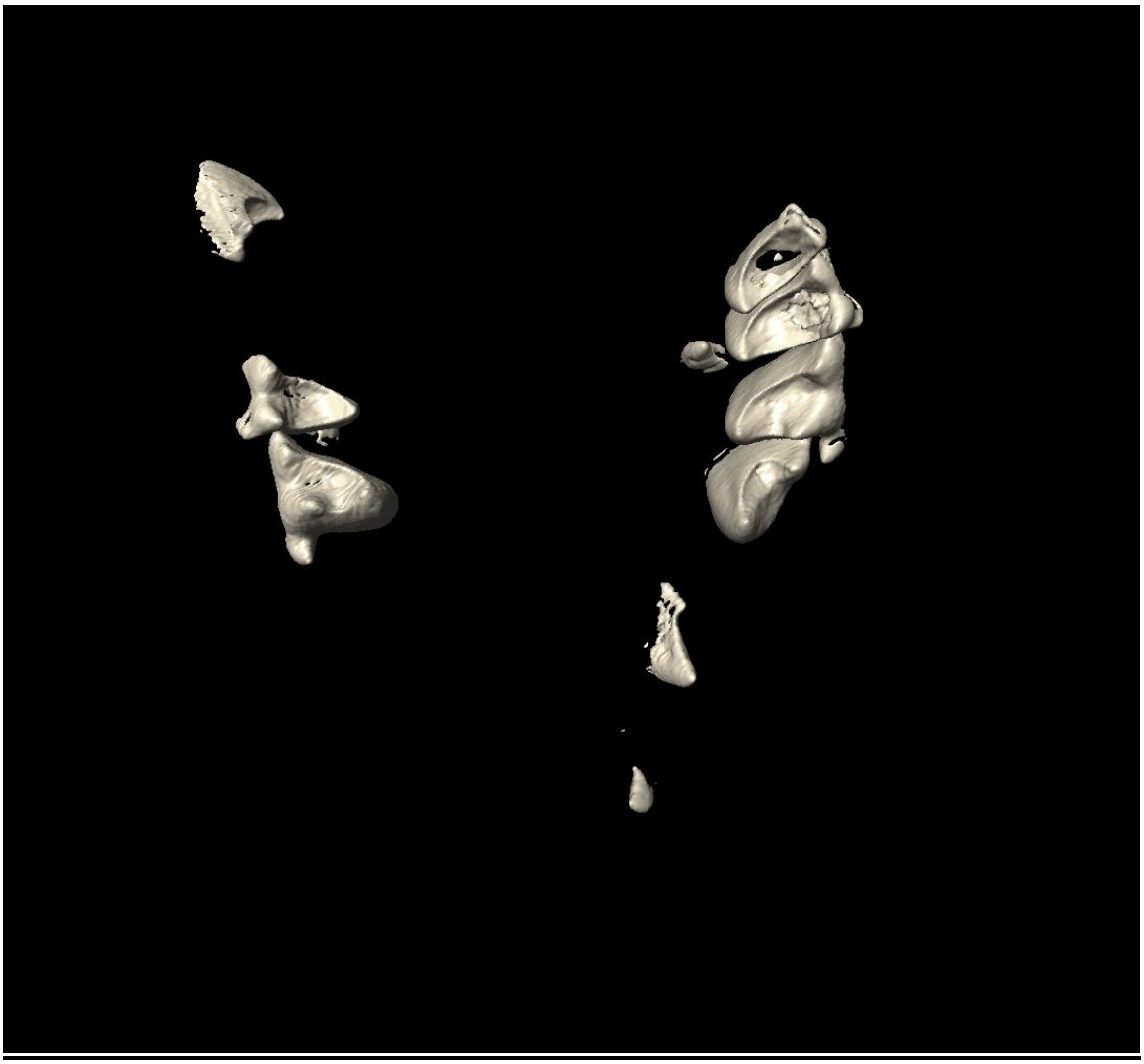

Figure 9. Occlusal View – 3D reconstruction of the present maxillary dentition for specimen MPCA-PV 482.

Lower Dentition

i1 Description

Evidence of the first lower incisors is preserved on the right-hand side as a natural mold. No remnant of the tooth itself is recognized. The mold is preserved on the mesial most extent of the concretion and copies a portion of what would have been the dorsal aspect of a large and very procumbent tooth. The impression of the tip of the tooth is not preserved, so the total length remains unknown. The impression indicates that the tooth was relatively straight and not curved. It was a robust element, several times larger than the preserved last incisor (i3), running on or very close to the midline, and parallel to the major axis of the symphysis. It is unclear how far back it extended but it does not seem to reach the distal most portion of the symphysis. There is no evidence to determine if this is a permanent or a deciduous element; however, the adult first lower incisor agrees with the general morphology present in this specimen, being procumbent and relatively large.

i3 Description

There is only one preserved lower incisor as we interpreted as a last lower incisor. Based on other specimens of *Cronopio* in the collection, we know that *Cronopio* has at least three lower incisors, rendering this the lower di3 (deciduous). The tooth is preserved as a floater directly mesial to the element we identify as a deciduous canine. Although clearly out of place, it is preserved in a more or less natural orientation with the tip of the tooth pointing dorsally and the root ventro-laterally. It is a robust element, blunt, and

semi-spatulated. The tooth has a single cusp with no mesial or distal accessory cusps. The buccal face is somewhat vertical while the lingual has a gentler slope determining a thicker lingual surface for the tooth. The mesial and distal edges of the tooth are somewhat sharp, and they were likely aligned with the major mesio-distal axis of the jaw. We are uncertain how deep the crown was, but we believe that the bulk of what is preserved is enamel representing the crown. There is thickened enamel in the postero-labial part of the tooth. Root formation is present noted by a distinct difference in the radiopacity of the enamel and root structures.

dc Description

The tooth we define as a canine has a morphology that contrasts heavily with that of the upper published canine of *Cronopio* (Rougier et al., 2011). The lower canine was not known at the time of the original publications; however, additional specimens show that as in the type the lower canines are single-rooted, sharp, very-long teeth. This is not the case with this element, and this contrast in morphology in addition to the overall stage of development of the specimen is what leads us to identify this tooth as a deciduous canine. Only the right dc is known, and it appears to have been preserved in place and represented only by its crown with no mineralization of the roots present. The canine is preserved as a single cuspid tooth with a convex mesial slope and a straighter more vertical distal slope. It is broad and flattened bucco-lingually with a blunt buccal crest descending from the tip of the cusp inferiorly which determines a thicker and shorter mesial portion of the canine and a flatter and longer distal portion of the tooth. The lingual surface of the canine is flat to slightly convex and does not appear to have a clear

delineation of the crown neck. It is a tooth much larger than the lower incisor and the anterior lower premolars. It is likely that it became a fairly large and prominent tooth, and what is preserved represents only a small portion of the crown surface. The mandibular bone in this area is either not preserved or not ossified enough to show in the CT images. The canine was located mesial to the distal end of the mandibular symphysis. It is common in mammals that the root of the canine extends distally at least to the level of the symphysis which was also likely the case in this specimen which appears to be confirmed by the loosely preserved fragments of the dentary.

