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**A Pandemonium of Pantodonts:
The anatomy of *Pantolambda* with notes on
body size and behaviour**

by

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Abstract

Pantodonts, a group of herbivorous Paleogene mammals traditionally united by the 'double-v' cusp and crest arrangement of their upper premolars, have a long history of study with the first fossils reported in the mid-1800s. Despite the existence of nearly complete skeletons known from multiple genera, little work has been done on this group outside of description with some speculation about their paleobiology. This narrow focus of previous work arises in part because the taxonomy and systematics of the group (particularly that of the large-bodied *Coryphodon*) has historically been quite difficult to resolve. A provisional phylogenetic definition for Pantodonta is proposed here. The best way to tackle this issue is targeted redescriptions of both historical and new specimens with an eye towards constructing a phylogenetic hypothesis for the clade.

To this end, I present descriptions of new specimens of *Pantolambda*, from the San Juan Basin, New Mexico, USA. In particular, the specimens NMMNH P-27844, a juvenile of *P. bathmodon*, preserving its deciduous dentition, and NMMNH P-57738, a partial skeleton of *P. cavirostrum* preserving a nearly complete forelimb, provide an expanded understanding of the morphology of these animals. The deciduous premolars of *Pantolambda* bear some interesting similarities to the permanent dentition of the putative pantodonts, the cyriacotheriids, including the orientation of the preparacrista, the texture of the enamel, and the location of the metaconules. Additionally, a partial braincase and scapula of *P. intermedium* are described and a case is made for its validity as a species.

Body size is a foundational characteristic of living organisms that correlates with a variety of physiological, life history, and population-level features. In pantodonts, it is particularly interesting because of their rapid achievement of large body sizes after the Cretaceous-Paleogene mass extinction. A variety of existing body size proxies (stylopodial circumference, dental measurements, and occipital condyle widths) were evaluated for pantodonts. The results of this analysis evidenced that there is a disconnect between long bone and dental proxies within the pantolambdids and barylambdids, but that the discrepancy is less within the coryphodontids. This

mismatch is hypothesized to arise from the exaggerated small skull to body proportions in the former two groups.

The behaviour and community structure of *Pantolambda bathmodon* was further evaluated by examining NMMNH L-1079, a collecting pan below a pantodont bone bed. The minimum number of individuals (MNI) of the quarry on the basis of the calcanea was four. Further insight into the assemblage arose from palaeohistological sampling which increased the MNI of the pantodont individuals to six and allowed us to understand aspects of the demographics of the pantodont group. The ages of the group ranged from 2 to 5 years old with one lower molar root potentially coming from an 11 year old individual. This spread in ages and the relatively low amount of fluvial transport of the bones hints that *Pantolambda bathmodon* engaged in grouping behaviour and was likely gregarious. This sort of gregarious behaviour has been observed in other pantodonts like *Alcidedorbignya* and *Corpyhodon* and thus, occurs across the entire size range of the clade.

The palaeohistological sections used in the taphonomy study also give insight into the life history of *Pantolambda*. It gave birth live well-developed young and experienced a rapid pace of life. The short generations entailed by this pace of life can be speculated to have contributed to the rapid rise of pantodonts to large body size in the post-extinction landscape of the Paleocene.

Lay Summary

Sixty six million years ago, an asteroid struck the earth and kicked off the single worst day in prehistory. In the wake of the Cretaceous-Paleogene (K-Pg) mass extinction, dinosaurs went extinct and mammals diversified. Shortly after the extinction, mammals had ballooned in body size to reach over 100 kg – a stark contrast to their Mesozoic ancestors who never reached more than ~12 kg.

Pantodonts, an enigmatic group of Paleocene mammals, were among the first mammals to grow to large body sizes. These animals have been known for over 150 years with the first fossils being discovered off the coast of Essex, UK in the 1840s. However, the family relationships and paleoecology of these large herbivores remains understudied. The single most important priority for further work on pantodonts is to carefully revisit their anatomy with an eye to resolving their phylogeny.

To this end, some new pantodont fossils from the San Juan Basin in New Mexico, USA have been described. These fossils spanned a juvenile *Pantolambda bathmodon* still with its baby teeth, a series of teeth and fragmentary bones of *Pantolambda intermedium*, and the hand and forearm of *Pantolambda cavirictum*. All of these pieces of *Pantolambda* help us think about the taxonomy (the way that individual fossils are named and grouped) of the genus or the broader relationships of the group. For example, the baby teeth of *Pantolambda bathmodon* are similar to the adult teeth of the cyriacotheriids, a group of animals that is less definitively part of the pantodont clade. I make an argument for the relationship between these groups by looking at those anatomical similarities.

The paleobiology of pantodonts, particularly *Pantolambda*, was also investigated. The body size of these animals was explored using both the dimensions of the long bones and their teeth. It was found that some pantodont groups (pantolambdids and barylambdids) had a mismatch between estimates from those two types of measurements. That mismatch is possibly because these animals have proportionally small heads for their bodies.

The behaviour of *Pantolambda* was also investigated by looking at a series of bone fragments from a single locality. By counting the minimum number of individuals in the assemblage, a group of at least four and likely up to six pantodonts was found to have been present. The mixture of different bone types indicates the pantodont's bones didn't travel far from where they died. Therefore it is likely that they lived in social groups. This finding is interesting because small pantodonts like *Alcidedorbignya* and large pantodonts like *Coryphodon* also live in groups. Therefore, this sort of social behaviour seems to be fundamental to pantodonts as a clade.

Finally, the life history of *Pantolambda* was also explored by cutting up its bones and teeth. *Pantolambda* gestated for around seven months, was born with its eyes open, and weaned about a month after birth. It grew up fast and only lived for around two to five years. This rapid pace of life leads to short times between generations. It is possible that these short generations were one of the factors influencing pantodonts' rapid rise to large body sizes.

Declaration of Own Work

I declare that I am the sole author of this thesis. This work has not been submitted, in whole or in part, for any other degree or professional qualification. The descriptions and analysis reported here are my own work, except where work supporting a jointly-authored publication has been included. The contributions of others to this project are detailed here and indicated in the main text. I confirm that appropriate credit has been given within this thesis to the contributions of others.

The paleohistological data and analyses referenced in Chapter 3 (section title 'Taphonomy of NMMNH L-1079, San Juan Basin, New Mexico, USA') were previously published in Nature as "The origin of placental mammal life histories" by Gregory F. Funston, Paige E., dePolo, Jakub T. Sliwinski, Matthew Dumont, Sarah L. Shelley, Laetitia E. Pichevin, Nicola J. Cayzer, John R. Wible, Thomas E. Williamson, James W. B. Rae, and Stephen L. Brusatte (Appendix III). Paige dePolo is the student and author of this thesis. Stephen Brusatte (primary), Thomas Williamson (external), and Sarah Shelley supervised the thesis. The concept of the paleohistology study was developed by Gregory Funston and Stephen Brusatte. My contributions to the work were (a) providing input into study design and hypothesis testing, (b) identification of the *Pantolambda* material and support in selecting specimens from the L-1079 quarry for sectioning, and (c) contributing to drafting and editing the manuscript.

Additionally, specimen photographs taken by Tom Williamson and Greg Funston form the basis for some figures within this thesis. These photographs are used with permission of the original photographers. When the source images are not my own, credit to the photographer is given in the figure captions. Similarly, a skeletal reconstruction by Sarah Shelley is used as figure base. This reconstruction was created as a result of iterative conversations between Sarah and myself about the anatomy of the animal and is used with permission.

Paige dePolo

November 2023

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The years I have spent working on this thesis have been, to put it mildly, an adventure. I'm not sure that I'm any smarter at the end of the process, but I reckon, more importantly, I'm a fair bit wiser. A truth that resonates throughout the experience is that it takes a village to do a science. This section is going to end up longer than the average thesis acknowledgments. I regard that as a celebration of all the good humans who helped make this piece of work happen.

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~

"Besides, without leaving, she never would have met all the friends she'd made elsewhere. Perhaps the ache of homesickness was a fair price to pay for having so many good people in her life."

- Sissix, Becky Chambers, *The Long Way to a Small Angry Planet*

Land Acknowledgement

This thesis cruxes around specimens of *Pantolambda* from the San Juan Basin in northwestern New Mexico, USA. The San Juan Basin is the ancestral homeland of the Navajo (Diné), Ute, Pueblo, and Jicarilla Apache. Members of these peoples were the first humans to recognize fossils in the San Juan Basin.

These peoples live today, and I acknowledge and respect their stewardship of the land in the past, present, and future. The work of reparation does not end with a land acknowledgement and, as a scientist and scholar, I commit to intentionally incorporating the knowledge and needs of indigenous nations in my future work.

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Institutional Abbreviations

AMNH = American Museum of Natural History, New York City, New York, USA

BYU = Brigham Young University Museum of Paleontology, Provo, Utah, USA

CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

FMNH = Field Museum of Natural History, Chicago, Illinois, USA

IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

MCZ = Museum of Comparative Zoology, Harvard, Massachusetts, USA

MHNC = Muséum National d'Histoire Naturelle, Paris, France

NMMNH = New Mexico Museum of Natural History, Albuquerque, New Mexico, USA

UCMP = University of California Museum of Paleontology, Berkeley, California, USA

UM = University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA

USNM = Smithsonian Institution of Natural History, Washington DC, USA

YPM = Yale Peabody Museum, New Haven, Connecticut, USA

Common Anatomical Abbreviations

Dentition:

L = left

R = right

d = deciduous

i = lower incisor

I = upper incisor

M = lower molar;

M = upper molar

p = lower premolar

P = upper premolar

A note on spelling with this thesis:

UK spelling is used throughout with the exception of the geologic time periods

'Paleocene' and 'Paleogene' where the spelling used in North America and mainland Europe is used. This decision is made largely for consistency with the original etymology of the word (Pulvertaft, 1999).

A note on the ethos of this thesis:

My scientific practice has been strongly influenced by the experience of conducting research during the COVID-19 pandemic and the general maelstrom of the last few years. Those challenges and difficulties are reflected both in what is contained in this thesis and what is omitted. While no contemporary reader needs reminding of the world being knocked askew, I think about the decades-old theses that I've pored over during the last few years and about how future readers might lack our current shared context. So, Appendix I represents a reflective practice account written iteratively over the last few years. It's a snapshot of where I have been, where I am now, and where I envision these experiences directing my science going forward.

Geological Time Scale and North American Land Mammal Ages (NALMAs)

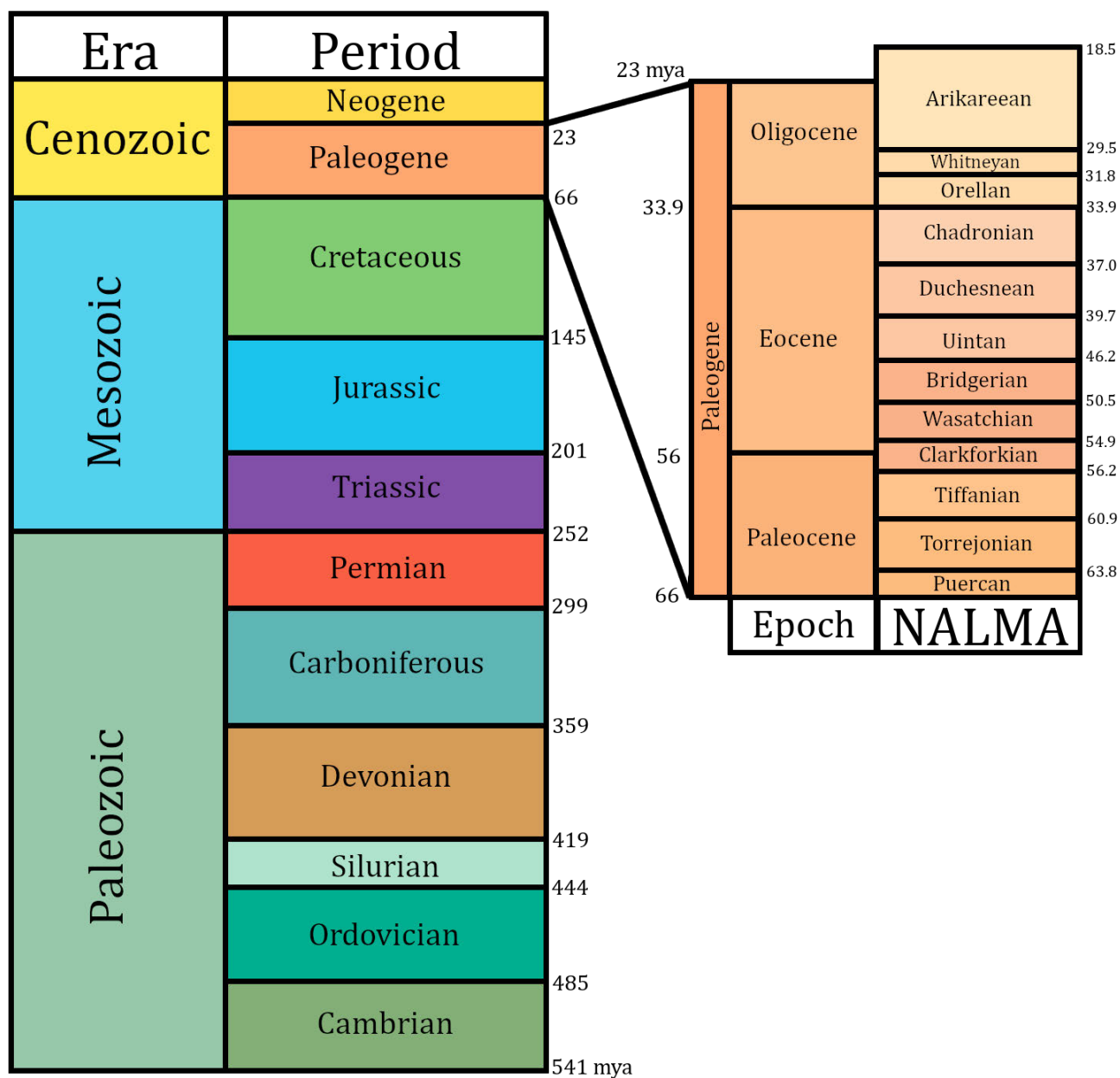


Figure i.1: A generalized time scale illustrating the geologic time periods mentioned in text. Abbreviations: mya = million years ago, NALMA = North American Land Mammal Age. Figure adapted from the BGS Geologic Time Scale (<https://www.bgs.ac.uk/discovering-geology/fossils-and-geological-time/geological-timechart/>, accessed Nov. 2023) and Barnosky et al. (2014).

Chapter 1:

Setting the Stage



Cañada Alamito, San Juan Basin, New Mexico (taken May 2018)

"...there is opened to our view a subject interesting to man who thinks; a subject on which to reason with relation to the system of nature; and one which may afford the human mind both information and entertainment."

- James Hutton, 1875, *The System of the Earth*

Mammals seem ubiquitous in the world today. They flap through the air, swim in the vastness of the ocean, climb trees, glide between branches, run at blinding speeds, hold so still that communities of algae grow in their fur, and burrow through the ground. A mammal wrote this thesis and a mammal is currently reading it. If you looked in the mirror today, you would see a mammal peering back at you.

Background (What is a Mammal?)

Mammals, warm-blooded furred animals that typically give birth to live young and nourish them with milk, are some of the most recognisable organisms in Earth's modern ecosystems. Their wide diversity of body forms and lifestyles is captured in roughly 6500 extant species (Burgin et al., 2018; American Society of Mammalogists, 2022). A constellation of anatomical features including the presence of body hair and mammary glands, three middle ear bones (the malleus, incus, and stapes), a specialised jaw joint between the dentary and squamosal, and a complex brain with the cerebrum including a six-layered neocortex characterize extant mammals (McKenna and Bell, 1997; Aboitiz et al. 2003; Aboitiz and Montiel, 2007). Additionally, extant mammals are endothermic, use a diaphragm to help with the tidal respiration of their lungs, and possess four chambered hearts (McKenna and Bell, 1997; Vaughan et al., 2015). It is the unique intersection of these features that create the 'mammal-ness' we so easily recognise in today's world.

While extant mammals are recognised from the combination of many traits, the key feature traditionally used for defining a mammal in the fossil record is the existence of a single point of articulation between the lower jaw and the skull at the dentary-squamosal joint (e.g. Kermack and Musset, 1958; Simpson, 1959a; Simpson, 1960; Kermack and Kermack, 1984). The presence of this joint, in contrast to the articular-quadrato joint of pre-mammaliaform cynodonts like *Thrinaxodon* (Parrington, 1946; Crompton, 1972) and the double articulation (paired articular-quadrato and dentary-squamosal) of *Probainognathus* (Romer, 1970; Crompton 1972) distinguishes 'true' mammals from closely-related (and ecologically very similar) mammaliaforms in the fossil record (Kielan-Jaworowska et al., 2004; Kemp, 2005). The evolution of this unique jaw joint proceeds in tandem with the development of the definitive

mammalian middle ear as the articular and quadrate become repurposed as the malleus and the incus, respectively (Hopson, 1966; Allin, 1975).

Since the anatomical features that characterise mammals evolved piecemeal along the synapsid lineage (Sidor and Hopson, 1998), difficulties in clearly classifying fossils as mammalian on the basis of anatomy arise, particularly when the relevant portions of the skull or jaw of fossil taxa are unavailable. One solution to this taxonomic challenge is the employment of a crown-group definition for Mammalia as introduced by Rowe (1988). Under this definition, Mammalia is defined as “comprising the most recent common ancestor of living Monotremata (Ornithorhynchidae and Tachyglossidae) and Theria (Marsupialia and Placentalia), and all of its descendants” (Rowe, 1988, p. 247). In this analysis, Mammalia was supported by 37 unambiguous anatomical characters including both cranial features like the absence of squamosal suspensorial notches and postcranial features like the fusion of cervical ribs to the postaxial vertebrae and the presence of a patella and corresponding groove on the femur (Rowe, 1988). Under this ancestry-based framing, fossils can then be placed within a cladistic framework to determine their placement within or outside of Mammalia. While the nuances of the taxonomic framework used to define Mammalia are critical in the study of Mesozoic mammals and important to contextualising the evolutionary history of later members of the group, the clade of Paleocene mammals on which this thesis focuses sit comfortably within the crown group. Pantodonts are mammals regardless of whether the taxonomic group is defined on the basis of anatomical features or cladistics.

Extant mammals can be divided into three groups based on their reproductive strategies: monotremes (which lay eggs), marsupials (which give birth to less developed young), and placentals (which give birth to well-developed young) (McKenna and Bell, 1997). Eutherian mammals include extant placentals and all extinct mammals that share a more recent common ancestor with placental mammals than with marsupials (metatherians) (Archibald, 2001). These different and highly specialised reproductive strategies give strong support for common ancestry within each of these broad groups that has been further corroborated by investigation of genetic sequences. The broad phylogenetic relationships of

Mammalia are well-defined. Monotremata branches off the stem of the mammal family tree first (Messer et al., 1998; van Rheede et al., 2006; Zhou et al., 2021) with Theria subsequently arising and then splitting into Metatheria and Eutheria (dos Reis et al., 2012). However, while many intraordinal relationships within Eutheria are clear, some remain stubbornly unresolved (Foley et al., 2016). In order to investigate the processes affecting mammal evolution, we first must wrestle with clarifying the patterns that it follows.

Uncertainties around Placental Mammal Phylogeny

Genetic sequences divide modern placental mammals into four main groups: Afrotheria, Xenarthra, Laurasiatheria and Euarchontoglires (Madsen et al., 2001; Murphy et al., 2001a, Murphy et al., 2001b; Springer et al., 2004). Afrotheria is composed of elephants, hyraxes, golden moles, elephant shrews, manatees, aardvarks, and related animals while Xenarthra encompasses armadillos, anteaters, sloths, and related animals (Springer et al., 1997; Stanhope et al., 1998; Murphy et al., 2001b). Laurasiatheria spans a broad swath of the mammal family tree from cetaceans and ungulates to carnivorans, shrews, moles, hedgehogs, pangolins, and bats while Euarchontoglires captures rodents, lagomorphs, primates, scandentians, and relatives (Murphy et al., 2001b).

While the extant members of these groups are clear, the broader relationships between these modern groups are unresolved in molecular phylogenies (Springer et al., 2004; Murphy et al., 2007; Nishihara et al., 2009; Meredith et al., 2011; Song et al., 2012; McCormack et al., 2012; O'Leary et al., 2013; Foley et al., 2016). The main topologies debated for these supraordinal relationships are summarised in the Exafroplacentalia, Epitheria, and Atlantogenata hypotheses (Foley et al., 2016; Murphy et al., 2021; Fig. 1) The Extrafroplacentalia hypothesis posits that Afrotheria diverged from other placental mammals first and was followed by Xenarthra (Murphy et al., 2001b; Springer et al., 2003; McCormack et al., 2012; Fig. 1a) while the Epitheria hypothesis suggests the reverse - that Xenarthra was the first branch from the placental root followed by Afrotheria (Kriegs et al., 2006; O'Leary et al., 2013; Fig. 1b). Both hypotheses suggest that the final divergence of placental supraorders occurred between Euarchontoglires and Laurasiatheria. In contrast, the

Atlantogenata hypothesis suggests a branching between the clades Euarchontoglires + Laurasiatheria and Afrotheria + Xenarthra with subsequent splits between each of these supraordinal groups (Hudelot et al., 2003; Hallström et al., 2007; Arnason et al., 2008; Morgan et al., 2013; Tarver et al., 2016; Fig. 1c). Most recently, a large-scale genomic analysis of placental relationships using whole genomes of 241 placental mammals found support for the Atlantogenata hypothesis and suggests that continental fragmentation might have played a role in the initial isolation of these lineages (Foley et al., 2023).

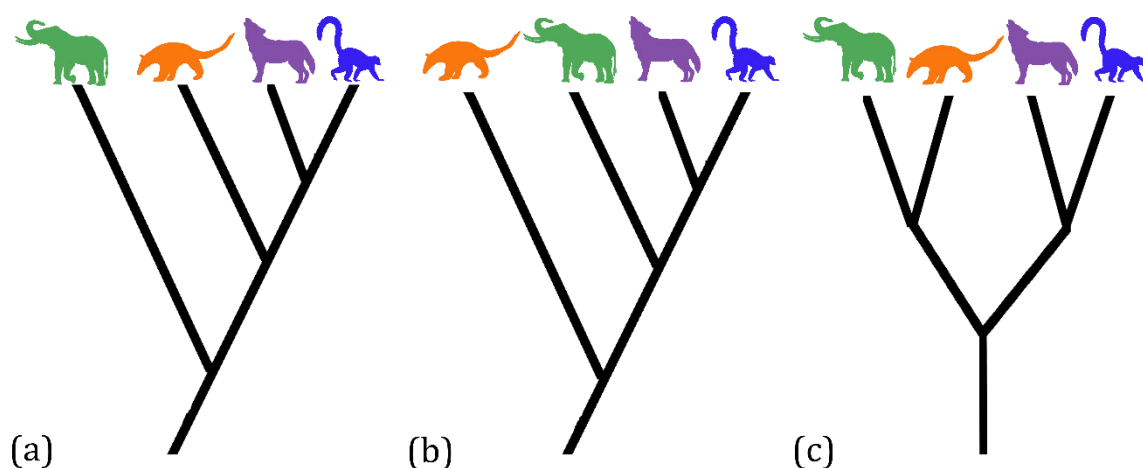


Figure 1: The three central hypotheses for the supraordinal relationships between placental mammals with (a) the Exafroplacentalia hypothesis, (b) the Epitheria hypothesis, and (c) the Atlantogenata hypothesis. Afrotheria denoted by green elephant, Xenarthra by orange anteater, Laurasiatheria by purple wolf, and Euarchontoglires by blue lemur. All silhouettes from Phylopic (www.phylopic.org) and used under a CC 1.0 license (by Chuanxin Yu (*Loxodonta africana*), Ferran Sayol (*Lemur catta*), Tracy A. Heath (*Canis lupus monstrabilis*), and Xavier A. Jenkins (*Tamandua mexicana*)). Figure concept adapted from Shelley (2017).

Understanding what these supraordinal relationships are and when these key divergences occurred is critical for testing different hypotheses about the timing and tempo of the mammalian radiation after the Cretaceous-Paleogene (K-Pg) extinction. Initially, the lines of evidence used to investigate the mammal phylogeny (fossils of extinct animals and genetic sequences of extant animals) seemed to hint at radically different stories with regard to when key radiations of mammals happened (Springer, 1997; Kumar and Hedges, 1998; Douzery et al., 2003; Bininda-Emonds et al., 2007). Although more recent work has narrowed the differences between these estimations considerably, discrepancies with regard to the timing and the tempo of the placental mammal radiation still remain (dos Reis et al., 2012; Goswami, 2012; Foley et al., 2016; Springer et al., 2019).

Three main hypotheses are at the crux of active debate in this area: the explosive hypothesis, the short fuse hypothesis, and the long fuse hypothesis (Archibald and Deutschman, 2001; Foley et al., 2016; Fig. 2a-c). The explosive hypothesis represents the classical story of the radiation where the majority of placental diversification occurred after the extinction of the dinosaurs as mammals filled the vast number of vacant ecological niches (Simpson, 1937a), but it has also been advocated for by modern studies because of the paucity of clear placental fossils from the Cretaceous (Wible et al., 2007; O’Leary et al., 2013). In contrast, molecular clock studies show an earlier point of origination for these mammals. Both the short and long fuse hypotheses suggest that the Cretaceous was when the main orders of placental mammals originated and that the major intraordinal diversifications occurred after a lag period. The short fuse model posits that intraordinal diversification of placental mammals also occurred during the Cretaceous while the long fuse model puts forward the idea that this diversification happened after the K-Pg boundary (Archibald and Deutschman, 2001; Springer et al., 2003; dos Reis et al., 2012; dos Reis et al., 2014).

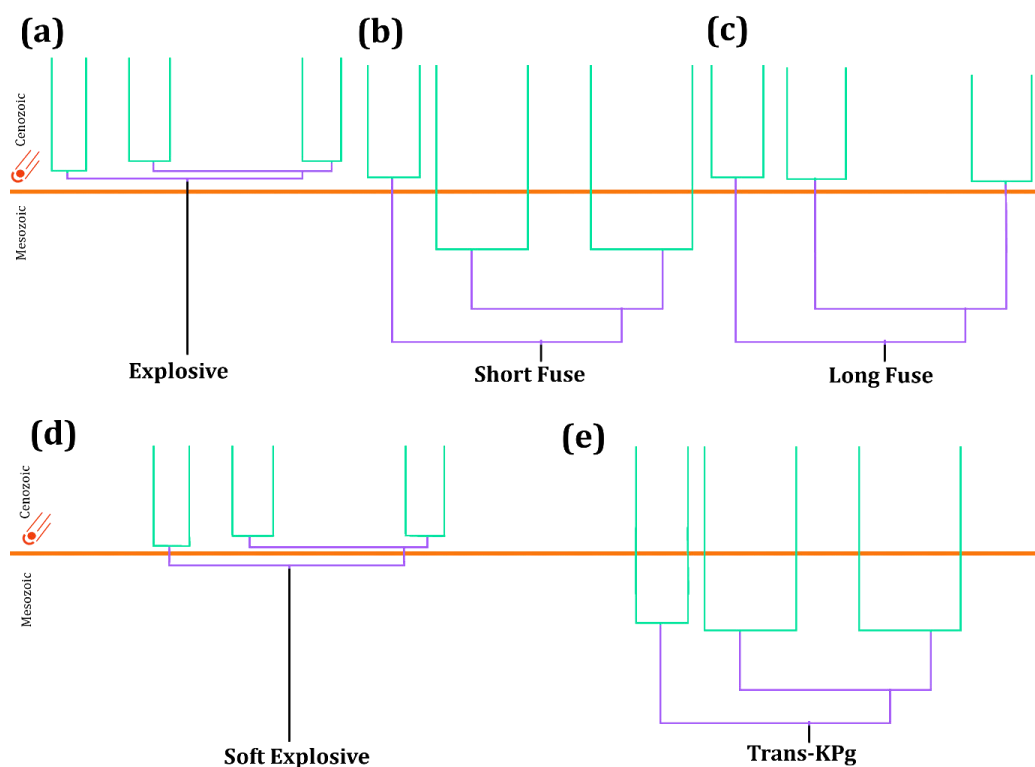


Figure 2: Simplified representation of the five hypotheses for the timing and tempo of the placental mammal radiation with (a) the explosive hypothesis, (b) the short fuse hypothesis, (c) the long fuse hypothesis, (d) the soft explosive hypothesis, and (e) the trans-KPg hypothesis. The black line represents the placental stem, the purple lines represent interordinal divergences, and the green lines represent intraordinal divergences.

Two additional hypotheses for the timing and tempo of this radiation extend and nuance the discussion. The soft explosive hypothesis suggests that supraordinal divergences (i.e. at the level of Xenarthra, Afrotheria, etc.) occurred in the Cretaceous but most interordinal and all intraordinal divergences happened in the Paleogene (Phillips, 2016; Phillips and Fruciano, 2018; Fig. 2d). Essentially, as implied by the name, the soft explosive hypothesis weakens the necessity of all key placental divergences occurring post-K-Pg extinction and represents a middle ground between strict explosive and long-fuse models. In contrast, the trans K-Pg hypothesis suggests that the K-Pg extinction did not have an influence in mammal evolution with steady rates of interordinal diversification beginning in the Cretaceous and being maintained through time (Liu et al., 2017; Fig. 2e). While it also occupies a middle ground between the explosive hypothesis and the long fuse hypothesis in terms the timing of key divergences, in essence, the trans K-Pg hypothesis represents an opposite end member to the explosive hypothesis in the emphasis placed on the extinction as a driver of placental mammal evolution. The trans-KPg hypothesis instead suggests that the evolution of angiosperms (Liu et al., 2017) played a greater role in influencing mammal diversification. Overall, the long fuse model seems to be most supported hypothesis in molecular studies but conflicts with morphological phylogenies placing Cretaceous eutherians outside of crown Placentalia (Springer et al., 2019). Indeed, a recent Bayesian analysis of phylogenomic data found the origination of crown Placentalia in the late Cretaceous with the majority of ordinal diversification in the Paleogene, a pattern consistent with the long-fuse model (Álvarez-Carretero et al., 2022).

Ultimately, these questions about the topology and the timing and tempo of the placental radiation remain open and are the ongoing focus of intensive discussions around the most thoughtful way to employ different methods (Murphy et al., 2021). We can gain further traction these persistent questions about mammal phylogeny through the careful incorporation of fossil mammals from the Paleocene in phylogenetic analyses. The strange mammals that lived during this time period are challenging to work with for several reasons including poorly constructed taxonomic groupings (wastebasket taxa) and uncertainty in how certain clades fit into the

broader mammal phylogeny. This uncertainty about the placement of Paleocene mammals is compounded because many groups do not appear to have any extant descendants (Rose, 2006). Additionally, in the case of wastebasket taxa, the groupings lump together different animals that may not have close evolutionary relationships. These groups serve to further obfuscate understanding of phylogenetic relationships because, unlike with monophyletic clades, including several representatives in a phylogenetic analysis does not give insight into the broader relationships of the whole group. Some wastebasket groupings include 'condylarths' and 'cimolestids' (McKenna and Bell, 1997; Rose, 2006). Since the interrelationships between Paleocene mammals and their relationships to modern taxa are poorly resolved, they are often excluded from broader scale phylogenetic analyses of placental mammals (Goswami, 2012).

However, this action results in an incomplete picture of the evolution of placental mammals, particularly during a pivotal time in their evolution in the post-extinction landscape. Ultimately, questions about what characteristics of certain organisms favored their survival over others or about the evolution of adaptations must be underpinned by robust phylogenetic hypotheses (Harvey and Purvis, 1991). The minimisation or exclusion of Paleocene mammals from placental mammal phylogenies weakens the resultant reconstructions of how modern mammal clades arose and interpretations about what factors influenced their diversification. A clearer understanding of Paleocene mammals will inform their placement within the mammal phylogeny and allow for more accurate reconstructions of the evolutionary radiations of placental mammals. Ultimately, these deep questions about the phylogeny of placental mammals must be informed by incorporating information from the deep and varied fossil record of this group.

Mammals in the Mesozoic

Mammals¹ possess a deep evolutionary history. The long evolutionary walk to mammals began in the Carboniferous with the divergence of synapsids from

¹ Here, the word mammals is used in a broad sense (i.e. outside of a strict crown-group definition) to encompass both mammals and mammaliaforms (all of the branches of the synapsid lineage present in the Mesozoic). This approach is taken to capture the fullest sense possible of the ecology of these animals.

sauropsids (Benton and Harper, 2009). Synapsids – animals that possess a single hole in the skull for jaw muscles – then passed through several evolutionary grades (pelycosaurs, therapsids, and cynodonts) where characteristics strongly associated with ‘mammalness’ were acquired piecemeal (Hopson, 1994). ‘True’ mammals first appeared around 220 million years ago in the late Triassic (Gill et al., 2014). In the Mesozoic, the acquisition of some core mammalian features (e.g. the definitive mammalian middle ear) likely occurred multiple times in their evolutionary history (Luo et al., 2017; Mao et al., 2021; Wang et al., 2021).

Mesozoic mammals were most likely predominantly nocturnal (Hall et al., 2012; Maor et al., 2017). However, contrary to the dated conception that these night-dwelling creatures were unspecialised insectivores, these mammals explored a variety of ecologies (Luo, 2007). This ecomorphological diversity can be seen in examining different locomotion styles employed by Mesozoic mammals. *Fruitafossor* and *Docofossor* were adapted for digging (Luo and Wible, 2005; Luo et al., 2015). The haramiyid *Arboroharamiya* and the docodont *Agilodocodon* were arboreal and took to the trees (Zheng et al., 2013; Meng et al., 2015). The scansorial eutherian *Eomaia* could negotiate uneven terrains and climb (Ji et al., 2002). *Volaticotherium*, *Maiopatagium*, and *Vilevolodon* all possessed a patagium (a furry membrane between front and hind limbs) which indicates they could glide between branches (Meng et al., 2006; Luo et al., 2017, Meng et al., 2017). *Castorocauda* and *Liaconodon* took to the water and exhibit semi-aquatic adaptations (Ji et al., 2006; Chen and Wilson, 2015). Summing these observations together, their postcranial skeletons evidence that multiple locomotor modes were employed by Mesozoic mammals which reflect a wide diversity of ways in which these animals occupy their environments (Chen and Wilson, 2015).

Similarly, a diversity of ecologies can be seen with the feeding strategies employed by Mesozoic mammals. While many Mesozoic mammals likely did engage in insectivory, some appear to have specialised between hard-bodied and soft-bodied insect prey (Gill et al., 2014). A myriad of food resources were available to other mammals. For example, *Fruitafossor* exhibits specialised teeth for eating colonial insects similar to modern armadillos (Luo and Wible, 2005). Gliders like

Maiopatagium were likely herbivorous (and specifically feeding on plant soft tissues) and the metatherian *Glasbius* was likely a frugivore (Kielan-Jaworowska et al., 2004; Meng et al., 2017). *Agilodocodon* might have gnawed bark to feed on sap while *Vintana* munched roots, nuts and seeds (Schultz et al., 2014; Meng et al., 2015). Carnivory also evolved multiple times in Mesozoic mammals. *Castorocauda*'s molars are specialised for feeding on fish (Ji et al., 2006). The large metatherian, *Didelphodon vorax*, potentially occupied a predator-scavenger niche (Wilson et al., 2016) while *Repenomamus* has been found with the bones of baby dinosaurs in its gut (Hu et al., 2005) and, possibly, frozen in the act of preying upon *Psittacosaurus* (Han et al., 2023). These diverse diets were, in part, supported by novel anatomical features. The acquisition of tribosphenic molars² helped multiple mammal lineages to explore novel ways of feeding by allowing for shearing, crushing, and grinding (Patterson, 1956; Crompton, 1971; Davis, 2011).

For nearly 140 million years, Mesozoic mammals quietly explored different ecological niches and modes of life while being overshadowed in terms of size by dinosaurs, which have also received much more attention from both palaeontologists and the public. Throughout the Mesozoic and in the final days of the Cretaceous, mammals were thriving in these small-bodied niches and exhibited much of the ecological diversity seen in modern mammals.

Effects of the Cretaceous-Paleogene (KPg) Extinction on Mammal Lineages

66 million years ago, an asteroid struck the earth at Chicxulub, Mexico and initiated the Cretaceous-Paleogene (K-Pg) mass extinction event (Alvarez et al., 1980; Schulte et al., 2010). The combination of a global heat pulse and wildfires, catastrophic tsunamis, and a dust cloud that blocked out the light of the sun for several years resulted in the collapse of food webs and the decimation of marine and terrestrial ecosystems (Pope et al., 1997; Kring, 2007; Morgan et al., 2022; Santa Catharina et al., 2022). Iconic Mesozoic fauna like non-avian dinosaurs, marine

² Tribosphenic molars show a distinctive arrangement of cusps, crests, and basins. The shearing function that arises from the occlusion of the lower molar trigonid with the crests of the corresponding upper molar is coupled with a novel grinding function arising from the development of a large, lingual cusp (protocone) on the upper molar to occlude with a heel-like talonid on the lower molar (Luo et al., 2001).

reptiles like mosasaurs, and ammonites went extinct (Bardet, 1994; Landman et al., 2014; Brusatte et al., 2015). The Age of the Mammals had dawned.

Although several lineages survived the extinction, mammals were also significantly affected by the impact event with between ~45-66% of known diversity disappearing across the K-Pg boundary (Archibald and Bryant, 1990; Sheehan and Fastovsky, 1992; Alroy, 1999) and possibly up to 90% (Longrich et al., 2016).

Metatherians were strongly affected by the K-Pg extinction event with the North America fauna being particularly hard hit and evidencing only a single taxon in the immediate aftermath of the extinction (Williamson et al., 2014). Multituberculates also experienced a loss of diversity across the K-Pg as a result of decreased diversification rates from those of the Late Cretaceous (Pires et al., 2018).

Unsurprisingly, mammalian survivorship across the K-Pg boundary appears to have been influenced by aspects of their ecology. For example, while the morphological disparity of therians increased in the late Cretaceous, the K-Pg extinction saw a selectivity among mammals with dietary specialists like those that engaged in strict carnivory or herbivory more likely to go extinct (Wilson, 2013; Grossnickle and Newham, 2016). In particular, metatherians with specialised dentitions were strongly affected while eutherian generalists survived and then radiated again in the post-extinction landscape (Grossnickle and Newham, 2016). Additionally, the broader dietary range encompassed by omnivorous to herbivorous multituberculates did not appear to be directly affected by the extinction event (Wilson et al., 2012). Similarly, the substrate preference of mammal also appears to have played a role in survivorship with nonarboreal animals preferentially surviving the extinction (Hughes et al., 2021). Dietary generalist, ground-dwelling mammals made it through what has been called the single worst day in earth history and the lean years immediately following it.