Right p2 Description

The p2 is a simple tooth preserved only on the specimen's right-hand side and is missing on the left. It is a simplified shape that is present also in the two following premolars. The tooth is represented only by its crown which was not fully erupted. The main central cusp, the protoconid, is relatively blunt with a heavily convex mesial slope and a more vertical distal slope. The cross-section of the tooth approaches a "D" shape with a relatively flat lingual surface and a strongly convex labial surface. The mesial half of the tooth is thicker and more rounded while the distal portion is narrower and somewhat more blade-like. The mineralization of the crown is not complete, and the area near the presumptive neck is not yet to be mineralized. There appears to be the beginning of a distal accessory cusp in this tooth which is not fully connected with the main body of the premolar. If this is the case, the p2 follows the same overall pattern present in p3 and p4. The distal heel would be small, un-basined, and not very well developed distally. The p2 is small, the smallest of the preserved premolars, but about the same size as the deciduous

canine at this stage. In the specimen, there is no evidence of a mesial accessory cusp, but it is possible that at least a thickening was present as such a feature can be seen in the succeeding premolars that have the same general pattern.

Right p3 Description

The p3 is preserved on both sides of the specimen. Their state of mineralization seems to be similar. Neither of them has any roots developed, and these teeth sit very close to the bottom edge of the dentary. The tooth is premolariform with a main central cusp, the protoconid, that is sharp and slightly postclive. As in the preceding premolar, the mesial slope is longer, less vertical, and rounded, while the distal slope is narrow, more vertical, and sharp. These differences on the two main crests are also reflected in the nature of the crown of the premolar where the mesial half of the tooth is more robust and rounded while the distal half is narrower and approaching - even more than in the p2 - the shape of a blade is common in other premolars of *Cronopio* and the lingual face is relatively flat or slightly convex while the labial is strongly convex with a distinct labial bulging. There are two accessory cusps in the p3, a smaller mesial one and a larger and somewhat basined distal one. The mesial one is well preserved on the left-hand side but does not appear to be recognized on the right. The mechanical preparation of the specimen shows more of a slope that would be consistent with the specimen's left side. The mesial cusp is low, blunt, and in line with the main crest coming down from the protoconid. There appears to be a small, mesio-buccal cingulum, but it is not clear on the lingual side. On the distal half of the tooth, the distal crest descending from the protoconid is thickened and turned slightly lingual as it approaches the embrasure

separating the main cusp from the distal accessory cusp. This thickening does not amount to a distinct cusp, but it is in the position where a metaconid were to be expected. The thickening produces a gibbous outline to the distal crest as it veers lingually. The distal accessory cusp is distinct, sharp, and linked to a flattened surface connecting it to the main slope of the tooth. This basin is small but functionally meaningful. The rims of the basin are formed by two or three nubby thickenings of enamel along the disto-buccal edge of the basin. Roots are not preserved but the shape of the tooth suggests that two roots were likely present.

Right p4 Description

p4 is present on both jaws and in similar state of development. It is fairly immature perhaps to a larger degree than the preceding tooth where there are no roots present in either one of them. Only the beginning of the roots is shown on the specimen's left side, but there are none present on the right. The p4 is a large tooth with a tall and sharp crown which has not finished mineralizing and has no evidence of roots. As an overview, the p4 can be described as a larger version of the p3, with a central, main, dominant protoconid and small mesial and distal cusps. The dominant cusp, the protoconid, is flanked, as in the case of the p3, by two crests. A blunter and thicker mesial one and a sharper and thinner, distal. The mesial half of the tooth is thick forming a rounded face of a triangle stretching from the mesial accessory cusp to the protoconid and to the buccal mesial corner of the tooth. The distal half, as in the preceding premolar, is more bucco-lingually compressed with a relatively vertical slope face suggestive of a more sectorial (cutting) function. The mesial accessory cusp is better shown on the

specimen's left premolar. It is similar to that of the p3, extending mesially as a platform that is higher than the level of the distal accessory cusp and its talonid. Preservation does not allow for the recognition of cingula near the base of the tooth, and it is unknown if they were present. On the distal slope of the tooth, the distal crest veers medially in a somewhat sharp way reaching the distolingual corner of the main cusp, the protoconid. This is reminiscent of the morphology seen in molars, but no distinct metaconid can be recognized. This area is damaged on the left premolar and appears to be complete on the right, but only a tiny bump is present in the area where a metaconid would be expected. The distal talonid is not very well preserved in either one of the teeth, but it was at least as long as the one of the p2 with a distinct cusp and at the very least it has a very small basin surface. The left premolar shows that two roots were present and were bucco-lingually compressed and antero-posteriorly long with an embrasure located slightly mesial to the position of the protoconid.

Right p5 (dp5?) Description

The crowns of p5 are complete and in position on both jaws. Like other teeth in the specimen, they are missing fully developed roots, but cervical portions of them are present in this position. The p5s are fully moralized premolars as is common in other meridiolestidans. The morphology of this tooth does not closely match that of the adult and it is likely a deciduous element, but at present, we do not make a definitive choice about it and for simplicity we use the term p5. The tooth is much larger, longer, and wider than the preceding premolars and slightly longer than the m1, the longest of the molars. The tooth is also the tallest of the series as preserved. The p5 is composed by a

broad trigonid and a low single cuspid un-basined talonid. The trigonid is formed by a distinct protoconid, a metoconid, and a much smaller and lower paraconid. These three cusps form a triangle with a right angle at the back of the tooth with the main mesio-distal axis of the dentary and the imaginary plane connecting the metaconid and the protoconid. The protoconid is the largest of the cusps with a sharp and transverse metacristid and a much lower but longer paracristid. The labial face of the protoconid is strongly convex while the lingual face is almost flat with a small bulging along the midline of the cusp and two depressions running parallel to the paracristid and metacristid. This central bulge descending from the protoconid merges with the base of the metaconid. Thus, dividing the trigonid into a mesial portion and a distal portion. The distal portion of the trigonid is circumscribed by the protoconid, its bulge, the metaconid base, and the metacristid. In some meridiolestids, this connection is more prominent, and a well-defined basin can be recognized such as in *Quirogatherium* (Bonaparte, 1990) but this is not the case in *Cronopio*. This subdivision is just insinuated but not fully realized. The metaconid is the second most robust cusp of the trigonid but is lower and smaller than the protoconid with a broader base. The metacristid climbs the distal slope of the erect cusp of the metaconid to reach the apex of the cusp. A well-developed and deep metacristid notch is present between the protoconid and the metaconid. The notch is rounded and not very sharp, lacking any suggestion of a carnassial notch. A poorly defined ridge extends mesially along the lingual margin of the p5. This ridge loses integrity before reaching the paraconid. The paraconid is poorly expressed as a cusp being mostly a procumbent, slightly thickened lingual end of the paracristid. The mesial

portion of the trigonid comprised between the paracristid, the mesial slope of the paraconid, and the distal slope of the paraconid is broadly opened lingually.

On the mesio-lingual face of the tooth, at the cervical area, there is a single mesial cusp heel present. This anterior accessory cusp is the homolog of the "E" cusp of other mammals, no cusp "F" can be recognized. A very small cingulum appears to project distally from the cusp "E" without reaching the level of the embrasure between the paraconid and metaconid. Distally, there is a relatively large talonid. The talonid appears to have no sharp cusps and no basin. The talonid cusp is represented by a thickening of the crest marking the lingual boundary of the talonid which extends medially and ventrally to circumscribe a broad wear area on the distal face of the tooth. This slope is similar to that found in other dryolestoids. The vertical development of the talonid is extensive, and it will provide a large surface area of contact for the paracone. On the lingual surface, there is no indication of a cingulum along the distal half of the tooth.

The roots are not fully formed, but what is present suggests the presence of two roots, an anterior one that is mesio-distally elongated, and a distal one that is bucco-lingually broad and mesio-distally compressed.

General Lower Molar Description

There are three lower molars present in our *Cronopio* specimen MPCA-PV 482 and they are preserved on both sides of the lower jaw. The right lower jaw retains all of the crowns in a near-life position while the left m3 is floating posterior to m1 and m2. All of the specimens are pristine, showing no wear and incomplete root development. Roots are better mineralized in the m1 almost to the same degree on the m2 and not yet present

in the m3. None of the teeth appear to have been functional and were still enclosed in the jaw/oral soft tissue at the time of death. The occlusal surface area diminishes posteriorly as well as overall size and height. The general pattern of the molars is similar, and all three of the molars are size variations of the same motif. The lower molars have a distinct trigonid formed by the classical three-main cusps of Mammalia lower dentition – a protoconid (tall, dominant, and massive) on the buccal apex of the molar triangle. A very large and erect metaconid which approaches the size of the protoconid, and a much smaller and procumbent paraconid. A talonid is present in all of the lower molars as a small distal extension from the distal slope of the molar. All of the talonids have a single cusp and lack a basin. The trigonid basin is open lingually by a deep notch between the metaconid and the paraconid. All of the molars possess a mesio-lingual accessory cusp – Cusp E – which does not continue into a cingulum either on the lingual aspect of the tooth or the mesial slope of the trigonid. All of the molars contact each other providing a loose interlocking at the base of the teeth.

Right m1 Description

The first lower molar is the largest, tallest, and also the longest of all of the lower molars making the m1 the widest tooth of the whole dentition. The m1; however, is smaller and shorter than the last premolar, p5. The paracone is slightly recumbent with a sharp tip and a relatively narrow base. The m1 differs from the preceding premolar, p5, by its more constricted nature and sharper overall pattern. Stimming from the protoconid, there are two sharp crests - the mesially directed protocristid and the medially directed post prototcristid. These two crests form the mesial and distal boundaries of the trigonid

and are interrupted halfway by notches. The mesial one develops between the low paraconid and protoconid while the distal one develops between the protoconid and the better developed metaconid. As in the case of the last premolar, the labial face of the protoconid is very convex while the lingual is flatter but subdivided by a faint ridge descending form the apex of the cusp. This small ridge allows for the recognition of the mesial portion of the trigonid basin and a distal portion of the same. The mesial portion develops between the base of the metaconid, the paraconid, the pre protocristid, and the paracristid. The space opens lingually via the notch between the paraconid the metaconid. The second area, more distal within the trigonid, has the mesiobucally oriented slope of the metaconid as its lingual boundary and the post protocristid and the distal portion of the protoconid slope as its distinguishing features. This portion of the trigonid is higher than the more mesial one. The metaconid is much smaller than the protoconid - erect with a barely sloping distal face with a robust bulging base inside the trigonid and a rounded and blunt ridge directed mesially towards the notch between this cusp and the paraconid. The post paracrista / metacrista is nearly transverse to the major axis of the jaw. The smallest of the major cusps of the trigonid, the paraconid, is a low cusp that projects mesially beyond its face and has an almost horizontal paracristid. It is a more distinct cusp and somewhat sharper than in the p5. It continues with the mesial slope of the paraconid at the base of the crown. There is a small accessory cusp, cusp E, which is embricated with the proceeding tooth in such a way that the talonid of the preceding element is labial to this cusp. This relationship is preserved and repeated in all of the molars. Cusp E is distinct, rounded, and helps to circumscribe a light dorso-ventral embrasure on the mesial face of the trigonid that facilitates molar contact. On the distal

portion of the tooth, the talonid is present and relatively well-developed for the condition present in dryolestoids with a gutter like surface running along the distal face of the post-protocristid and metacristid. There is no distinct cusp in the talonid but only a thickening of the distal most portion of the labial edge of the structure. This “gutter-like" surface of the talonid is not basined and is served for the contact with the opposing paracone of the upper molars. No wear is visible on this surface. The talonid does not appear to continue with any kind of cingulum.

The m1 has a single root which is incompletely mineralized, but at this stage is about equal to the height of the crown itself. The root occupies the full width of the lingual face of the molar and it is roughly triangular in cross section extending labially to support the protoconid.

Right m2/m3 Description

The m2 and m3 are similar in shape to the m1, but they decrease in size distally. The protoconid is recumbent on the lower molars, and the paraconid is slightly procumbent with a sharp tip and a relatively narrow base. The right m3 is out of place and tilted mesially so that it partially overlaps the talonid of the m2, and this is an artifact. The metaconid on the m2 differs slightly from the metaconid on the m1. It is shorter and broader at its base as well as rounder on the lingual face. The paraconid on both the m1 and m2 are about the same size. The paraconid in the m3 is slightly smaller than that of the m2 while the metaconid is much shorter and tilted slightly to the distal which opens the lingual embrasure of the trigonid basin. The talonid of the m2 and m3 are of similar size than that of the m1 not showing any pronounced reduction in size. The distal crest,

marking the end of the postcingulid, is not well preserved or mineralized in the m3, but appears to have been present. There is still a faint presence of a lingual ridge on the protoconid similar to that described on the m1.

The lower molars are in a pre-eruptive arrangement. The m2 is single rooted, and the presence of this root suggests that it is close to eruption. The root of the m2 is shorter than the length of the crown. There is no evidence that the roots have started to mineralize in the m3.

Upper Dentition

General Upper Description

The upper dentition is incomplete and preserved more poorly than the lower dentition. The top and front of the snout having been lost during fossilization. There is no evidence in the specimen of the upper canine or incisors. Only on the specimen's right side we have the anterior premolar dentition preserved while the P5 is present on the right and the left sides. The posterior molars are more perturbed by the fossilization process in the upper dentition than the lower with both M3s recovered as incompletely mineralized crowns floating in the matrix far from their original position. The right M2 is mostly in place while the left M2 has fallen out of its alveolus or crypt and is floating far posteriorly from an approximate natural position. The skull as a whole is flattened, and ossification appears to be poor which given the precocious nature of the lower dentition explains the larger degree of artifactual preservation for the uppers.

Right P2 Description

The crown of the P2 is lanceolate in shape with a very sharp cusp and is very compressed bucco-lingually. The P2 shows no accessory cusps of any kind. It is easily comparable to the characterization by Rougier et al. 2011, in the original description of *Cronopio*.

Right P3 Description

The P3 is also a simple tooth with a convex labial surface and a flat to concave lingual surface dominated by a central cusp, the paracone, and showing a small distal talonid that is continuous with the relatively vertical posterior crest of the paracone. The front of the tooth is more robust and rounded while the distal portion of the tooth is compressed and sharp providing a tear-drop cross section for this element. The talonid is not basined and no distinct cusps can be recognized here. There is a large diastema between this element and the preceding P2 as well as with the P5. A feature also seen in *Cronopio* (Rougier et al. 2011). No roots are distinguishable either in the P2 or the P3, but the very lone nature of the P3 suggests that 2 roots were present in this specimen and two roots were described for both the P2 and the P3 in Rougier et al. 2011. The upper P3 is a tall sharp tooth shown in MPCA 454 to be the longest of the upper teeth.