Mammals in the Paleogene

In the wake of the K-Pg extinction, mammals diversified into the post-apocalyptic world emptied of its non-avian dinosaurs and other Mesozoic fauna. Of the wide diversity of Mesozoic non-therian mammals, only multituberculates saw post-

extinction success and experienced a peak in their diversity in the middle Paleocene (Weil and Krause, 2008). The origins of the majority of the Paleocene's post-extinction fauna are much more equivocal and, as always, more fossils are needed to unpick the nuances of these relationships (Rose, 2006). Less equivocal is that a substantial amount of ecological diversity was quickly established among the Paleocene fauna. 'Condylarths' were abundant in the post-extinction fauna and, as a group, occupied a range of ecological niches from slow-moving *Peripitychus* with a dentition adapted to eating tough food (Shelley et al., 2018) to *Phenacodus* and *Ectocion* which developed "incipient cursorial adaptations" (Rose, 1990, p. 127). Plesiadapiforms like *Torrejonia* and putative early primates like *Purgatorius* (Chester et al., 2015; Chester et al., 2019) exhibit adaptations for climbing and arboreality. Taeniodonts like *Wortmania* likely were fossorial and ate roots and tubers (Coombs, 1983; Williamson and Brusatte, 2013). Tillodonts were suggested to have a similar diet and might have used their incisors to pull up these more fibrous foodstuffs (Gingerich and Gunnell, 1979). Large-bodied pantodonts occupied herbivorous browsing niches (Lucas, 1998). Mesonychians are reconstructed as cursorial predators and additionally might have engaged in ossiphagy (O'Leary and Rose, 1995; Stefen, 1997). Finally, the bizarre South America Native Ungulates (SANUs) were broadly herbivorous, but likely ranged in diet specialisation from animals that ate more coarse grass to those that ate less abrasive fruits and leaves (Croft et al., 2020).

By the Eocene, the early representatives of extant placental mammal groups are more easily discernable in the fossil record. For example, clear examples of artiodactyls, perissodactyls, and euprimates all appear at the beginning of the Eocene. Indeed, the base of the Eocene is marked biostratigraphically by the appearance of many of these groups across the Holarctic due to migration along northerly land bridges (Bowen et al., 2002; Smith et al., 2006; Bai et al., 2018). As seen in previous time periods, these mammals occupied a variety of niches including fossorial, cursorial, and arboreal ecologies. Additionally, in the Eocene, mammals bridged some final ecological frontiers that Mesozoic mammals had not breached with the evolution of powered flight in bats and the invasion of fully aquatic lifestyles

with whales (Simmons et al., 2008; Thewissen et al., 2009; Rietbergen et al., 2023). By the end of the Eocene, while many of the mammals still appeared strange and fantastical, we have clear evidence of the existence of the extant groups we see today.

Mammal Body Size Through Time

While mammals explored a variety of ecological niches through the Mesozoic, their overall body size remained small. The upper limits of mammal body size were reached in the Cretaceous with the marsupial *Didelphodon vorax* possessing a skull up to 12.2 cm long and reaching an estimated mass of 1.6-5.2 kg (Gordon, 2003; Wilson et al., 2016), the gondwanathere *Vintana sertichi* reaching an estimated mass of ~9 kg (Krause et al., 2014), and the triconodont *Repanomamus giganticus* reaching an estimated mass of 12-14 kg (Hu et al., 2005).

The maximum mammalian body size radically changed after the K-Pg extinction. Within ~500,000 years of the impact, in the Puercan, the peripitychid *Ectoconus* had achieved estimated body sizes of up to 100 kg (Shelley, 2017; Flynn et al., 2020), a nearly ten-fold increase from its Mesozoic predecessors. Shortly thereafter, in the Torrejonian, mammal body size underwent another step change with the appearance of pantodonts like *Pantolambda cavirictum* (Williamson, 1996). With lumbering *Barylambda* (Tiffanian) and *Coryphodon* (Clarkforkian), pantodonts remained the largest mammals known on earth for the remainder of the Paleocene (Simons, 1960; Smith et al., 2010).

In the Eocene, pantodonts were replaced as the largest mammals in terrestrial ecosystems by dinoceratans like uintatheres and perissodactyls like brontotheres (Lucas and Schoch, 1998a; Smith et al., 2010). Giant rhinos like *Indricotherium*, *Paraceratherium*, and *Dzungariotherium* mark the largest terrestrial mammals ever seen with estimated weights between 14-34 tonnes (Alexander, 1989; Gingerich, 1990; Li et al., 2022). Mammal body size only exceeds these limits in the aquatic realm with whales being differently affected by gravity than terrestrial animals. Despite these excursions into extreme body size, the majority of mammals that have lived in earth history remain relatively small. In the wake of the K-Pg extinction,

small mammals experienced a similar diversity increase to larger mammals (Benevento et al., 2023) and, indeed, in modern ecosystems, the modal size class of terrestrial mammals ranges below 100 g (Blackburn and Gaston, 1998).

Therefore, the achievement of large body sizes by mammals becomes a hinge point in reflecting on post-extinction evolutionary dynamics within the group. For example, interestingly, in the initial ballooning of enigmatic mammals to large body sizes in the Paleocene, their brain sizes did not keep pace (Bertrand et al., 2022).

Essentially, as these animals evolved bigger bodies, their brains did not get big at the same rate. Thus, the relative brain size of Paleocene mammals decreased in the wake of the extinction (Bertrand et al., 2022). This pattern possibly reflects niche filling in the wake of the extinction with larger relative brain sizes appearing in members of modern mammal groups as the ecosystems became more saturated (Bertrand et al., 2022). As one of the first groups of mammal to grow to truly large body sizes after the K-Pg extinction³, pantodonts represent an excellent natural laboratory for reflecting on these dynamics.

Systematic Review of Pantodonta: Piecing Together the Pantodont Puzzle

I here present a systematic review of our current state of knowledge of pantodonts, reflect on some of the challenges in studying them, and set forth priorities for future research. While previous workers have provided more targeted looks (Simons, 1960; Lucas, 1984a) and the clade has been surveyed in Cenozoic mammal reference books (Lucas, 1998; Rose, 2006), this review marks, to my knowledge, the first attempt at a comprehensive synthesis of research on the clade.

What is a pantodont?

Pantodonts are an enigmatic group of Paleocene mammals and were some of the first mammals to grow to truly large body sizes after the K-Pg extinction (Simons, 1960; Rose, 2006). These generally heavily-built, quadrupedal mammals ranged from omnivorous to herbivorous (Dawson, 2012). Pantodonts are traditionally

³ And as possessors of teeny, tiny brains. Savage and Long (1986) adapt Jerison (1973, Table 11.1) in suggesting that *Coryphodon* might have had a roughly 90 g brain in a 500 kg body.

recognised by the double-V shaped morphology of their upper premolars (Muizon and Marshall, 1992; Fig. 3a, b). Specifically, the triangular, submolariform upper premolars have two large, well-developed cusps (a centrally-located paracone and a lingual protocone). Bucally-directed anterior and posterior crests originate from each cusp (the pre- and postparacrista from the paracone and the pre- and postprotocrista from the protocone). In occlusal view, this combination of crests and cusps results in the double-V shape. This dental synapomorphy is not observed in other eutherian mammals (Lucas, 1998; Muizon *et al.*, 2015). Additionally, the upper molars of many pantodonts are characterised by distinctive, wing-like preparacristae and postmetacristae (Clemens, 2017). Pantodonts had an extensive global distribution and are found in North and South America, Europe (England, Belgium, and France), and Asia (Kazakhstan, Mongolia, and China) (Dawson, 2012; Muizon *et al.*, 2015). Pantodonts went extinct during the middle Eocene period (~49 mya) and have no extant descendants (Lucas, 1998; Rose, 2006).

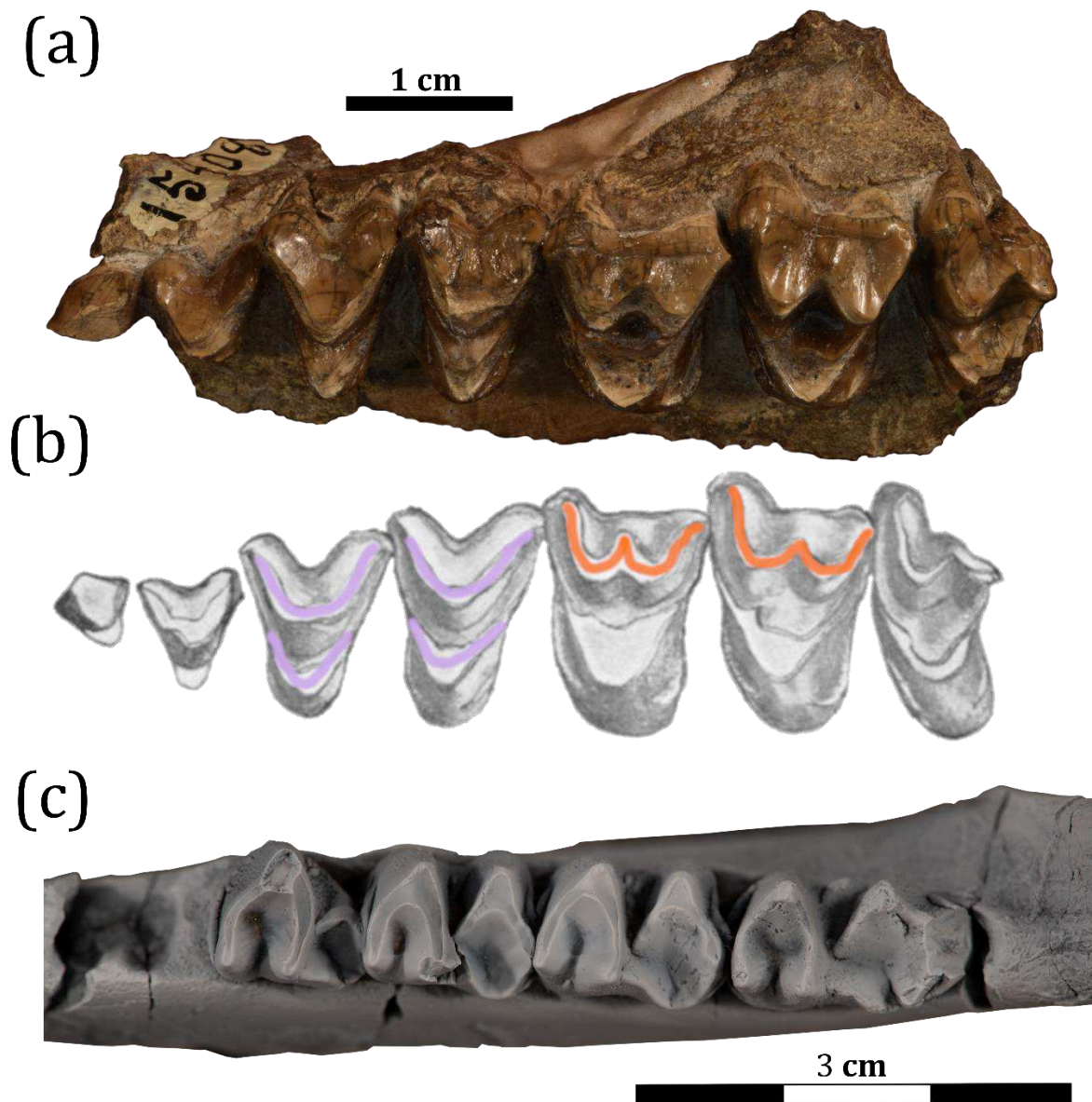


Figure 3: The key dental synapomorphy of pantodonts illustrated by the teeth of *Pantolambda bathmodon*. In (a), the upper dentition of USNM 15408 and (b) a sketch of this same dentition from Simons (1960) show the 'double-v' morphology of the upper premolars. Light purple outlines highlight the arrangement of the cusps and crests of the penultimate and ultimate premolars and orange outlines highlight the w-shaped ectoloph of the molars. In (c), the occlusal view of NMMNH P-72346, some additional features of the lower dentition are evident. The 'v' shapes created by (i) the anteroposteriorly narrow trigonids and the well-developed hypoconid on the talonid marked the inspiration for the name *Pantolambda*. Upper scale bar (1 cm) pertains to (a) and (b) and the lower scale bar (3 cm) to (c).

History of Study

Pantodonts have been studied for over 150 years with the lower molars of *Coryphodon eocaenus* marking the first fossil from the clade entered in the scientific record (Owen, 1845; Owen 1846). Interestingly, this first specimen (Fig. 4) was dredged out of the sea off the coast of Essex, England (between St. Osyth and Harwich) and referred to the London Clay due to its coloration and pyritisation (Owen, 1846). Additional early specimens of *Coryphodon* from France were

described by Blainville (1846) and Hebert (1856). The study of pantodonts can then be roughly broken into pulses of research driven by enthusiastic researchers and the recovery of key specimens.

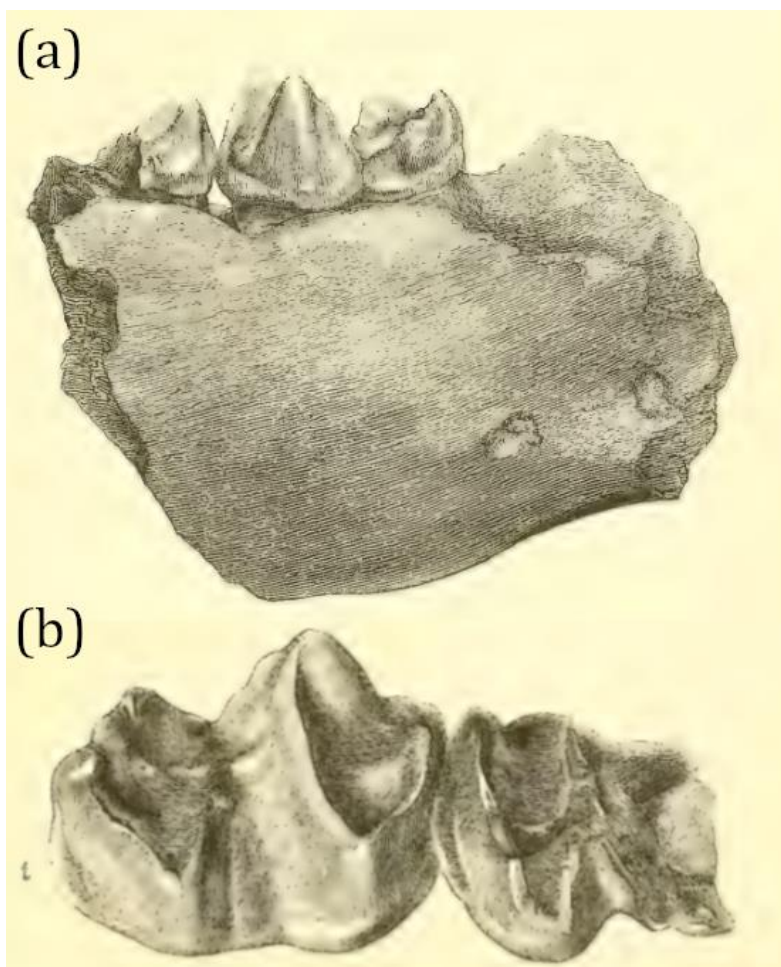


Figure 4: The type specimen of *Coryphodon eocaenus* in (a) buccal and (b) occlusal view as depicted in Owen (1846, Fig. 102, 103). This illustration emphasizes the structure of the trigonid and talonid that allowed early workers like Cope (1883c) to recognize the relationship between *Coryphodon* and *Pantolambda*.

The first flurry of research activity was driven by the work of E. D. Cope, H.F. Osborn, and others from the 1870s until the late 1890s. These studies resulted in the description of *Pantolambda* (Cope, 1882a; Cope, 1883a; Cope, 1883b; Cope, 1888; Osborn and Earle, 1895) and an expanded understanding of the anatomy of *Coryphodon* (e.g. Cope, 1872a; Cope, 1872b; Cope, 1873a; Marsh, 1876; Marsh, 1877; Cope, 1877a; Cope, 1877b; Cope, 1884a; Cope, 1889; Osborn and Wortman, 1892; Marsh, 1893; Osborn, 1898a; Osborn, 1898b). Additionally, a recognition of anatomical resonances between the different genera of pantodonts across North America and Europe began to develop with Cope (1882a; 1883c) emphasising the

similarities in the lower dentition of *Pantolambda* and *Coryphodon* even while initially hesitating to assign the genus *Pantolambda* to Pantodonta because of characteristics of the astragalus. Owen (1878) also engaged with the discoveries of *Coryphodon* in North America by reflecting on the implications of its small brain for its overall ecology.

As the Paleogene faunas of North America were further explored, the full diversity of pantodonts on the continent was more clearly realised. A hint of this diversity was seen with the report of fragmentary material of *Titanoides* from North Dakota (Gidley, 1917) which was, at that point, the largest mammal known from the Paleocene. Then, from the 1930s until the 1960s, workers like Bryan Patterson, Glenn Jepsen, and Elwyn Simons expanded our understanding of medium-large bodied pantodonts with the description of taxa like the barylambdids (Patterson, 1933; Patterson, 1934; Patterson, 1935; Patterson, 1937; Patterson, 1939a; Patterson and Simons, 1958) and further reflections on both the dentition and postcrania of *Coryphodon* (Patterson, 1939b) and *Titanoides* (Jepsen, 1930; Simpson, 1937b; Patterson, 1939a). This work culminated in the publication of the results of Simons' doctoral studies (1960) – an authoritative synopsis on Paleocene pantodonts focused on the detailed comparison of the variations in skeletal anatomy across the clade and reflections on their taxonomy.

As the discovery of new taxa in North America began to lull, the hotbed of pantodont discovery and descriptive work shifted to Asia. Starting in the 1950s, a myriad of pantodont specimens were recovered and new species described from areas like the Anhui (Huang, 1977; Qiu and Li, 1977; Huang, 1978; Chow and Wang, 1978; Wang et al., 1992; Huang and Chen, 1997; Huang and Zheng, 1997; Huang, 2003; Wang et al., 2016), Guangdong (Chow et al., 1973; Chow et al., 1977; Tong, 1982; Ting et al., 1996; Huang and Zheng, 2003), Jiangxi (Chow, 1959; Tong, 1979; Wang, 1979; Wang and Ding, 1979; Li, 2005), Sichuan (Xu, 1976), Ningxia (Ding et al., 1987), Hunan (Gao, 1975; Wang, 1975) and Shandong (Chow and Qi, 1982; Wang, 1994; Tong and Wang, 2006) provinces and the Xinjiang (Chow and Hu, 1956; Tong, 1978; Tong, 1989) region of China. Additionally, pantodonts have been recovered from Paleogene rocks of Inner Mongolia (Zhou et al., 1976; Chow and Qi,

1978; Qi, 1990; Paepen et al., 2021), Mongolia (Flerov, 1952; Kielan-Jaworowska, 1968; Flerov and Dashzeveg, 1974; Dashzeveg, 1980; Yo et al., 2023), and Kazakhstan (Gabounia, 1962; Klebanova, 1964; Gabounia, 1977). These studies vastly expanded our understanding of the radiation of endemic Asian pantodonts and mark pioneering work by scholars like Minchen Chow, Ban-yue Wang, Demberlyin Dashzeveg, Suyin Ting, Yuanqing Wang, and others.

A subsequent flurry of research activity in the 1980s and 1990s that, in part, sought to synthesise the North American, European and Asian pantodont records cruxes around doctoral work by Spencer Lucas that primarily focused on the genus *Coryphodon* (Lucas and O'Neill, 1981; Lucas, 1982; Lucas, 1984a; Lucas, 1984b; Lucas, 1984c; Lucas, 1986; Lucas and Schoch, 1987, Lucas and Tong, 1987; Lucas 1989; Lucas and Schoch, 1990). Most recently and unexpectedly, the small-bodied pantodont, *Alcidedorbignya inopinata* has been described from the Tiumpapa of Bolivia (Muizon and Marshall, 1987; Marshall and Muizon, 1988; Muizon and Marshall, 1992; Muizon et al., 2015).

These pulses of research activity have resulted in a dizzying array of animals being described from four continents encompassing an order of magnitude range in body sizes from small-bodied *Harpyodus* and *Alcidedorbignya* to bulky *Coryphodon* and *Barylambda*. A sense of the wide diversity of pantodonts can be derived by examining their current taxonomy.

Pantodont Taxonomy

Beginning in the Torrejonian (Paleocene) and extending into the Clarkforkian (Eocene), definitive pantodonts known from extensive dental and cranial material are present in the fossil record. Simons (1960) divided Paleocene pantodonts into four main taxonomic groups: Pantolambdidae (*Pantolambda*, *Caenolambda*); Barylambdidae (*Barylambda*, *Haplolambda*, *Leptolambda*, *Ignatiolambda*), Titanoideidae (*Titanoidea*), and Coryphodontidae (*Coryphodon*) (Fig. 5). The groups Harpyodidae (*Harpyodus*), Bemalambdidae (*Hypsilolambda*, *Bemalambda*), Pastoralodontidae (*Pastoralodon*, *Altilambda*), and Pantolambdodontidae (*Archaeolambda*, *Pantolambdodon*) were included by McKenna and Bell (1997) to

recognise the additional discoveries from Asia in the latter portion of the 20th century.

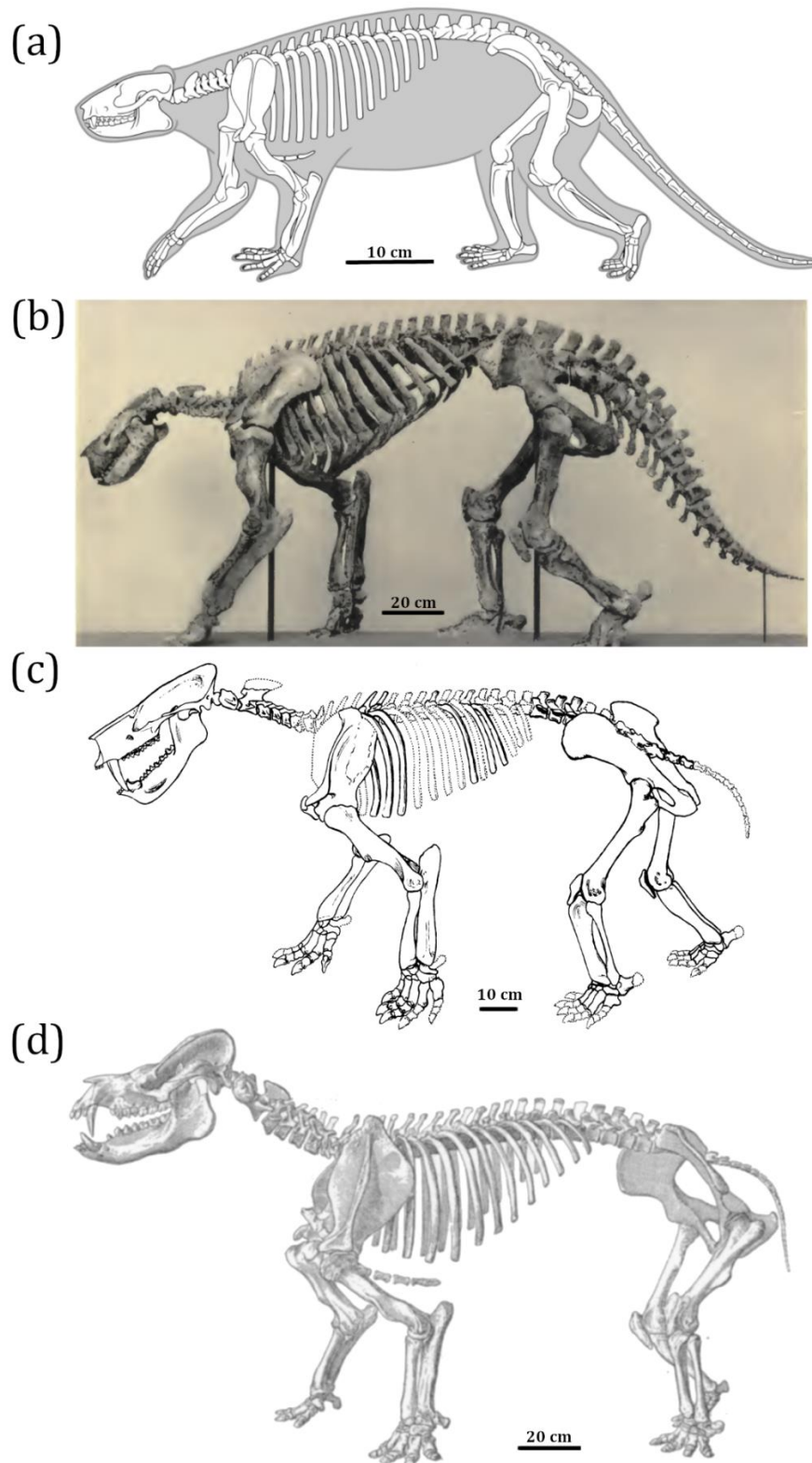


Figure 5: Representatives of the key North American pantodont groups with (a) *Pantolambda bathmodon*, (b) *Barylambda faberi*, (c) *Titanoides*, and (d) *Coryphodon*. Images are sourced from (a) reconstruction by Sarah Shelley, (b) Patterson (1939a), (c) Simons (1960), and (d) Osborn (1898a)

The family Pantolambdidae is typified by the genus *Pantolambda*. *Pantolambda* was originally recognised on the basis of fossils from the San Juan Basin in New Mexico, USA (Cope, 1882a) and is regarded as the most primitive North American pantodont genus (Simons, 1960; Muizon and Marshall, 1992; Williamson, 1996). While *Pantolambda* is known primarily from the San Juan Basin of New Mexico (Matthew, 1937; Williamson, 1996), it has also been reported from Gidley Quarry and the Crazy Mountain Field, Montana (Douglass, 1902a; Douglass, 1902b; Douglass, 1908; Simpson, 1935; Simpson, 1937c), North Dakota (Lloyd and Hares, 1915), and the Bighorn and Carbon Basins of Wyoming (Leite, 1994; Secord, 1998). The other pantolambdid genus, *Caenolambda*, was defined based on an elongated cranium with narrow nasals and a strongly developed sagittal crest (Gazin, 1956). The dentition of *Caenolambda* is strikingly similar to that of *Pantolambda* with the key difference appearing to be size and a relatively wider protocone on the upper molars resulting in a more quadrangular outline of the teeth (Gazin, 1956; Simons, 1960). In fact, an isolated tooth from Saunders Creek, Alberta that likely belongs to *Caenolambda* was originally referred to *Pantolambda* despite being larger than those of *Pantolambda cavirictum* because of the striking structural resemblance (Russell, 1948; Simons, 1960). The dentition of *Pantolambda* seen as a structural ancestor to *Coryphodon* (Cope 1883c; Simpson 1929) and it has been further suggested that *Pantolambda cavirictum* might be ancestral to *Caenolambda* (Simons, 1960). *Caenolambda* was subsequently raised as a possible ancestor to *Barylambda* and *Haplolambda* (Gingerich and Childress, 1983).

The barylambdid pantodonts are typified by *Barylambda*, the largest (~650 kg) Paleocene pantodont (Simons, 1960; Lucas, 1998). This animal was originally described as *Titanoides faberi* (Patterson 1933), but later referred to a new genus on the basis of distinct dental differences from *Titanoides primaevus* (Patterson 1937). Generally speaking these large-bodied pantodonts have small heads with a short facial region, a widely flaring pelvis, and an extremely robust tail with well-developed chevrons (Patterson 1939a; Simons, 1960). Dentally, *Barylambda* has canines with a triangular cross-section, broad, high crowned lower molars and subrectangular, subequally sized upper molars (Patterson, 1933; Patterson, 1939a;

Gingerich and Childress, 1983). Another smaller-bodied barylambdid pantodont, *Haplolambda quinni*, occurs in the same locality in which the type of *Barylambda faberi* was found and is distinctive in having small canines (Patterson 1939a). These two pantodont genera were contemporaneous and seem to have successfully co-existed.

The other barylambdid genera recognised by Simons have been regarded more skeptically by later workers. *Leptolambda schmidt* was originally distinguished from *Barylambda* on grounds of having smaller canines, more spatulate incisors, and a less robust skeleton with distinctive proportions (Patterson and Simons, 1958). The type specimen of this genus was found in Colorado's Plateau Valley (like *Barylambda* and *Haplolambda*,) and referred specimens derived from Polecat Bench in Wyoming (Patterson and Simons, 1958). Gingerich and Childress (1983) recognised variations between the type designated by Patterson and Simons (1958) and the referred specimens. The larger specimen from Plateau Valley was therefore synonymised with *Barylambda faberi* while the specimens from Polecat Bench were placed in the new species *Barylambda churchilli* on basis of the overall size of the cheek teeth (Gingerich and Childress, 1983). This focus on similarities across the dentition appears to neglect postcranial differences observed between the genera (Patterson and Simons, 1958; Lucas, 1982). *Ignatiolambda barnesi* was described based on a shattered maxilla and mandible and a crushed left manus and considered distinctive from other barylambdid pantodonts based on the pronounced protocone on the upper molars, the relatively large size of the canines, and on the size and shape of its phalanges (Simons, 1960). Gingerich and Childress (1983) similarly argued that *Ignatiolambda barnesi* was not distinctive enough to be separable from *Haplolambda quinni*, another medium-sized, late Tiffanian-aged pantodont. Barylambdid pantodonts have also been reported from Utah (Miller, 1986) and more southerly localities like Texas (Schiebout, 1974) and Punta Prieta in Baja California (Morris, 1966; Ferrusquia-Villafranca, 1984) and, while meriting more study, indicate a fairly broad geographic distribution of the group across the Paleocene basins of North America.

Titanoideidae encompasses a single genus. Although *Titanoidea* was originally thought to be allied with titanotheres on the basis of its lower dentition (Gidley, 1917), the 'v' shaped arrangement of crests around the pronounced paracone and protocone of its upper premolars support the placement of the genus within Pantodonta. However, *Titanoidea* departs from the pantolambdid and barylambdid bauplan in several striking ways. In particular, *Titanoidea* possesses sabre-like upper canines that extend past the lower edge of the dentary and antero-posteriorly elongated, bladed lower canines (Patterson, 1939a; Lucas 1998). Patterson (1939a, p. 353) was so struck by the lower canine of *Titanoidea* that he described it as an "altogether unique tooth." *Titanoidea* also has claw-like unguals on its manus in contrast to the blunted hoof-like unguals of other pantodonts (Patterson, 1939a; Coombs, 1983). *Titanoidea* is further distinguished from barylambdids on basis of the low crowns of its narrow lower molars (Gingerich and Childress, 1983).

The last of Simons' pantodont groups, Coryphodontidae, marks the acme of both geographic and temporal ranges for the clade. *Coryphodon* is the most widely distributed pantodont genus. It is the latest occurring pantodont genus in North America and is also found in the Eocene of Europe and Asia (Gervais, 1859; Chardin, 1927; Cailleux, 1945; Simons, 1960; Zhai, 1978). *Coryphodon* exhibits a wide latitudinal distribution and is found from Ellesmere Island, Canada (West and Dawson, 1977) to the southern reaches of the United States including Texas (Lucas, 1989), Alabama (Westgate, 2001), and Mississippi (Beard and Dawson, 2009). The diversity of coryphodontids is greater in Asia than on other continents. The Asian fauna includes *Hypercoryphodon*, *Asiocoryphodon*, *Heterocoryphodon* and *Eudinoceras* across the late Paleocene-Eocene of China and Mongolia (Osborn and Granger, 1931; Osborn and Granger, 1932; Xu, 1976; Lucas and Tong, 1987; Mao and Wang, 2012). During the late Paleocene and early Eocene, *Coryphodon* is one of the largest land animals known in North America (Lucas, 1998).

Asian pantodonts exhibit a similar wide diversity in forms to their North American counterparts. The first Asian pantodont described, *Archaeolambda planicanina*, was found in the Paleocene Nemegt Basin, Mongolia (Flerov, 1952). Although Simons (1960) synonymised *Archaeolambda planicanina* with *Haplolambda quinni* on basis of

its lower dentition, this synonymy was quickly challenged on the basis of different characteristics of the upper dentition and the maxilla (Kielan-Jaworowska, 1968). The later discovery of a nearly complete *Archaeolambda* specimen (Huang, 1977) supports the inference that these two genera are indeed distinct. The discovery of more complete material of *Archaeolambda* and additional dentitions of animals like *Nanlingilambda* (Tong, 1979), *Pastoralodon* (Chow and Qi, 1978), and *Altilambda* (Chow and Wang, 1978) further clarified interrelationships between endemic Asian taxa (Huang, 1995).

In particular, the taxonomic status of *Pantolambdodon* within Pantodonta was secured by these later discoveries. A pantodont affinity was tentatively proposed when the taxon was originally described on the basis of lower dentitions from Mongolia (Granger and Gregory, 1934) and later authors had noted the similarities between the lower dentition of it and *Archaeolambda* (Kielan-Jaworowska, 1968; Chow and Qi, 1978). The discovery of associated upper and lower dentitions of *Pantolambdodon* further illustrated a morphological similarity to *Archaeolambda* and supported the inference of a radiation of this group of Asian endemic pantodonts (Dashzeveg, 1980).

In both North America and Asia, a radiation of endemic pantodonts is clearly reflected in the fossil record. Indeed, Asian pantodonts appear to follow a similar trajectory to North American pantodonts with regard to the evolution of large body sizes with smaller-bodied, more gracile taxa like *Harypodus* (Qiu and Li, 1977) and *Bemalambda* (Chow *et al.*, 1973) giving way to the rhinoceros-sized, graviportal *Eudinoceras* and *Hypercoryphodon* (Osborn, 1924; Osborn and Granger, 1932; Mao and Wang, 2012). The coryphodontid *Eudinoceras* achieved a fairly extensive geographic range and is reported from Mongolia, China, and Kazakhstan (Young, 1934; Chardin and Young, 1936; Gabounia, 1977; Tong and Tang, 1977). Although later workers have begun to integrate some Asian pantodonts into more comprehensive analyses of pantodont diversity and phylogeny (Lucas, 1998; Muizon and Marshall, 1992; Scott, 2010; Muizon *et al.*, 2015), full incorporation of these animals has been stymied by the dizzying diversity of taxa named, limited images in the literature, and their sometimes dubious affinities. For example, Flerov (1957)

suggested that '*Procoryphodon*' was a pantodont but later work evidenced its synonymy with *Phenacolophus*⁴ (Simons, 1960; McKenna and Manning, 1977). In contrast to their relatively sparse occurrences in North America, pantodonts mark one of the most common mammal groups in Paleocene deposits in China (Wang et al., 2016). Targeted revision and further osteological descriptions of the Asian pantodonts, potentially building from the foundation of the doctoral work of Wang (1993), represent fruitful avenues for future research.

In the late 20th century, the geographical range of pantodonts was dramatically extended from the Holarctic (North America, Europe, and Asia) to South America with the announcement and description of *Alcidedorbignya inopinata* (Muizon and Marshall, 1987; Muizon and Marshall, 1992). This small-bodied (~580 g) pantodont is the most abundant animal found in Bolivia's Tiupampan fauna and is known from hundreds of teeth and post-cranial elements (Muizon and Marshall, 1992; Muizon et al., 2015). *Alcidedorbignya* marks the only pantodont genus to date that has been comprehensively researched with the employment of many of the tools of the modern palaeontology renaissance including phylogenetic analyses using both parsimony criteria and a molecular backbone and the employment of CT scanning to understand the internal structures of the brain and its dental ontogeny (Muizon et al., 2015; Muizon and Billet, 2022).

The following overview does not represent an exhaustive list of all taxa referred to Pantodonta. Some animals with more debated membership within the clade will be detailed further in the '*Pantodont Affinities and Phylogenetic Relationships*' section (below).

Challenges in Pantodont Systematics

While many genera of pantodonts are known from nearly complete skeletons (*Pantolambda*, *Alcidedorbignya*, *Bemalambda*, *Archaeolambda*, *Barylambda*, *Titanoides*, *Coryphodon*), little work on their biology or ecology beyond the initial anatomical descriptions has been conducted. This tendency to leave the work at

⁴ The precise affinity of *Phenacolophus* – an 'archaic ungulate' - remains unresolved. Recent work (Mao et al., 2016) suggests the phenacolophids might be a group of stem altungulates.

description can be explained by reflecting on a core challenge associated with studying these animals. While, the preceding taxonomic summary presents a neat overview of the main pantodont genera, the alpha taxonomy of this clade is a valley of tears. Lucas (1982; p. 337) describing the state of pantodont taxonomy as “currently verging on chaos” and Muizon and Marshall (1992, p. 510) echoed that opinion with the observation that “pantodont systematics is chaotic and confusing”. These issues within pantodont taxonomy can be most clearly seen by considering the thorny problem of *Coryphodon*.

As previously noted, *Coryphodon*, the first named pantodont genus, possesses the widest geographical distribution with specimens found in North America, Europe, and Asia (Owen, 1845; Dawson, 2012). It was a common component of late Paleocene and Eocene ecosystems and occupied a large, browsing ecological niche (Lucas, 1998; Rose, 2006; Hooker and Collinson, 2012). However, despite its presence in a number of well-studied Eocene faunas (e.g. Bighorn Basin, USA (Schankler, 1980; Rose et al., 2012); San Juan Basin, USA (Simpson, 1951); Ellesmere Island, Canada (West and Dawson, 1977; Dawson, 2012); Abbey Wood, UK (Forster-Cooper, 1932; Hooker, 2010); Turpan Basin, China (Zhai, 1978)), the taxonomy of these large-bodied pantodonts remains challenging. Over the last 150 years of study, a myriad of different species (Table 1) have been erected within this genus with several defunct genera also subsumed under the priority of *Coryphodon*.