Right P4 Description

Evidence of the P4 is present on the specimen's right and left side, but only the right one is materially present, the left is represented by its natural mold, or endocast, in the rock which has been partially recovered digitally. The premolar is in an early stage of

development and the crown itself has not been completed. There is no evidence of any kind of root formation. The element is high within the maxilla and probably only the tips of the paracone were piercing through the bone. Like in the lower elements, there is no evidence of wear in any of the upper teeth. In our specimen, the lack of the anterior accessory cusp renders the length of the actual element incomplete. The mesial cusp is the parastyle noted by Rougier et al. 2011. The P4 is a sharp, tall tooth dominated by an acute paracone which has a relatively long and recumbent mesial slope and two crests coming down distally from it. Of these two crests, the most clear and sharp crest links the paracone with the metastyle which is positioned distal and labially. This is the homolog of the postparacrista of the upper molars. There is a rounded embayment on this crest but not a distinct notch. This embayment is closer to the position of the metastyle than to the paracone. The metastyle is a relatively short but sharp cusp with a long distal slope. The metastyle is also connected to the paracone via a blunt and not very distinct crest that would be homologous with a similar rise in the labial slope of the paracone of the more posterior molars. This is the "medianer graad" or centrocrista (median ridge) of other dryolestoids. In *Cronopio*, this median ridge fails to manifest itself as a sharp crest, but it is expressed as a gentle elevation of the trigon. Between this crest and the postparacrista there is a shallow basin homolog of the distal half of the basin of the molars. The labial surface of the P4 is convex and in part would correspond to the mesial portion of the trigon basin of the molars. The overall structure of the P4 is remarkably similar to that of the molars except for the absence of the stylocone which results on a trigon that is open mesially. In either of the two P4s, there is not any evidence of the anterior accessory cusp which can be considered a serial homolog of the parastyle of P5 and the molars. The P4 is

set obliquely with regard to the main direction of the molars. This tooth will follow the general shape of the snout and palate indicated by the abrupt widening of the middle palate at the level of P5 and the narrow morphology of the snout. The distal slope of the metastyle is connected with the small and low posterior accessory cusp. A homolog of which is present in the P5 which cannot be easily recognized in the molars.

Right P5 Description

The P5 is a fully molariform tooth that is well preserved on the right and left side. It is the largest tooth of the upper post-canine series, and as is the case with the last lower premolar as it could be a deciduous element. The P5 is a triangular tooth in occlusal view. The boundaries of this triangle are formed by a large and dominant paracone, a subequal stylocone, and a much smaller metacone. To this rough triangle an anterior parastyle and a posterior accessory cusp add small buccal wings. The posterior accessory cusp is much lower than the metastyle and appears to be a cingular cusp; therefore, we do not recognize it as an accessory metastyle, a feature present in other dryolestoids. There is no lingual cingulum on any of the molariform teeth. No wear or roots are present for any of them either. As in many dryolestoids, the lingual aspect of molariform teeth is higher than the buccal portion of the tooth. The main lingual cusp is the paracone which is sharp, conical, and recumbent. Two crests extend from this cusp forming the margins of the pseudo-trigon. One is direct mesio-buccally – the preparacrista, and a second one directed distobuccally, the postparacista. The preparascrista is relatively vertical and has a deep notch separating it from the stylocone which is also sharp and prominent. The mesial face of the pseudo-trigon is vertical, tall, and sharp. The lingual face of the paracone is sharply

convex which gives the cross section of this cusp in the CT images a “D” shape. The buccal slope of the paracone is slightly convex insinuating the presence of a poorly developed median ridge which is far less clear than that in the P4, but more distinct than what can be seen in the M1 and M2. The portion of the pseudo-trigon that is mesial to the slope of this bulge of the paracone is circumscribed by the preparacrista and the distolingual slope of the stylocone which is mostly flat or slightly convex. The stylocone is pyramidal in shape with a sharp apex with a flat mesial slope and a long but relatively sharp distal slope. The stylocone is located at the buccal margin like in many Laurasia (northern continent) drlyolestoids unlike many of the meridiolestids showing what is presumed to be the ancestral condition for the South America taxa. Continuing mesially from the base of the stylocone, there is a small parastylar lobe that is much higher in position than the trigon. This parastlylar lobe has a small distinct conical parastylar cusp that is not connected with a cingulum appearing to be a self-standing structure. The parastylar lobe has a distinct shape and is characteristic of the P5 in *Cronopio*. The distal crest, the postparacrista, is less sharp than the preparacrista and runs more horizontally and dorsally that the latter. It connects with a much smaller metastyle and helps to delineate the distal edge of the pseudo-trigon and the distal slope of the trigon overall. There is no notch along its surface being by and large a continuous, smooth, curved structure. The metastyle is a small pyramidal cusp with a flat distal face that is part of the trigon distal surface, a somewhat flat mesiolingual surface that produces the narrowing of the embrasure of the pseudo-trigon and a rounded buccal face continuous with the buccal margin of the tooth. Neither the metastyle nor the stylocone develop a buccal cingulum. The metastyle is about half the height of the stylocone. The small distal accessory cusp

present at the cingulum level is blunt and found at the intersection of the buccal margin of the tooth and the distal edge of the trigon.

Right M1 Description

Both M1s are preserved in the specimen showing no evidence of wear and no roots. The M1 is a smaller and shorter tooth than the P5. Unlike the preceding premolar, it is very compressed mesiodistally so that the crest stemming from the paracone, the pre- and postparacrista, are almost parallel to each other during most of their lengths. The occlusal view of the tooth is however triangular. Its shape is dictated by the small parastyle and the distal deflection of the metastyle and the distal slope of the cusp. The paracone is a tall, sharp cusp out of which a long and relatively shallow preparacrista extends buccally. There is no notch present. The preparacrista reaches bucally with a mesially located stylocone. As in the P5, the lingual face of the paracone is convex and the buccal surface mostly flat. No clear traces of a median crest are seen. The stylocone is as tall as the paracone. It is conical slightly procumbent with a flat mesial wall and a long more gradual distal slope stretching towards the pseudo-trigon buccal embrasure. The buccal surface of the stylocone is extremely convex and continues mesially into the minute parastylar lobe which extends as a small heel overlapping buccally in the metastylar area of the P5. There is not a distinct parastylar cusp just a rounded thickening in the parastylar lobe. There is no evidence of a preparastylar cingulum. The postparacrista is similar in development to the preparacrista, but it has a deeper concavity near the base of the paracone. The postparacrista runs along the vertical edge of the distal face of the pseudo-trigon reaching the small metastyle at the buccodistal corner of the

crown. The metastyle is pyramidal with a flat distal face continuous with the distal face of the pseudo-trigon and a flat mesial lingual surface. A blunt crest descends distally from the metastyle and produces a moderate bulge near the neck of the crown. Between the stylocone and the metastyle, the buccal embrasure of the pseudo-trigon is present which in the case of the M1 is much wider and shallower than in the P5. There is no clearly recognizable distal accessory cusp in the M1.

Right M2 Description

The M2 is preserved in situ in the specimen on the right but preserved in the matrix on the left side. It is a slightly smaller tooth than the M1 further compressed mesio-distally so that the pre- and postparacrista are parallel during most of their length. The occlusal view is subtriangular with three cusps. A prominent paracone lingually and two similarly sized bucally, the stylocone and the metastyle. There is no parastylar lobe or cusp nor a distinct bulge of the distal portion of the metastyle. The tooth is shorter than the M1 and the preceding molariform teeth. The paracone is sharp and lingually convex and slightly recumbent. The pseudo-trigon is smooth forming a concave surface delineated mesially by a preparacrista and distally by a deeper postparacrista. Both crests are convex and without notches. The preparcsita at the mesiobuccal corner merge into the stylocone and the postparacrista with the metasyle on the distobuccal margin of the crown of the tooth. There is no clear embrasure opening the pseudo-trigon buccally in the M2. The crest connecting the stylocone and metastyle is low and blunt. The closure of the basin being formed by the margin of the bases of the cusps. No cingulum or cingular structure is recognized in the M2.

Right M3 Description

Both M3s are partially preserved as floaters in the matrix. They are in an immature state of development. The M3 has completed the mineralization of the paracone and its immediate surrounding area, but the labial aspects of the tooth have yet to be completed. The M3 was a tooth much smaller than the M2 with a functional paracone which was the dominant cusp of the crown. The tooth is further buccolingually compressed compared to the M2 – a general trend in the dentition.

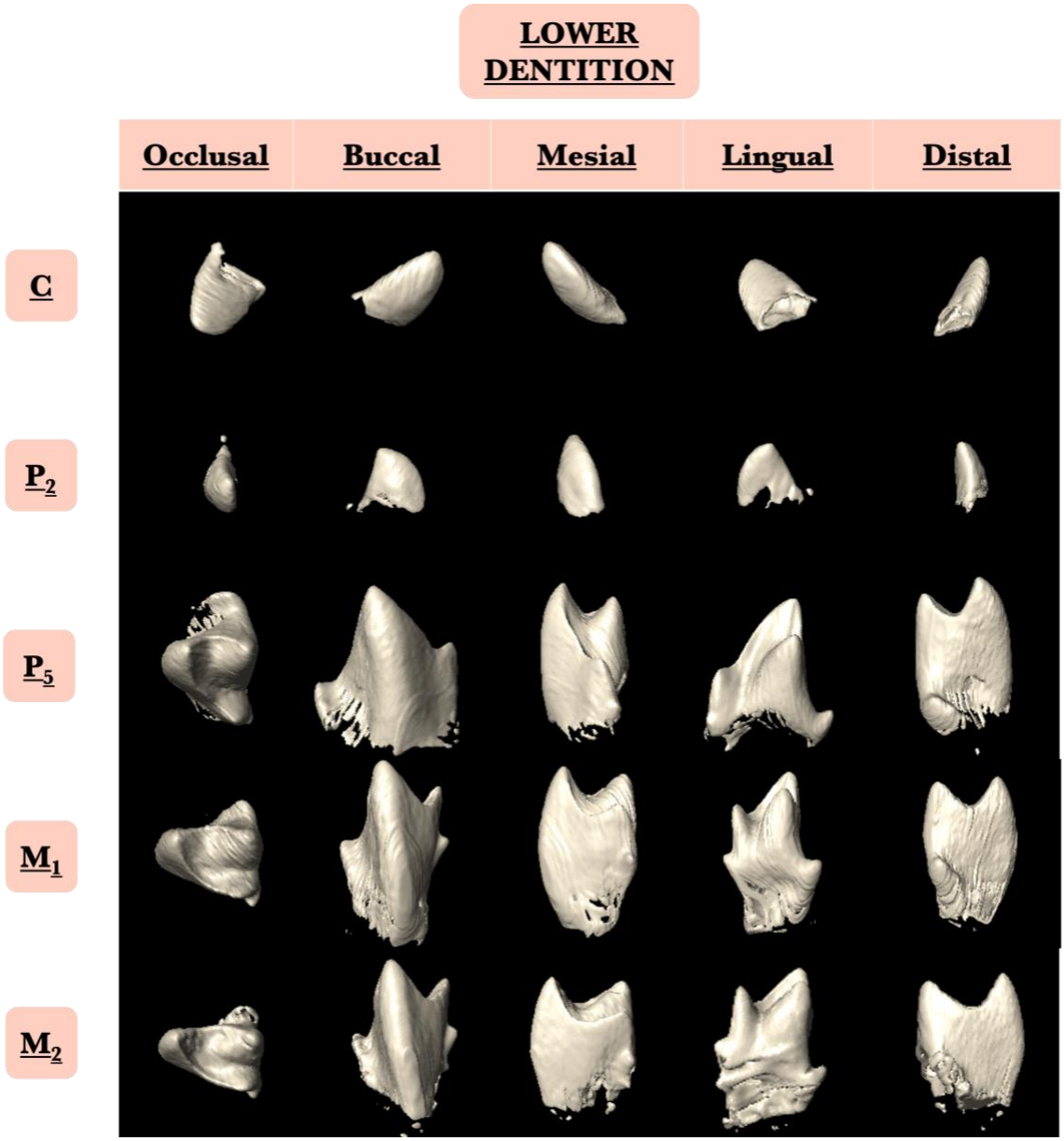

Figure 10. 3D reconstruction of the present mandibular dentition for specimen MPCA-PV 482 from all views.

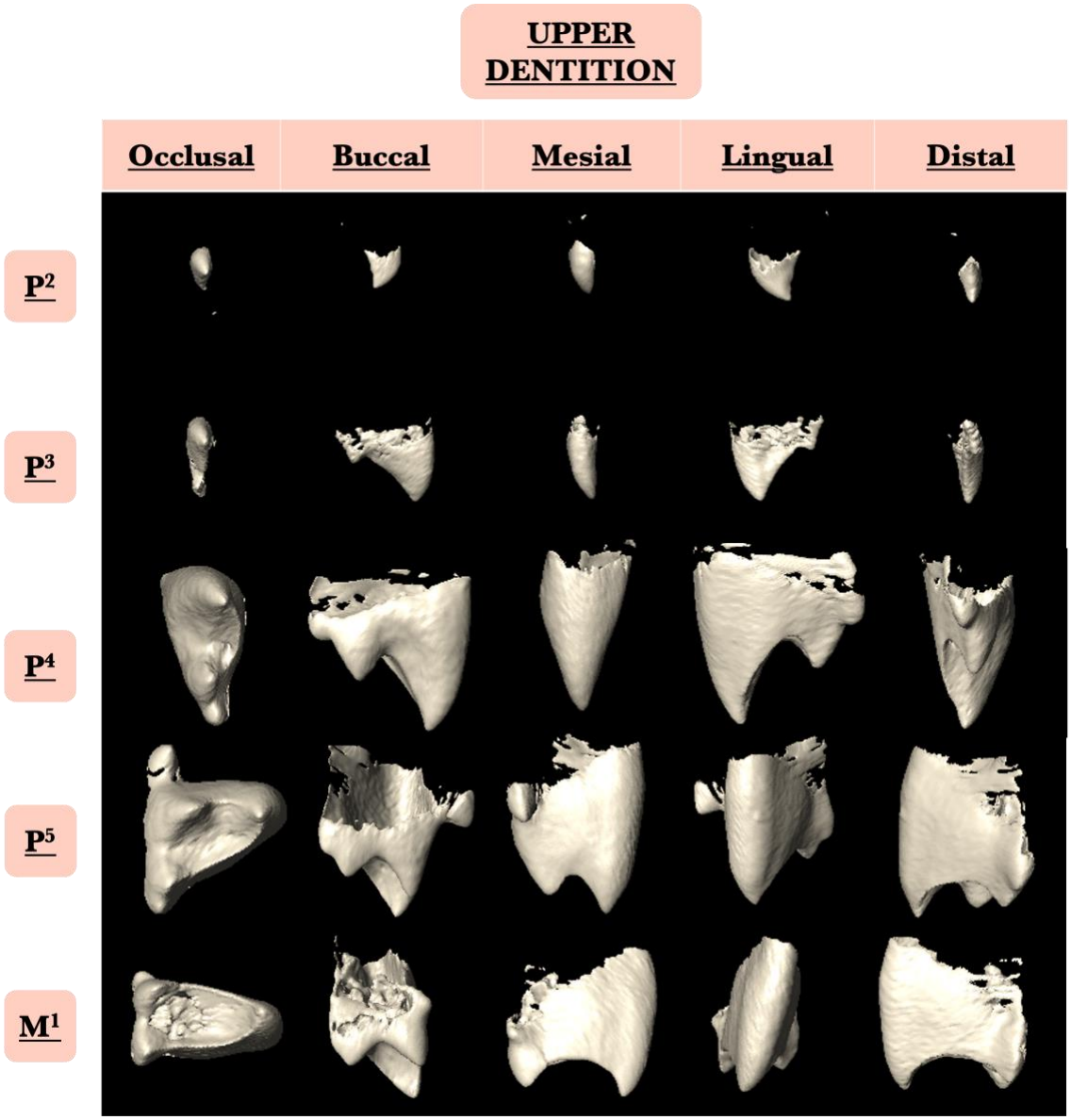

Figure 11. 3D reconstruction of the present maxillary dentition for specimen MPCA-PV 482 from all views.