Table 1: Summary of All Named 'Coryphodon' Species (updated from Lucas, 1984a)

Species	Reference
<i>Coryphodon eoacaenus</i>	Owen, 1845
<i>Lophiodon anthracoides</i>	Blainville, 1846
<i>Coryphodon oweni</i>	Hebert, 1856
<i>Bathmodon radians</i>	Cope, 1872a
<i>Bathmodon semicinctus</i>	Cope, 1872a
<i>Metalophodon armatus</i>	Cope, 1872c
<i>Bathmodon latipes</i>	Cope, 1873a
<i>Bathmodon brevipes</i>	Cope, 1873b
<i>Bathmodon simus</i>	Cope, 1874
<i>Bathmodon molestus</i>	Cope, 1874
<i>Bathmodon lomas</i>	Cope, 1874
<i>Bathmodon elephantopus</i>	Cope, 1874
<i>Bathmodon latidens</i>	Cope, 1875a
<i>Bathmodon cuspidatus</i>	Cope, 1875a
<i>Coryphodon hamatus</i>	Marsh, 1876
<i>Coryphodon obliquus</i>	Cope, 1877b
<i>Coryphodon lobatus</i>	Cope, 1877b
<i>Manteodon subquadratus</i>	Cope, 1882b
<i>Ectacodon cinctus</i>	Cope, 1882b
<i>Metalophodon testis</i>	Cope, 1882b
<i>Coryphodon anax</i>	Cope, 1882b
<i>Coryphodon repandus</i>	Cope, 1882b
<i>Coryphodon curvicristis</i>	Cope, 1882b
<i>Coryphodon marginatus</i>	Cope, 1882b
<i>Bathmodon pachypus</i>	Cope, 1883d
<i>Coryphodon croydonensis</i>	Newton, 1885
<i>Coryphodon ventanus</i>	Osborn, 1898a
<i>Coryphodon wortmani</i>	Osborn, 1898a
<i>Coryphodon singularis</i>	Osborn, 1898a
<i>Coryphodon gosseleti</i>	Malaquin, 1899
<i>Coryphodon flerowi</i>	Chow, 1957
<i>Coryphodon proterus</i>	Simons, 1960
<i>Coryphodon ninchiashanensis</i>	Chow and Tung, 1965
<i>Coryphodon tsaganensis</i>	Reshetov, 1976
<i>Coryphodon dabuensis</i>	Zhai, 1978
<i>Manteodon youngi</i>	Xu, 1980
<i>Coryphodon ryani</i>	Morgan et al., 1995
<i>Coryphodon pisuqi</i>	Dawson, 2012

The majority of species of *Coryphodon* were erected on the basis of isolated upper and lower dentitions with differences in both the upper and lower ultimate molars of particular note. The presence or absence of features like a metastyle, postprotocrista, and entoconid and the development and orientation of crests like

the hypolophid and the preparacrista-postmetacrista all have played a role in distinguishing *Coryphodon* species historically (Lucas, 1984a). Many of these identified diagnostic characters (e.g. the development of the metastyle and the presence of the entoconid) arise from variations that have been demonstrated to be labile within both individuals and populations (Earle, 1892a; Osborn, 1898a; Lucas, 1984a).

This issue of specific versus individual variation within *Coryphodon* was articulated by Earle (1892a). He attempted the first revision of the genus after examining the extensive collection of *Coryphodon* material at the AMNH and subsumed the genera *Bathmodon* and *Metalophodon* under *Coryphodon* (Earle, 1892b). Cope (1893) remained committed to the multiple genera and species he had named and rebutted Earle's critique by arguing that observational errors were made in the act of synonymising the majority of the taxa. Osborn (1898a) extended the work of Earle (1892b) by subsuming *Manteodon* and *Ectacodon* under *Coryphodon* in his revision of the genus. Despite these early efforts, Patterson (1939b, p. 97) observed that there remained "no adequate idea of what characters may safely be regarded as having specific value" when it came to *Coryphodon*. Later, other workers echoed the need for taxonomic revision of *Coryphodon* (McKenna, 1960; Simons, 1960; Delson, 1971).

Around a century after the first attempts to clarify the taxonomy of *Coryphodon*, several other workers approached the issue with different revisions of the genus proposed. Operating under a strict morphological species concept, Lucas (1984a, 1984b) surveyed the diversity of *Coryphodon* species and suggested that there were eight valid ones: *Coryphodon eocaenus*, *C. anthracoides*, *C. oweni*, *C. simus*, *C. molestus*, *C. lobatus*, *C. subquadratus*, and *C. proterus*. The validity of these species was largely based on assessing the size and characteristics of the molars. Critical diagnostic criteria for the upper molars include the orientation of the centrocrista (postparacrista-premetacrista) on the ultimate upper molar and the presence or absence of lingual cingula, postprotocristae, and metaconules. On the ultimate lower molar, the presence of an entoconid and the relative development and orientation of the hypolophid are diagnostically salient (Lucas, 1984a; Lucas, 1984b). Species of

Coryphodon originally defined on the basis of postcrania rather than dentitions were deemed *nomen vanum*⁵ because of the lack of diagnostic features in the posterior portions of the skeleton (Lucas, 1984b).

Uhen and Gingerich (1995) subsequently criticised this taxonomic approach on the basis that there were relatively few morphological characters differentiating different species and because it was decoupled from the stratigraphic context for the specimens. Focusing on the constrained geographic area of the Bighorn and Clarks Fork Basins, these authors recognised five species of *Coryphodon* (*C. proterus*, *C. eocaenus*, *C. radians*, *C. armatus*, *C. lobatus*) and the small European species, *C. oweni*, on the basis of overall body size and morphological features like the presence or absence of an entoconid and the development of bilophodonty on the ultimate lower molar. However, the emphasis on size information in these species divisions could potentially fall prey to intraspecific variation as a result of sexual dimorphism. In particular, metric information from the ultimate molars is postulated to be particularly subject to sexual dimorphism and therefore less suitable for taxonomic work (McGee, 2002). Later, another scheme for organising *Coryphodon* was introduced that focused on specimens from Europe (Hooker, 2010). In this scheme, Hooker (2010) upheld the distinctiveness *C. oweni* as a species but synonymised *C. eocaenus* and *C. anthracoides* (sensu Blainville, 1846). He also questioned the breadth of *C. eocaenus* as defined by North American workers. In toto, there remains little consensus about which species of *Coryphodon* might constitute meaningful taxonomic units and which specimens belong to individual species.

At its heart, the taxonomy of *Coryphodon* remains difficult to resolve because of both the inertia induced by the deep history of study of the genus and the abundance of material available for assessment. The lack of overlapping elements between the myriad of type specimens and the demonstrable variation of both dental and postcranial features within clear populations (Lucas, 1984a; McGee,

⁵ A *nomen vanum* ("empty name") as defined by Simpson (1945, p. 27) is a name where "the proper application of which cannot now be determined" that, in practice, "can only be either ignored or listed as indeterminate." In essence, a *nomen vanum* is a name whose validity cannot be determined with present information, but could potentially be clarified with the discovery of new material. In the case of *Coryphodon* species erected on the basis of postcrania, potential for further clarification seems low.

2002; McGee and Turnbull, 2010) mean that this problem of meaningfully separating species of this genus remains intractable.

Despite this lack of resolution, the taxonomy of *Coryphodon* is an important problem with which to wrestle because this genus has the widest geographical and temporal range of any pantodont and represents the largest amount of pantodont material available for study. If aspects of its taxonomy can be more satisfactorily resolved, *Coryphodon* represents a group of animals that holds the potential for underpinning broader palaeobiological interpretations of evolution. *Coryphodon* holds particular potential for further investigating how larger mammals might respond to rapid changes in environment (D'Emic et al., 2020). For example, *Coryphodon* appears to diminish in body size across the Paleocene-Eocene boundary which could reflect a response to global warming (Rea et al., 1990).

While the 100+ years of taxonomic problems presented by *Coryphodon* are the most striking, similar taxonomic instability can be found in examining the fine details of many other pantodont genera. The separation of the barylambdid genera is disputed (see *Pantodont Taxonomy* section). The taxonomic status of *Caenolambda* was questioned by Gingerich and Childress (1983) based on the many similarities between its upper cheek teeth and those of *Haplolambda* and *Barylambda* although no strong determination of its validity was made. *Titanoides* spans multiple species known from fragmentary dentitions (Simons, 1960) and the genus has been observed to be badly oversplit (Lucas, 1982). Additionally, many of the named Asian taxa are in need to taxonomic revision in context of the more wholistic view of the endemic pantodont radiation on that continent provided by the last half century of study. In part due to this lack of clarity around pantodont taxonomy, a comprehensive species-level phylogeny of this group evaluated using modern cladistic methods has never been constructed. Furthermore, while their affinities have been speculated at for over 150 years, the broader phylogenetic position of pantodonts within the mammal family tree remains enigmatic.

Pantodont Affinities and Phylogenetic Relationships

The first pantodont to be scientifically reported, *Coryphodon eocaenus*, was regarded as a primitive perissodactyl due to the superficial similarity between its teeth and those of a tapir (Owen, 1845). This idea of a perissodactyl affinity for *Coryphodon* persisted through the 1800s (Owen, 1846; Marsh, 1877). When *Coryphodon* material was found in North America, Cope (1872d) initially reflected that the dentition appeared to mix perissodactyl and ruminant (=artiodactyl) features. Cope subsequently constructed the suborder Pantodonta (1873a) and grouped it with Dinocerata (including uinatheres) to form the order Amblypoda (1875a). Cope then placed *Pantolambda* within Amblypoda through the creation of the suborder Taligrada (1883c) and, later, included Periptychidae within the suborder (1897). Amblypoda cruxed around the relationships between the bones of the carpus and tarsus (Cope, 1884b). The similarity between the postcrania of *Pantolambda* and *Periptychus* was further noted by Matthew (1897). The relationship with Dinocerata and separation of Pantolambdidae in Taligrada with Periptychidae and Coryphodontidae as the only family within Pantodonta was upheld in Osborn (1898a). These taxonomic groupings were challenged and subsequently abandoned by later workers (Simpson, 1929; Patterson, 1939a, Simons, 1960). As more primitive uinathere fossils were found, the similarity of dinoceratans to pantodonts was judged to be the result of convergence rather than shared ancestry (Wood, 1923; Simpson, 1929). Simpson (1945) subsequently placed pantodonts with the group Paenungulata which also included dinoceratans, pyrotheres, proboscidiens, embrithopods, and sirenians.

The spectre of pantodont affinities continued to be raised during the latter half of the 20th century. In his monographic study of Paleocene pantodonts, Simons suggested that the group had subungulate affinities and positioned *Deltatherium* as a close relative (1960). Although Matthew (1937) grouped *Deltatherium* with *Chriacus* in Arctocyoniidae [subgroup Oxyclaenidae], Simons (1960) noted that the upper molars of pantodonts are generally similar to those of *Deltatherium* and observed common features between the petrosal of it and *Titanoides*. *Deltatherium* later was included without clear justification within the suborder Pantodonta

(McKenna, 1975). *Deltatherium* has alternatively been postulated to be a arctocyoniid condylarth that “did give rise to the pantodonts” (Van Valen, 1978, reference Fig. 2; Van Valen, 1988, p.38; Fig. 6a) or a sister taxon to them (Lucas, 1998).

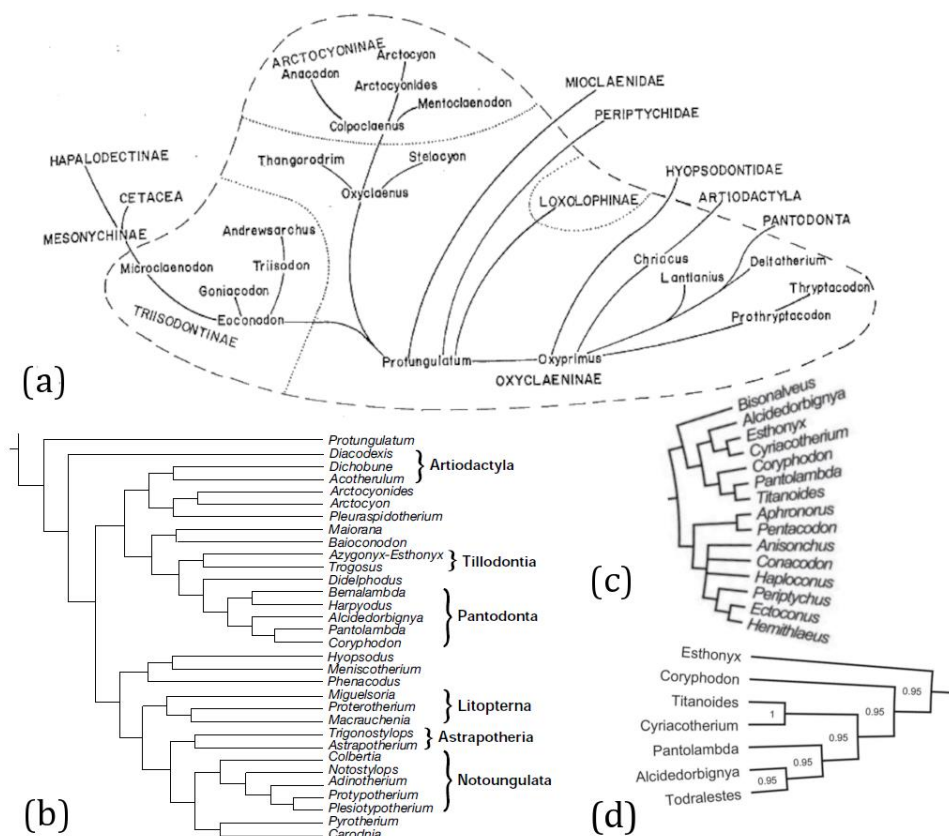


Figure 6: An illustration of some of the diversity of opinions about the relationship of pantodonts to other Paleocene mammals and their in-group relationships with (a) pantodonts hypothesized as closely related to *Deltatherium* within a broader ‘arctocyoniid’ clade (Van Valen, 1978, Fig. 2), (b) pantodonts forming a monophyletic group that has the sister taxon *Didelphodus* and is closely allied with tillodonts (Muizon et al., 2015, Fig. 122), (c) North American pantodonts as sister taxa to peripitychids (Halliday et al., 2017, Fig. 4), and (d) pantodonts are sister taxa to *Esthonyx* (a tillodont), but the inclusion of the pantolestid, *Todralestes*, within the clade breaks its monophyly (Halliday et al., 2019, Fig. 1).

Didelphodonts⁶ and tillodonts have also been examined as potential close relatives to pantodonts. A relationship of pantodonts to didelphodonts was suggested by the inclusion of both groups within the order Cimolesta (McKenna, 1975). However, this relationship was challenged based on differences within the foot structure of these two groups with pantodonts not possessing the lepticimorph structure (characterised in part by a large trochlear arc of the astragalus, the absence of an astragalar foramen, and strong reduction of the fibular facet of the calcaneum and the groove associated with the plantar calcaneocuboid ligament) of other purported cimolestids

⁶ Didelphodontia (McKenna, 1975; McKenna and Bell, 1997) encompasses the grouping of small cimolestids like *Cimolestes*, *Procerberus*, and *Didelphodus*.

(Szalay, 1977). Szalay (1977) instead supported an affinity between pantodonts and arctocyonids based on the tarsus. The idea of didelphodonts being reasonable pantodont relatives remained persistent. The first cladistic analysis of the different pantodont genera made the *a priori* decision to use *Didelphodus* as an outgroup when determining the polarity of characters within the group (Lucas, 1982). Furthermore, when the dentition of *Alcidedorbignya inopinata* was described in detail, didelphodonts were again raised as potentially the closest sister group to pantodonts despite the lack of a clear synapomorphy uniting the groups (Muizon and Marshall, 1992).

The affinity of pantodonts and tillodonts was first noted by Gazin (1953) on the basis of similarities between the cheekteeth of tillodonts and both *Deltatherium* and *Pantolambda*. These resemblances were subsequently inferred to more likely be the result of convergence with the ancestry of tillodonts suggested as more likely to be found with “arctocyonid condylarths” (Gazin, 1953). The potential relationship between pantodonts and tillodonts was then raised in discussions of Chinese pantodonts based on comparisons of the upper and lower molars of these groups (Chow *et al.*, 1977; Chow and Wang, 1979; but see Ting and Zheng, 1989 for an alternative perspective). In reflecting on the characteristics of the primitive members of both groups, Chow and Wang (1979) made Tillodontia a suborder within Pantodonta. Muizon and Marshall (1992) further argue that tillodonts and pantodonts may share common ancestry based on the shared characters of brachydont molars and semimolariform penultimate and ultimate premolars with ‘v’ shaped protocones. These workers also noted that *Deltatherium* is not a pantodont since the ectoloph of the ultimate upper premolar is straight instead of clearly ‘v’ shaped (Muizon and Marshall, 1992). Lucas (1993; 1998) and Lucas and Schoch (1998b) suggested that while tillodonts and *Deltatherium* were also not part of Pantodonta, they may be closely related since, like the early Asian pantodonts, *Harypodus*, *Pastoralodon*, and *Archaeolambda*, tillodonts also began developing dilambdodonty in their upper molars. Notably, links between *Deltatherium* and tillodonts are also suggested through absence of P1 and a molariform ultimate

premolar (Lucas, 1998). Pantodonts and tillodonts are resolved as sister groups in several recent phylogenetic analyses (Wang and Jin, 2004; Muizon *et al.*, 2015).

Ultimately, all of these hypotheses about pantodont affinities adopted a strict morphology-based definition of pantodonts that focused on the key synapomorphy of the 'double v' of the crests of their upper premolars (Simons, 1960; Lucas, 1982; Muizon and Marshall, 1992). Although pantodonts are generally regarded as a monophyletic grouping (Simons, 1960; Muizon *et al.*, 2015), their in-group relationships to one another and their position on the broader mammal family tree remain mysterious. This confusion over where pantodonts fit into the phylogeny of mammals has not been clarified by the use of larger, more comprehensive datasets with a broad taxon sampling. In fact, different phylogenetic analyses of the relationships between Paleocene mammals place pantodonts in radically divergent places on the tree from being a sister group to *Didelphodus* with the resulting pantodont-*Didelphodus* clade sister to Tillodontia (Muizon *et al.*, 2015; Fig. 6b) to being a sister taxa to Peripitychidae (Halliday *et al.*, 2017, Fig. 6c) or *Esthonyx* (Halliday *et al.*, 2019, Fig. 6d).

Recently, a study investigating the phylogenetic position of *Alcidedorbignya inopinata*, showed evidence that pantodonts were potentially laurasiatherians, and recovered pantodonts and tillodonts as closely related (Muizon *et al.*, 2015). However, this study used a limited number of pantodont genera with the Asian pantodonts represented by *Harypodus* and *Bemalambda* and the North American pantodonts by *Pantolambda* and *Coryphodon*. Another analysis focused on the relationships between Cretaceous and Paleocene eutherians and incorporated the pantodont genera *Pantolambda*, *Alcidedorbignya*, *Cyriacotherium*, *Titanoides*, and *Coryphodon* (Halliday *et al.*, 2019). However, the in-group relationships recovered from this phylogeny do not correspond with general morphological observations, with the highly derived, Late Paleocene to Eocene-aged pantodont *Coryphodon* appearing as the most basal member of the group and large-bodied *Titanoides* appearing as sister to the tiny, disputed *Cyriacotherium* (Halliday *et al.*, 2019). Furthermore, the monophyly of Pantodonta is not upheld because the pantolestid *Todralestes* appears nested deep within the clade as the sister taxon to

Alcidedorbignya (which is recovered as the most derived pantodont)(Halliday *et al.*, 2019). To date, no fully comprehensive in-group phylogeny has been constructed for Pantodonta and the relationships of this group to other contemporary mammals are unclear.

Constructing an in-group phylogeny of pantodonts marks the single most important research priority for conceiving of pantodonts as a clade rather than as individual, interesting animals. The phylogeny can then be used to investigate such questions as: (1) whether the sister group to pantodonts is comprised of tillodonts, didelphodonts, *Deltatherium*, or another group of Paleocene mammals and where they might fit into the broader mammal family tree and (2) which of the putative pantodonts might be appropriately included within the clade.

Putative Pantodonts and the Curious Case of the Cyriacotheriids

The oldest ostensibly pantodont-like tooth currently known is assigned to the species *Crustulus fontanus* and comes from late Puercan-aged (Pu 3, ~65.5 ma) Tullock Member of the Fort Union Formation, Montana, USA (Clemens, 2017). Although the isolated upper molar shows features that are typically associated with early pantodonts, namely an ectoflexus dividing the styler shelf, the tooth lacks the distinct precingulum and enlarged postcingulum observed in pantodonts like *Bemalambda*, *Harpyodus*, *Pantolambda*, and *Alcidedorbignya* (Clemens, 2017). Additionally, the shape of preparacrista and postmetacrista of the tooth are characteristic of pantodonts. This tooth was regarded as belonging to a pantodont in earlier assessments (Wilson, 2014; Muizon *et al.*, 2015), but Clemens (2017) cautions that it may belong to a pantodont or other animal located somewhere within the broader pantodont + tillodont clade hypothesised in previous literature (Chow and Wang, 1979; Lucas, 1998). The affinity of *Crustulus* has not yet been tested in a phylogenetic analysis.

One of the strangest purported pantodont groups from North America is the cyriacotheriids (*Cyriacotherium* and *Presbytherium*). These small, enigmatic creatures differ from other pantodonts in having strongly molariform penultimate and ultimate premolars and molars with pronounced dilambdodonty (Rose and

Krause, 1982; Scott, 2010). Cyriacotheriids have been found in Torrejonian to Clarkforkian-aged strata from Wyoming, USA and in Saskatchewan and Alberta, Canada (Rose and Krause, 1982; Scott, 2010). The presence of a strongly developed metacone with a W-shaped ectoloph separating it from the protocone on the upper premolars apparently contrasts with the 'v' shaped morphology that is strongly conserved within the premolars of all other pantodonts.

For this reason, the placement of cyriacotheriids within Pantodonta has been contested by several subsequent workers (Lucas, 1982; Van Valen, 1988; Lucas, 1998). Lucas (1982) claimed that the upper molar ectoloph was only superficially similar to that of pantodonts and that the animal lacked the critical 'double v' synapomorphy of the upper premolars. Thus, he excluded *Cyriacotherium* from the analysis of pantodont relationships *a priori*. Van Valen (1988) lent support to this idea by suggesting that *Cyriacotherium* was more likely a "mixodectid insectivoran" based on the 'w' shaped ectoloph of its posterior premolars (p. 37). Lucas then reiterated his thoughts on the affinity of cyriacotheriids by arguing that the characters originally used to align them with pantodonts were either primitive or present in other mammal groups, implying that they could be homoplastic, and suggested a better placement for the group could be found with the dermopterans (1998).

Cyriacotherium spp. was first incorporated into a cladistics analysis in Zack (2009). In this work, the status of *Cyriacotherium* as a pantodont was consistently supported rather than it being more closely allied with plagiomenids or mixodectids. Zack (2009) placed particular emphasis on this result because this relationship for *Cyriacotherium* (often nested within the group as a fairly derived pantodont) was supported despite superficial similarity of the upper molars between cyriacotheriids and plagiomenids (due to the strong dilambdodonty). Shortly thereafter, Scott (2010) reported *Presbyterium*, a new genus of cyriacotheriid from the early Paleocene (To2) of Alberta, Canada and suggested that this earlier animal represented a transitional form between more primitive pantodonts like *Pantolambda* and *Bemalambda* and the heavily derived *Cyriacotherium*. This contention was made on the basis that, although *Presbyterium's* penultimate and ultimate premolars are

semimolariform (and therefore depart from the 'typical' pantodont condition), they do not exhibit the extreme dilambdodonty and molarisation of *Cyriacotherium*. In a phylogenetic analysis based on dental characters, *Presbyterium* was recovered as sister to *Pantolambda* and that grouping was sister to *Alcidedorbignya* (Scott, 2010). This arrangement was in part supported on the basis of synapomorphies like a pronounced ultimate premolar metaconid.

Zack's (2009) matrix was subsequently incorporated into the matrices used in Halliday et al. (2017, 2019). The placement of *Cyriacotherium* varies within the strict consensus trees of the publications. *Cyriacotherium* was first recovered as sister taxon to the 'dermopteran' clade (*Elpidophorus* + (*Plagiomene* + *Worlandia*)) in an unconstrained analysis (Halliday et al., 2017). The taxon was subsequently recovered as a derived pantodont and the sister taxon to *Titanoides* (Halliday et al., 2019). Notably, Pantodonta is not a monophyletic grouping in this later case with the pantolestid, *Todralestes*, recovered as sister taxon to *Alcidedorbignya* (Halliday et al., 2019). As can be seen with these results, the position of *Cyriacotherium* remains labile within analyses with a broader taxon sampling.

The deciduous teeth of definitive pantodonts (Simons, 1960; Lucas and Tong, 1987; Lucas and Schoch 1990; Muizon and Marshall, 1992) lend some ancillary support to the argument that the cyriacotheriids represent derived pantodonts. The deciduous ultimate premolars of *Alcidedorbignya*, *Barylambda*, *Titanoides*, *Coryphodon*, and *Heterocoryphodon* have a more molariform nature than the permanent teeth that replace them with a distinctly separated paracone and metacone connected by a 'w' shaped ectoloph. While this molarisation of the deciduous premolars is to be expected in mammals, the slightly asymmetrical structure of these teeth is reminiscent of that of *Cyriacotherium*'s permanent premolars. A similar echo of this reflection of more primitive patterns is seen when Cope (1884b) notes that the ultimate deciduous premolar of *Coryphodon* is molariform and resembles the molars of *Pantolambda*.

The relationships of some of the Asian taxa are also worth assessing in a broader phylogenetic context. For example, in their original description of *Plethorodon*,

Huang and Zheng (1987) considered it a pantodont-like mammal and refrained from assigning it to either Pantodonta or Tillodontia. Some later workers (Muizon and Marshall 1992; Wang, 1993; Wang et al., 1998) leaned towards a tillodont affinity for *Plethorodon*, but others (Ting, 1998; Tong et al., 2003) disputed this inference and retained it within Pantodonta. In a small analysis considering early tillodonts, pantodonts, and *Deltatherium*, *Plethorodon* was placed within the tillodonts as a sister taxon to *Lofochaius* (Wang and Jin, 2004). It is worth analysing this enigmatic animal and others like *Dysnoestodon* (Zhang, 1980) in a larger scale analysis to further investigate the possibility pantodont affinity and elucidate the probable stem of the pantodont-tillodont grouping.

The question at stake in considering these putative members of the group, particularly the cyriacotheriids, is essentially: 'what characteristics diagnose a pantodont?' The distinct double-v shapes of their penultimate and ultimate premolars are a key synapomorphy that has traditionally diagnosed the clade (Muizon and Marshall, 1992; Lucas, 1998). However, these features are either unknown (in the case of the molar associated with *Crustulus*) or not present (in the case of the 'w' shaped ectolophs of cyriacotheriid premolars) in the purported pantodonts investigated. If these taxa are robustly recovered within Pantodonta, then the synapomorphies supporting this clade will need to be clarified with more nuance. There exists utility in moving from a strictly morphology-based diagnosis of the group to a phylogenetic definition of pantodonts and clarifying this definition marks a major priority for further research. A phylogeny-based definition of Pantodonta would be flexible to potential character loss in the further evolution of the group and allow less rigidity in group membership. This flexibility could then allow for new discoveries to be more easily incorporated within the pantodont pantheon.

Using a stem-based definition, Pantodonta could provisionally be conceptualized as the most inclusive clade including *Alcidedorbignya* but excluding (1) *Cimolestes*, (2) *Didelphodus*, (3) *Palaeoryctes*, (4) *Apatemys*, (5) *Conoryctes*, (6) *Esthonyx*, (7) *Aphronorus*, (8) *Periptychus*, (9) *Prodinoceras*, and (10) *Arctocyon*. Taxa (1)-(7) were selected as representatives of other 'cimolestid' groups (sensu McKenna and

Bell, 1997). Taxa (8)-(10) were selected for exclusion because of their superficial postcranial resemblances to pantodonts. This provisional definition of Pantodonta sets up a framework for the group that is independent of the presence or absence of the 'key' upper premolar synapomorphy that has traditionally defined it.

In summary, the outstanding questions that exist around pantodont phylogeny are (1) the relationships between different pantodont genera, (2) where pantodonts fit in the broader context of the mammal family tree, and (3) how best to define and diagnose this group in response to the nuance provided by later discoveries.

Without a detailed hypothesis about the pattern of their evolution, we are not able to meaningfully grasp the processes and drivers of evolution within this group. In particular, a revised phylogeny for the group would allow for more detailed reflections on the evolution of large body sizes within the group and how this group's evolution might have been influenced by changes in the climate. Although the framework for understanding the whole group's evolutionary context is still lacking, previous workers have reflected on the specific ecology of individual taxa within the group.

Pantodont Ecology and Palaeobiology

Pantodonts were among the first Paleocene mammals to grow to truly large body sizes (Rose, 2006). However, the specifics of body size within this group have rarely been rigorously estimated. Initially, workers used broad comparisons to animals like sheep and tapirs to contextualise these animals (e.g. Cope, 1884b; Marsh, 1877). Later, pantodonts were included in broader investigations of the best proxies for body size estimation in extinct animals (e.g. Damuth, 1990; Gingerich, 1990). Since body size is correlated with many other aspects of an animal's paleobiology and pantodonts are notable in evolutionary history for achieving large sizes for their moment in time, targeted investigation of the most appropriate ways of estimating body size in this clade is an important avenue for future research.

Pantodonts occupied the large herbivore niche in mid-Paleocene through mid-Eocene mammal faunas (Gingerich and Childress, 1983). The relatively low crowns of the

cheek teeth within the group supports a general inference that pantodonts typically consumed softer vegetation (Coombs, 1983) and were browsers rather than grazers (Lucas, 1984a). However, these animals appear to have explored multiple feeding strategies within the browsing niche. For example, the suggestion that *Titanoides* used its claw-like unguals, sabre-like upper canines and bladed, antero-posteriorly elongated lower canines for a diet of root and tubers (Patterson, 1939a; Coombs, 1983) contrasts with more folivorous diet proposed for cyriacotheriids on basis of their molariform ultimate premolars (Rose and Krause, 1982). *Bemalambda* is similarly posited to have eaten more delicate foliage (Chow et al., 1977). Most evocatively, the discovery of a skull of *Pantolambdodon* with highly retracted nasals leads to the inference that this animal might have had a tapir-like proboscis (Ding et al., 1987) and engaged in a similar feeding strategy. Additionally, the feeding ecologies of coryphodontids have been repeatedly speculated on with Owen (1846, p. 304) suggesting that *Coryphodon* ate “the coarser kinds of vegetable substances.” Patterson (1939b) suggested that the canines of *Coryphodon* might have been used for uprooting succulent plants that grew near bodies of water. Transverse grooves on the back of the canines could indicate that these animals pulled at stems and passed them through the diastema between canine and cheek teeth (Simons, 1960; Lucas, 1984a). Flerov (1957) extended that suggestion to other coryphodontids by speculating that *Eudinoceras* and *Hypercoryphodon* also fed on aquatic plants. Other hypotheses for pantodont feeding appear to be more inexplicable with suggestions of omnivory in *Coryphodon* (Cope, 1877b) and an insectivorous feeding strategy proposed for *Archaeolambda* due to superficial similarities between its upper dentition and that of bats (Flerov, 1952).

Upon closer examination, a similar diversity in proposed locomotion strategies and postcranial adaptations exists within Pantodonta. The later, larger members of the group like *Coryphodon* evidence graviportal specialisations in the postcrania, particularly the pes (Osborn, 1898a; Gregory, 1912). However, different movement strategies have been proposed for smaller-bodied taxa. Among the Asian taxa, *Archaeolambda tabiensis* (Huang, 1977) is suggested to be arboreal (Lucas, 1998) while the humerus of *Bemalambda* suggests digging adaptations (Rose, 2006).

Alcidedorbignya may have had a scansorial habit combining a general terrestrial lifestyle with the ability to both climb and adopt a bipedal stance (Muizon et al., 2015). The unique postcrania of *Barylambda* also have led to various speculations about its locomotion and lifestyle. Some workers reflect that it might have had ground sloth-like habits (Flerov, 1952) and been capable of bipedal browsing (Scott, 1937; Lucas, 1998). In contrast, Patterson evocatively hypothesised that *Barylambda* might be “a semi-aquatic form, inhabiting soft rather swampy ground” where its “large feet would have been useful in locomotion” and its “very powerful, laterally compressed tail could have functioned as an effective swimming organ” (Simons, 1960, p. 70). The majority of habitus hypotheses for different pantodonts remain purely speculative.

Evidence of gregariousness is also observed in different populations of pantodonts. For example, *Coryphodon* is known from multiple quarries that include multiple individuals (Lucas, 1984a; McGee, 2001; McGee, 2022; McGee and Turnbull, 2010) and the abundance of juvenile pantodonts found at Tiupampa has raised the idea of a nearby breeding ground (Muizon and Billet, 2022). Additionally, sexual dimorphism has been interpreted in multiple pantodont genera including *Alcidedorbignya*, *Barylambda*, *Leptolambda*, and *Coryphodon* (Patterson and Simons, 1958; Lucas, 1984a; Uhen and Gingerich, 1995; Muizon et al., 2015). The combination of gregariousness and pronounced dimorphism supported a suggestion of a polygynous herd structure in *Coryphodon* (Lucas, 1984a). Additional evidence of intraspecific interactions can be found in a wound in the skull of *Coryphodon* that may have resulted from an antagonistic interaction (face-biting) with a conspecific (Lucas and Schoch, 1987). This posited interaction resonates with Cope’s (1877b, p.203) speculation that the animals were “formidably armed with tusks” in reference to their canines.

The microenvironment in which certain pantodonts lived has also been speculated upon. *Leptolambda* may have lived in a different, more marginal place within the basin than other barylambdids because its fossils are preferentially found in channel deposits rather than in mudstones which implies they have been transported in to the locality where they were subsequently unearthed (Patterson and Simons, 1958).

Similarly, a semi-aquatic habit for *Coryphodon* has been speculated, in part, because of recovery of its bones from fluvial deposits (Lucas, 1984a).

In each these aspects of pantodont ecology, it is clear that, with the exception of recent studies on *Alcidedorbignya*, the inferences remain relatively speculative and could benefit from clear hypothesis testing. Thus, an avenue for further work within this clade exists in investigating aspects of pantodont palaeoecology within a more quantitative framework. In particular, the unique and bizarre skeletons of the barylambdids promise to be a fertile ground for targeted functional analysis.

A Closer Look: Pantodont Endocasts

Early workers used casts of prepared brain cavities to begin to understand the brain structure of pantodonts (Marsh, 1876; Cope, 1877a; Marsh, 1877) and observed generally small brains in both *Coryphodon* and *Pantolambda*. In particular, the small size of the cerebral hemispheres of the brains of both taxa was noted (Marsh, 1877; Cope 1883b). In *Coryphodon*, the small cerebrum was initially contrasted with an inference that the animal had an expanded cerebellum (Marsh, 1876). However, later workers (Edinger, 1929; Tilney, 1931; references from Jerison, 1973) noted this apparent extent of the cerebellum was due to the removal of the auditory bullae during preparation. All told, pantodont brains were judged to be “of a very inferior type” (Marsh, 1876, p. 426) which supported a “low stage of development which suited a blissful condition of existence” (Owen, 1878, p. 222).

This brain structure of *Coryphodon* appears to remain consistent through ontogeny. The only morphological difference noted in an endocast of a juvenile *Coryphodon* is narrower cerebral hemispheres (Lucas and Schoch, 1990). Similarly, the structure of pantodont brains seems broadly conserved across genera. The dorsal surface of the endocast of *Pantolambda* resembles that of *Coryphodon* (Lucas, 1984a). In comparison with *Pantolambda*, the endocast of *Leptolambda* is found to be similar in terms of both its overall shape and in the absence of clear furrows along its surface (Edinger, 1956). The most striking feature of *Leptolambda*'s endocast is interpreted as large pituitary gland (Edinger, 1950a; Edinger, 1964) and further sectioning of its cranium showed the development of a large frontal sinus which might be evidence

of pneumatization of the skull (Edinger, 1950b). The endocast of *Alcidedorbignya* is elongated and narrow with a similar morphology to both *Pantolambda* and *Leptolambda* (Muizon et al., 2015). Notably, the endocast of this small-bodied pantodont occupies a greater volume of the skull than that of other, larger pantodonts (Muizon et al., 2015).

Pantodonts exhibit extremely low encephalisation quotients (EQs) across the full range of their body sizes (Table 2) (Jerison, 1973; Bertrand et al., 2022).

Table 2: Pantodont Encephalisation Quotients

Taxon	Encephalisation Quotient (EQ) (Jerison, 1973)	Phylogenetic Encephalisation Quotient (PEQ) (Bertrand et al., 2022)
<i>Pantolambda bathmodon</i>	0.16	0.10
<i>Leptolambda schmidtii</i>	0.16	0.11
<i>?Barylambda</i>	0.12	
<i>Coryphodon hamatus</i>	0.19	0.11
<i>Coryphodon elephantopus</i>	0.11	0.10
<i>Alcidedorbignya inopinata</i>		0.14
<i>Titanoides primaevus</i>		0.04

Muizon et al. (2015) calculated the encephalization quotient for *Alcidedorbignya* using a variety of equations and body size proxies with an average result of 0.42. This value is notably larger than those returned for all other pantodonts in previous and subsequent studies. This elevated EQ reflects the body mass equations used as Bertrand et al., (2022) recovered values for *Alcidedorbignya* that, while indeed being slightly higher, were more consistent with other pantodonts.

Taking a broader view across the Paleogene, Edinger (1964) noted that the evolution of brains appeared decoupled from the evolution of body size in these mammals. That finding was echoed recently in a large-scale analysis of fossil brains across the K-Pg boundary and through the Paleogene (Bertrand et al., 2022).

A Closer Look: Pantodont Dental Microstructure, Palaeohistology, and Stable Isotope Analyses

From the turn of the century a variety of destructive analytical methods have been leveraged to gain further insights into the ecology of pantodonts. For example, the distinctive enamel microstructure of the enamel of *Coryphodon* - constituted of

rounded prisms with subparallel interprismatic matrix arranged into a nested chevron or tree-like structure - was recognised (Koenigswald and Rose, 2005). Since *Coryphodon*-enamel has evolved across several mammalian lineages, the authors hypothesised the structure might be a strategy for strengthening a tooth against breakage (Koenigswald and Rose, 2005). This enamel microstructure has subsequently been employed to identify otherwise indeterminate tooth fragments from Ellesmere Island as belonging to this large-bodied pantodont (Eberle et al., 2020).

Palaeohistology represents another avenue for investigating pantodonts. Using palaeohistological sections of the upper dentition and comparisons to extant analogs, the growth and development of large-bodied Asian coryphodontids has been investigated (Mao et al., 2014) and, most recently, the life history of the relatively small-bodied pantodont, *Pantolambda bathmodon* was elucidated using a combination of palaeohistology and trace element geochemistry (Funston et al., 2022). The observation of a rapid pace of life in *Pantolambda* with rapid growth to adult body size within a year is broadly consistent with the inference that *Coryphodon* also grew rapidly and achieved nearly adult size before the loss of its deciduous dentition or the fusion of its long bone epiphyses (Lucas and Schoch, 1990). Similarly, speculations that *Coryphodon* might have given birth to a singleton offspring (Lucas, 1984a) find similar resonance with the expectations for *Pantolambda* (Funston et al., 2022). However, the rapid crown formation times found for *Pantolambda* contrast with the slower crown formation times (3-4 years for the ultimate upper molar) within *Asiocoryphodon*, *Heterocoryphodon* and *Eudinoceras* (Mao et al., 2014). These slower crown formation times were used to infer slower growth and a longer lifespan within these large-bodied pantodonts (Mao et al., 2014). These variable results across within different pantodont genera raise the question of the distribution of various life history strategies within the clade. The presence of osteologically immature specimens of other pantodont taxa including *Alcidedorbignya inopinata* (Muizon et al., 2015; Muizon and Billet, 2022), *Barylambda faberi* (Patterson, 1933), *Titanoidea* (Holtzman, 1978), *Archaeolambda* (Kielan-Jaworowska, 1968), and *Coryphodon* (Lucas and Schoch, 1990; McGee and

Turnbull, 2010) represents a significant avenue for future research into life history within this clade using palaeohistology.

The abundance of juvenile pantodonts specimens also means that their dental ontogeny can be investigated by reflecting on dental eruption patterns. In *Alcidedorbignya*, the deciduous dentition erupts near birth and the eruption of permanent premolars (replacement teeth) is interspersed with the eruption of molars (Muizon and Marshall, 1992; Muizon and Billet, 2022). This sequence is similar to that of *Coryphodon* where the permanent canines and premolars are in use before the ultimate molar erupts (Lucas and Schoch, 1990). In *Barylambda*, the eruption pattern is different with the first and second molar seeming to erupt before the replacement dentition and the incisors likely the last of the permanent dentition to erupt (Patterson, 1933; Patterson, 1934). The dental eruption sequence of *Coryphodon* was evaluated to predict that the first molar likely emerged when the animal was less than a year old (Smith, 2000). Under the hypothesis proposed by Schultz's Rule, this relatively early replacement of deciduous dentition in the eruption sequence was inferred to be a proxy for a slower life history (Smith, 2000). However, Schultz's Rule doesn't generalize uniformly across mammals (Godfrey et al., 2005) and might instead be more influenced by phylogeny than life history (Monson and Hlusko, 2018). Indeed, the similarity in dental eruption patterns between small-bodied *Alcidedorbignya* and large-bodied *Coryphodon* lead to the suggestion that, rather than reflecting a slower life history, this dental eruption pattern might instead be influenced by phylogeny and reflect a synapomorphy for the group (Muizon et al., 2015; Muizon and Billet, 2022).

Finally, stable isotope analyses are providing further traction on the persistent question of whether *Coryphodon* had a semi-aquatic habit. In a sample from the Bighorn Basin, *Coryphodon* exhibited more negative $\delta^{13}\text{C}$ values in its enamel than contemporaneous herbivores leading to speculation that it could have been feeding in a closed-canopy microenvironment rather than in more open woodlands (Koch et al., 1995). The $\delta^{18}\text{O}$ values of the same sample were also more negative than those of contemporaneous herbivores. These data were later reanalysed to determine that large-bodied members of the genus showed similar values to extant semiaquatic

mammals ('the hippo ecomorph'; Clementz et al., 2008). Additionally, in comparison with contemporaneous herbivores, low $\delta^{13}\text{C}_\text{E}$ values in *Coryphodon* enamel have been found in both mid- and high-latitude populations and are consistent with a diet of aquatic vegetation (Secord et al., 2008; Eberle et al., 2009). These analyses provide another line of evidence for the argument that the genus might have semiaquatic habits.

Insights from Trace Fossils

Due to the relatively large body sizes achieved by the early Paleocene (Torrejonian) within the group, pantodonts are one of the only clades of enigmatic Paleogene mammals that has an inferred ichnological record. The majority of the tracks in question are, with varying degrees of confidence, referred to large-bodied pantodonts like *Titanoidea* and *Coryphodon* (Mustoe, 2002; Lüthje et al., 2010; Henderson, 2015; Wroblewski and Gulas-Wroblewski, 2021). Interestingly, some footprints referred to pantodonts have been found in places where their body fossils are not yet known. For example, several gorgeous narrow-gauge trackways with a pentadactyl manus and overstepping pes are known from the island of Spitsbergen, Svalbard Archipelago and have been argued to derive from titanoideid pantodonts (Lüthje et al., 2010). Similarly, fairly large, circular tracks from both western Alborz and Birjand in Iran have been postulated to potentially belong to either a pantodont (*Coryphodon*) or dinoceratan (Abbassi and Lockley, 2004; Nadjafi et al., 2005; though see subsequent criticism by Mirzaie Ataabadi, 2007).

These footprints are often located in sediments that indicate a more water-logged, marginal environment. Although this pattern may partially indicate a preservational bias towards settings where footprints are more likely to be formed, it could also indicate evidence of a preference for these animals to exist in environments with more saturated sediments like mirey coal-swamps or brackish tidal platforms (Mustoe, 2002; Lüthje, 2010; Wroblewski and Gulas-Wroblewski, 2021). The occurrences of these tracks in more marginal sedimentary environments potentially provide an additional line of evidence for a more semi-aquatic habit for larger pantodonts. While footprints found in Paleocene sediments are more likely reflective

of pantodonts (Lüthje et al., 2010; Henderson, 2015; Wroblewski and Gulas-Wroblewski, 2021), those found in the Eocene tend to be more equivocal as dinoceratans become potential alternative candidates for large-bodied trackmakers (Mustoe, 2002; Abbassi and Lockley, 2004). These examples highlight that, although Paleocene track sites are rare in comparison to sites from later in the Cenozoic, they hold potential for more concretely understanding the geographic ranges achieved by large-bodied pantodonts and their environmental preferences.

Pantodont Biogeography

Pantodonts are interesting among Paleocene mammals because of their wide geographic distribution. As various continental faunas were described, the general consensus among previous workers supports an Asian origin of pantodonts (Flerov, 1952; Lucas, 1984c; Lucas and Williamson, 1995; Williamson, 1996; Beard, 1998; Lucas, 1998; Clemens, 2017). Rose (2006, p. 118) summed up the consensus by noting the “antiquity, diversity, and plesiomorphic state of Asian members of both Pantodonta and Tillodontia suggest that continent as a center of origin of these clades.”

However, the timing of the proposed dispersal of pantodonts from Asia is less clear, particularly in light the discovery of *Alcidedorbignya* in South America. While Muizon and Marshall (1987) suggested that *Alcidedorbignya* would support a South American origin for pantodonts with a subsequent northwards dispersal, this inference relied on an assumption of Cretaceous age for the Tiupampa fauna. With the age subsequently clarified as Paleocene, Muizon and Marshall (1992) noted that the continent of pantodont origins was difficult to determine but argued that the group originated in the late Cretaceous since *Alcidedorbignya* appears the Santa Lucia Formation (Tiupampan) of South America and appears more primitive than North America’s *Pantolambda bathmodon*. Williamson (1996) challenged this timing and argued that the presence of the earliest known North American pantodont, *Pantolambda intermedium*, in the Torrejonian of the Nacimiento Formation indicated that a Paleocene dispersal of pantodonts from Asia could not be ruled out. In the 1990’s, the Tiupampan SALMA (South American Land Mammal Age) was regarded as

early Paleocene (Puercan) (Muizon and Marshall, 1992; Marshall et al., 1997), but its age was subsequently revised to approximately the Puercan-Torrejonian boundary (Woodburne et al., 2014, reference Fig. 1). With this posited younger age of the Tiupampan SALMA, the balance of evidence appears again to favour a Paleocene dispersal of pantodonts from Asia to the Americas. However, if the Puercan-aged *Crustulus fontanus* is indeed a pantodont (Clemens, 2017), the first appearance of this group in the North America supports an earlier dispersal of the group. Further study of the Tiupampan fauna has again led to the suggestion that it might best be placed in the Puercan (Muizon and Ladavèze, 2020) and discussion of the challenges around dating this fauna and its implications continue (Muizon and Billet, 2022). Altogether, the first appearances of pantodonts in Asia (Shanguan ALMA; Wang et al., 2016), North America, and South America all lie within a narrow (late Puercan to early Torrejonian) range (Clemens, 2017) which implies a root for the pantodont family tree deeper in time. The timing of this first intercontinental dispersal of pantodonts is important because it has implications for the timing of the overall origin of this group.

A second intercontinental dispersal of pantodonts, that of *Coryphodon* across the Holarctic, is well-known (Dawson, 2012), but the point of origin of the animal is much more equivocal. Some workers argue for an Asian ancestry for *Coryphodon* (McKenna, 1980; Godinot, 1982; Krause and Maas, 1990) while Lucas (1984a) argues for a North American origin of the genus on the basis of its apparent close phylogenetic relationship with *Pantolambda* and *Caenolambda* and because the oldest fossils of *Coryphodon* are found in North America. Lucas (1984a) then suggests that *Coryphodon* dispersed via Arctic routes to Europe and Asia. A later biogeographic reconstruction of coryphodontid phylogeny argued that an Asian origin for this clade was unambiguously supported, but this inference appears to conflict with the hypothesised phylogenetic relationships of *Coryphodon* nested within a clade of North American pantodonts (Beard, 1988). In the case of both pantodont origins and of the dispersal of *Coryphodon*, a better understanding of the phylogenetic context of the clade will support more sophisticated biogeographic reflections.

Several smaller-scale questions about pantodonts could also be addressed by further clarification of their biogeography and stratigraphy. Although pantodonts of varying body sizes co-existed in the same environments (e.g. *Pantolambda cavirictum* and *P. bathomodon* in the San Juan Basin; *Barylambda faberi* and *Haplolambda quinni* in the Plateau Valley of Colorado), the spectre of competition between large-bodied pantodonts in North America has been raised (Simons, 1960; Gingerich and Childress, 1983). The appearance of *Coryphodon* in North American ecosystems (specifically the Plateau Valley sequence) seems coupled with the disappearance of another large-bodied pantodont, *Barylambda* (Gingerich and Childress, 1983). It is unclear whether direct competition between these different pantodonts or changes in environmental conditions is responsible for this ecological turnover (Gingerich and Childress, 1983). *Coryphodon* is similarly postulated to have been a potential agent in ecological turnover in Europe across the PETM (Hooker and Collinson, 2012). Smaller terrestrial mammals were suggested to be adversely affected by the reduction of ground cover through *Coryphodon's* feeding activities (Hooker and Collinson, 2012). These questions of ecosystem turnover naturally raise further questions about what specific mechanisms might have driven pantodont extinction and subsequent replacement in the large herbivore niche of ecosystems by members of modern mammal groups.

Both at the basin-level and intercontinentally, the patterns of dispersal within pantodonts bear further investigation when the clade's taxonomy and phylogenetic relationships are further clarified. A robust understanding of the stratigraphic context of these animals will also help with understanding the timing of these major evolutionary events.

Pantodont Biostratigraphy

Pantodonts have occasionally been used as biostratigraphic indicators and have supported the definition of several land mammal ages in both North America and Asia. For example, the first appearance of *Coryphodon* is used to help define the Clarkforkian North American Land Mammal Age (Wood et al., 1941; Rose, 1981). Similarly, the turnover of endemic Asian pantodonts was used to define both

Bemalambda and *Archaeolambda* zones within the Shanghuan Asian Land Mammal Age (Ting, 1998). The Asian coryphodontids (particularly *Eudinoceras*) were used to tentatively correlate between faunas across basins and *Coryphodon* was similarly used to help establish correlations across the Holarctic (Lucas, 1984a).

Archaeolambda has been useful for correlating upper Paleocene sequences in Mongolia (Dashzeveg, 1988). Most granularly, pantodonts have been historically used to help understand basin-level stratigraphy. For instance, Osborn (1909) divided the Nacimiento Formation of the San Juan Basin into the (now defunct) "*Deltatherium*" and "*Pantolambda* zones". The utility of pantodonts as biostratigraphic indicators lies in their fairly wide distribution both inter- and intra-continentially and potentially reflects the larger range sizes that would be expected from their large body sizes.

Future Steps and Conclusions

Pantodonts were among the first mammals to grow to large body sizes after the K-Pg extinction and were the biggest animals in mid-Paleocene to Eocene ecosystems. They have been studied for over 150 years and multiple genera are known from nearly complete skeletons. However, research on these enigmatic animals has rarely progressed beyond the initial descriptions of these bone and vague speculation about the implications for their ecology. The time is ripe for careful osteological descriptions of these animals with an eye toward clarifying their taxonomy and, armed with that information, the construction of a comprehensive in-group phylogeny of these animals. The apparent timing of their origins and diversification and their enigmatic phylogenetic relationships indicates that, despite their lack of extant relatives, pantodonts are important in resolving placental mammal phylogeny.

Pantodonts evolved progressively larger body sizes over the course of their evolutionary history across multiple endemic faunas (Simons, 1960). Within the context of a resolved phylogeny, this qualitatively observed trend could be assessed to determine whether this achievement of large sizes happened independently across multiple pantodont lineages or whether there was a single point of origin for this evolutionary event. Additional avenues for study of these animals include

clarifying the palaeobiology of individual members of the clade including feeding and locomotion strategies and further investigating how pantodonts responded to the rapid environmental changes associated with Paleocene hyperthermal events and the Paleocene-Eocene Thermal Maximum. Recent advances in both stable isotope geochemistry and palaeohistology evidence that there are several potential avenues for gaining a deeper understanding of both pantodont ecology and life history. The excellent record of pantodonts means that they hold the promise to be a good 'natural laboratory' for understanding how evolution works in a warm, post-extinction world.

This thesis represents an initial foray into the close examination of this exemplary group of animals.

Project Aims and Overview of Thesis Contents

In this thesis, I aim to begin building a solid framework for further investigation into the evolutionary history of pantodonts, an enigmatic yet important, clade of Paleocene mammals.

As evidenced in the systematic review of Pantodonta, many fundamental questions remain outstanding about these mammals. In this thesis, I aim to leverage anatomical descriptions of new material from the genus *Pantolambda* to explore the questions of:

- (1) Whether *Pantolambda intermedium* is a valid species and
- (2) Whether the characteristics of the deciduous dentition in definitive pantodonts can give us any additional insight into the affinity of the cyriacotheriids, a group of putative pantodonts.

I will then look at other, more fragmentary *Pantolambda* material from the SJB to investigate these animals as living, breathing organisms. I will explore:

- (3) Whether existing dental and postcranial proxies are appropriate for estimating body size in pantodonts and

- (4) What behaviors, social structures, and life history strategies may have existed within *Pantolambda bathmodon*.

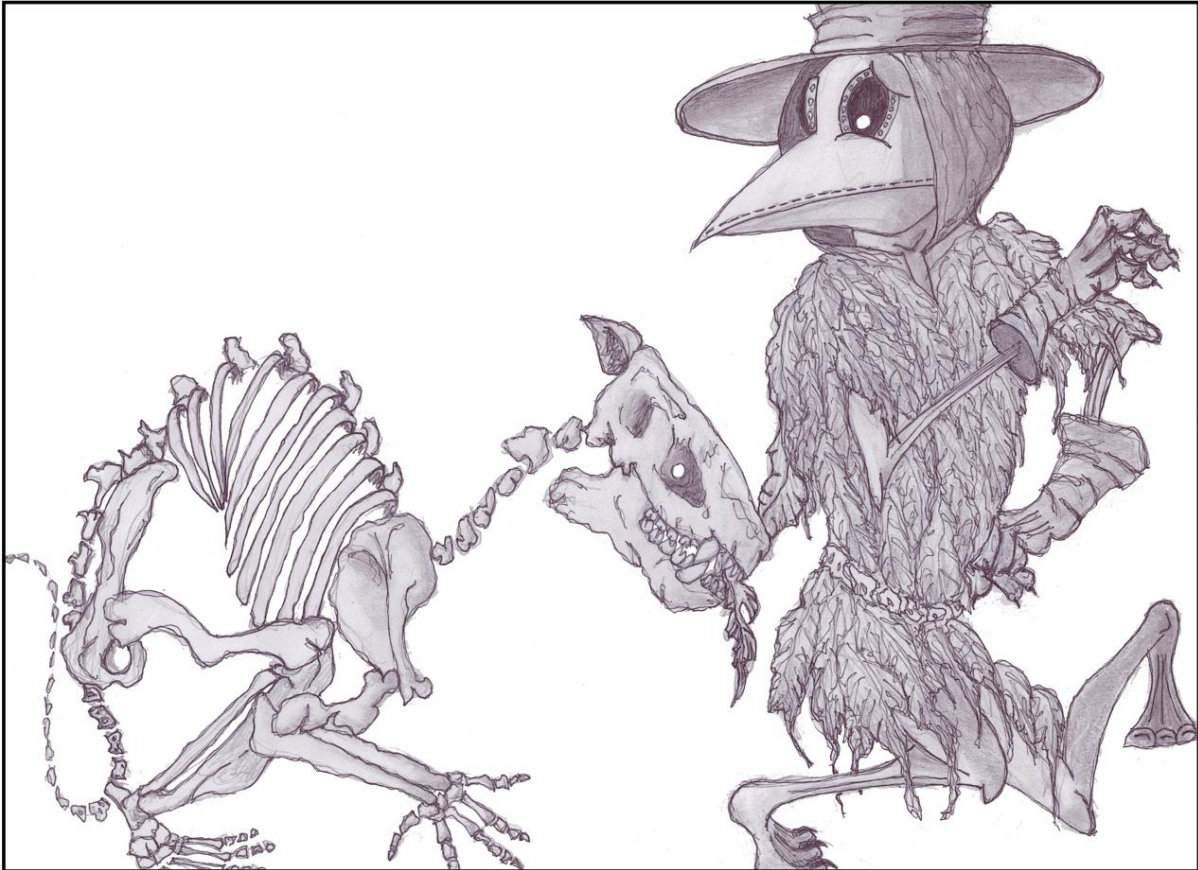
To summarize the contents of this thesis, Chapter 1 seeks to contextualise these animals within mammal evolutionary history and to systematically review the existing literature pertaining to them. Chapter 2 represents an anatomical study of new material from the genus *Pantolambda*, one of the earliest-appearing pantodont genera in North America, using exquisite fossils from the San Juan Basin of New Mexico, USA. Chapter 3 is focused on the palaeobiology of pantodonts: it investigates body size estimates within the clade, reflects on the taphonomy of a *Pantolambda bathmodon* bone bed from the San Juan Basin and presents additional information on *P. bathmodon*'s life history through palaeohistology. Starting from the foundation provided by this thesis, pantodonts can be more meaningfully explored as critical indicators of body size evolution in the wake of a mass extinction and as interesting animals in their own right.

Chapter Summary:

In this chapter, I have briefly surveyed the long evolutionary history of mammals from their synapsid ancestors through coexistence with non-avian dinosaurs in the Mesozoic. I have reflected on the unique post-extinction fauna of Paleocene mammals, seen how the rapid evolution of large body sizes fundamentally distinguished them from Mesozoic mammals, and systematically reviewed the current state of knowledge on pantodonts. Pantodonts were among the first mammals to grow to truly large body sizes after the K-Pg extinction and achieved a wide geographic distribution across four continents. The taxonomy of pantodonts remains challenging which has resulted in their limited incorporation in phylogenetic analyses and their palaeobiology and ecology remain understudied. Despite these challenges, pantodonts hold the potential to be a good natural laboratory to understand large mammal evolution in a post-extinction landscape.

Chapter 2:

***Pantolambda* from the San Juan Basin**



"Don't Do That" by Savannah Carpenter

"The aspect of external nature, as it presents itself in its generality to thoughtful contemplation, is that of unity in diversity, and of connection, resemblance, and order, among created things most dissimilar in their form; - one fair harmonious whole."

- Alexander von Humboldt, 1848, *Cosmos* (trans. Edward Sabine)

Introduction and Motivation:

The North American pantodont genus, *Pantolambda*, is known from three species: *P. bathmodon*, *P. intermedium*, and *P. cavirictum*. Fossils referred to this genus have been recovered from multiple localities across the Paleogene basins of the western United States including Gidley Quarry, Montana (Simpson, 1935), the Carbon Basin, Wyoming (Secord, 2008) and the San Juan Basin, New Mexico (e.g. Williamson, 1996).

Although it represents a baseline against which other pantodonts are compared (e.g. *Bemalambda* (Chow et al., 1977) and *Alcidedorbignya* (Muizon et al., 2015)), the genus *Pantolambda* has not been treated in detail since the monumental work of Matthew (1937). In the last close treatment of North American Paleocene pantodonts, Simons (1960) noted that Matthew's work had led a clear understanding of the anatomy of the genus. However, Simons (1960) also raised the spectre that this genus was potentially oversplit. He noted that, aside from the clear difference in size, the type specimen of *Pantolambda intermedium* found in Gidley Quarry was broadly consistent with the anatomy of *P. bathmodon* (Simons, 1960). Among several interpretations for this size difference, he raised the hypothesis that this more northerly occurrence could be "due to the operation of the ecologic principle known as Bergmann's rule" which states that "the more northern species or subspecies of a given type of animal tend to be larger than their more southern relatives" (Simons, 1960, p. 21).

In light of the discovery of new specimens of the genus *Pantolambda* from the San Juan Basin which reveal novel anatomy for the genus, the time is ripe for revisiting the osteology of this iconic pantodont. After surveying the broader context of the San Juan Basin, I describe the deciduous dentition of *Pantolambda bathmodon* (NMMNH P-27844), cranial and postcranial material referable to *Pantolambda intermedium*, and elements of the pectoral girdle and forelimb of *Pantolambda cavirictum* (NMMNH P-57738). This descriptive work further extends our understanding of the anatomy of the genus. I will additionally evaluate whether *Pantolambda intermedium* constitutes a valid species in response to Simons (1960) and in context of this new material.

The San Juan Basin, New Mexico, USA

One of the best places in North America to explore the evolution of pantodonts is the San Juan Basin, New Mexico, USA.

Geography and Geology

The San Juan Basin (SJB) spans $\sim 67,000$ km² across northwestern New Mexico and southeastern Colorado (KellerLynn, 2015; Fig. 7). It is a tectonically-formed foreland basin that began opening in the Cretaceous during the Laramide Orogeny (Chapin and Cather, 1981; Craigg, 2001; Pecha et al., 2018). The SJB is one of the most southerly of a string of contemporaneous basins formed during this orogeny (Dickinson et al., 1988). The more northerly Uinta Basin, Washakie Basin, Green River Basin, and Powder River Basin all derive from the same continental-scale event (Dickinson et al., 1988). The dominant lithologies recorded in the SJB Paleogene are clastic sedimentary rocks with mudstones, sandstones, and isolated pebbly conglomerates recording basin-scale river systems with corresponding floodplains (Williamson and Lucas, 1992; Williamson, 1996; Cather et al., 2019).

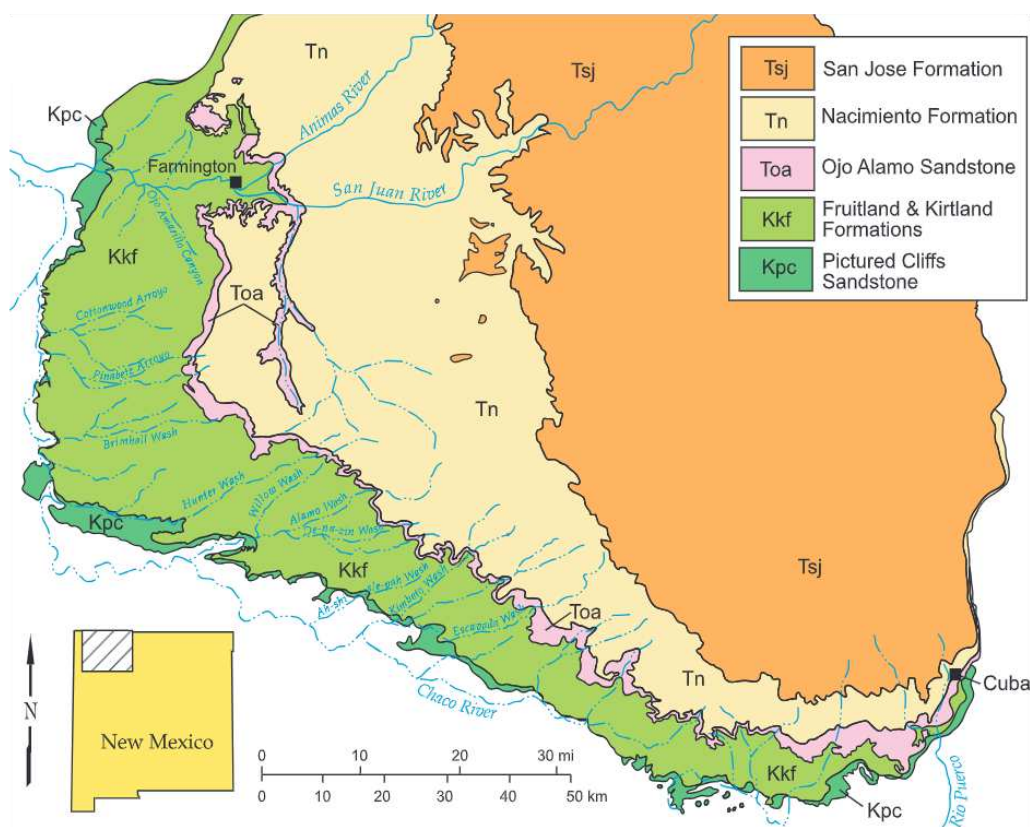


Figure 7: The geology of the San Juan Basin in northwestern New Mexico showing that the sediments tend to become younger towards the eastern portion of the basin (modified from Williamson et al., 2008).

When the San Juan Basin began subsiding in the Cretaceous, accommodation space was created and the Fruitland and Kirtland Formations were deposited (Cather, 2004). Both formations consist of interbedded channel sandstones, siltstones, and shales (Craig, 2001). These formations record abundant dinosaur remains including hadrosaurids, ankylosaurs, ceratopsians, pachycephalosaurs, sauropods, and theropods (Sullivan and Williamson, 1999; Lucas et al., 2000; Farke and Williamson, 2006; Williamson and Weil, 2008; Carr and Williamson, 2010; Burns and Sullivan, 2011; Williamson and Brusatte, 2014; Williamson and Brusatte, 2016). The Ojo Alamo Sandstone spans the K-Pg boundary with the Naashoibito Member in the Cretaceous and the Kimbeto Member in the earliest Paleocene (Powell, 1973; Cather et al., 2019). The Nacimiento Formation spans the majority of the Paleocene (Puercan to Tiffanian) in the San Juan Basin (Williamson, 1996; Cather et al., 2019). The Nacimiento Formation can be up to 530 m thick and is unconformably overlain by the Eocene San Jose Formation (Baltz, 1967; Smith, 1992). The lithologies of the San Jose Formation are broadly consistent with the Nacimiento Formation and were deposited in similar fluvial environments (Smith, 1992; Craig, 2001).

The dominant flow direction within the SJB is to the south and southeast in the Kimbeto Member of the Ojo Alamo Formation but presents as more variable in the overlying Nacimiento Formation (Sikkink, 1987; Cather et al., 2019). Palaeocurrent indicators in the upper Arroyo Chijuillita Member, the Ojo Encino Member, and the Tsosie Member of the Nacimiento Formation show flows to the north and east-northeast (Williamson, 1996; Cather et al., 2019). Higher in the section, in the Escavada Member of the Nacimiento Formation, the flow direction switches back to a predominantly southeasterly direction (Cather et al., 2019). Similarly, the palaeocurrents in the San Jose Formation are directed southwards (Smith and Lucas, 1991; Smith, 1992). These variations in flow patterns are likely, in part, tectonically-influenced and related to local areas of rapid subsidence within the basin resulting from the continental-scale orogeny (Cather et al., 2019). These fluvial systems were complicated and resulted in a large amount of heterogeneity in the depositional environment.

In this thesis, I focus on fossils from the Nacimiento Formation. The Nacimiento Formation has traditionally been divided into three members (the Arroyo Chijuillita Member, the Ojo Encino Member, and the Escavada Member) (Williamson and Lucas, 1992; Williamson, 1996). Following, a recent revision of the stratigraphy, the middle portion of the Nacimiento Formation in the southwestern part of the basin was defined as the Tsosie Member (Cather et al., 2019). In this same revision, the Kutz Member (exposed in the northern part of the basin at Kutz Canyon) conformably overlies the Kimbeto Member of the Ojo Alamo Formation and is conformably overlain by the Angel Peak Member (Cather et al., 2019). In sum, this revision created more nuance within the pre-existing Arroyo Chijuillita and Ojo Encino Members to reflect lithological variations across the geographic extent of the basin. Specifically, the Ojo Encino Member is restricted to variegated mudstones and sandstones and the thick channel sands previously assigned to that member are referred to the Tsosie Member (Cather et al., 2019). The more recent stratigraphy will be used throughout this thesis when referring to specimen localities.

Williamson (1996) established a biostratigraphic framework for the Nacimiento Formation of the San Juan Basin (Fig. 8) which will be broadly used in the current study. Table 3 illustrates the taxa that define each of these biozones.

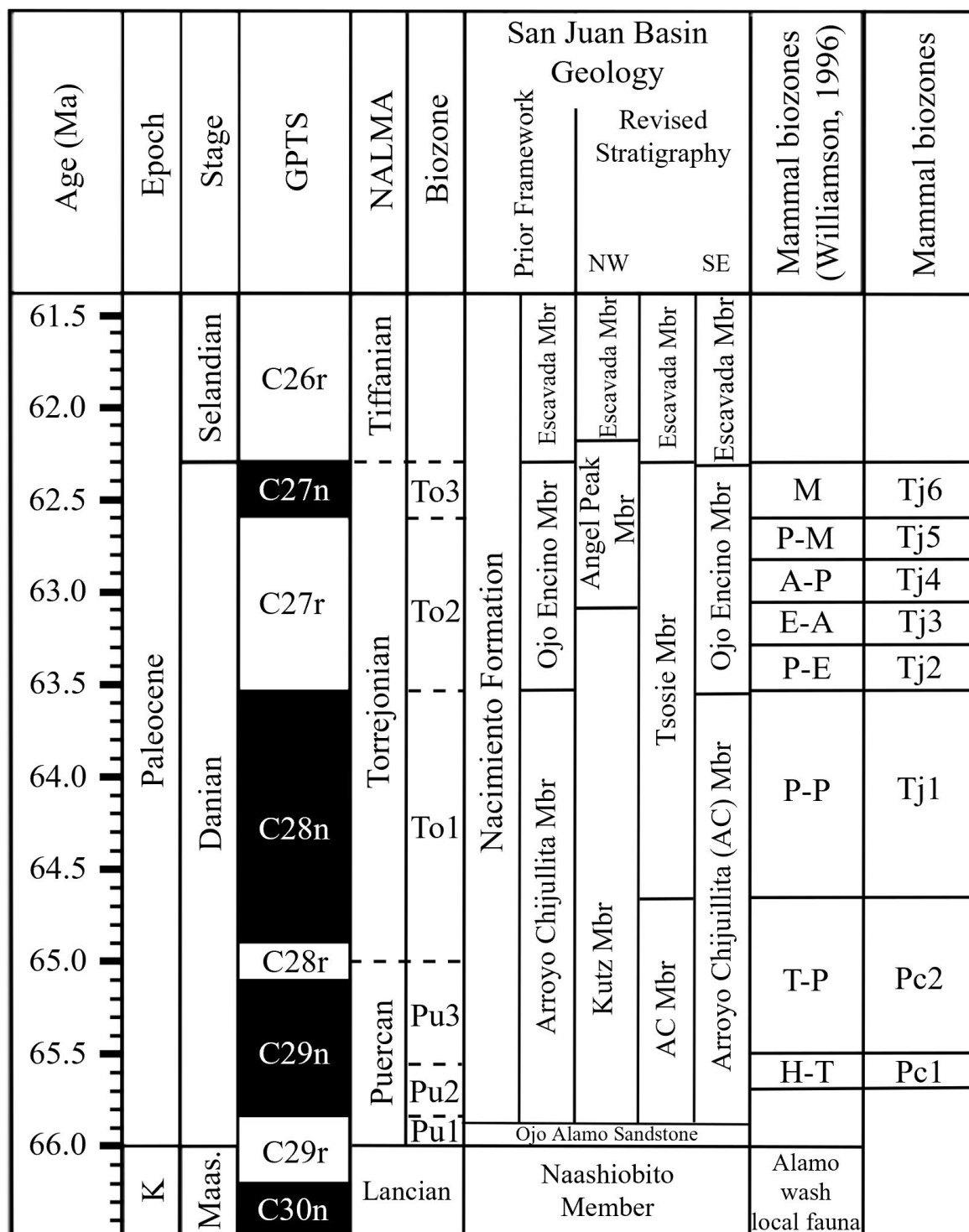


Figure 8: The latest Cretaceous and Paleocene stratigraphy, chronology and biostratigraphy of the San Juan Basin with the cross-basin lateral variation in the revised stratigraphic framework of Cather et al. (2019) illustrated. Image modified from Davis et al., (2016) with the Geomagnetic Polar Time Series (GPTS) from Ogg (2012) and North America Land Mammal Ages (NALMA) from Lofgren et al. (2004).

Table 3: Biostratigraphic Framework of the Nacimiento Formation, San Juan Basin, New Mexico
(adapted from Williamson, 1996)

Biozone		Defining Taxa
Tj6	<i>Mixodectes pungens</i> (M) zone	Interval between the first and last occurrence of <i>M. pungens</i> . Index taxa include <i>Pentacodon occultus</i> , <i>Plesiolestes wilsoni</i> , and <i>Pantolambda bathmodon</i> .
Tj5	<i>Pantolambda cavirictum</i> – <i>M. pungens</i> (P-M) zone	Interval between first appearance of <i>P. cavirictum</i> and <i>M. pungens</i> . Index taxa include <i>Huerfanodon torrejonius</i> .
Tj4	<i>Arctocyon ferox</i> – <i>P. cavirictum</i> (A-P) zone	Interval between first appearance of <i>A. ferox</i> and <i>P. cavirictum</i> . No taxa fully restricted to this biozone to serve as index fossils.
Tj3	<i>Ellipsodon grangeri</i> – <i>A. ferox</i> (E-A) zone	Interval between first appearance of <i>E. grangeri</i> and <i>A. ferox</i> . Index taxa include <i>Palaechthon nacimienti</i> .
Tj2	<i>Protoselene opisthacus</i> – <i>E. grangeri</i> (P-E) zone	Interval between first appearance of <i>P. opisthacus</i> and <i>E. grangeri</i> . Index taxa include <i>Palaechthon torrejonius</i> , <i>Triisodon crassiscuspis</i> , and <i>Pantolambda intermedium</i> .
Tj1	<i>Periptychus carinidens</i> – <i>P. opisthacus</i> (P-P) zone	Interval between first appearance of <i>P. carinidens</i> and <i>P. opisthacus</i> . Index taxa include <i>Protoselene griphus</i> and <i>Paromomys</i> sp.
Pu2	<i>Taeniolabis taoensis</i> – <i>P. carinidens</i> (T-P) zone	Interval between first appearances of <i>T. taoensis</i> and <i>P. carinidens</i> . Index taxa include <i>Oxyclaenus antiquus</i> , <i>Loxolophus priscus</i> , and <i>L. pentacus</i> .
Pu1	<i>Hemithlaeus kowalevskianus</i> – <i>T. taoensis</i> (H-T) zone	Interval between first appearances of <i>H. kowalevskianus</i> and <i>T. taoensis</i> . Index taxa include <i>Catopsalis foliates</i> , <i>Eoconodon gaudrianus</i> , <i>Oxyclaenus simplex</i> , and <i>Loxolophus kimbetovius</i> .

Today, the San Juan Basin is well-known for both Mesozoic and Cenozoic fossil-bearing rocks. Tantalising archaeological evidence from burials and pit houses hints that the original inhabitants of the SJB recognised and sometimes collected the fossils of weathering out of the landscape (Cope, 1875b, p. 172; Simpson, 1942, p. 133). The first western scientists to formally explore the basin were members of the Wheeler Survey with E. D. Cope beginning to prospect Eocene-aged strata along the Gallinas River in 1874 (Simpson, 1942; Kues and Lucas, 1993). In his exploration work, Cope may have been guided to some fossiliferous outcrops by the indigenous folks as there are records of him being shown *Bathmodon* (= *Coryphodon*) teeth by a man who was “possibly a Pueblo dweller” (Mayor, 2005, p. 135). David Baldwin collected the first Paleocene vertebrates from the SJB in 1879 (Simons, 1963) and, in the 1880s, Cope published a flurry of papers describing SJB fossils that he received from Baldwin (Simpson, 1981; Kues and Lucas, 1993). Further collection efforts were undertaken in the 1890s by the AMNH after the acquisition of Cope's collection (Tom Williamson, personal communication). In the late 1920s, G.G. Simpson first visited the SJB and, from the 1940s, took up the mantle of work in the basin and focused collection efforts in both the Nacimiento and San Jose Formations (e.g. Simpson, 1951; Simpson, 1959b). The results of the collection efforts of these researchers and many others sum to one of the best records of Paleogene mammals known globally. Indeed, the Puercan, Torrejonian, and Tiffanian North American Land Mammal Ages were defined on the basis of SJB rocks (Wood et al., 1941; Lofgren et al., 2004). Intensive research programs continue into the present through active work from the New Mexico Museum of Natural History and Science (NMMNH). This research program has been led by Thomas Williamson from the 1990s through today (e.g., Williamson 1996).

Paleocene Ecosystem of the San Juan Basin

In the Paleocene, San Juan Basin would have appeared radically different to its modern scrub brush-dominated, high desert ‘badlands’ landscapes. The climate in the SJB coincided with a tropical seasonal forest biome (Flynn and Peppe, 2019). Evidence from paleosols indicates a mean annual temperature reconstructed to $\sim 12^{\circ}$ C and mean annual precipitation estimated to be 1150-1372 mm/yr (Davis et al.,

2016). However, these paleosol derived values are likely underestimates because the presence of palms in the flora indicates temperatures were at least 14° C (Davis et al., 2016). Consistent with this inference, the MAT calculated from leaf-based indices was upwards of 23° C with MAP upwards of 1500 mm/year (Flynn and Peppe, 2019). Evidence from paleosol development indicates that this precipitation was most likely seasonal (Davis et al., 2016). This climate supported a wide range of plants including angiosperms (e.g. palms and plane trees (*Platanites*)), pteridophytes (particularly ferns) and conifers (Davis et al., 2016; Flynn and Peppe, 2019; Milligan et al., 2022). In addition to these macrofossils, pollen grains expand the understanding of the San Juan Basin ecosystem to include familiar trees like oaks and willows (Anderson, 1960). This warm and wet climate appears to have remained broadly stable through early portions of the Paleocene (Davis et al., 2016).