DISCUSSION

The juvenile specimen is poorly ossified, but a majority of the dentition is present in place with a few floating ultimate molars indicating an immature maxilla and dental series. The dentition is pristine with no evidence of wear and most or the totality of the crowns were enclosed by alveolar bone. The lower dentition is precocial regarding the upper: the m3 appears to be close to a pre-eruptive position, while the M3s are floating in the matrix. The M3 are represented by a crown only partially mineralized and are floating as a result from being dislodged from the maxilla, they were still far from completing the coronal morphology. The last premolars and the first two molars show the beginnings of root development, which are lacking in the last molars and still-erupting deciduous anterior premolars and canine. The roots are most developed in the last premolar which based on comparisons with the adult morphology is regarded as a deciduous. Given that the last premolar and first lower molar are likely erupting and, the specimen is technically a mid-late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and likely lactating, not yet weaned. Most of the dentition, if not all of it, was still likely fully below the gum line, of with only the most prominent cusp breaking through it. This is a condition similar to the developing 27-day old *Monodelphis domestica* (Figure 12). The developmental sequence does not easily

conform to known therian patterns and it is uncertain if it is viable as a pattern primitive for mammals in general (Diaz et al., 2008; Abdala et al., 2001; Urban et al., 2017) The specimen; however, shows that altricial birth is primitive for mammals, corroborating the expected condition for ancestral mammals (Rager et al., 2014; Wernerburg et al., 2016). The lack of wear in any dental position and the relatively complete stage of mineralization of most of the crown implies a prolonged lactating stage and a relatively late onset of weaning. Direct comparison of our specimen to other mammals is difficult given that no other Mesozoic mammals of a similar developmental stage is known. The dentitions of juvenile dryolestoids described by Martin (Martin, 1996; 1999) reflect a replacement of the premolar dentition before most of the molars are functional or developed which it is at odds with the condition in *Cronopio*. Using a phylogenetic bracket (Witmer, 1995) is in part undercut by the fact that tooth development in monotremes is rudimentary and ambiguous due to the complete (echidna) or early loss (platypus) of teeth. Fossil toothed monotremes are known, but their dental development is yet to be recorded by specimens. Marsupials are altricial, born with muscular forelimbs and a differentiated head and oral cavity which is roofed by a functional secondary palate that is not osteologically complete but separated from the oral cavity via soft tissue. Early dental development in marsupials follows a pattern in which the last DP erupts followed by incisors and anterior molars, distal teeth erupt later, and canines erupt late. Marsupials are peculiar among mammals because they only replace on tooth position, DP3/P3 (Lucket, 1993 a,b; Cifelli et al., 1996;1998). Our specimen does not appear to conform to this pattern because there is not a dramatic difference between the developmental stages of the dentition in general. Certainly, the last P and first M position are precocious

regarding the rest, but they appear to be all in a similar occlusal plane, in particular – the likely less distorted p5-m1-3. *Cronopio* is not much different in size to *Monodelphis* (VanNievelt and Smith, 2005) where eruption does not start until after the 30th day. The lack of wear and similar position of the teeth suggest that the crowns described here were likely unerupted or in the process of doing so. The eruption pattern present in placentals with deciduous teeth for every non-molar locus is likely primitive for Mammalia as a whole and is strikingly different to what we observe in the *Cronopio* specimen where no developmental buds are recognized. It is possible that such buds are not conspicuous at this early stage and a "placental" pattern may become evident at a later stage, but presently we have no evidence of it. We are only certain that the last premolar is deciduous, and likely the lower canine, but uncertain at present regarding other elements of the antemolar dentition.

This will provide us with a unique model for the establishment of modern mammalian tooth formulae, eruption pattern, and dental evolution. The timing of eruption in *Cronopio* is unlike that of placentals where a similar number of molars are present, but they develop much later with regard to the eruption of the last premolar/first molar (Figure 14). The pattern does not conform with that of marsupials either were the last molar is roughly synchronic with the replacement of the deciduous last premolar; in *Cronopio* the m3 is mineralized although the dp-last is yet to erupt. Monotremes are not very helpful, but they show that development of their transitory teeth in the jaw in a manner similar to *Cronopio* and therian, and this setting up of most of the dental elements before eruption is likely a primitive condition for Mammalia. The alternate patter of replacement of the antemolar dentition documented in Holartic dryolestids (Martin, 1997;

1999, Figure 13) is possible in *Cronopio* and by extension other meridiolestids but this stage is too early and does not yet present evidence of permanent antemolars or clear developmental crypts.

Figure 12. CT reconstruction of a 27-day old Monodelphis *domestica*. This individual was obtained from the Southwest Foundation for Biomedical Research (SFBR) in San Antonio, Texas where it was used as a test animal for cancer research (Macrini, 2000) http://digimorph.org/specimens/Monodelphis_domestica/day27/index.phtml

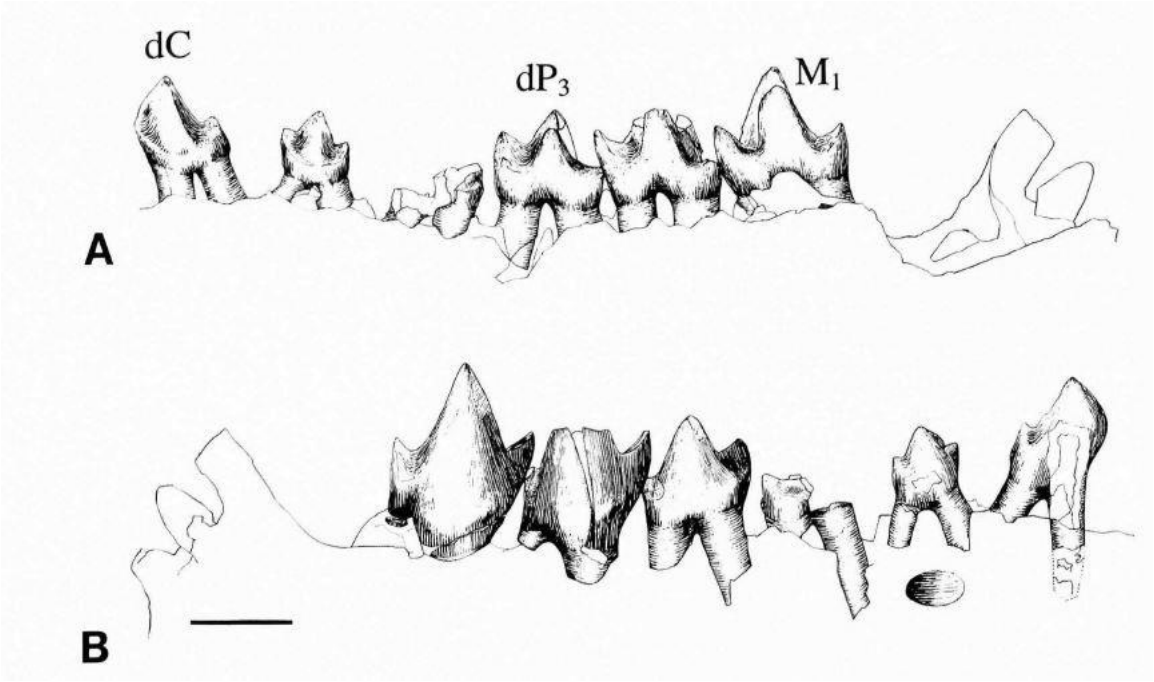

Figure 13. Juvenile lower jaw of *Dryolestes* (Martin et al., 1999).