A diverse fauna inhabited these lush forests and water systems. Gastropods (e.g. *Helix*, *Viviparus*) and bivalves (e.g. *Unio*) are recovered from channel sand deposits alongside abundant gar scales (Hartman, 1981; Sullivan and Lucas, 1986). Reptilians including crocodiles, turtles, and lizards and the bird, *Tsidiyazhi abini*, existed in this range of river and terrestrial environments (O'Neill et al., 1981; Sullivan and Lucas, 1986; Lyson et al., 2016; Kspeka et al., 2017). A myriad of enigmatic mammals is present throughout the Paleocene Nacimiento Formation. The mammal fauna, in particular, was astonishingly diverse and includes multituberculates (*Taeniolabis*, *Kimbetopsalis*), metatherians (e.g. *Swaindelphys*, *Peradectes*), 'condylarths' (e.g. *Periptychus*, *Tetraclaenodon*, *Deuteronodon*, and *Mioclaenus*), taeniodonts (e.g. *Wortmania* and *Psittacotherium*), arctocyonids (e.g. *Chriacus*), and plesiadapiforms and their close relatives (e.g. *Torrejonia* and *Mixodectes*) (Matthew, 1937; Williamson, 1996; Williamson and Taylor, 2011; Williamson and Brusatte, 2013; Williamson et al., 2016; Chester et al., 2017; Shelley et al., 2018).

Pantodonts represent a small but distinctive subset of the Paleocene and Eocene fauna of the San Juan Basin (Williamson, 1996). The earliest appearing pantodont in the basin was *Pantolambda intermedium* (Tj2; Williamson, 1996). *Pantolambda cavirictum* and *Pantolambda bathmodon* are first recorded in the basin in Tj5 and Tj6, respectively (Williamson, 1996). *Pantolambda bathmodon* is exclusively present

in the redbeds associated with Tj6 and is regarded as an index fossil for this biozone (Williamson, 1996; Leslie et al., 2018). The pantodont *Coryphodon* is also observed in the San Juan Basin from the Eocene San Jose Formation (Simpson, 1951; Lucas, 1984a).

In sum, we can envision the Paleocene environment of the San Juan Basin as a lush, subtropical forest with a diverse and intriguing menagerie of animals occupying various niches within the ecosystem. The exceptional preservation of mammals in this basin, and the extensive history of study (spanning nearly 150 years) marks the San Juan Basin as an excellent place for investigating questions of early Cenozoic mammal evolution. We'll now turn our focus to both historical and new specimens of *Pantolambda* from the San Juan Basin.

Historical Context of the Genus *Pantolambda*:

The genus *Pantolambda* was founded on the basis of a lower dentition of *P. bathmodon* preserving the penultimate and ultimate premolars and the first molar (AMNH 3956) (Cope, 1882a) and subsequent treatments (Cope 1883b; Osborn, 1898a) elucidated the majority of the postcranial skeleton of this species. Cope (1883a) also named the larger species, *Pantolambda cavirictum*, on the basis of a nearly complete mandible. *Pantolambda intermedium* (Simpson, 1935) is the only species of *Pantolambda* named on the basis of material from outside the San Juan Basin. It remains the most poorly known species.

After the initial flurry of discovery, Matthew (1937) monographically treated the fauna of the San Juan Basin including *P. bathmodon* and *P. cavirictum* and Simons (1960) set the anatomy of *Pantolambda* in conversation with that of other pantodonts. Most recently, Muizon et al., (2015) described the basicranium and auditory region of *Pantolambda bathmodon* to support a monographic treatment of *Alcidedorbignya inopinata*.

Etymology:

The etymology of *Pantolambda* was not explicated in Cope's original descriptions. Since I am following Williamson (1996) in correcting a mismatch in the gender of the

genus and species names of these animals, I am write a few sentences here to unpack the nomenclatural nuance.

The genus name *Pantolambda* is derived from the Greek παντο- (panto-) meaning “all” and Λ/λ (lambda; the eleventh letter of the Greek alphabet). This name, “all-lambdas” or “all- Λ” reflects the strong ‘v’ shapes of both the trigonid and the talonid on the lower molars.

The species name *bathmodon* is derived from the Greek βαθμός (bathmos) meaning “step, stair, rank” and ὀδοῦς (odous) meaning “tooth”. This name roughly can be transcribed as ‘stepped tooth’ and refers to the pronounced elevation of the trigonids above the talonids in the genus. The species name *cavirictus* is derived from the Latin *cavus* meaning ‘cave’ and *rictus* meaning ‘jaws/open mouth’⁷. The ‘cave-like open mouth’ likely refers to the large, nearly complete mandible on which the species was erected. Simpson (1935) did explicate the species name for *intermedius* as coming from the Latin *inter* (between) + *medium* (middle) to mean “in the middle” referring to its middling body size.

When a Greek word is transliterated directly to Latin without changes (ICZN Article 30.1.2), the resulting epithet takes on the gender. “Lambda” is a neuter word. For this reason, Cope’s original ‘*cavirictus*’ is written as ‘*cavirictum*’ here. Similarly, Simpson’s ‘*intermedius*’ is referred to as ‘*intermedium*.’ While ‘*bathmodon*’ is technically a masculine species name as well, I have not been able to discern a clear avenue for making ὀδοῦς neuter the allows the name to be recognizable. For nomenclatural stability, this gender mismatch between the genus and species names is retained in the following discussion.

Materials and Methods:

The general abbreviations for the dentition used in this thesis are located on pg xviii. This thesis follows the suggested dental notation of McKenna (1975) which has been adopted by some later workers (e.g. Wible et al., 2009; Shelley et al., 2018; though see alternative perspectives in Lockett, 1993 and Cifelli, 2000). Under this scheme,

⁷ I like to conceptualize this word in this context as ‘gaping maw’.

the first and second premolars are denoted P/p 1 and P/p 2, respectively, and the penultimate and ultimate premolars are denoted P/p 4 and P/p5, respectively. This nomenclature reflects the assumption that the P/p 3 observed in basal eutherians is a retained deciduous tooth (McKenna, 1975). In the genus *Pantolambda*, four premolars are present and are thus labeled P/p 1, P/p 2, P/p 4, and P/p5 from the anterior to the posterior portions of the tooth row. The standard eutherian terminology summarized by Szalay (1969, Fig. 1) is adopted in describing the cusps, crests, and fine details of the teeth. Anatomical nomenclature was drawn from Miller's Anatomy of the Dog (Evans and de Lahunta, 2013) and recent monographs on the pantodont, *Alcidedorbignya inopinata*, (Muizon et al., 2015) and the periptychid, *Periptychus carinidens* (Shelley et al., 2018).

NMMNH P-27844 is a partial skeleton of *Pantolambda bathmodon* consisting of fragments of the skull roof, left and right maxillae, isolated vertebrae including the axis, humeri, ulnae, radiae, carpal bones, the distal epiphyses of the femur, distal tibia, isolated metapodials and phalanges. The skeleton was found at Escavada Wash in the Tsosie Member of the Nacimiento Formation. NMMNH P-19774 and NMMNH P-72117 represent tooth and jaw fragments referred to *Pantolambda intermedium*. A partial scapula (NMMNH P-21647) and brain case (NMMNH P-21646) are also referred to *P. intermedium*. All of these specimens were found at Kutz Canyon which is stratigraphically low in the Nacimiento Formation (Tj2). NMMNH P-57738 is a partial skeleton of *Pantolambda cavirictum* consisting, in part, of maxillae, vertebrae, scapula, clavicle, tibia, an articulated forelimb, manus, and unguals. The skeleton was found in the Ojo Encino Member of the Nacimiento Formation.

Systematic Palaeontology:

MAMMALIA Linnaeus, 1758

EUTHERIA Gill, 1872

PANTODONTA Cope, 1873

PANTOLAMBDIDAE Cope, 1883

Pantolambda Cope, 1882

Deciduous Dentition:

Tooth Row Position Justification:

The right maxilla of NMMNH P-27844 consists of a dP2-dP5 and M1 (Fig. 9). Although the deciduous dentition of *Pantolambda bathmodon* has not been previously described, several lines of evidence lead to these inferred tooth row positions. Most critically, the unworn M1 is wholly consistent with *Pantolambda bathmodon* (see description below). Additionally, an examination of the alveoli anterior to the tooth supports this interpretation. A broad alveolus exists anterior to the dP2. Anterior to this alveolus, a flattened edge evidences a second, larger alveolus that sits more buccally in the jaw. The relative positions of these alveoli are consistent with the position of the P1 as immediately adjacent and posterolingual to the canine in *Pantolambda bathmodon* (Matthew, 1937).



Figure 9: The right maxilla of NMMNH P-27844 consisting of dP2, dP4, dP5, and M1 (anterior oriented to the right of the image). These deciduous premolars are the first known for this taxon. Scale bar is 1 cm long. Specimen photo courtesy of Greg Funston.

Description

dP2: The second deciduous premolar (dP2) possesses a more simplified crown shape than the subsequent permanent tooth. dP2 has three roots and a triangular cross-section that is dominated by a pronounced, lingually situated paracone. The pre- and postparacristae of the paracone are moderately developed with both crests extending buccally to the edge of the tooth. The buccal slope of the paracone encompassed by these cristae is flattened and also extends to the edge of the tooth. The buccal cingulum is weakly developed. The tooth has a weak ectoflexus and the metastylar lobe extends further distally than the parastylar lobe extends mesially. A small, weakly developed protocone can be seen on the distolingual side of the paracone. The dP2 does not have a precingulum and, aside from the slight bulge that constitutes the protocone, a postcingulum also has not developed. Overall, the distal extension of the metastylar lobe and the distolingual position of the protocone result in an asymmetry of the tooth within the maxilla. Flattened wear facets are developed along both the pre- and postparacrista.

The dP2 is broadly similar to its permanent successor in *Pantolambda bathmodon* (Fig. 10; NMMNH P-19544; AMNH 16663) in having an overall triangular cross-section and three roots. Similarly, both the dP2 and P2 are dominated by a large paracone with a flattened sloping buccal side. However, the ectoflexus of the P2 is more developed than that of the dP2 and forms a sharp 'v' shape rather than a weak 'u' shape. This shape is due to the more buccal extent of both the metastylar and parastylar lobes in the P2.

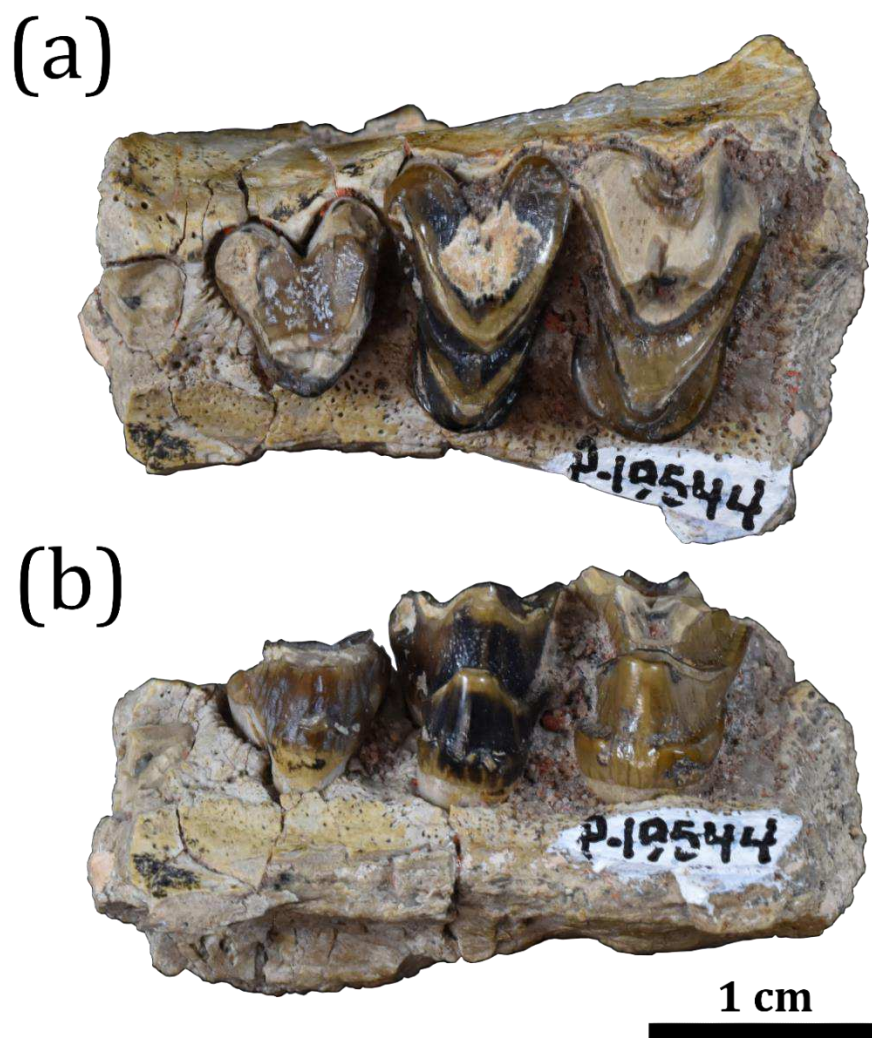


Figure 10: The adult premolars of *Pantolambda bathmodon* as illustrated by the left maxilla of NMMNH P-19544. The single root of p1 is present with the crowns of P2, P4, and P5. The anterior of the maxilla is oriented to the left of the image.

The dP2 of *Pantolambda bathmodon* differs from that of *Alcidedorbignya inopinata* (MHNC 1210; MHNC 8423; Muizon and Marshall, 1992; Muizon and Billet, 2022) in terms of the number of roots and its cross section. The dP2 of *Alcidedorbignya* is single-rooted and has a simpler, more peg-like crown. While these teeth are notably different in terms of their morphology, this difference is unsurprising given that a single-rooted P2 is an autapomorphy for *Alcidedorbignya* (Muizon et al., 2015). The dP2 of *Pantolambda* is similar to the dP2 of *Barylambda faberi* (FMNH P-14637) in terms of both its triangular cross-section, the distolingual position of a small protocone, and the metastylar crest extending distally. The dP2 of *Pantolambda* differs from *Barylambda* in both having a less pronounced ectoflexus and a less developed parastylar lobe. The dP2 of *Pantolambda* is very similar to that of

Coryphodon (AMNH 15797; Lucas and Schoch, 1990) in terms its overall morphology, but differs in its lack of a pronounced paracingulum.

dP4: The penultimate deciduous premolar (dP4) possesses a more simplified crown shape than the subsequent permanent tooth. dP4 has a triangular cross-section dominated by a pronounced, centrally located paracone. The pre- and post-paracristae are more strongly developed than those of dP2. Both cristae extend buccally to the outer edge of the tooth. At the buccal margin of the tooth, the preparacrista curves mesially to form a small, rounded preparastylar lobe. The surface of the preparacrista is smooth, but the surface of the postparacrista bears two low, weakly-developed cuspules slightly lingual to its termination along the buccal margin. Additionally, the postparacrista exhibits slight wrinkling in the enamel along its mesial margin. The buccal slope of the paracone is flatted along the central axis of the tooth but slightly concave overall. This concavity is caused by the raised, wing-like pre- and postparacristae. A clearly developed, shallow ectoflexus is present. A shelf-like buccal cingulum extends along the entire buccal margin of the tooth. A small protocone is developed on the distolingual side of the crown. The preprotocrista is short and weakly developed, terminating before the lingual border of the paracone. The postprotocrista is characterized by a flattened wear facet. The weak postprotocrista transitions into a poorly developed postcingulum which extends to the distobuccal edge of the tooth. A slight paracingulum extends lingually along the outer margin of the tooth from the parastylar lobe. Clear wear facets along the exterior edges of the pre- and post-paracristae are present and the apex of the paracone is abraded.

The dP4 of *Pantolambda bathmodon* is broadly similar to its permanent successor in its prominent paracone and triangular cross-section. However, it departs sharply from the P4 in both the level of development and the position of the protocone. In the permanent dentition, the protocone is large and located slightly anterior to the central axis of the tooth (anterior to the apex of the paracone). The reverse is true for the dP4 with the apex of the paracone anterior to the protocone which is positioned distolingually. Additionally, the permanent successor of the dP4 has much more strongly developed pre- and postprotocristae. These crests contribute to the

'double-v' morphology of pantodont premolars, but are not well developed in the deciduous dentition.

The dP4 of *Pantolambda bathmodon* is strikingly different than that of *Alcidedorbignya*. The dP4 of *Alcidedorbignya* is an asymmetrical tooth with an exaggerated, distally extended, flattened metastylar lobe, while the parastylar and metastylar lobes for *Pantolambda bathmodon* are more subequal in size and extent. The exaggerated metastylar lobe of *Alcidedorbignya* appears similar to the pattern hinted at in *Barylambda* (although, this tooth in FMNH P-14637 is heavily abraded). The protocone of the dP4 of *Coryphodon* is similarly underdeveloped to that of the dP4 of *Pantolambda* but the overall shape of the tooth is more subquadrangular than triangular. This dP4 shape for *Coryphodon* results from the pre- and postparacristae being less strongly buccally directed (i.e. with a wider angle between them).

dP5: The ultimate deciduous premolar is molariform and subquadrangular in cross-section. Both the paracone and metacone are well-developed and subequal in size and height. The buccal slopes of both cusps are broken in the right maxilla and, therefore, fine details of the pre- and postparacristae are lost. The protocone is large and dominates the lingual margin of the tooth. Both a paraconule and metaconule are present in the tooth. The paraconule forms a distinct rounded cusp along the preprotocrista and is positioned slightly mesial to the peak of the paracone. The preparacrista becomes the preparaconular crista and continues along the mesial margin of the tooth to form the paracingulum before terminating at the parastyle. The metaconule is less pronounced than the paraconule (although still forming a more distinctly rounded cusp than in the subsequent molar series) and forms on the postprotocrista. A well-developed postmetaconular crista extends distally from the metaconule and becomes the metacingulum of the tooth. As the cristae transition to these basal cingula, they become shelf-like. The dP5 also preserves evidence of shelf-like pre- and postcingula. These cingula are distinct, but less pronounced than those of the molars. There is no lingual cingulum connecting these shelf-like cingula.

The permanent successor (P5) of *Pantolambda bathmodon* is a strikingly different tooth than the dP5. The P5 of *Pantolambda bathmodon* is triangular in outline and bears a centrally located paracone and a large, well-developed protocone. The dP5 can therefore be more productively compared with the M1 of the taxon. The tooth is broadly similar in shape and in the presence and arrangement of cusps and crests. The main difference lies in the development of the ectoflexus. The ectoflexus of dP5 narrower and more 'v' shaped than the flattened 'u' shape of M1. This configuration is caused by the more buccal extent of the parastylar and metastylar regions of the tooth.

Similar to the contrast seen with the dP4, the dP5 of *Pantolambda bathmodon* differs from that of *Alcidedorbignya* in being broadly symmetrical with parastylar and metastylar regions that are subequal in size. Although less extreme than in dP4, the metastyle of the dP5 of *Alcidedorbignya* is similarly distally extended. This feature results in an overall asymmetrical tooth. The dP5 of *Alcidedorbignya* is similar to the dP4 of *Pantolambda bathmodon*. The dP5 of *Barylambda faberi* is worn and abraded and it is difficult to draw much fine detail from the specimen. However, an interesting pattern arises in its relationship with its M1. As seen in the dP5 of *Pantolambda bathmodon*, the ectoflexus of *Barylambda* is more pronounced and 'v' shaped than the flattened structure observed in the M1 of that taxon. The dP5 of *Coryphodon* is more anteroposteriorly broad than the dP5 of *Pantolambda bathmodon*.

Permanent Dentition:

The first upper right molar (M1) is also present in NMMNH P-27844. The molar is nearly unworn with only the slightest mesowear developing on the preparacrista and the preprotocrista. Even another relatively unworn specimen (AMNH 15934; Fig. 11) captures a later wear stage where the enamel has been breached to expose the dentine along the preparacrista, postmetacrista, and centrocrista.

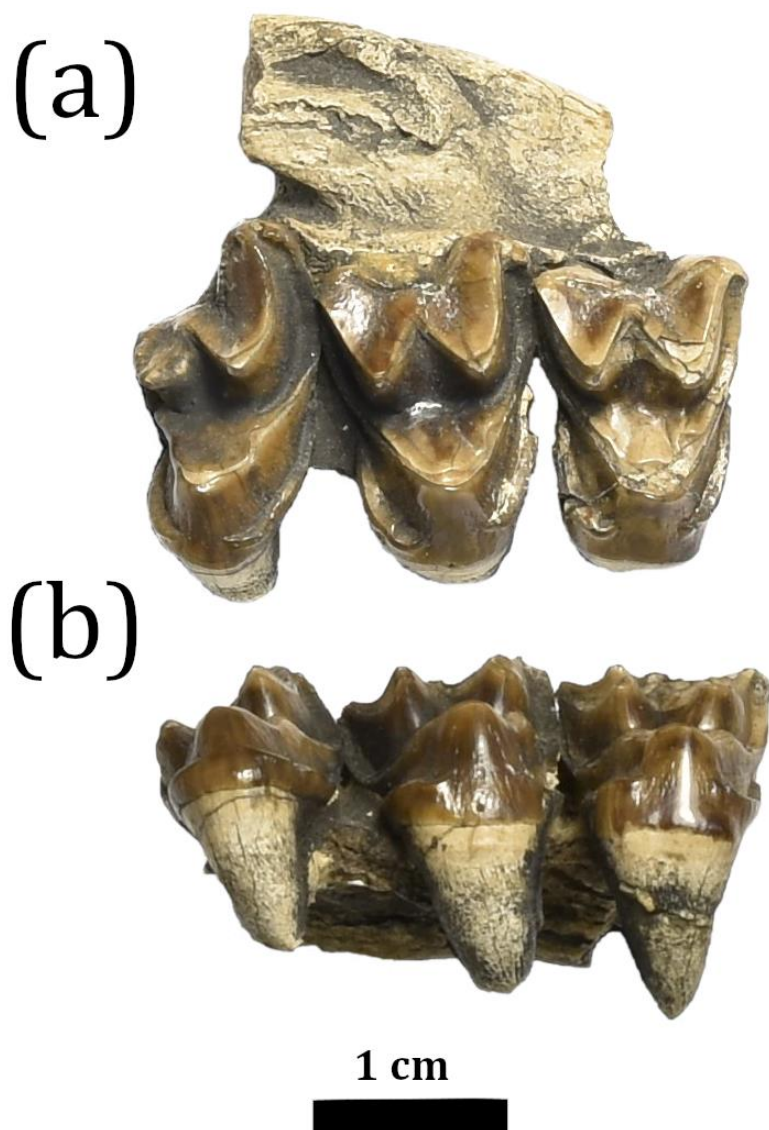


Figure 11: The upper M1-M3 of AMNH 15934 (anterior to the right). These teeth compare favorably with the M1 of NMMNH P-27844 and evidence that this juvenile specimen can indeed be referred to *Pantolambda bathmodon*.

Since the NMMNH P-27844 M1 presents a rare opportunity to see this tooth mostly unworn, I briefly describe it here and contrast it with the molars of *Pantolambda cavirictum* (Fig. 12). The M1 of *Pantolambda bathmodon* is a quadrangular tooth with three large roots (two buccal and one lingual). The paracone and metacone are large and subequal in height. The buccal edges of the cusps are flattened and slope down to a weak buccal cingulum. Wing-like, buccally directed cristae extend from the apices of these cusps. The postparacrista and the premetacrista (in combination, the centrocrista) form a low mesostyle at their intersection. The parastylar lobe of the M1 is more buccally directed than the metastylar lobe. This results in a shallow ectoflexus and a weakly L-shaped margin of the tooth. As seen in Fig. 11, the buccal

extent of the parastylar region becomes more pronounced throughout the molar series with the M2 having a strongly L-shaped margin.

The large protocone sits along the central axis of the M1. Well-developed pre- and postprotocristae extend from this cusp and, after becoming the para- and metacingulum, respectively, extend to the buccal margin of the tooth. A well-developed paraconule is present on the preprotocrista and a smaller metaconule is present on the postprotocrista. Shelf-like pre- and postcingula are present, but there is no lingual cingulum. These features are all present in AMNH 15934 and support the referral of NMMNH P-27844 to *Pantolambda bathmodon*.

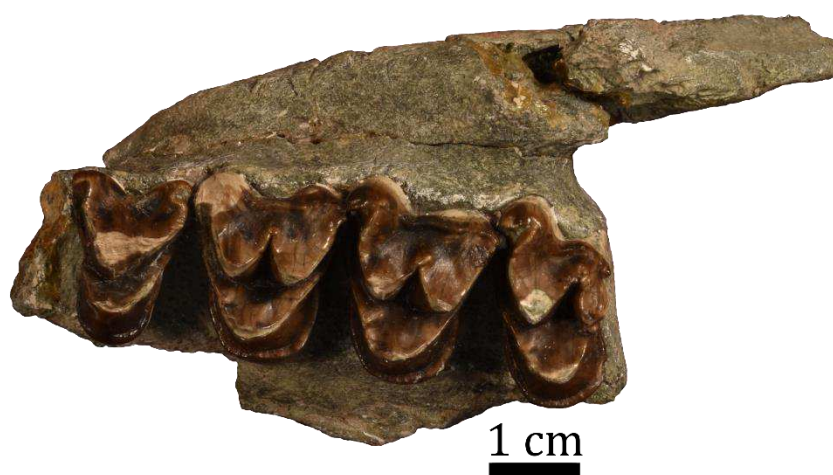


Figure 12: The upper dentition (P5-M3) of *Pantolambda cavirictum* (USNM 21327) (anterior to the left) illustrating some of the key differences between the species.

There are many resonances between the molars of *Pantolambda bathmodon* and those of *Pantolambda cavirictum* including the arrangement of the major cusps and wing-like crista that form a w-shaped ectoloph. A key difference between *Pantolambda bathmodon* and *Pantolambda cavirictum* is the latter possesses a shelf-like lingual cingulum connecting the pre- and postcingula. In addition to the stark size contrast between these taxa, this particular morphological distinction remains consistent through all of the specimens of these taxa that I have examined.

Thus, the right maxilla of NMMNH P-27844 both represents new anatomy for the genus in terms of the first deciduous dentition known and further corroborates existing molar observations. In addition to its bearing deciduous premolars, the osteological immaturity of NMMNH P-27844 is evidenced because it has not yet fused the epiphyses of several long bones including the humeri, radiae, and ulnae and because its midline cranial suture is contacting but not fused (Fig. 13).



Figure 13: The posterior portion of the frontal of NMMNH P-27844. The central axis of the specimen shows where the left and right frontals are contacting but not yet fused.

Although the deciduous dentition differs from the permanent dentition, the postcranial morphology of P-27844 is broadly concordant with that of more mature individuals of *Pantolambda bathmodon*. Some minor differences between the juvenile and adult skeleton appear to be a lower sagittal crest along the parietals and a straight radius rather than one that exhibits more sigmoidal curvature. Notably, even at an early ontogenetic stage, this individual already possessed the robust forelimbs and overall body proportions of adults.

I have examined the upper dentition of *Pantolambda* through the lens of NMMNH P-27844. Aspects of the lower dentition can be elucidated through considering the specimens that have been referred to *Pantolambda intermedium*.

Pantolambda intermedium is the most poorly known species of this genus. It previously was only known from the type specimen (a fragmentary dentary preserving m1-2; Fig. 14) and some additional isolated teeth referred to the species (e.g. Leite, 1994). In addition to being intermediate in size between *P. bathmodon* and *P. cavirictum*, the lower dentition of *Pantolambda intermedium* differs from its congeners in two key ways.



Figure 14: USNM 8384, the type specimen of *Pantolambda intermedium* in (a) occlusal and (b) lingual views.

Pantolambda intermedium possesses a well-developed entoconid on m1-2. Additionally, a small diastema is present in the dentary between p1 and p2. In

contrast, *P. bathmodon* (Fig. 15) lacks an entoconid on the mesiolingually sloping postcristid of its lower m1-2. Furthermore, the lower dentition of *P. bathmodon* is tightly spaced and no diastema is present between its lower premolars. These same anatomical features also distinguish *P. intermedium* from *P. cavirictum* (Fig. 16) which possesses a large diastema between p1 and p2 and a less developed entoconid on the m1-2.



Figure 15: The lower dentition of *Pantolambda bathmodon* (NMMNH P-72346) in (a) lingual and (b) occlusal views. The open lingual margin of the talonid on m1-2 is particularly clearly illustrated in this specimen. Photos courtesy of Tom Williamson.



Figure 16: The lower dentition of *Pantolambda cavirictum* (AMNH 3691) illustrating the weak entoconid and the large diastema between the p1 and p2.

The presence of *Pantolambda intermedium* in the San Juan Basin is recognized with the worn dentary (NMMNH P-19774). Fortuitously, this specimen preserves m1-2 (Fig. 17a, b) which enables direct comparison with the type specimen of the species, USNM 8384 (Fig. 14). Despite extensive wear obliterating the trigonid cusps and large portions of the talonid, some lingual enamel remains in the talonid basin. The large entoconid that defines the species is present on both the m1 and the m2. The presence of this well-developed entoconid distinguishes this specimen from the dentition of *P. bathmodon* and *P. cavirictum*. Additionally, while the presence of a diastema cannot be evaluated from the NMMNH P-19774 dentary, these worn teeth show another subtle difference from the m1 and m2 of *P. cavirictum*. The lingual margins of the trigonid and talonid of the m1 and m2 of NMMNH P-19774 are subequal in size. While this similarity in size between the mesial and distal regions of the molar is similar to the shape observed in *P. bathmodon*, the lingual margin of the trigonid of *P. cavirictum* is narrower than the lingual margin of the talonid in both the m1 and m2. Thus, NMMNH P-19774 is further distinguished from the dentition of *P. cavirictum*.

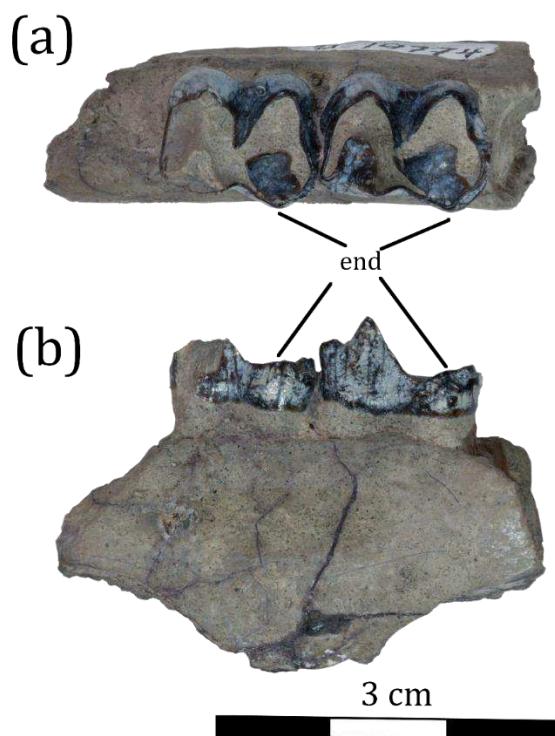


Figure 17: NMMNH P-19774, a right dentary preserving extremely large entoconids despite the highly abraded enamel of the trigonid and the buccal edge of the talonid. Abbreviation: end = entoconid.

An additional isolated left m3 (NMMNH P-72117; Figure 18a-e) expands our understanding of the anatomy of *Pantolambda intermedium*. P-72117 consists of a partial, narrow trigonid with a wide talonid basin that is shallower than in *P. bathmodon*. The postcristid is more cuspidate than that seen in the m3 of *P. bathmodon* with both a small entoconid developing near the hypoconulid and entoconulid present. The paraconid is large and raised to nearly the same elevation as the metaconid which is similar to the condition in *P. bathmodon*.

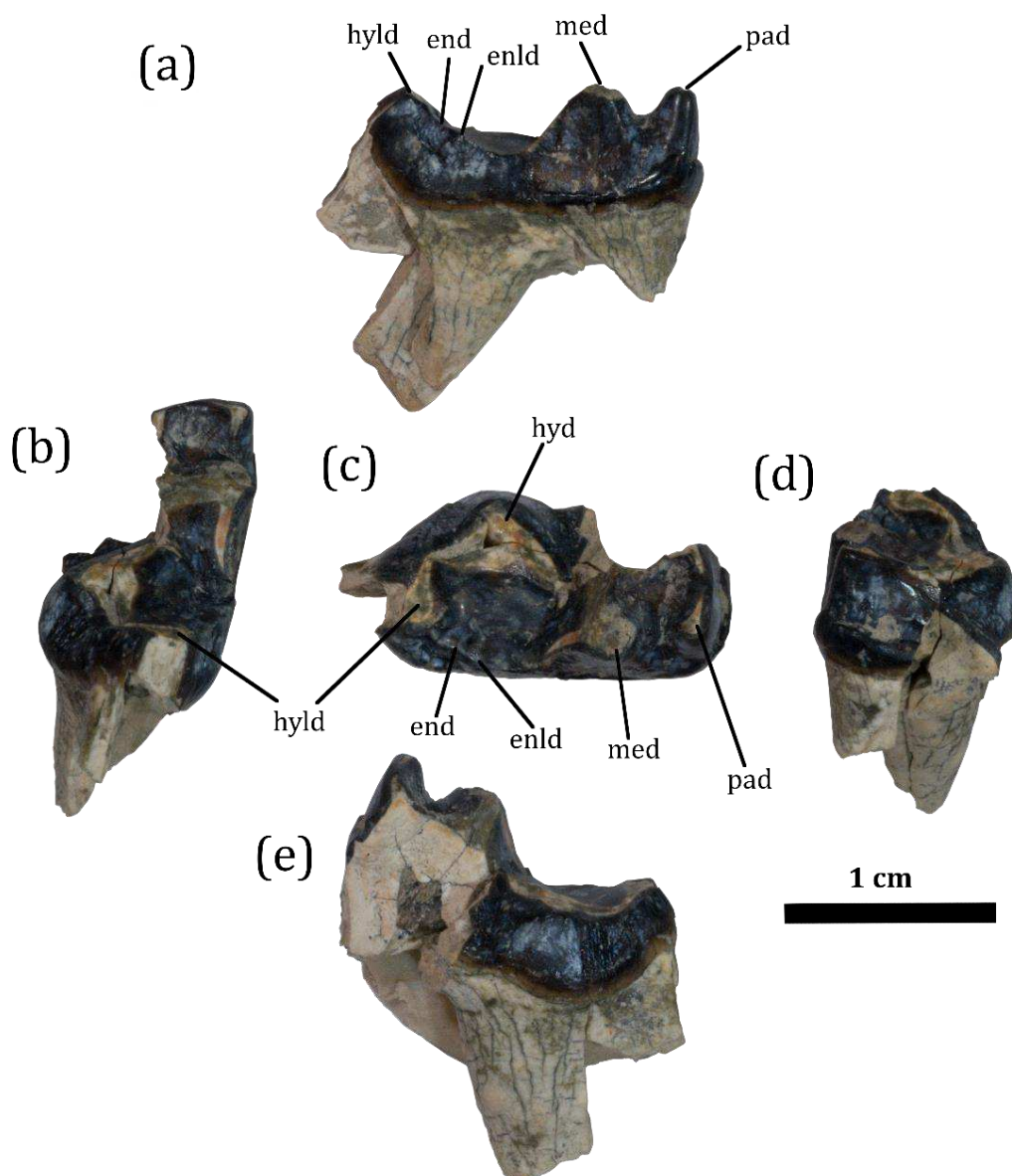


Figure 18: NMMNH P-72117, an isolated m3 referred to *Pantolambda intermedium* in (a) lingual, (b) mesial, (c) occlusal, (d) distal, and (e) buccal views. Abbreviations: end = entoconid, enld = entoconulid, hyld = hypoconulid, med = metaconid, and pad = paraconid.

The San Juan Basin also yields the first clear postcrania known for *Pantolambda intermedium*. A concreted, partial braincase (NMMNH P-21646; Fig. 19) preserves the posterior portion of the skull roof and the left occipital condyle. The braincase bears low sagittal and nuchal crests similar to *P. bathmodon*. As seen in *Pantolambda bathmodon*, the nuchal crest has a shallow posterior slope. Immediately ventral to the sagittal crest, several temporal foramina are present. Similar levels of vascularization appear in *P. bathmodon*, *Alcidedorbignya* (Muizon et al., 2015), and *Bemalambda nanshiungensis* (Chow et al., 1977). The moderate temporal vascularization of these smaller pantodonts contrasts with more intense vascularization extending onto the lateral surfaces of the parietals of the large-bodied pantodont, *Titanoides* (FMNH 8655).

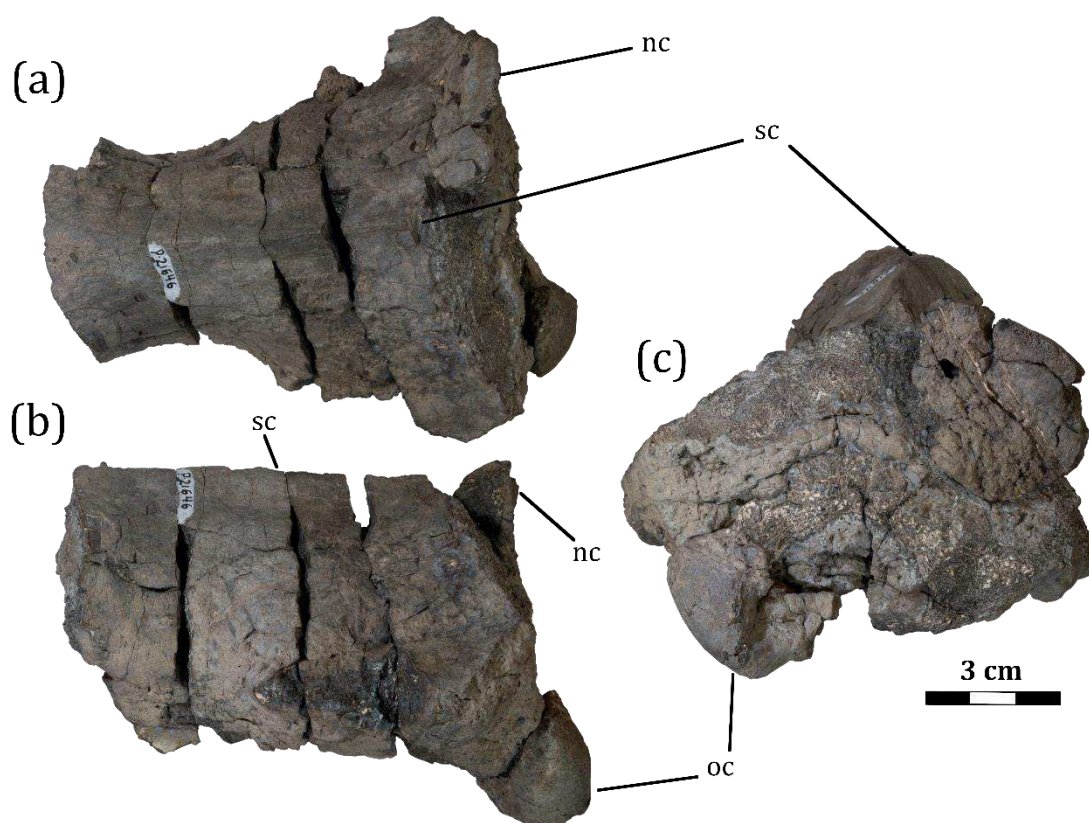


Figure 19: The partial braincase of NMMNH P-21646 showing low sagittal and nucha crests. Abbreviations: nc = nuchal crest, oc = occipital condyle, and sc = sagittal crest.