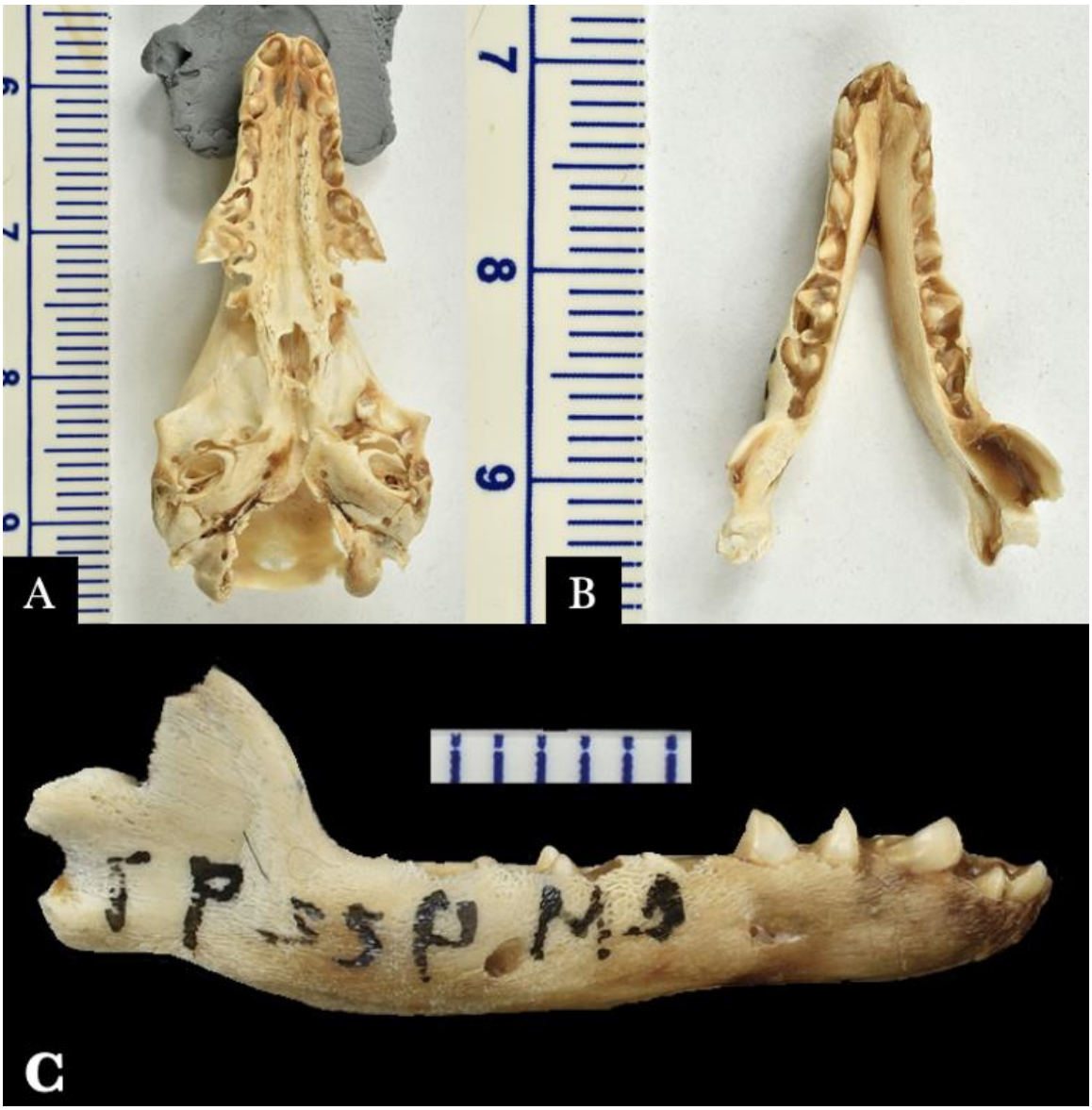

Figure 14. *Potamogale* CM 42297 (courtesy of John Wible). A) Occlusal view of the maxilla, B) Occlusal view of the mandible, C) Buccal view of the right jaw.

SUMMARY

The study of Mammalian evolution is an important to understanding the life histories and development of the living taxa we know today. The characteristics provided by more in-tact or complete specimens allows us to re-interpret published data and make more supported assumptions about this species' life history as well as evaluate the evolution of soft character and produce a reconstruction of the major biological attributes of the extinct taxa. The discovery of this juvenile *Cronopio dentiacutus* specimen MPCA-PV 482 has provided a more detailed understanding of its dental morphology – one of the main features used to interpret mammalian relationships. The juvenile stage of the specimen and its pristine condition is remarkable thus allowing us to compare life stages and development to related taxa including the sequence of tooth eruption. The eruption sequence present at this stage for *Cronopio dentiacutus* does not draw parallels to published and known sequences of other therian species thus increasing the curiosity surrounding this mammal species.

CONCLUSION

The crown morphology of *Cronopio* is now known in detail, greatly improving the anatomy of individual teeth hampered by wear and damage in the original descriptions. *Cronopio* is a sharp-toothed meridiolestid not too different from similar taxa like *Leonardus* or *Groebertherium* from the classical late Cretaceous localities (Bonaparte, 1986; 1990; 1994). The adult are remarkable by the presence of single roots in the molars, a condition shared with the Miocene meridiolestid *Necrolestes* (Wible and Rougier, 2017), roots are not developed well enough in the juvenile to determine their condition. Given that the last lower molar crown is almost fully mineralized and close to begin erupting, not too far from occlusal position, the specimen is technically a late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and not yet weaned. The teeth would not come in contact with each other, similar to the condition seen in the juvenile 29-day old opossum. The developmental sequence does not easily conform to known therian patterns and it is uncertain if it is viable as a pattern primitive for mammals in general or therians in particular.

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APPENDICES

Presentations & Talks

The Society of Vertebrate Paleontology 80th Annual Meeting Virtual 2022
Poster Presentation

TITLE:
TOOTH ERUPTION AND MORPHOLOGY IN EARLY MAMMALS: A JUVENILE DRYOLESTOID SKULL FROM THE LATE CRETAEOUS OF SOUTH AMERICA.