The braincase illustrates that the size variations observed between the dentitions of *Pantolambda bathmodon*, *P. intermedium*, and *P. cavirictum* are similarly expressed in body proportions (Fig. 20). *Pantolambda intermedium* is $\sim 1.3\times$ larger than *P. bathmodon* in terms of linear measurements and *P. cavirictum* is $\sim 1.5\times$ larger than

P. bathmodon. The consistent anatomical differences between the dentitions of these animals coupled with the systematic size variations associated with those differences supports the validity of *P. intermedium* as a distinct species despite its limited fossil record.

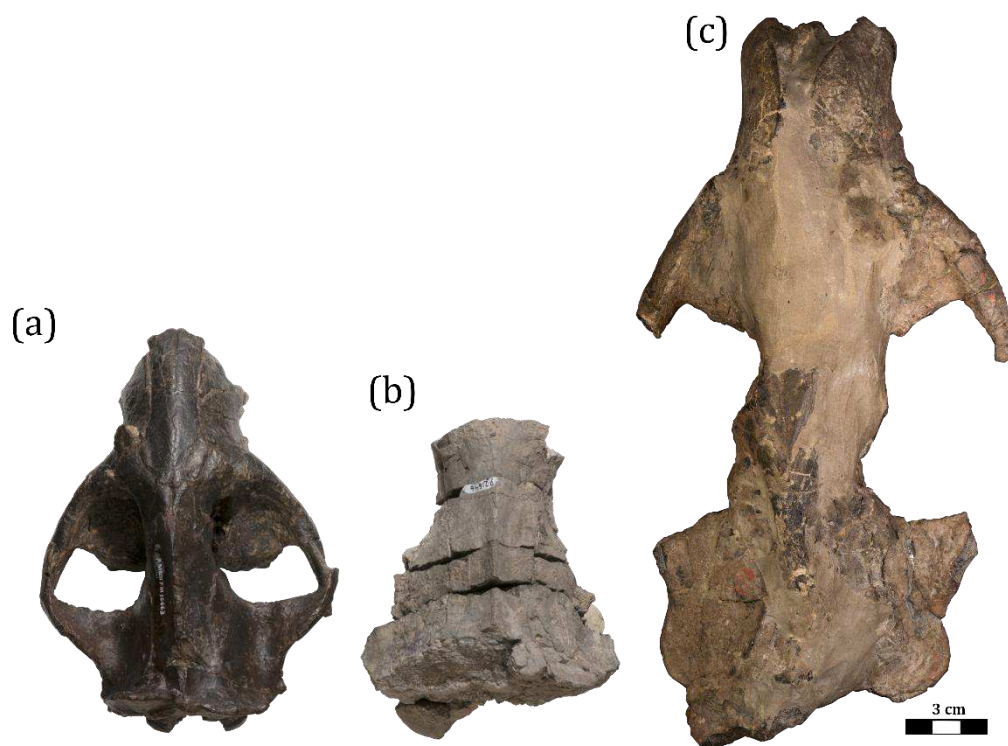


Figure 20: The relative size variations within *Pantolambda* can be visualized by observing the crania of (a) *P. bathmodon* (AMNH 16663), (b) *P. intermedium* (NMMNH P-21646), and (c) *P. cavirictum* (AMNH 963). Photo (a)/(b) courtesy of Tom Williamson.

The final specimen referred to *Pantolambda intermedium* was found in close association with the braincase (NMMNH P-21646). A partial scapula (NMMNH P-21647) preserves the glenoid region and the distal portion of the scapular body (Fig. 21). The glenoid cavity is an elongated oval that tapers anteriorly to a prominent, triangular supraglenoid tubercle. A coracoid process distinct from the tubercle is not present. *P. bathmodon* possesses similar scapular morphology. There is broad correspondence between the scapulae of *P. cavirictum* (Fig. 22) and *P. intermedium* as well. *P. cavirictum*'s scapula differs from both smaller congeners in having a more bulbous supraglenoid tubercle that extends further distally from the glenoid cavity.

The condition in *Pantolambda* contrasts with other pantodonts. *Alcidedorbigna* possesses a relatively small tubercle distinct from a rounded coracoid process. The larger-bodied pantodonts, *Barylambda* and *Coryphodon* exhibit both a prominent tubercle and a well-developed coracoid process.

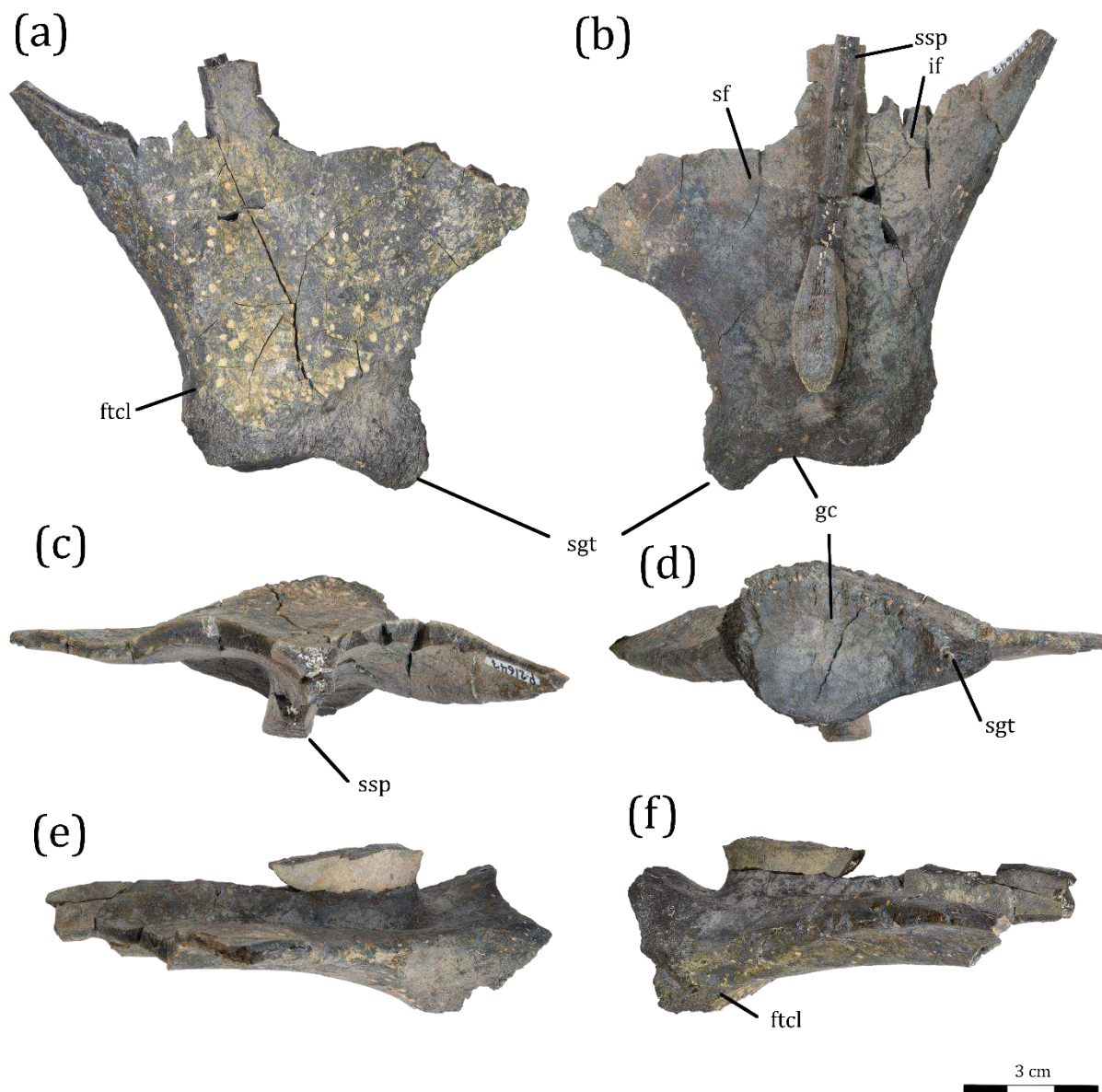


Figure 21: A partial scapula of *Pantolambda intermedium* (NMMNH P-21647) in (a) medial, (b) lateral, (c) proximal, (d) distal, (e) anterior, (f) posterior views. Scale bar = 3 cm. Abbreviations: ftcl = fossa for the origin of the caput longum of the triceps, gc = glenoid cavity, if = infraspinus fossa, sf = supraspinatus fossa, sgt = supraglenoid tubercle, ssp = scapular spine

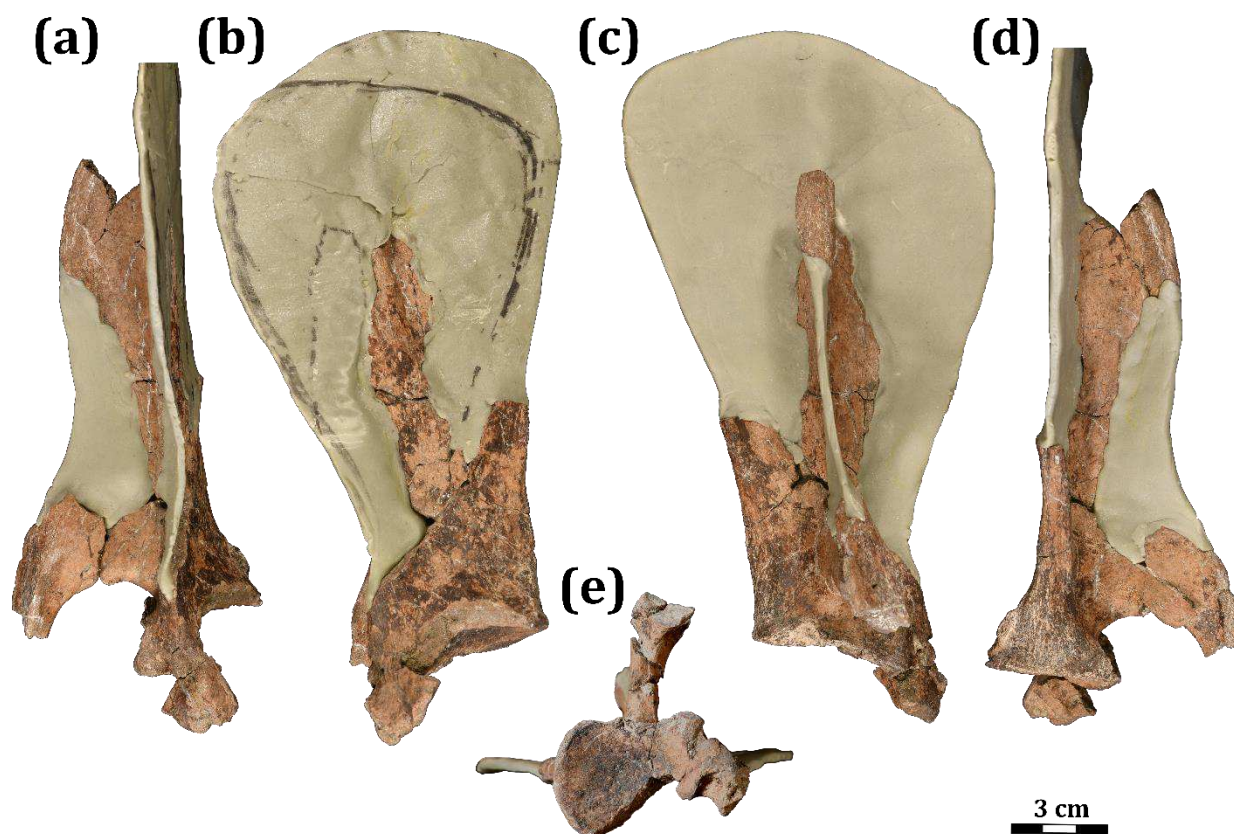


Figure 22: A partial scapula of NMMNH P-57738 in (a) posterior, (b) medial, (c) lateral, (d), anterior, and (e) distal views.

Reflecting on the scapula leads to reflections on the final specimen in this treatment, NMMNH P-57738. This specimen of *Pantolambda cavirictum*, in part, preserves a scapula, clavicle, and articulated forelimb.

The clavicle of NMMNH P-57738 is preserved still in articulation with the humeral head (Fig. 23). The bone is overall stout and robust and has a rounded cross section that contrasts with the more flattened, slender presentation of the clavicle in *Pantolambda bathmodon* (Fig. 24) and *Alcidedorbignya* (Muizon et al., 2015). The sternal (medial) end of the clavicle widens to a rounded surface with an anteriorly directed process while the acromial (lateral) end forms a flattened oblique surface. A similar pattern is observed in *Pantolambda bathmodon* with the acromial end forming a smaller, but similarly flattened oblique surface. The clavicle of *P. bathmodon* differs in the sternal end being flattened with a more straight margin rather than a rounded end.

Notably, although the sternum is not known in *P. cavirictum*, the manubrium of *P. bathmodon* (Fig A1-A2) does not preserve clear articular surfaces for the clavicle.

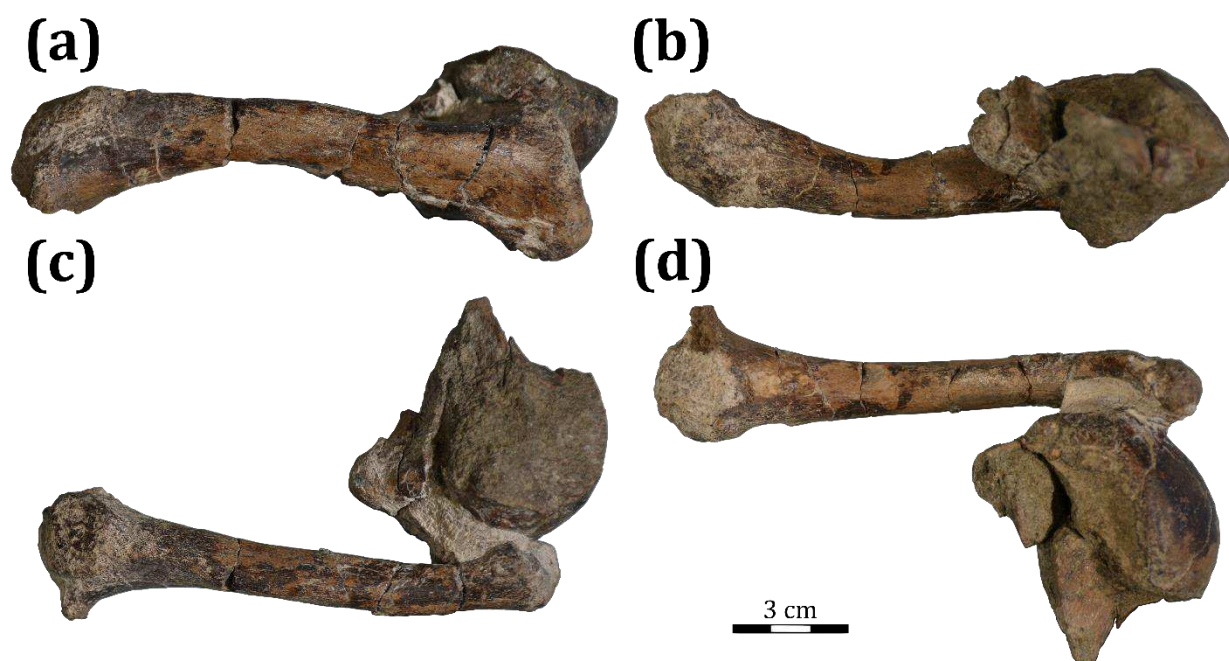


Figure 23: The right clavicle of *Pantolambda cavirictum* (NMMNH P-57738) in preserved in articulation with the humeral head in (a) anterior (b) posterior (c) dorsal and (d) ventral views. Photos courtesy of Tom Williamson.

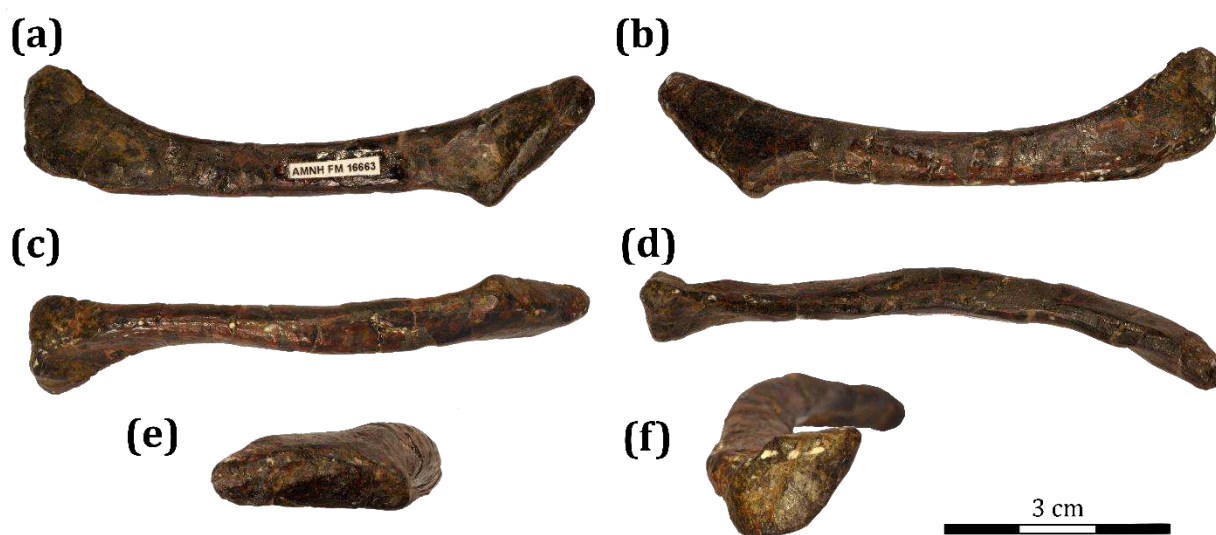


Figure 24: The clavicle of *Pantolambda bathmodon* (AMNH 16663) in (a) posterior, (b) anterior, (c) dorsal, (d) ventral, (e) lateral, (f) medial views.

NMMNH P-57738 also preserves the majority of an articulated forelimb (Fig. 25) consisting of a complete radius and ulna and the distal portion of a humerus. These bones are stout and evidence the robust forelimbs associated with the genus. Although the radius is less sinusoidal in *P. cavirictum* than in *P. bathmodon*, both possess a strongly developed pronator crest.



Figure 25: The articulated forelimb of *Pantolambda cavirictum* (NMMNH P-57738).



Figure 26: The right manus of NMMNH P-57738 in dorsal view. The bones of the carpus have been rotated slightly out of life position on this specimen.

Manus: The right manus of NMMNH P-57738 (Fig. 26) consists of the scaphoid, lunate, cuneiform, unciform, magnum, centrale, trapezium, trapezoid, metacarpals I-V, proximal phalanges I-IV, and intermediate and distal phalanges I-V (Fig. 1). The only bones not present in this specimen are the pisiform and proximal phalanx V. The bones were found in association and nearly in articulation. The carpal bones are rotated out of articulation and digits I and V slightly displaced so that the lateral edges of their metacarpals face dorsally. Interestingly, the radius and ulna of this specimen were found reversed from life position relative to the manus with the radius adjacent to the cuneiform and the ulna to the scaphoid. This arrangement underscores that some skeletal complexes of this specimen are preserved in association but not direct articulation. The manus has been prepared so that the dorsal aspects of the bones are visible.

The manus of *Pantolambda cavirictum* is pentadactyl and mesaxonic with the primary axis of the foot passing through the third digit. The manus shows the primitive alternating arrangement of carpals with the lunate and unciform showing a clear contact (Gregory, 1910; Novacek and Wyss, 1986). However, contact between the scaphoid and the magnum is precluded by the centrale. This carpal arrangement is also observed in *Pantolambda bathmodon*. The probable phalangeal formula of *Pantolambda cavirictum* conforms to the primitive mammal condition (2-3-3-3-3?).

Scaphoid: The scaphoid is the medialmost of the proximal carpals. In this specimen, the scaphoid has rotated out of life position and around the medial edge of the manus. It has a broad, square-shaped radial facet which with the radial facet of the lunate creates a smooth rectangular surface. There is a saddle-shaped depression between the radial facet and another small, bulbous protrusion (the palmar tubercle). This saddle shape extends from the proximal to the palmer surface of the bone and could be where the flexor carpi radialis sat. The dorsal surface of the bone is anteroposteriorly shortened, mediolaterally elongated, and roughly barbell-shaped. The scaphoid's distal edge comes into contact with several bones. Proceeding from lateral to medial, the contact with the centrale is short and straight, with the trapezium concave, and with the trapezoid concave to flat. The medialmost side of the distal edge flattens into a small facet where the prepollex fits.

Lunate: The lunate articulates with the lateral surface of the scaphoid. The radial facet of the lunate, located on its proximal surface, is square-shaped with straight dorsal, plantar and medial margins and a concave lateral margin. The radial facet is a slightly concave surface and is subequal in size to the radial facet of the scaphoid. The dorsal surface of the lunate is overall rectangular in shape with the long axis extending mediolaterally. The margin of the radial facet forms the entirety of the dorsal surface's proximal side. The lateral margin of the lunate is angled mediolaterally and forms a straight contact with the cuneiform. The distal margin of the lunate's dorsal surface is broad, and flat to slightly concave and contacts with the unciform. A small, concave dip in the distal margin marks where the magnum contacts the lunate. The distal portion of the medial margin is straight and abuts the centrale. The most proximal portion of the medial margin forms a small convex surface. This surface marks the small dorsal contact between the lunate and the scaphoid.

Cuneiform: The proximal surface of the cuneiform is characterized by two, concave facets separated by a low ridge. The medial facet (ulnar facet) is subrectangular with straight long edges and convex short edges. The surface of the ulnar facet is saddle-shaped with the high points located along the long edges of the rectangle. The pisiform facet is located lateral to the ulnar facet. It forms an L-shape in proximal view and widens dorsally. The dorsal surface of the cuneiform is proximodistally compressed, mediolaterally elongated, and rectangular. The dorsal surface has two indentations, each located directly under the facets on the proximal surface. The free lateral margin of the cuneiform is slightly convex. The distal margin is composed of two slightly concave facets at a shallow angle to one another. The medial margin of the cuneiform (which contacts the unciform) is small and convexly curved.

Unciform: The unciform is an irregular pentagon with five surfaces visible in dorsal aspect: the lateral margin and contacts with the cuneiform, lunate, magnum, and metacarpal IV and V. The lateral margin of the unciform (which marks the edge of the proximal row of carpals) is a small, slightly convex surface. The contact between the unciform and the cuneiform is oriented proximolaterally and is convex and

scoop-shaped. The articular surface between the unciform and the lunate is a broad, flattened plane. The contact with the magnum is a similarly flattened surface. The distal margin of the unciform forms a broadly straight edge with a slight convex bend demarcating the places where metacarpals IV and V articulate. The two longest edges of the unciform are the contacts with the cuneiform and the metacarpals. The lunate and the magnum contacts are smaller and approximately subequal in extent. The lateral margin is the smallest side of the unciform.

Magnum: The magnum is a small bone with a trapezoidal dorsal surface. Its lateral edge is straight and forms a short contact with the unciform. The magnum has a small contact with the lunate that forms a convex edge. A short concave edge contacts with the centrale. The shortest edge of the magnum (which contacts the trapezoid) is proximodistally-oriented and straight. The distal edge of the magnum rests on metacarpal III. Plantar from the dorsal surface, the magnum forms a shallowly dipping rod-like projection that appears to sit ventral to the lunate and the centrale. This projection is smooth-surfaced and saddle-shaped.

Centrale: The centrale wedges between and slightly distal to the lunate and the scaphoid in the manus. The dorsal surface of the centrale is shaped like a right-angled trapezoid. The longest edge of the centrale is located on its medial side and contacts the trapezoid. The centrale-trapezoid contact is straight. Laterally (moving counterclockwise) from that edge, is a short slightly concave articular surface that contacts with the magnum. A straight, flat facet of similar length to the centrale-magnum contact marks where the centrale abuts the lunate. The scaphoid facet of the centrale angles distomedially from the lunar facet and is, like most of the other surfaces of the bone, straight-edged and flattened. The centrale is one of the smallest carpal bones in terms of its dorsal exposure (subequal in size to the magnum), but is elongated plantarly and extends into the palm.

Trapezoid: The trapezoid has rotated about 90° counterclockwise from its original life position. The dorsal surface of the trapezoid is shaped like a right triangle with a convexly curved hypotenuse. The lateral tip of the triangle flattens into a small facet which articulates with the magnum. The distal edge of the element makes up the

long side of the right angle and is slightly concave. It forms a contact with metacarpal II. The medial edge is straight and forms the contact with the trapezium. The proximal edge represents the hypotenuse of the triangle and has a moderate convex curve. The proximal edge forms the contact with centrale laterally and the scaphoid medially.

Trapezium: The trapezium is the medialmost of the distal carpal bones. In this specimen, it is displaced medially and rotated in the same manner as digit I. The dorsal surface is roughly heart-shaped, with the concave distal edge resting on metacarpal I. The distal portion of the lateral edge is proximo-distally oriented, straight, and contacts with the trapezoid. The proximal portion of the lateral edge is straight and angled medially. This edge abuts the scaphoid. The contact with the scaphoid continues to the proximal edge of the element. The medialmost portion of the proximal edge flattens into a small facet where the prepollex sesamoid sits. The free, medial margin of the trapezium is small and slightly convex.

Metacarpals: The five metacarpals articulate to form a series of slightly concave surfaces with which the distal carpal bones articulate. The metacarpals are dorso-palmarly compressed. The proximal ends of the metacarpals have a weak u-shape in dorsal view which forms a slightly raised lip and is bounded on the outer edges by flattened angled facets. These angled facets mark where the metacarpals contact the adjacent metacarpals and are present on the lateral side of metacarpal I, the lateral and medial sides of metacarpals II, III, and IV, and the medial side of metacarpal V.

Proximal Phalanges: The proximal phalanges are trapezoidal in shape in dorsal view. The proximal edge of the phalanx is longer than the distal edge with the proximodistal length falling in between these two measurements. The phalanges are dorso-palmarly compressed. The dorsal surface of the phalanges is saddle shaped and dips toward the center from raised lips on the proximal and distal edges. Both the proximal and distal surfaces of the phalanges are slightly concave. The lateral and medial margins taper proximodistally and have a generally straight outline. This outline is only slightly broken by the presence of tubercles and impressions.

On the lateral edge of proximal phalanx IV, there is a flattened surface near the proximal end and concave facet near the distal margin. This distal facet is ellipsoidal and broadens toward the dorsal surface. The proximal margin of this facet forms a weak tubercle. On the medial side of the phalanx, the proximal flattening is less pronounced, but a similarly shaped distal facet that is excavated slightly deeper into the bone can be observed. Proximal phalanx II proves to be the mirror of phalanx IV in terms of the lateral and medial indentations with the flattened surface on the proximal side more pronounced on the medial side. In proximal phalanx III, there are two indentations on the lateral and medial margins which were likely for the interosseous tendons which connect to the extensor digitorum lateralis. The lateral and medial margins between these indentations are slightly concave. Proximal phalanx I is rotated and broken such that details of its lateral and medial margins are indeterminate and proximal phalanx V is missing from the specimen.

The proximal phalanges of *Pantolambda cavirictum* are more robust than those of many Paleocene mammals. Muizon *et al.* (2015) used the ratio between the proximal mediolateral width of the phalanx and its proximodistal length to quantify this quality. *Pantolambda cavirictum* (1.0) proves more robust than *Pantolambda bathmodon* (0.78) and much more robust than *Alcidedorbignya* (MHNC 8372; 0.47). The shafts of proximal phalanges of *Alcidedorbignya* have uninterrupted straight edges and do not exhibit any clear tubercles or marks on the bone where the interosseous tendons may have sat. Additionally, when transitioning from the proximal end to the central shaft, the phalanges of these animals show more pronounced convex curvature than those of *Pantolambda cavirictum*.

Intermediate Phalanges: The intermediate phalanges are shorter proximodistally than the proximal phalanges. They exhibit a similar tapering from a broad proximal end to a narrower distal end which results in a roughly trapezoidal shape in dorsal view. More precisely, the lateral and medial margins of the intermediate phalanges form an 'hourglass-shape'. Moving proximodistally, the margins initially are bulging and convex, then pass through an inflection point to become straight to slightly concave. The dorsal edge of the distal end has a raised lip with a subtle, flattened

space centered along the long axis of the element. This flattened surface is probably where the tendon of the extensor digitorum communis would rest.

Distal Phalanges (Unguals): The distal phalanges of *Pantolambda cavirictum* are dominated by a dorso-palmarly flattened, ungual process. They are longer proximodistally than mediolaterally. The distal phalanges are larger than the intermediate phalanges and similar in size to slightly larger than the proximal phalanges. The ungual crest of these phalanges is negligible and can mainly be seen in their slightly concave articular surface that contacts with the intermediate phalanges. Pronounced longitudinal fissures extend more than halfway lengthwise up the ungual and divide its distal portion into two distinct lobes are present on distal phalanges II and IV. The lateral ungual phalanges (I and V) are substantially smaller than II, III, and IV and lack a distinct fissure, instead coming to slightly asymmetric points.

Sesamoids: Between the scaphoid and the trapezium, there is a small sesamoid (prepollex). The bone has flattened facets where the scaphoid and the trapezium articulate. The surfaces of these facets form a right angle (90°). The exposed surface of the prepollex is comparable in size (albeit slightly smaller) to that of the centrale. This sesamoid likely formed in association with the musculus abductor pollicis longus and is found within most pentadactyl mammalian groups (Le Minor, 1994). An additional sesamoid that is slightly smaller than the prepollex is located below the distal portion of metacarpal V. The sesamoid is small (approximately the size of the lateral edge where metacarpal V broadens distally), rounded, and has a concave articular surface where the medialmost portion of the palmar surface of metacarpal V rests.

Discussion and Concluding Remarks:

These snapshots of new anatomy further our understanding of the genus *Pantolambda* and suggest additional reflections on the broader milieu of pantodont evolution.

The maxilla of NMMNH P-27844 shows that the penultimate and ultimate upper premolars of the deciduous dentition are strongly molariform as observed in the

deciduous dentitions of other pantodonts (e.g. *Alcidedorbignya*, *Coryphodon*) with a 'w' shaped ectoloph being present rather than the distinctive 'v' shapes of the adult premolars. This observation, in and of itself, is unsurprising as the deciduous premolars of eutherian mammals tend to be more molariform than their permanent successors (Luo et al., 2004; e.g. *Hyracodon*; Tanner and Martin, 1972). This similarity of form between the deciduous premolars and the molars results from the two sets of teeth being developmentally integrated (Zeigler, 1972). More interestingly, the deciduous premolars of NMMNH P-27844 show some similarities to the adult dentitions of both *Presbytherium* and *Cyriacotherium*, the cyriacotheriids that have been controversially posited as pantodonts⁸, in how they develop aspects of their 'molariform' character.

In particular, the angulation of the mesial 'v' of the ectoloph (formed by the preparacrista and postparacrista) and the texture of the ectoloph crests of NMMNH P-27844 are notable. In the most detailed rebuttal of the hypothesis that *Cyriacotherium* is a derived pantodont, Lucas (1998) argued that the way the upper premolar ectoloph developed was fundamentally different. Lucas (1998, p. 277) observed that, for *Cyriacotherium*, the "ectoloph V's [are] narrow anteroposteriorly" and that the "ectoloph crests [are] cuspidate" with the "enamel of molariform cheek teeth crenulated" and noted these features were not present in pantodonts. We can investigate the presence or absence of these features in more detail by examining the deciduous dentition of pantodonts. In NMMNH P-27844, the angulation of the mesial 'v' of the dP5 is $\sim 61^\circ$ while that of the mesial 'v' of the M1 was $\sim 75^\circ$. This difference in angulation arises from the more bucco-lingually directed preparacrista of the dP5. This orientation of the preparacrista more along the bucco-lingual axis of the ultimate premolar falls subtly between the more anteriorly-directed crista observed in the adult molars of *Pantolambda bathmodon* and the buccally-directed cristae in *Presbytherium* (Scott, 2010) and *Cyriacotherium* (Rose and Krause, 1982).

The enamel of the dP4 of NMMNH P-27844 is also more textured than that of the P4 of the permanent dentition (e.g. NMMNH P-19544; Fig. 10). In addition to general

⁸ See discussion in Chapter 1: 'Putative Pantodonts and the Curious Case of the Cyriacotheriids' for further context.

wrinkling of the enamel along the buccal slope of the paracone, this enamel texture results in some topography along the shearing crests of the tooth (particularly the postparacrista). While these bumps do not become fully cuspidate, they result in a wavy surface along apical edge of the crest. Due to the loss of the majority of the paracone and metacone enamel of the dP5, these features could not be fully evaluated on this tooth. However, the dP5 of *Alcidedorbignya* shows some texturing in the enamel on the pre- and postprotocristae and the development of an additional ?cusp lingual to the parastyle (Muizon and Billet, 2022, Fig. 7). In *Presbyterium*, we see an intermediate stage between the wavy development of the apical surface of the posterior shearing crest of *Pantolambda* and the strongly cuspidate crests of *Cyriacotherium*, with the presence of small cusps along the buccal extent of the postmetacrista. *Presbyterium* also evidences more wrinkled enamel on the cheek teeth overall than either *Alcidedorbignya* or *Pantolambda*⁹. Finally, the placement of the paraconule and metaconule on the dP5 of *Pantolambda*, positioned nearly flush with the bases of the paracone and metacone, respectively, is similar to the placement of these cusps in *Presbyterium* and *Cyriacotherium*. The grading in the shapes and positioning of tooth features between the molars of *Pantolambda*, *Presbyterium* and *Cyriacotherium* noted by Scott (2010) are further corroborated by features of the deciduous upper premolars of NMMNH P-27844.

Furthermore, while not strictly linked to the characteristics of the juvenile dentition, the placement of the mesostyle within the genus *Pantolambda* is notable for this reflection. The mesostyle of *Cyriacotherium* is nearly flush with the buccal margin of the tooth resulting in a strongly 'v' shaped centrocrista (Rose and Krause, 1982). This labial position of the molar metastyle is argued to be a core difference between how pantodonts and *Cyriacotherium* construct their 'w' shaped ectolophs (Lucas, 1998). However, the location of the mesostyle is variable across individuals within *Pantolambda* from more centrally located between the paracone/metacone and the buccal margin (e.g. NMMNH P-27844, Fig. 9; USNM 15408, Fig. 3; USNM 21327, Fig.

⁹ However, the enamel of the M1 of NMMNH P-27844, particularly on the buccal slope of the tooth is textured (contra the presentation of the M1 in AMNH 15934). The M1 of NMMNH P-27844 represents the most unworn upper molar known for *Pantolambda* (Funston et al., 2022). Speculatively, the low relief enamel wrinkles present on more unworn teeth of *Pantolambda* could be abraded throughout an animal's lifetime which would lead to their variable presentation in more mature individuals.

12) to nearly flush with the buccal margin (AMNH 16663; AMNH 15934, Fig. 11). The latter state is similar to the placement of the mesostyle in *Cyriacotherium* along the buccal margin of the tooth (essentially intersecting with the buccal cingulum). The overall form of the centrocrista of *Pantolambda* remains more 'u' shaped because of the narrower ectoloph 'v's observed in *Cyriacotherium*. In sum, these additional anatomical observations of the deciduous and permanent dentitions of *Pantolambda* further corroborate the phylogenetic arguments made by Zack (2009) and Scott (2010). The hypothesis that the cyriacotheriids are pantodonts remains to be further tested within a pantodont-focused phylogenetic framework.

Speculatively, the retention of the juvenile characteristics of more molariform premolars that are broadly present in Pantodonta could inform a potential evolutionary pathway to the still-controversial cyriacotheriids. Van Valen (1988, p. 37), while still supporting a mixodectid affinity for *Cyriacotherium* notes that it is "probably not impossible developmentally for such a transition to occur from one direction or the other" with regard to the evolution of a 'w' shaped ectoloph from a 'v' shaped one.

This transition in dental structure to the retention of the juvenile molariform characteristic can speculatively be supported by reflecting on the functional pressures on teeth imposed by shifts in the ecology of a species. Rose and Krause (1982) developed the suggest that *Cyriacotherium* had a more folivorous diet. Mammals adapted to more folivorous diets are observed to develop long shearing crests often with thin enamel (which increases the available shearing surfaces when it is pierced to expose the dentine) (Kay, 1975; Kay and Hylander, 1978; Rose and Krause, 1982; Strait, 1997; Fleagle, 2013). The nature of these shearing crests reflects the mechanical properties of the food stuff with longer blades more appropriate for slicing through less brittle foodstuffs (Strait, 1997). Cusps serve to provide additional points of contact for trapping and subsequently propagating cracks within tough foodstuffs (Luke and Lucas, 1983) and a greater cusp relief is observed in folivores (Boyer 2008). All told, the teeth of folivorous animals tend to have a more complex occlusal surface (more cusps and crests) to allow for processing challenging foods (Evans et al., 2007). These features of elongated

shearing blades with abundant cusps are present in the upper molars of *Cyriacotherium* to create a much more complex occlusal surface than observed in definitive pantodonts. Notably when considering the adaptations of premolars of the cyriacotheriids, the dietary shift to folivory places specific shearing pressures on the premolars (Kay and Hylander, 1978) with these teeth engaging earlier in the chewing stroke than the molars (Kunz and Ingalls, 1994).

The body size of the cyriacotheriids should also be taken into account. Pantodonts are broadly considered to be herbivorous browsers (Lucas, 1998), but the majority of the animals in the clade achieved much larger body sizes than that of *Cyriacotherium*. It is possible that the specialization of the teeth of *Cyriacotherium* might not indicate a dietary shift as much as reflect an energetics-driven need to more efficiently process vegetation (i.e. by reducing the particle size of the food prior to swallowing) (e.g. Parra, 1978). Essentially, the form of the juvenile dentition of these animals might indicate that the appropriate developmental framework was in place for the evolution of a smaller-bodied, pantodont that remained specialized for eating grass or leaves. These dietary hypotheses could be further tested by conducting microwear studies on the dentitions of *Pantolambda*, *Presbyterium* and *Cyriacotherium* to explore whether there were any differences in the foodstuffs these animals were processing.

The other material described in this thesis finds its utility from a taxonomic perspective. Further description of the postcranial anatomy of *Pantolambda cavirictum* is useful because the historical postcranial specimens for this species are fragmentary (Simons, 1960, p. 17). Indeed, some prior workers (Patterson, 1939a, p. 356; Simons 1960 p. 17) suggest that eventually *P. cavirictum* might be deemed different enough from *P. bathmodon* to be separated into a new genus. Simons (1960, p. 17) reserves the decision until a “really complete skeleton of *Pantolambda cavirictu[m]*” is found. The exquisitely preserved and extensive postscrania of NMMNH P-57738 represents an opportunity to begin evaluating this hypothesis. Although, NMMNH P-57738 exhibits some differences from *P. bathmodon* that are reflective of its achieving a larger body size (e.g. the robusticity of its forelimb bones and the reduction of the curvature of the radius), the bones described herein is

broadly similar to those of *P. bathmodon*. In particular, the complete manus of NMMNH P-57738 does not differ from the anatomy known for *P. bathmodon*. Further work on this specimen will encompass the vertebrae and the fragments of the hindlimb.

Another interesting implication of the new material described regards the biogeography of the genus, particularly when it comes to the distribution of *Pantolambda intermedium*. The distinctive dental characteristics of *Pantolambda intermedium* and their correspondence with size support its validity as a species. The definitive presence of *Pantolambda intermedium* in the San Juan Basin challenges the prior hypothesis that this species might represent a larger morph of *Pantolambda bathmodon* consistent with body size trends predicted by Bergmann's Rule (Simons, 1960). The presence of *P. intermedium* in New Mexico in a similar environment to and at the same latitude as both *P. bathmodon* and *P. cavirictum* further supports its distinction from the other two morphs as a unique species.

P. intermedium occurs stratigraphically lower (Tj2) than the other two species of *Pantolambda*, representing the lowest occurrence of pantodonts in the San Juan Basin. In contrast, *P. cavirictum* occurs in Tj5-6 biozones while *P. bathmodon* is restricted to the Tj6 biozone (Williamson, 1996; Flynn et al., 2020). An isolated tooth tentatively referred to *P. intermedium* has also been reported from the Bighorn Basin of Wyoming (Leite, 1994) and further hints at a wider distribution of the taxon.

This series of anatomical descriptions is intended as a springboard for a later full revision of the genus. The bulk of the anatomical work on this taxon occurred between the 1880s and the 1940s and, therefore, it is valuable to revisit these older specimens with the broader perspective of pantodonts that have been discovered in the latter half of the 20th century and in the new millennium. In particular, further study of the partial skeleton of *Pantolambda cavirictum*, NMMNH P-57738 represents an opportunity to unify previously fragmentary historical specimens and provide additional insight into postcranial variations within the genus beyond simple size differences.

Chapter Summary:

In this chapter, I surveyed the San Juan Basin, New Mexico, USA as an ideal place to investigate the genus. We've have taken stock of the geological and geographical context of the area and reflected on the other animals that occupied Paleocene ecosystems alongside pantodonts. I then summarized the historical context of study of the genus *Pantolambda*.

I have described and figured new specimens from the San Juan Basin that give us further insight into the anatomy of this genus. We have examined the first deciduous dentition known for the genus from a juvenile skeleton of *Pantolambda bathmodon*. This dentition served as a springboard for reflecting on the similarities between the deciduous premolars of pantodonts and the permanent premolars of the cyriacotheriids. The first cranial and postcranial material from *Pantolambda intermedium* is formally described. The presence of *Pantolambda intermedium* in the San Juan Basin is confirmed and its validity as a species is supported. Finally, we examined the articulated forelimb and manus of *Pantolambda cavirictum*. This specimen expands our relatively poor understanding of the postcrania of this large-bodied animal and holds future potential to unite the fragmentary historical specimens referred to this species. These specimens illustrate the continued value of San Juan Basin for yielding critical information about *Pantolambda*, an iconic North American pantodont genus.

Chapter 3:

Animals Alive



Pantolambda Cuddle Puddle by Taliesin Coleman

"At midnight in the museum hall
The fossils gathered for a ball
There were no drums or saxophones,
But just the clatter of their bones,
A rolling, rattling, carefree circus
Of mammoth polkas and mazurkas.
Pterodactyls and brontosauruses
Sang ghostly prehistoric choruses.
Amid the mastodontic wassail
I caught the eye of one small fossil.
'Cheer up, sad world,' he said, and winked-
'It's kind of fun to be extinct.' "

- Ogden Nash, 1949, "Fossils"

While the skeleton constitutes core data for vertebrate palaeontologists, a full understanding of animals arises from more than their bones alone. In this chapter, I synthesize together several analyses investigating the paleobiology of *Pantolambda bathmodon* including body size, grouping behaviour, and life history to provide a more complete picture of it as a living animal.

In the first analysis, I will leverage the excellent fossil record of pantodonts (including multiple skeletons with crania, forelimbs, and hindlimbs) to evaluate whether existing dental and postcranial proxies for body size are appropriate for estimating body size in pantodonts. After this broad focus across pantodont genera, I will narrow my attention to *Pantolambda bathmodon* by investigating the taphonomy of a single site from the San Juan Basin of New Mexico. Through this taphonomic analysis, I will explore what behaviors and social structures this species might have had. This chapter will conclude with a closer look at the palaeohistology and inferred life history strategies for *Pantolambda*.

Some of the data presented in this chapter have been previously published in a study lead by Greg Funston where I was a contributing author (Funston et al., 2022). That paper relies on the specimens on which this thesis is based and is included in Appendix III of this thesis. Some of the results from that paper underpin further reflections and analysis in this chapter. Details of my contribution to Funston et al., (2022) are provided in the 'Declaration of Own Work' statement (pg. v).

How Big Did They Get?: Reflections on Pantodont Body Size

Importance of Body Size

Body size is a fundamental parameter for understanding the biology and ecology of animals (McMahon and Bonner, 1983; Schmidt-Nielsen, 1984). In mammals, body size can be correlated to a wide variety of physiological and life history parameters including basal metabolic rate, daily energy expenditure (i.e. field metabolic rate), gestation period, and lifespan (Kihlström, 1972; Western, 1979; Lindstedt and Shaeffer, 2002; White and Seymour, 2003; Ernest, 2003; Brown et al., 2004; Nagy, 2005; Speakman, 2005; Clarke et al., 2010). In broad strokes, larger mammals have slower mass-specific metabolic rates (Savage et al., 2007), longer gestation periods

(Kihlström, 1972), and longer lifespans than their smaller counterparts (Western, 1979). Locomotion is also influenced by body size (McMahon, 1975; Biewener, 1989; Schaeffer and Lindstedt, 2013; Cloyed et al., 2021). Larger animals are able to move more efficiently (i.e. less energy expenditure per gram of muscle to move the same distance) while smaller animals typically exhibit more agility and manoeuvrability (Biewener, 1989; Cloyed et al., 2021). Larger mammals also have more extensive home ranges¹⁰ than smaller mammals (Harestad and Bunnell, 1979; Lindstedt et al., 1986).

Body size also correlates to population-scale features. For example, body size appears to exhibit an inverse relationship with population density in mammals and larger mammals have a relatively lower local abundance than smaller mammals (Damuth, 1981; Blackburn and Gaston, 1999). Body size also correlates with the intrinsic rate of increase of a population which reflects the growth rate of a population when not limited by density-dependent factors (Fenchel, 1974). Several foundational theories of biogeography also centre on how the body size of different animals scales with physical features of their landscape. For example, Bergmann's Rule postulates that warm-blooded animals in cooler climates will be larger than animals with a similar bauplan from warmer regions¹¹ (Freckleton et al., 2003; Meiri and Dayan, 2003; though see McNab, 1971 and Blackburn et al., 1999 for additional influences and nuances). Additionally, the landmass area where populations live appears to influence the extremes (largest and smallest) of mammal body size present (Marquet and Taper, 1998). The interplay of landmass area and body size can also be seen when considering the island rule. Here, a trend of dwarfism in typically larger species and gigantism in typically smaller species exists in relation to island area (Lomolino, 2005). In each of these cases, the body size, particularly of endothermic animals like mammals appears fundamentally linked to the physical characteristics of the environments they inhabit.

Body size can also be linked to the level of extinction risk in mammals (Cardillo et al., 2005; Burger and Ginzburg, 2009). This risk arises from the combination of

¹⁰ The home range is defined as an "area normally traversed by an individual animal or group of animals during activities associated with feeding, resting, reproduction, and shelter-seeking" (Harestad and Bunnell, 1979.)

¹¹ For a recent translation of Bergmann's original German text formulating the rule, see Table 2 of Watt et al. (2009).

aspects of their physiology (e.g. longer gestation times), ecology (e.g. lower population density) and environmental factors resulting in larger mammal populations being less resilient to environmental disruption and more susceptible to extinction (Cardillo et al., 2005).

All told, when seeking a deeper understanding of animals as living organisms, body size is a critical data point for beginning to interrogate, predict, and reflect on a myriad of other interesting aspects of their biology and ecology.

Body Size Estimations from Fossils

While determining the body size of (most) extant animals is relatively straightforward, estimating the body sizes of extinct organisms presents more difficulty. We're not able to bring a scale back in deep time and instead must try to flesh out an understanding of the bones as available to us. The majority of the current approaches to estimating body mass of extinct animals are empirically derived rather than being drawn from and situated in a strong theoretical framework (Hopkins, 2018).

Reasonably estimating the body size of an extinct animal holds the potential to give insight into what it might have been like as a living organism. The quantitative renaissance in estimating body size in fossils began when Gould (1975) made the connection that the size of the tooth surface area in mammals seemed to broadly correlated with their body size. Subsequently, body size in mammals has been estimated in a variety of ways including through dental equations (e.g. Legendre, 1986; Legendre, 1989; Damuth, 1990; Janis, 1990), limb bone scalings or articular surface areas (Anderson et al., 1985; Gingerich, 1990; Ruff, 1990; Ruff, 2003), skull length (e.g. Reynolds, 2002), distance between the occipital condyles (Martin, 1980; Engelman, 2022), and tarsal dimensions (Tsubamoto, 2014; Tsubamoto, 2019). These estimation strategies typically result from the use of linear measurements or areas as proxies. A final way to estimate body size in extinct animals is through the use of convex hulls (Sellers et al., 2012; Brassey, 2017).

A core challenge in estimating body size from fossils arises when trying to determine the best proxies for extinct group with no extant descendants and unique combinations of anatomical features. Additionally, phylogeny has been demonstrated to have a strong influence on the different proxies (Legendre 1986; Hopkins, 2008). Despite these challenges, estimating body size from fossils remains a worthwhile endeavour. Currently, a decent strategy seems to be using multiple proxies to generate estimates and then reasoning through which result might be most appropriate to the organism.

Previous Body Size Estimates for Pantodonts

In the broader narrative of mammal evolution in the world of the Paleocene, pantodonts find a common framing as one of the first mammals to grow to large body sizes after the K-Pg extinction. However, precise estimates of the body size of the members of this clade are relatively sparse and remain poorly constrained.

Initially, body size estimates for pantodonts relied on general comparisons to extant mammals. These comparisons sometimes resulted in wildly different assessments. For example, Cope (1882a, p. 418; 1883b, p. 559) suggests that *Pantolambda bathmodon* was “about as large as a sheep.” However, he subsequently reassessed that claim to suggest that *P. bathmodon* was “about the size of a coyote” and *P. cavirictum* was “as large as a South American tapir, or nearly equal to the smallest species of *Coryphodon*” (Cope, 1884b, p. 1113). Using a composite skeleton, Osborn suggested *P. bathmodon* was “about the size and proportions of a large Wolverine [sic] (*Gulo luscus*)” (1898a, p. 184). Simons’ (1960, p. 17) posits a third set of fairly similar comparisons - that *P. bathmodon*’s body size was “that of a fox” while *P. cavirictum*’s was “that of a tapir.” Similar comparisons were used to estimate the size of various species of *Coryphodon*. A common comparator was a tapir (Cope, 1877, p. 203; Marsh, 1877, p. 84). Other comparison animals included the ox and Javan rhinoceros (Cope, 1872a, p. 418; Cope, 1877, p. 203).

Additionally, early workers sometimes reported the dimensions of mounted skeletons (often resulting from composite specimens) when trying to get a sense of how large pantodonts might have been. Osborn estimated that *Pantolambda bathmodon* was

about 2 ft, 9 in. long excluding its tail (0.84 m) and 1 ft. 1 $\frac{3}{4}$ in. at the withers (0.35 m; 1898a, p. 184) and similarly used a composite mount of *Coryphodon radians* from the Wind River Basin to estimate a length of 2.38 meters and height of 1.03 meters at the withers (1898b). A slightly smaller *Coryphodon* estimate of six feet (1.8 m) in length and three feet (0.91) in height arises from Marsh (1893).

These mount-derived estimates have the advantages of being more quantitative than extant animal comparisons and linked directly to the bones. However, they are limited by (a) unspoken assumptions that the individual specimens composited are relatively the similar sizes and (b) decisions made during the mounting process about the stance and posture of the animals.

In the mid-late 1900s, as quantitative methods for estimating the body size of fossil mammals became more broadly applied, pantodonts were occasionally included among the extinct mammals assessed. For example, Jerison (1973) used body lengths and the assumption of a heavy habitus to estimate the body mass of *Pantolambda bathmodon* (30 kg), *Leptolambda schmidtii* (205 kg), *Barylambda* (620 kg), *Coryphodon hamatus* (270 kg), and *Coryphodon elephantopus* (540 kg). Other studies estimating body size in pantodonts include Damuth (1990) (which surveyed *Pantolambda bathmodon*, *Barylambda faberi*, and *Coryphodon testis*) and Uhen and Gingerich (1995)'s investigation of *Coryphodon*.

Lucas (1998) reports body sizes of 7 kg for *Archaeolambda*, 150 kg for *Titanoides* and 650 kg for *Barylambda* but the reasoning for these estimations is not clear. Recently, Mao et al. (2014) used Legendre (1989)'s ungulate equations to estimate body masses for three Asian coryphodontids – *Asiocoryphodon conicus* (600 kg), *Heterocoryphodon flerowi* (1000 kg) and *Eudinoceras mongoliensis* (1400 kg).

While multiple estimates of pantodont body sizes exist in the literature, the most appropriate proxies to use for understanding these animals remain opaque. This challenge fundamentally arises from some of the unusual body proportions exhibited by the group and from pantodonts lacking extant descendants. These challenges can clearly be seen in the inconsistencies Gingerich (1990) found in estimating the body size of *Coryphodon* using limb bone proxies. Gingerich (1990) noted that this

disconnect likely in part arose from *Coryphodon* having proportionally shorter and stouter limb bones than those of the extant animals from which the limb bone regressions were derived.

Reflections on Pantodont Body Size Estimates

Determining appropriate metrics for estimating body size in pantodonts is important, in part, because they were among the largest animals in Paleocene. Constraining how big 'big' is in this context holds the potential to provide further insight into the structure of these early mammal-dominated ecosystems. Since pantodonts are notable for multiple genera being known from nearly complete skeletons, I aimed to evaluate limb bone and dental estimates across pantodont genera within the same skeleton.

Materials and Methods:

To underpin this reflection, I took dental measurements using digital calipers (0.01 mm accuracy) and measured limb bone circumferences either using a flexible tape measure (1 mm gradations) or by wrapping a slip of paper around the bone, marking the circumference, and measuring with calipers. The specimens for which a humerus, femur, and lower jaw were available were *Pantolambda bathmodon* (AMNH 16663), *Barylambda faberi* (AMNH 32511), *Titanoides primaevus* (FMNH P-15520), and *Coryphodon armatus* (UM 21691). Additionally, limb bone measurements in the absence of a skull were taken from a mounted skeleton of *Barylambda faberi* (FMNH FM P-14945¹²) and *Coryphodon molestus* (AMNH 48163). I was unable to locate the lower jaw of AMNH 48163 when I visited the collection in 2022, but it was described and measured in Lucas (1984a). Finally, dental and postcranial measurements for *Alcidedorbignya inopinata* were taken from Muizon et al. (2015). This taxon sampling encompasses representatives from each of the main groups of North and South American pantodonts.

The body size of quadrupedal tetrapods can be estimated is using long bone (humerus and femur) circumferences (Campione and Evans, 2012; Eq. 1). In this

¹² The skull of the Field Museum *Barylambda* mount was made of plaster and dental measurements were not tabulated.

equation, body mass (BM) is in grams and the stylopodial circumference (C_{N+F}) is in millimeters (mm). The stylopodial circumference is calculated by taking the sum of the minimum circumference of the shaft of the humerus and the minimum circumference of shaft of the femur.

$$\log(\text{BM}) = 2.749(\log(C_{H+F})) - 1.104 \quad (\text{Eq. 1})$$

Campione and Evans (2012) demonstrated that the relationship between these stylopodial bones and body mass is strongly conserved and not clearly influenced by stance or phylogeny. The independence of the relationship from phylogeny and its broad applicability across tetrapods¹³ steps outside the challenge posed by the lack of extant relatives for pantodonts in applying equations more specific to mammals. In this current reflection, the results of this equation will be point of comparison against which other metrics are judged for their utility for different pantodont genera.

Additionally, mammal-specific stylopodial scaling equations relating humerus length (H_L ; Eq. 2) and femur length (F_L ; Eq. 3) to body mass (Campione and Evans, 2012) were used to generate a postcranial body mass estimate for *Alcidedorbignya*. In these equations, both H_L and F_L are in millimeters.

$$\log(\text{BM}) = 2.8626(\log(H_L)) - 1.8476 \quad (\text{Eq. 2})$$

$$\log(\text{BM}) = 2.993(\log(F_L)) - 2.341 \quad (\text{Eq. 3})$$

A suite of dental equations was also calculated for each taxon based on the regressions of Legendre (1986), Legendre (1989), and Damuth (1990). For all the equations presented below, the dental measurements are in millimeters and the resulting body masses (BM) are in grams.

The final body mass proxy investigated was occipital condyle width (OCW; Engelman, 2022). This metric was calculated for *Pantolambda bathmodon* and select pantodont

¹³ Although, I am assuming this equation as the baseline for the analysis above, it should still be regarded with the skepticism afforded all body mass proxies. For a critique of this equation, see Bates et al. (2015) for instances with large sauropods where the equation appears to systematically overestimate the size of these animals in relation to volumetric estimates. Some of the limitations of this equation in this setting likely arise from the fact that the measurements of sauropod dinosaurs fall outside the range of the extant animals from which the regression lines of Campione and Evans (2012) were originally derived.

taxa. Some of these taxa (e.g. *Hypercoryphodon thompsoni* and *Eudinoceras kholobolchiensis*) were not included in other measurement categories because of limited or non-existent postcranial material.

Results:

Table 4 illustrates the body mass estimates from these limb bone proxies for different pantodont genera.

Table 4: Limb Bone Estimates of Body Size for Different Pantodonts

Taxon	Specimen Number	Hum. Circ. (mm)	Fem. Circ. (mm)	Body Mass (kg)
<i>Pantolambda bathmodon</i>	AMNH 16663	57.01	64.46	42.29
<i>Barylambda faberi</i>	FMNH P-14945	228	250	1827.0
<i>Barylambda faberi</i>	AMNH 32511	205	221	1331.2
<i>Titanoidea primaevus</i>	FMNH P-15520	157	168	632.7
<i>Coryphodon armatus</i>	UM 21691	146	140	445.2
<i>Coryphodon molestus</i>	AMNH 48163	132	134	364.8
		Hum. Len. (mm)	Fem. Len. (mm)	Body Mass (kg)
<i>Alcidedorbignya inopinata</i>	MHNC 8372	43.64	51.7	0.7 ^a
				0.6 ^b
<i>Pantolambda bathmodon</i>	AMNH 16663	130.3	157.4	16.1 ^a
				17.2 ^b

Notes: Abbreviations are as follows: Hum. = humerus, fem. = femur, circ. = circumference, len. = length ^a denotes humerus body mass estimate and ^b denotes femur body mass estimate.

The body sizes estimated from stylopodial circumferences are, generally speaking, larger than those previously reported in the literature. For example, *Pantolambda bathmodon*'s 42 kg weighs in at much bulkier than the more svelte 10.4-14.2 kg estimated by Damuth (1990). The stylopodial estimate for *Pantolambda* was more similar to the 30 kg estimated by Jerison (1973). Similarly, *Barylambda*'s weighty 1,827 kg from limb bone dimensions was over twice as heavy as previous estimates (620 kg, Jerison, 1973; 650 kg, Lucas, 1998). *Titanoidea* was also much heavier than Lucas (1998)'s previous estimate of 150 kg. In contrast with the other North American pantodonts, the estimates of the *Coryphodon* specimens fell within ranges previously estimated for the taxon.

Body size estimates for *Pantolambda bathmodon* based on long bone lengths were smaller values that were more consistent with those from previous dental equations.

This pattern of high values deriving from limb bone circumference and low values deriving from limb bone lengths reflects the robust nature of these bones and their relatively short and stout proportions (similar to that observed for *Coryphodon* by Gingerich (1990)).

Tables 5-10 illustrate the body size estimates for the different pantodont taxa being considered as recovered from the suite of dental equations (tooth measurements in Table A1.i-iii).

Table 5: Body Size Estimates for *Pantolambda bathmodon* (AMNH 16663)

Linear Proxy	Empirical Data	Equation	BM (kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	20.92
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	27.88
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	21.29
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	9.86
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	31.33
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	32.62
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	26.73
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	28.27
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	31.76
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	456.24
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	12.45
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	15.52
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	22.97
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	11.76

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Pantolambda bathmodon* resulting from dental proxies ranged from 9.86 kg to 32.62 kg (excluding the extreme outlier estimate of 456.24 kg arising from the m1-3 length for ungulates regression). None of the reasonable body size estimates from the dentition approached the 42 kg threshold suggested by stylopodial circumferences. Most dental estimates exceeded the humerus and femur length estimates.

Table 6: Body Size Estimates for *Barylambda faberi* (AMNH 32511)

Linear Proxy	Empirical Data	Equation	BM(kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	550.43
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	577.06
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	333.98
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	160.85
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	471.29
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	489.48
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	657.41
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	714.60
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	465.41
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	23600.77
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	315.31
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	278.78
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	342.73
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	252.35

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Barylambda faberi* resulting from dental proxies ranged from 160.85 kg to 714.60 kg (excluding the truly spectacular outlier estimate of 23,600.77 kg arising from the m1-3 length for ungulates regression). None of the reasonable body size estimates from the dentition approached the >1000 kg threshold suggested by the stylopodial circumference estimate.

Table 7: Body Size Estimates for *Titanoides primaevus* (FMNH P-15520)

Linear Proxy	Empirical Data	Equation	BM(kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	181.06
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	205.95
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	130.99
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	62.24
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	187.48
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	194.88
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	221.26
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	238.29
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	186.80
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	14227.83
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	136.92
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	192.49
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	136.73
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	137.41

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Titanoides primaevus* resulting from dental proxies ranged from 162.24 kg to 238.29 kg (excluding the outlier estimate of 14,227.83 kg arising from the m1-3 length for ungulates regression). None of the reasonable body size estimates from the dentition approached the 632.7 threshold suggested by the stylopodial circumference estimate.

Table 8: Body Size Estimates for *Coryphodon armatus* (UM 21691)

Linear Proxy	Empirical Data	Equation	BM(kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	325.31
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	354.47
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	214.51
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	102.66
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	304.74
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	316.62
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	392.77
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	425.07
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	302.22
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	24185.71
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	189.05
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	283.82
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	221.92
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	200.13

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Coryphodon armatus* resulting from dental proxies ranged from 102.66 kg to 425.07 kg (excluding the outlier estimate of 24,185.71 kg arising from the m1-3 length for ungulates regression). The body size estimate resulting from stylopodial circumferences (445.2 kg) falls just above the range circumscribed by the dental estimates.

Table 9: Body Size Estimates for *Coryphodon molestus* (AMNH 48163)

Linear Proxy	Empirical Data	Equation	BM(kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	309.62
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	338.59
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	205.76
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	98.41
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	292.50
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	303.92
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	374.20
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	404.81
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	290.19
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	22687.26
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	178.22
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	270.84
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	213.03
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	168.34

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Coryphodon molestus* resulting from dental proxies ranged from 98.41 kg to 404.81 kg (excluding the outlier estimate of 22,687.26 kg arising from the m1-3 length for ungulates regression). The body size estimate resulting from stylopodial circumferences (364.8 kg) falls within the range of the dental estimates.

Table 10: Body Size Estimates for *Alcidedorbignya inopinata* (MHNC 8372)

Linear Proxy	Empirical Data	Equation	BM(kg)
m1 Area (mm ²)	All Mammals ^a	$\ln(\text{BM}) = 1.827(\ln(\text{m1 area})) + 1.81$	0.90
m1 Area (mm ²)	Herbivores ^a	$\ln(\text{BM}) = 1.693(\ln(\text{m1 area})) + 2.694$	1.51
m1 Area (mm ²)	Large Mammals ^a	$\ln(\text{BM}) = 1.538(\ln(\text{m1 area})) + 3.115$	1.51
m1 Area (mm ²)	Mammalia ^b	$\ln(\text{BM}) = 1.56(\ln(\text{m1 area})) + 2.2470$	0.67
m1 Area (mm ²)	All Ungulates ^b	$\ln(\text{BM}) = 1.5147(\ln(\text{m1 area})) + 3.6049$	2.31
m1 Area (mm ²)	Ungulates with exclusions ^b	$\ln(\text{BM}) = 1.5133(\ln(\text{m1 area})) + 3.6515$	2.41
m1 Area (mm ²)	All Herbivores ^b	$\ln(\text{BM}) = 1.7894(\ln(\text{m1 area})) + 2.2224$	1.23
m1 Area (mm ²)	Herbivores with exclusions ^b	$\ln(\text{BM}) = 1.8046(\ln(\text{m1 area})) + 2.2109$	1.26
m1 Area (mm ²)	All ungulates ^c	$\log(\text{BM}) = 1.50(\log(\text{m1 area})) + 1.60$	2.40
m1-3 Length (mm)	All ungulates ^c	$\log(\text{BM}) = 4.14(\log(\text{m1-m3 length})) - 0.60$	26.88
m1 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.17(\log(\text{m1 length})) + 1.04$	1.29
m1-3 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.03(\log(\text{m1-3 length})) - 0.39$	1.95
m1 Area (mm ²)	Non-selenodont ^c	$\log(\text{BM}) = 1.51(\log(\text{m1 area})) + 1.44$	1.71
p5-m2 Length (mm)	Non-selenodont ^c	$\log(\text{BM}) = 3.12(\log(\text{p5-m2 length})) - 0.43$	1.48

Notes: Equations derived from: ^aLegendre (1986), ^bLegendre (1989), and ^cDamuth (1990).

The body mass estimates for *Alcidedorbignya inopinata* resulting from dental proxies ranges from 0.67 kg to 2.41 kg (excluding the outlier estimate of 26.88 kg arising from the m1-3 length for ungulates regression). The body size estimates arises from humerus and femur lengths (0.6-0.7 kg) fall at the low end of the range of estimates from the dentition.

The estimations of body mass on the basis of occipital condyle widths (OCW) are reported in Table 11. OCW measurements for the taxa are listed in Table A.2.

Table 11: Occipital Condyle Width Body Mass Estimates on AMNH Pantodonts

Taxon	Specimen Number	BM (kg) ^a	BM (kg) ^b	BM (kg) ^c	BM (kg) ^c
<i>Pantolambda bathmodon</i>	AMNH 1663	19.07	19.33	19.56	19.58
<i>Barylambda faberi</i>	AMNH 32511	534.88	545.54	489.49	537.93
<i>Pantolambda bathmodon</i>	AMNH 2549	25.71	26.07	26.11	26.35
<i>Pantolambda cavirictum</i>	AMNH 965	84.12	85.50	82.02	85.57
<i>Coryphodon molestus</i>	AMNH 48164	195.13	198.64	184.85	197.47
<i>Hypercoryphodon thompsoni</i>	AMNH 26384	1515.66	1548.87	1338.38	1514.45
<i>Eudinoceras kholobolchiensis</i>	AMNH 21744	2107.65	2155.16	1840.21	2101.66

Notes: All OCW equations from Engelman (2022): ^aAll species regression, ^bTherians regression, ^cSpecies >1000g regression, ^dUngulates regression

The OCW mass estimated for *Pantolambda bathmodon* is similar to that which results from femur and humerus length-based estimates. The OCW mass estimated for *Barylambda faberi* falls within the range of its dental estimates. On the basis of this proxy, the Asian coryphodontids appear to have achieved >1000 kg body sizes multiple times.

Discussion and Avenues for Future Work

This analysis makes concrete the striking size range that pantodonts achieved during their evolutionary history from small-bodied *Alcidedorbignya* (~1.5 kg) through the more middling-sized *Pantolambda* and *Titanoidea* to hulking *Barylambda* and the Asian coryphodontids (>1000 kg by some metrics). However, on closer examination, several inconsistencies between proxies and areas for further research emerge.

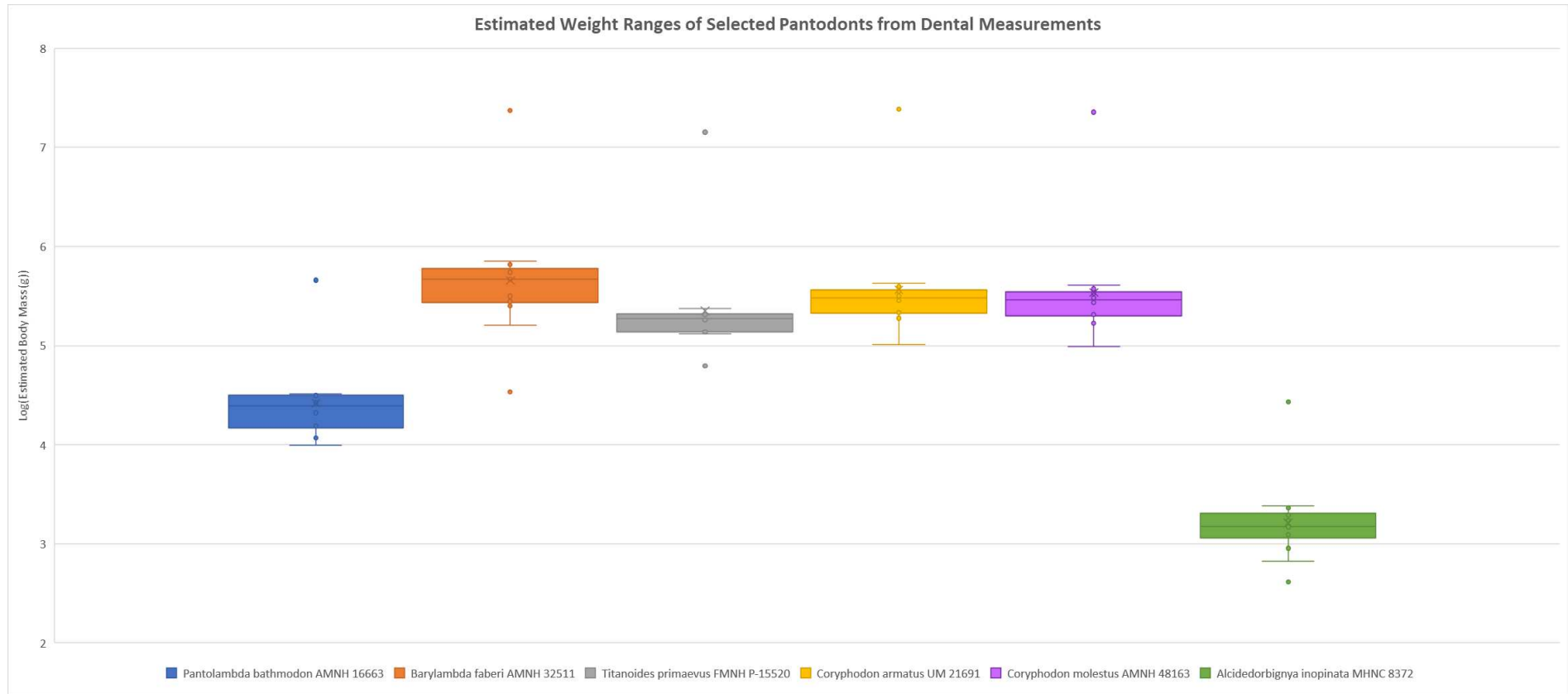


Figure 27: A box and whisker plot showing the range of body mass estimates of *Pantolambda bathmodon*, *Barylambda faberi*, *Titanoides primaevus*, *Coryphodon armatus*, *C. molestus*, and *Alcidedorbignya inopinata*. The box and whisker plots particularly highlight the strong outlying overestimate generated for each taxon by the 'all ungulates, m1-3 length' equation of Damuth (1990).

The most striking inconsistency between the dental proxies evaluated in this analysis can be seen in the m1-3 length regression for 'all ungulates' (Damuth, 1990). This equation systematically yields outlier estimates more than an order of magnitude higher than other proxies across the entire range of pantodont molar sizes input into the equation (Fig. 27). Shelley (2017) found a similar discrepancy in the equation while estimating the body size of *Periptychus*. Both the pantodonts studied and *Periptychus* fall well within the range of possible 'ungulate' body sizes covered by the equation. The largest ungulate in the dataset evaluated appears to be *Loxodonta africana* with a body size around 2,860 kg (Damuth, 1987). Since the extinct animals here fall within the size range here, I hypothesize that there is an error within the coefficients of the equation as present in Table 12.4 of Damuth (1990). However, the original dataset would need to be explored in more detail to resolve the discrepancy.

Aside from this notable outlier, in *Pantolambda*, *Barylambda*, and *Titanoidea*, the dental equations appear to systematically underestimate what is expected from postcranial equation focused on the stylopodial circumference. I think that this disconnect develops because of another interesting aspect of pantodont body proportions. Pantolambdids, barylambdids, and (to a less extent) titanoidids all have proportionally smaller heads on their robust bodies. This condition develops to its particular extreme with *Barylambda*.

Barylambda's very tiny head and correspondingly tiny teeth (relative to its body size) is corroborated by the dental estimates all being less than half the stylopodial circumference estimate. This pattern implies that the dental estimates for these pantodonts potentially underestimate the reality of their body size. The potential of dental estimates to systematically underestimate body sizes within this group is notable because the barylambdids were the biggest mammals seen up to that point in evolutionary history. Determining whether the >1000 kg estimate from the postcrania is reasonable is important for understanding body size evolution within these largest of large pantodonts.

This inference of the influence of head proportions on dental estimates is supported by the exception to pattern observed. In this sample, *Coryphodon molestus* does not show the same disconnect between estimates from postcranial and dental proxies (the values overlap) and the postcranial estimate of *Coryphodon armatus* is only ~20 kg higher than the upper bound of the range of estimates established from the dental equations. The greater congruence between these difference proxies arises from the different body proportions of these animals. Put simply, the head of *Coryphodon* is not comically small relative to its body (Fig. 5). Indeed, Osborn (1898a) comments on the large size of the head in this genus. For this reason, dental equations may be more suitable for estimating body sizes in *Coryphodon* than in other pantodonts.

The difference in proportions between *Coryphodon* and other pantodonts can be seen by comparing the stylopodial circumference (which gives a sense of how robust the limb bones are) with the length of the first lower molar (which can be conceptualized as a proxy for the overall size of the head). *Coryphodon*'s m1 measurements consistently fall above the 'trendline' between *Pantolambda* and *Barylambda* (Fig. 28).

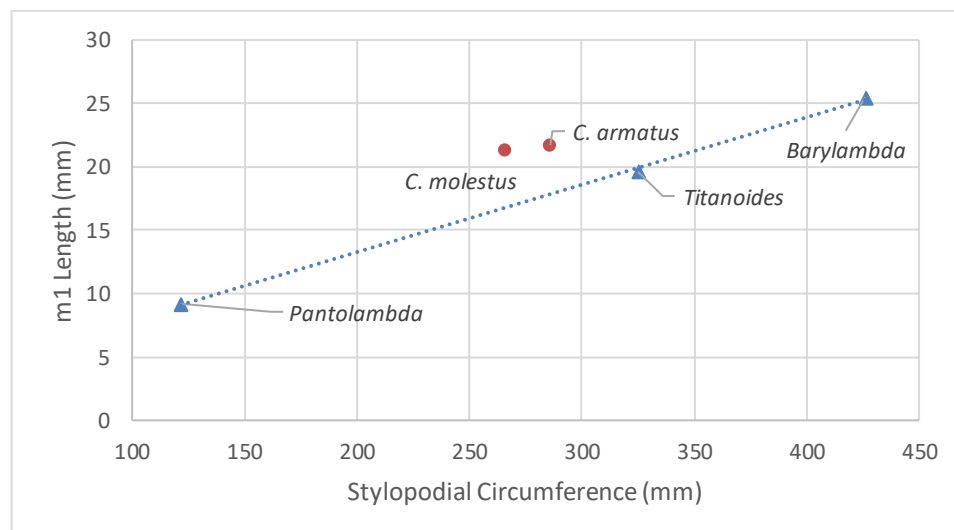


Figure 28: A bivariate plot of stylopodial circumference against the length of m1 (both in mm) for the pantodonts for which both pieces of data are known. This plot illustrates that the body proportions of *Coryphodon* are different than those of *Pantolambda*, *Titanoides*, and *Barylambda*.

As seen with other extinct organisms (e.g. Reynolds, 2002), a tension exists between different proxies for body size estimation in pantodonts. The most critical observation from this brief reflection is that the relationships between these proxies

varies within the clade. The most appropriate proxies for estimating body size in pantodonts should be sought at a more granular level (i.e. what is the best metric for barylambdids vs. coryphodontids). At the end of this reflection, I remain agnostic about what existing proxies might be best for estimating body sizes in pantodonts. Due to the limited sample size of this study¹⁴, it is difficult to definitively determine whether limb bone circumferences or dental proxies are more appropriate to each case. Another method needs to be employed to gain additional traction on this question and, luckily, pantodonts have the fossil record with which we could investigate it.

An avenue for future work on pantodont body masses lies in volumetric estimates on the basis of the multiple skeletal mounts that exist. One way to employ volumetric estimates lies in creating convex hulls around 3D models of the skeleton (Sellers et al., 2012; Brassey, 2017). Convex hull techniques have been applied to extant animals spanning from primates to birds (Brassey and Sellers, 2014) to mounted skeletons of ornithischian dinosaurs (Brassey et al., 2015) to early hominins (Brassey et al., 2018). These estimates essentially 'shrinkwrap' the skeleton so provide an effective minimum estimate of what size the animal might have achieved. Convex hulls hold the potential to remove some of the assumptions around how analogous different proxy measurements are for extinct animals with no appropriate living analogues (like pantodonts). While these methods are limited because of the requirements of complete skeletal reconstruction which demands an exceptionally complete fossil record (Hopkins, 2018), they are potentially appropriate for pantodonts where multiple mounted skeletons exist. The information exists to use this method for further investigating pantodonts, particularly some of the biggest North American taxa like *Barylambda faberi* (FMNH P-14945) and *Coryphodon* (e.g. MCZ 3420; Patterson, 1939b).

Although body size is an important metric for understanding the physiology and ecology of an organism, it is not the only avenue for conceptualizing an animal alive.