AUTHORS:
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ABSTRACT:
Meridiolestids are a diverse and distinct clade of Cretaceous–Miocene South American dryolestoid mammals ranging in size from small shrew-sized insectivores to relatively large dog-sized omnivores. *Cronopio dentiacutus* from the Cenomanian La Buitrera locality (Candeleros Fm., Argentina) is the best known of them, represented by skull material and associated jaws. A juvenile skull referred to *Cronopio dentiacutus*, based on tooth size and morphology, was collected from the type locality. The specimen, a small concretion, includes the skull and both articulated lower jaws. The fossil is poorly ossified and partially flattened; CT scanning reveals most of the dentition in place and a few floating teeth. Damage has occurred rostrally and no upper canines or incisors are present. Skull length is estimated at 16mm (adults are 27mm). The body of the jaw and snout are short and lack large diastemata, which characterize *Cronopio* adults. There is no clear evidence of replacement teeth in mandibular or cranial crypts, and there is no striking difference in thickness or gross appearance between the enamel of molars and that of teeth regarded as deciduous. None of the pristinely preserved teeth show any evidence of wear. The alveolar process is a paper-thin sheet of bone covering the bulk of the anterior dentition, while a broad Meckelian groove runs along the medial side of the dentary reaching the symphysis. The m3 appears to be close to occlusal position, while the M3s are floating in the matrix. The last premolars and the first two molars show the beginnings of root development, which are lacking in the last molars and still-erupting anterior premolars and canine. The anterior premolars and the sole preserved canine are deciduous. The dc is a broad labiolingually compressed crown and the dps are more complex than the permanent premolars in adult specimens. A lower incisor, further along in development, is preserved directly mesial to the dc, although it does not appear to be in

life position. Given that the last lower molar is erupting and close to occlusal position, the specimen is technically a late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and likely not fully weaned. The developmental sequence does not easily conform to known therian patterns and it is uncertain if it is viable as primitive for mammals in general.
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International Association for Dental Research 99th General Session & Exhibition Virtual 2021 – Poster Presentation

TITLE:
Dental Development and Morphology in Early Mammals

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ABSTRACT:
Mammalian tooth development and eruption is one of the most distinctive features of the group and was established early on in evolutionary history and is well-documented by fossils. We studied here a juvenile skull from the Late Cretaceous of South America (about 90 myr) identified as *Cronopio* dentiacutus, only distantly related to living marsupials and placentals. Computerized Tomography (CT) X-Ray was taken, and the data were processed with Avizo software. The specimen was manually segmented using differences in the radiopacity of rock, bone, and enamel and was then three-dimensionally rendered, with emphasis on dental and mandibular tissues. Morphology, tooth position, and eruption stage was determined for each tooth. A sequence of eruption was established by a combination of data from CT scanning and direct observation. The juvenile specimen is poorly ossified, but a majority of the dentition is present in place with a few floating ultimate molars indicating an immature maxilla and dental series. The dentition is pristine with no evidence of wear. The lower dentition is precocial regarding the upper: the m3 appears to be close to occlusal position, while the M3s are floating in the matrix. The last premolars and the first two molars show the beginnings of root development, which are lacking in the last molars and still-erupting deciduous anterior premolars and canine. Given that the last lower molar is erupting and close to occlusal position, the specimen is technically a late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and likely not fully weaned. The developmental sequence does not easily conform to known therian patterns and it is uncertain if it is viable as a pattern primitive for mammals in general.

Research!Louisville 2021 – Louisville, KY
Poster Presentation

TITLE:
COMPUTER TOMOGRAPHY (CT) EXAMINATION OF A JUVENILE DRYOLESTOID FROM THE CRETACEOUS OF SOUTH AMERICA

AUTHORS:
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ABSTRACT:
Dryolestoids, an extinct group of mammals, are closely related to the origin of modern marsupials and placentals (Theria) showing the origin of many dental features seen in most modern mammals today, including humans. We recovered a juvenile skull and jaws of the dryolestoid, *Cronopio dentiacutus*, from the early Late Cretaceous (90-95 My) bearing a mostly intact dentition. For the first time, we can describe a nearly pristine associated upper and lower dentition and get a glimpse of early tooth development and replacement in basal mammals. Tooth replacement, dental formula, and tooth morphology are central to the understanding of the evolution and feeding strategies of mammals in general. We hypothesize that (1) the specimen, represented by a skull and jaws semi- articulated, is a juvenile of *Cronopio dentiacutus* – a 90 My old member of an endemic group of mammals known as meridiolestids; (2) the completeness of the specimen and its developmental stage will provide a sequence of eruption and replacement similar to previously known dryolestids and unlike what we see in living therians; (3) we expect dryolestoid morphology and eruption pattern to be more similar to therians than to monotremes; and (4) we expect the mid- sequence complex teeth to be premolars and bear evidence of its latter replacement indicated by developing crypts, replacement developing teeth, different morphology when compared with an adult or any other evidence of eruption. A Computer Tomography (CT) Scan was taken of the juvenile specimen, encapsulated in rock, measuring 1.75 cm across. Using differences in the radiopacity of rock, enamel, and bone (via CT imaging) the dentition and associated jaw structures was digitally extracted. Avizo was used to produce a 3D reconstruction and rendering. Crown morphology, tooth formula, and eruption pattern were analyzed in a phylogenetic context. Given that the last lower molar is erupting and close to occlusal position, the specimen is technically a late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and not yet weaned. The developmental sequence does not easily conform to known therian patterns and it is uncertain if it is viable as a pattern primitive for mammals in general.

American Association for Dental, Oral, and Craniofacial Research Annual Meeting & Exhibition 2022
Atlanta, GA – Interactive Talk

TITLE:
Tooth Eruption And Development in Mesozoic Mammals From South America

AUTHORS:
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ABSTRACT:
We recovered a juvenile skull and jaws of a small dryolestoid mammal from the early Late Cretaceous (90-95 My) bearing a mostly intact dentition. We describe a nearly pristine associated upper and lower dentition highlighting early tooth development and replacement in basal mammals. We hypothesize (1) the specimen is a juvenile of *Cronopio dentiacutus* – a 90 My old endemic group of meridiolestid mammals; (2) dental development pattern and eruption sequence will be similar to eutherians (placental) mammals and likely plesiomorphic for Mammalia; (3) cladotheria dental morphology and eruption pattern will be more similar to therians than to monotremes; and (4) mid-sequence complex teeth characteristic of meridiolestids would be premolars. 3D reconstruction and rendering of the dentition was produced using a Computer Tomography (CT) Scan and Avizo software. The specimen (1.75 cm across) remains encased in rock, but additional information regarding tooth position was produced by mechanical preparation and optic photography. Differential radiopacity of rock, enamel, and bone (via CT imaging) is good regarding highly indurated tissues (dental) but not so for craniomandibular bone. The specimen is a late juvenile *Cronopio,* given that the crown of the last lower molar is close to completion, and it would be expected to erupt soon or be in the process of erupting. Although none of the molars are likely to have cut through the gum, the crowns are close to occlusal position, showing an orientation like that in the adults. Particularly, the unusual and absolute lack of wear in addition to the small size, proportions, and overall poor ossification of the jaw and skull suggest the specimen is not yet weaned. Eruption and developmental sequence is autapomorphic, differing from monotremes and therians, but sharing aspects of marsupial juvenile development that do not extend into the adult metatherian pattern.

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NATIONAL MEETING PRESENTATIONS:

1) The Society of Vertebrate Paleontology 80th Annual Meeting Virtual 2022
    a. Poster Presentation
2) International Association for Dental Research 99th General Session & Exhibition Virtual 2021
    a. Poster Presentation
3) Research!Louisville 2021 – Louisville, KY
    a. Poster Presentation
4) American Association for Dental, Oral, and Craniofacial Research Annual Meeting & Exhibition 2022 – Atlanta, GA
    a. Interactive Talk