¹⁴ This study is further limited in its applicability across the clade because the range of variation of body shapes of the Asian pantodonts is not taken into account. In particular, the body masses of pantodonts like gracile *Archaeolambda tabiensis* (Huang, 1977; IVPP V4333) would benefit from similar assessments.

By examining the taphonomy of unusual fossil assemblages, we can gain insight into the behaviour of extinct animals.

Taphonomy of NMMNH L-1070, San Juan Basin, New Mexico, USA

The Paleocene Nacimiento Formation in the San Juan Basin (New Mexico, USA) preserves one of the most detailed records of mammal faunas during the time immediately following the K-Pg extinction. The Nacimiento Formation is composed of alternating siltstones, sandstones, and redbeds from alluvial floodplain deposits (Williamson, 1996; Cather et al., 2019). Generally speaking, these clastic rocks undergo 'badlands' style weathering - eroding out of steep cliffs and accumulating in topographic lows such as shallow pans.

One such pan (NMMNH L-1079) is found on the East Flank of Torreon Wash (Fig. 29). L-1079 was discovered in the late 1970's and has been repeatedly visited for additional surface collection.

L-1079 is notable for a profusion of fossils including abundant teeth and postcrania from *Pantolambda bathmodon*. The observation that multiple pantodonts in the assemblage has led to the suggestion that this animal might be gregarious (Williamson, 1996).

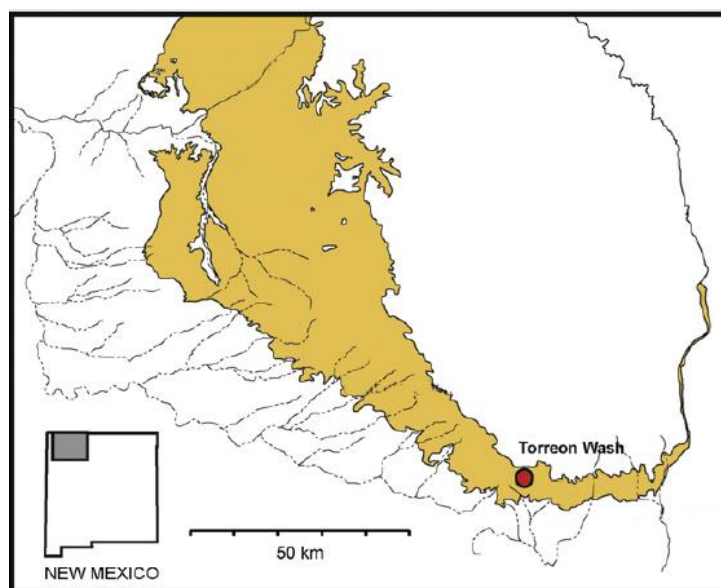


Figure 29: A map of the San Juan Basin in northwestern New Mexico (USA) showing the Nacimiento Formation's extent (light tan) and NMMNH L-1079's location at Torreon Wash (red dot). Image adapted from Silcox and Williamson (2012).

Materials and Methods:

This work focuses on fossils from the NMMNH collection. Additionally, I made two collecting trips to the L-1079 pan in the 2018 and 2019 field seasons where additional material was recovered and incorporated in the analyses. Using a Jacob staff, I measured a stratigraphic section through the area above and below the L-1079 pan. The thicknesses of sedimentary layers were determined under the assumption that they were flat-lying (no dip).

The majority of the material assigned to *Pantolambda bathmodon* was personally examined and the element identifications verified. In some cases, this work resulted in revising the original identifications on the specimen labels. While these revisions had the most bearing on the dental elements used for minimum number of individuals estimates (see below), they also had implications for the postcrania assigned to the taxon. In many cases, the elements grouped under *Pantolambda bathmodon* included bones from other taxa (e.g. the NMMNH P-19672 patellae, Fig. A9). I adopted a conservative strategy in tallying the material from this locality and only included definitive pantodont material in the later analyses.

Additional L-1079 material referred to other, non-pantodont taxa was tallied from the results of a locality search in the NMMNH database. The non-pantodont material was not loaned to the University of Edinburgh during the course of this project. Since I have not personally examined these specimens, I am (1) trusting the identifications listed in the database¹⁵ and (2) conservatively tallying the number of fragments assigned to each species. As with *Pantolambda bathmodon*, this conservative tallying strategy likely results in an underestimate of the number of individuals of other species present in the quarry.

The minimum number of *Pantolambda bathmodon* individuals in the assemblage was calculated by counting repeated elements within the assemblage (Shotwell, 1955; Badgley, 1986). Voorhies Groups (Table 12) were used to investigate the amount of fluvial influence within the assemblage (Voorhies, 1969; Behrensmeyer, 1975). In

¹⁵ I depart from the NMMNH specimen labels by following McKenna (1975) in referring to the penultimate premolar as P/p4 and the ultimate premolar as P/p5 rather than their original labels of P/p3 and P/p4. This decision was made for consistency with other sections of the thesis.

the process of making these estimates, I aimed to make the most conservative assessments (lowest) possible. Only tabulated postcrania in this analysis when I was able to definitively identify them to the element level and confidently refer them to *Pantolambda bathmodon*. Within Voorhies original groups, there was double counting of the dentary with the mandible appearing in Group III and the ramus appearing in Group II+III. In this analysis, where the postcrania are extremely fragmentary and elements are inferred to be present on the basis of small pieces (e.g. the number of femurs present was assessed by counting the heads). Thus, the number of dentaries was used to assess both the number of mandibles and the rami.

Table 12: Voorhies Groups

Group	I	II	III	I + II	II + III
Elements	Ribs Vertebrae	Femur Tibia Humerus Radius Metapodials Pelvis	Skull Mandible	Scapula Phalanges Ulna	Ramus

Sedimentology and Stratigraphy

L-1079 forms in a topographic low at the base of a steep cliff (~5-10 m tall) (Fig 30). Directly above the pan, the cliff does not extend above a horizon of large concretions; however, fossils from higher in the section can be washed onto the pan from the more southerly portion of the exposure. Since the flat pan of L-1079 accumulates material washing in from the overlying beds, this assemblage has likely experienced some mixing between different stratigraphic layers.



Figure 30: The cliff directly above L-1079 samples approximately 7 meters of stratigraphic section. The layer from which the *Pantolambda bathmodon* material derives is highlighted with a purple circle. Photo credit: Tom Williamson.

Although the fossils from L-1079 are found on the medium to coarse-grained, white sandstone of the pan, a concentration of bones was observed in the cliff 0.82 –1.05 m higher. The bone-bearing horizon is less than 1 meter thick. The bone-bearing layer is composed of a cliff-forming, gray mudstone.

L-1079 is located near the top of the Nacimiento Formation ~14.4 meters below the upper black mudstone of the Ojo Encino Member. Fig 31 presents a measured section illustrating the stratigraphic relationships at this locality and Table A3 summarizes the units measured. This locality belongs to the *Mixodectes pungens* biostratigraphic zone (M zone; Tj6), the youngest zone in the formation.

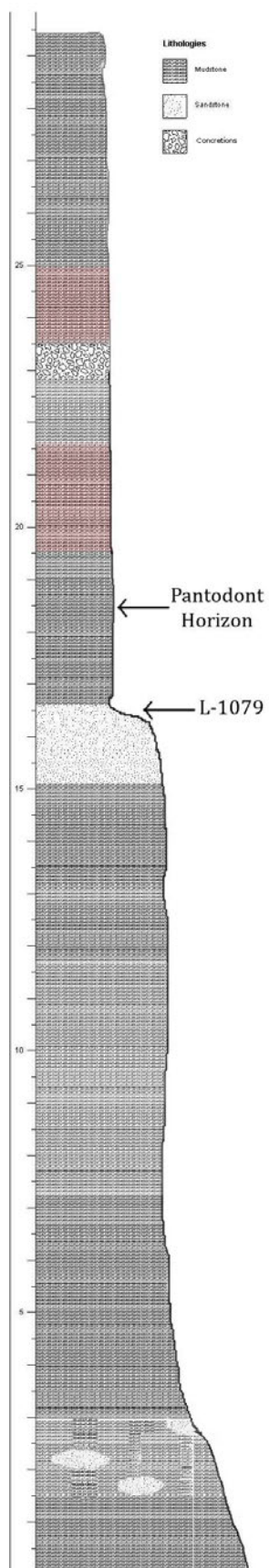


Figure 31: A measured section through the L-1079 locality placing it in broader context. The section is dominated by mudstones and fine grained sandstones with some lenses of coarser-grained material that are not laterally continuous.

On the basis of magnetostratigraphy, the L-1079 pan is dated to ~62.28 Ma with an estimated sedimentation rate of 87 m/myr (Leslie et al., 2018) . The level from which the bones derive is estimated to be a nearly contemporaneous age at ~62.29 Ma.

Taxa Present and Minimum Number of Individuals

At least 2,223 bone fragments and teeth from multiple taxa have been recovered from L-1079 (Table A4-6). Identifiable teeth were used to make an estimate of the minimum number of individuals of each taxon present. These values were then summed to generate a total minimum number of individuals for the quarry.

Abundant teeth and postcrania of the small-bodied pantodont *Pantolambda bathmodon* are present at L-1079. Indeed, a concentration of pantodont bones have been observed weathering out of a clear layer within the overlying bluff (Tom Williamson, personal communication). The *Pantolambda* teeth found at L-1079 are listed in Table A.4. These teeth were then tabulated by tooth position to more easily assess repeating elements. Tooth fragments referable to *P. bathmodon* but not sufficiently diagnostic for tooth position were not tabulated. The resulting tallies (organized by tooth position) are presented in Table 13.

Table 13: *Pantolambda bathmodon* Tooth Position Tallies:

Definite Identification										
RI1	RI2	RI3	RC	RP1	RP2	RP4	RP5	RM1	RM2	RM3
								I	I	II
LI1	LI2	LI3	LC	LP1	LP2	LP4	LP5	LM1	LM2	LM3
					II	I	II	I	II	I
Ri1	Ri2	Ri3	Rc	Rp1	Rp2	Rp4	Rp5	Rm1	Rm2	Rm3
II	II	I			I		I	I	I	III
Li1	Li2	Li3	Lc	Lp1	Lp2	Lp4	Lp5	Lm1	Lm2	Lm3
II	I		I	I	I	II	III	II	III	III
Indefinite Identification										
c/C	I?	i?	LM?	Rm?	M?					
IIII	I	I	II	I	I					

The total number of teeth tallied for *Pantolambda bathmodon* is 54. The most frequently occurring teeth in the sample are Rm3 (NMMNH P-19653, NMMNH P-19654, NMMNH P-19662), Lp5 (NMMNH P-19654; NMMNH P-19681; NMMNH P-

69890), Lm2 (NMMNH P-19541, NMMNH P-19663, NMMNH P-21561), and Lm3 (NMMNH P-19663, NMMNH P-69921, NMMNH P-69892). The minimum number of individuals of this taxon on the basis of the dentition is three.

However, the MNI of *Pantolambda bathmodon* can be further investigated by examining the postcrania of the animal. The calcaena fragments contained in P-19680 are of particular interest. This specimen consisted of eight *Pantolambda bathmodon* calcanea (Fig. 32) and one fragmentary tuber calcanei from a smaller taxon. Two complete right calcanea (Fig 32a, b) are present in the sample. Additionally, four fragmentary tuber calcanei (two right and two left) are present (Fig. 32e-h). Two additional fragments preserve other portions of the calcaneal body. The first preserves the sustentacular and cuboid facets of a left calcaneum (Fig. 32c) and the second is an isolated ?fibular facet from a ?right calcaneum (Fig. 32d).

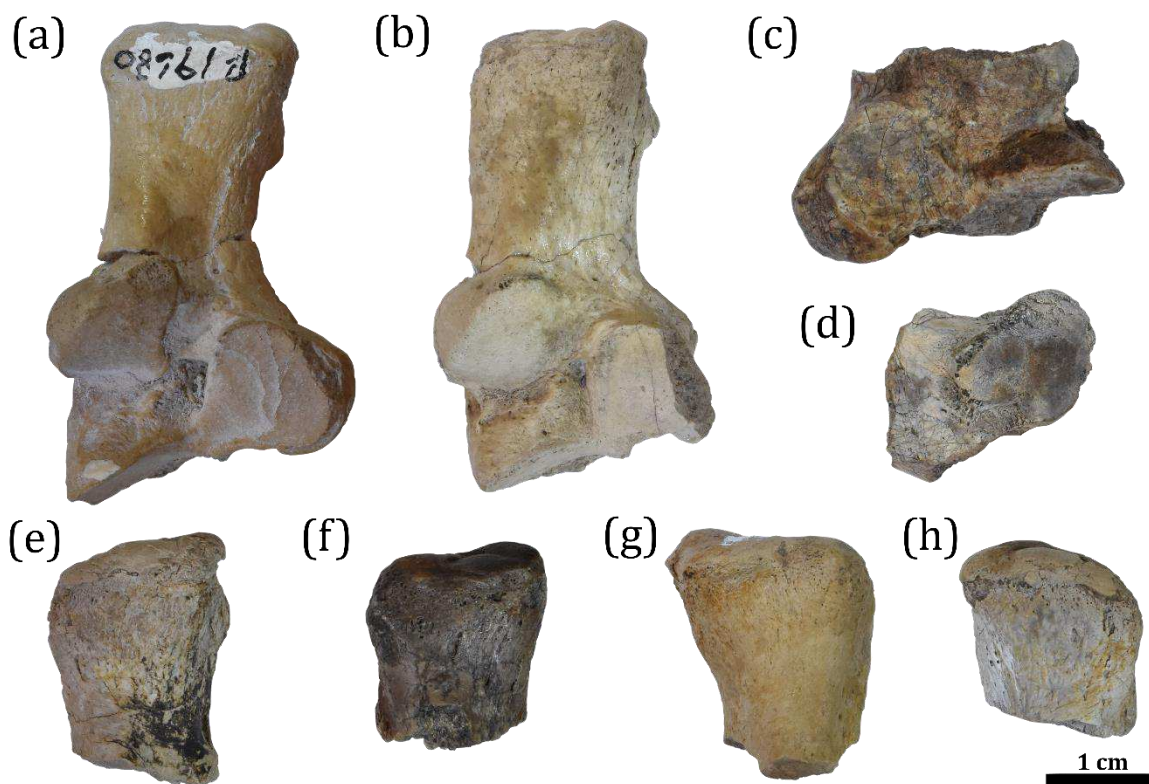


Figure 32: *Pantolambda bathmodon* calcanea from the L-1079 assemblage with (a) the most complete and (b) a second nearly complete right calcanea in dorsal view and several additional fragments. These fragments spanned (c) the sustentacular and cuboid facets, (d) a ?fibular facet, (e, f) two right tuber calcanei (e, f) and (g, h) two left tuber calcanei.

On the basis of the repetition of the tuber calcanei of the right calcaneum, the MNI of *Pantolambda bathmodon* is four.

The L-1079 sample also preserves abundant dental fragments from the condylarth, *Tetraclaenodon puercensis* (Table A5). Unidentified tooth fragments were excluded from the subsequent tallies for tooth positions within *Tetraclaenodon puercensis* (Table 14).

Table 14: *Tetraclaenodon puercensis* Tooth Position Tallies

Definite Identification						
RP1	RP2	RP4	RP5	RM1	RM2	RM3
		I	I	II	II	III
LP1	LP2	LP4	LP5	LM1	LM2	LM3
		I	II	I	III	III
Rp1	Rp2	Rp4	Rp5	Rm1	Rm2	Rm3
			III	III	III	III
Lp1	Lp2	Lp4	Lp5	Lm1	Lm2	Lm3
			I	I	II	I
Indefinite Identification						
m?	Lm?	LM?	Rm?	P?	Rp?	m3
I	III	II	IIII	II	I	I
P5	RM?	Rdp5	M3	canine	m2	m2?
I	II	I	I	I	I	I
m1	P5	M?				
I	I	I				

The total number of teeth tallied for *Tetraclaenodon puercensis* is 63. The minimum number of individuals based on definite teeth is four with Rm3 marking the key tooth. However, this MNI can be increased by examining the tabulated value for 'Rm?' (total = 5). Rm1 and Rm2 were each tabulated at three specimens. If the most conservative estimate is made (that Rm? is distributed equally between Rm1, Rm2, and Rm3), then an additional individual of *Tetraclaenodon* must be present. Thus the revised MNI for *Tetraclaenodon puercensis* is five¹⁶.

The assemblage at L-1079 also encompassed teeth from both therians (eutherians and metatherians) (Table 15) and multituberculates (Table 16).

¹⁶ A deciduous lower ultimate premolar (P-19514) is present in this sample of *Tetraclaenodon* teeth, but an additional individual was not tabulated in the MNI for this taxon because the ultimate premolar is hypothesized to be the last portion of the permanent dentition to erupt (West, 1971, Fig. 22). Therefore, it is reasonable to assume an individual could have possess both its molars and this tooth simultaneously.

Table 15: Therian Teeth from L-1079

Taxon	Specimen Number (NMMNH)	Specimen Identification	Most abundant tooth (#)	Total # of teeth	MNI
Eutherians					
<i>Mixodectes</i> sp.	P-15280	M? – isolated		2	1
<i>Mixodectes</i> sp.	P-15391	Rm3			
<i>Acmeodon secans</i>	P-19532	Lm? – isolated		1	1
<i>Arctocyon ferox</i>	P-54630	(16) canine + bone frags		1	1
<i>Mimotricentes subtrigonus</i>	P-54397	Rp5-pt.m1	Rm1 (2), Rm3(2)	6	2
<i>Mimotricentes subtrigonus</i>	P-54339	Rm1-3			
<i>Mimotricentes subtrigonus</i>	P-19602	Lm? – isolated			
<i>Mimotricentes subtrigonus</i>	P-19615	Lp5			
<i>Mimotricentes subtrigonus</i>	Uncat.	Rm3			
<i>Mioclaenus turgidus</i>	P-19621	Rm2-m3, dentary frags		4	1
<i>Mioclaenus turgidus</i>	P-19517	Rp? – isolated			
<i>Mioclaenus turgidus</i>	P-19511	Rp? – isolated			
<i>Promioclaenus acolytus</i>	P-15398	Rm1 + mandible frags		2	1
<i>Promioclaenus acolytus</i>	P-69887	RP5			
<i>Promioclaenus lemuroides</i>	P-77381	Lm2	Rm2 (2)	7	2
<i>Promioclaenus lemuroides</i>	P-77379	Rp4-m2			
<i>Promioclaenus lemuroides</i>	P-19506	Rm2			
<i>Promioclaenus lemuroides</i>	P-57817	Lm(1/2?)			
<i>Dissacus navajovius</i>	P-15279	RM1 – isolated		2	1
<i>Dissacus navajovius</i>	P-15395	P? partial – isolated			
<i>Anisonchus</i> sp.	P-45004	(3) tooth fragments (C, Lp2, other)		3	1
<i>Periptychus carinidens</i>	P-19227	Lm2? – isolated		3	1
<i>Periptychus carinidens</i>	Uncat.	2 lower premolars			
<i>Conoryctes comma</i>	P-41519	Left dp5, m1-2		3	1
Taeniodont indet.	P-19513	Tooth Fragment		1	-
<i>Torrejonia</i>	Uncat.	Dentary		2	1
Metatherians					
<i>Swaindelphys encinensis</i>	P-69888	Lm2		1	1

38 eutherian and metatherian teeth (excluding those of *Pantolambda bathmodon* and *Tetraclaenodon puercensis*) were tallied (e.g. Fig. 33). The minimum number of individuals yielded was 15. The high number of individuals in proportion to the teeth is due to many of the taxa being defined on the basis of 1-3 teeth.

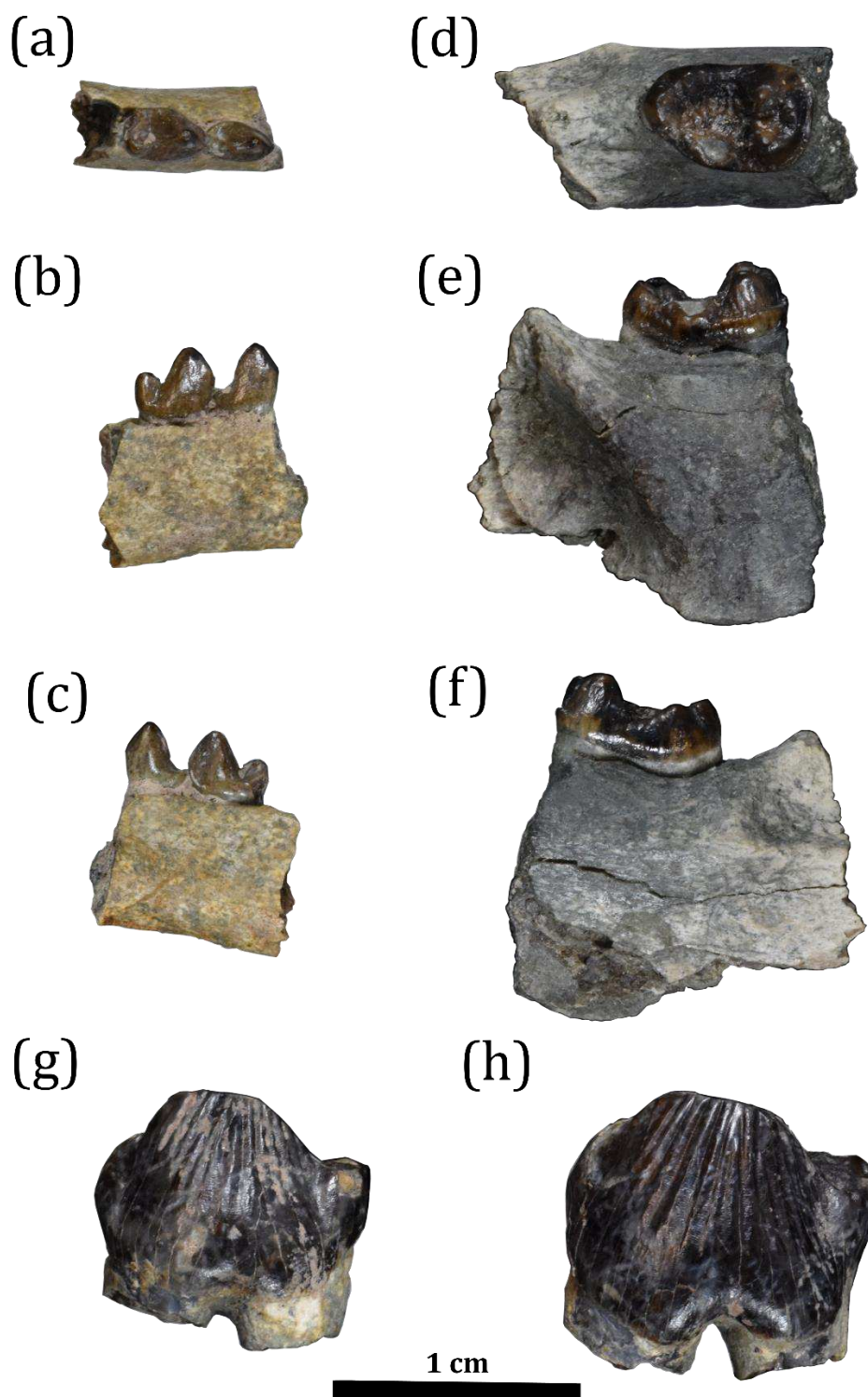


Figure 33: Examples of some of the other mammals found in the L-1079 assemblage with the left dentition of *Torrejonia* in (a) occlusal, (b) lingual, and (c) buccal views, the right ultimate molar of *Mimotricentes* in (a) occlusal, (b) buccal, and (c) lingual views, and (g, h) two *Peripitychus* premolars in buccal view. All specimens uncatalogued. Identifications of *Torrejonia* and *Mimotricentes* shared by Tom Williamson.

Additionally, ten isolated multituberculate teeth are also present at L-1079 (Table 16).

Table 16: Multituberculate Teeth at L-1079

Taxon	Specimen Number (NMMNH)	Specimen Identification	Most abundant tooth (#)	Total # of teeth	MNI
Multituberculate	P-19522	I? (isolated)		4	1
Multituberculate	P-19526	I? (isolated)			
Multituberculate	P-19529	I? (isolated)			
Multituberculate	P-69884	I? (isolated)			
Multituberculate	P-19619	i? (isolated)		2	
Multituberculate	P-19605	P? (isolated)			
Multituberculate	P-19521	P? (isolated)			
Multituberculate	P-19531	M? (isolated)		2	
Multituberculate	P-19527	M? (isolated)			

Since the generalized multituberculate dental formula is 1-3.0-1.1-4.2/1.0.1-4.2 (Rose, 2006), the MNI of multituberculates is most conservatively estimated to be one. The multituberculates known from the San Juan Basin include taeniolabids (*Taeniolabis*, *Kimbetopsalis*, *Catopsalis*), ptilodontids (*Kimbetohia*; *Ptilodus*), and neoplagiaulacids (Matthew, 1937; Weil and Krause, 2008; Williamson et al., 2016). Whether using the dental formula of Taeniolabididae (2.0.1.2/1.0.1.2), Ptilodontidae (2.0.4.2/1.0.2.2), or Neoplagiaulacidae (2.0.4.2/1.0.1–2.2) (Krause et al., 2020), the conservative MNI estimate of one multituberculate in the assemblage is upheld.

The overall mammal MNI (estimated from 160 total teeth) is 25. On the basis of the dentitions, *Tetraclaenodon puercensis* is the most abundant taxon with a MNI of five, followed by *Pantolambda bathmodon* (MNI = 4), *Mimotricentes subtrigonus* and *Promioclænus lemuroides* are the next most abundant taxa (MNI = 2). Other taxa present include *Acmeodon secans*, *Mioclænus turgidus*, *Dissacus navajovius*, *Periptychus carinidens*, and *Conoryctes comma*. Several multituberculate teeth and an isolated tooth of the marsupial *Swaindelphys encinensis* give evidence of non-eutherian mammals.

In addition to the mammalian remains, crocodile teeth, vertebrae and osteoderms (e.g. P-19520, P-54398, P-19666), squamate vertebrae (e.g. P-19616; P19539), shell fragments from platysternoid turtles (P-54625), and gar scales (P-19664; Fig. 34) were also recovered from L-1079 and indicate that these vertebrates were minor components of the fauna. Assuming, that there is at least one individual from each

of these group, the non-mammal MNI is 4. An additional, tiny (3 mm long axis) alligatoroid tooth was found among the bone fragments of P-19691 (Fig. 34e, f). Its small size indicates that it must have come from a very young juvenile (hatchling?) and thus another individual is added to the total non-mammal MNI (5). In addition to the vertebrate material, isolated invertebrate material (6 gastropod shells and 1 fragmentary/unprepared gastropod) is also reported from the locality.

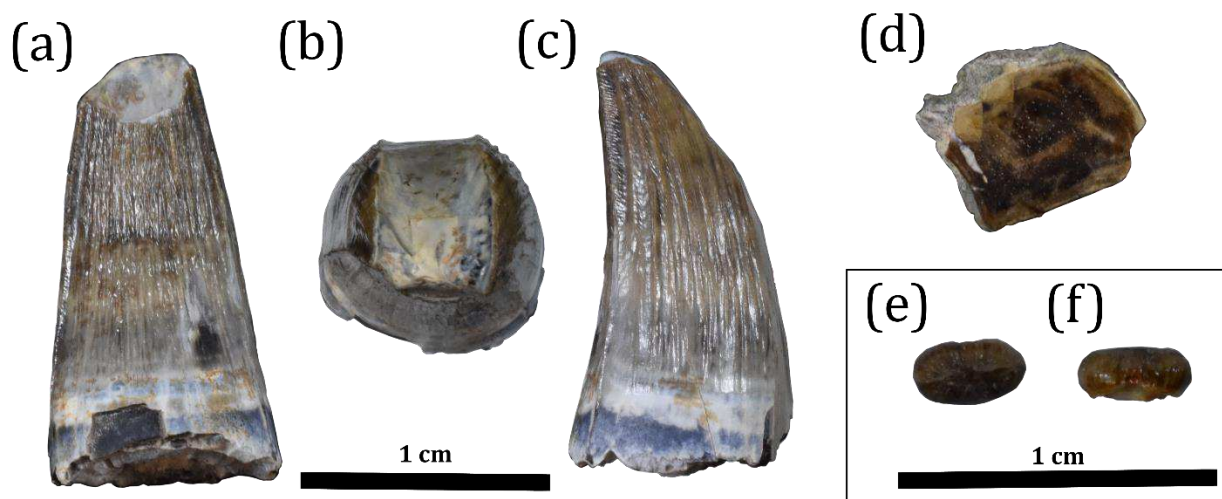


Figure 34: An assortment of non-mammalian vertebrate material from the L-1079 with an alligator tooth (uncatalogued) in (a) posterior, (b) apical, and (c) lateral view, (d) a gar scale (uncatalogued), and a tiny alligatoroid tooth (P-19691) in (e) apical and (f) lateral view.

In conclusion, the total minimum number of individual vertebrates (mammals + reptiles + fish) at L-1079 is 30. This estimate is likely a large underestimate given the low percentage (~7%) of identifiable dental material relative to the overall number of fragments recovered from the quarry.

The strict minimum number of individuals estimate (reliant on tabulating repeating elements) can be nuanced by taking into account additional observations. In the case of *Pantolambda bathmodon*, I will now detail some additional reflections on the number of individuals represented at L-1079 in context of the relative wear on the teeth and paleohistology.

Further Nuance on MNI of Pantolambda bathmodon: Relative Wear

The most conservative estimate of the MNI comes from considering repeated instances of the same element within an assemblage (Shotwell, 1955; Voorhies, 1969). However, additional observations can be brought to bear on the question to

generate a less conservative (but potentially more realistic) estimate. One strategy is considering whether teeth from different tooth row positions could reasonably come from the same individual on the basis of their relative amounts of wear. The amount of wear at different tooth row positions in the same individuals will vary based on factors like the timing of dental eruption and the mechanisms of the animal's chewing.

Pantolambda bathmodon exhibits consistency in the pattern of wear seen in the ultimate premolar and the molars across multiple individuals (AMNH 15934; AMNH 16663; NMMNH P-72346; USNM 15408). In brief, the first molar (M1/m1) is consistently the most worn of the posterior cheek teeth. The amount of wear decreases posteriorly with the ultimate molar (M3/m3) substantially less worn. The first molar is also more worn than the ultimate premolar (P5/p5). This premolar typically exhibits a similar amount of wear to the second molar and more wear than the ultimate molar.

The *Pantolambda bathmodon* teeth recovered from the L-1079 assemblage exhibit different stages of wear, from nearly unworn upper premolars (NMMNH P-19544) to intermediately worn upper molars (NMMNH P-19545) to extremely worn upper molars (NMMNH P-19546). These wear stages were divided into three qualitative categories (Fig 35).

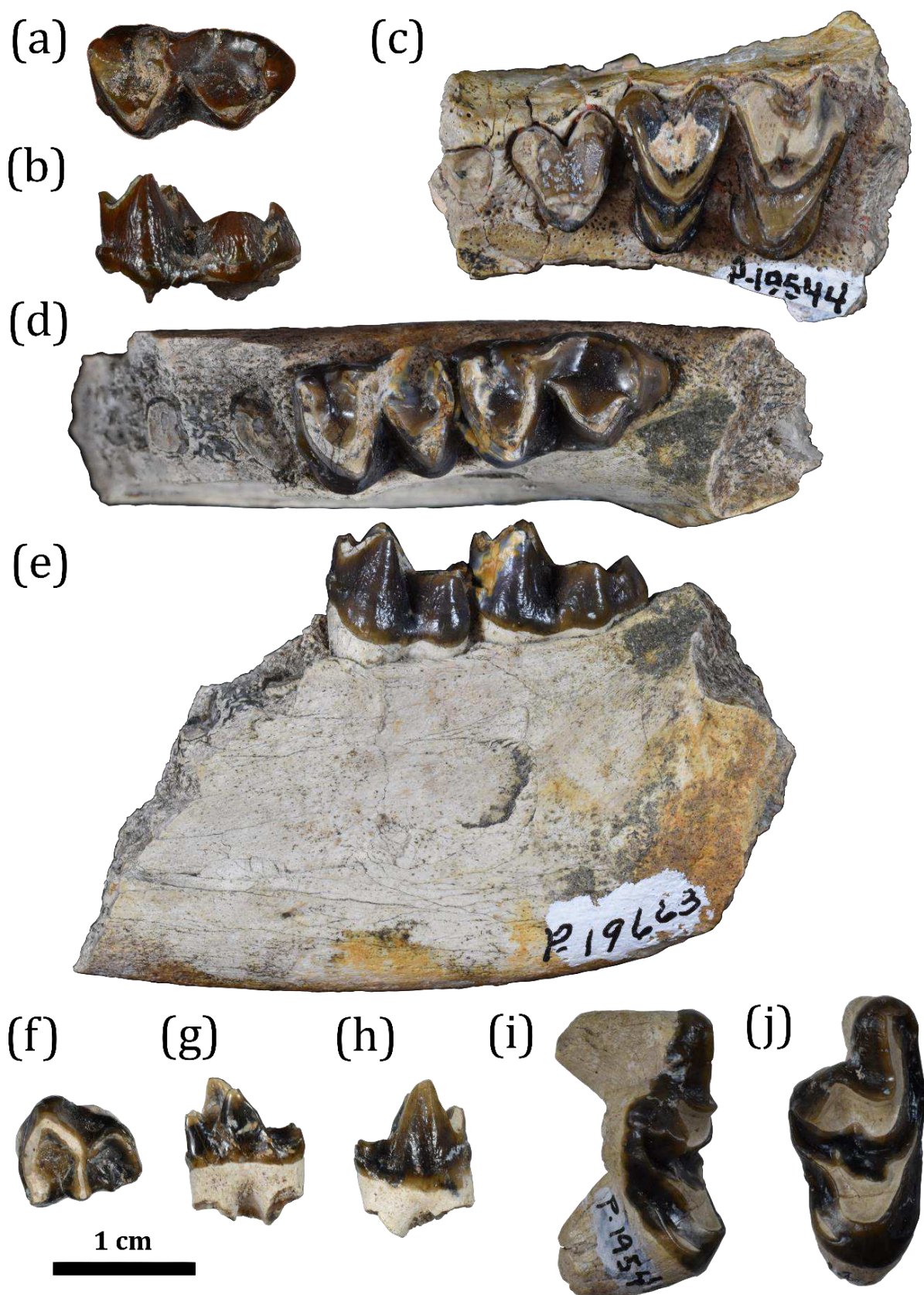


Figure 35: Wear stages of the L-1079 *Pantolambda bathmodon* teeth with Wear Stage 1 illustrated by NMMNH P-69921 (a) occlusal view and (b) buccal view and NMMNH P-19544 (c) in occlusal view. Wear Stage 2 is exemplified by NMMNH P-19663 in (d) occlusal and (e) buccal views and NMMNH P-19617 (f) occlusal, (g) lingual, and (h) buccal views. P-19546 in (i) anterior and (j) occlusal view shows a tooth at Wear Stage 3.

Wear Stage 1 represents the least worn teeth in the assemblage. Teeth at this wear stage (a) preserve the apices of their major cusps, (b) preserve some crests where the enamel has not been pierced to expose dentine (although flattened wear facets are developed on the enamel), and, on crests where the dentine is exposed, (c) preserve the narrow margins of the crest. No basining is present in the dentine. Specimens that exemplify this wear stage include NMMNH P-69921 (Fig. 35a, b), NMMNH P-19544 (Fig 35c), and NMMNH P-69889.

The upper premolars of NMMNH P-19544 help illustrate the range encompassed by Wear Stage 1. In P5, the paracone and metacone are broken by later erosion, but the protocone is preserved. The pointed apex of this cusp is preserved. No wear facet has developed on the preprotocrista and a slight flattened facet that does not pierce the enamel is developed on the postprotocrista. This state reflects the most unworn of the pantodont teeth of this assemblage. P4 is more worn with wear facets developing on all of the crests that contribute to the pantodont 'double-v'. The facet is least developed on the postprotocrista (enamel not breached) with some dentine beginning to shine through the enamel on the preprotocrista and the postparacrasta. The facet on the preparacrasta is most developed with the dentine exposed. Despite the breaching of the enamel, the apices of both the paracone and the protocone are well-developed. This P4 lies close to an upper limit for Wear Stage 1.

Wear Stage 2 (the intermediate stage) marks further advancement of wear along tooth crests through the more extensive exposure of the dentine. Teeth at this wear stage (a) show some flattening or rounding in the apices of the cusps (particularly the protocone of upper molars and the trigonid of lower molars) that results in the exposure of dentine and (b) have the enamel pierced to expose the dentine along the majority of the extent of the crests. Specimens that exemplify this wear stage include NMMNH P-19663 (Fig 35d, e), NMMNH P-19617 (Fig 35 f, g, h), and NMMNH P-19540. Wear Stage 2 differs from Wear Stage 3 because the exposures of the dentine remain relatively narrow and the apices of the cusps are still partially developed.

NMMNH P-19663 illustrates Wear Stage 2. In Lm2, the enamel of the paracristid, protocristid, and cristid obliqua is breached. Of these cristids, the protocristid shows the most broad dentine exposure. The protoconid apex is rounded and the hypoconid apex is flattened. The wear is less pronounced in Lm3 shows an overall similar pattern but the exposure of the dentine is more narrow. In this case, Lm3 would mark one of the 'least worn' presentations of Wear Stage 2.

Wear stage 3 marks the most extreme erosion of the enamel. Teeth at this wear stage exhibit (a) low cusps where the apices are worn away and large portions of the dentine are exposed, (b) widening of dentine exposure on large crests and the breaching of the enamel on smaller crests, and (c) basining in the dentine. This wear stage marks a striking change in the topography of the tooth from the original height of the major cusps.

NMMNH P-19546 exemplifies this wear stage (Fig. 35i, j). In this molar, the enamel has been worn through to the dentine from the apex of the paracone, along the centrocrista across the metacone, and along the postmetacrista until the buccal margin of the tooth. Furthermore, the pre- and postprotocristae are worn to the dentine buccally past the bases of the paracone and metacone and the enamel of the precingulum has been breached to a lesser extent. Finally, a wear facet has developed on the postcingulum but not yet pierced the enamel. As a result, both the protocone and the centrocrista are basined. The distal portions of the protocone and the metacone remaining the most elevated portions of the tooth. The dentine basin of the centrocrista extends buccally until it nearly reaches the weak lingual cingulum and lingually to the base of the paracone and metacone (the outer edge of the trigon basin). In the case of this M3, more extreme wear (Stage 3+) could be expected to occur with on the M1 and M2. The upper end of this wear class is exhibited by NMMNH P-19625, an upper right molar (see Extended Data Fig. 5 of Funston et al., 2022).

The wear stages of the teeth of *Pantolambda bathmodon* are listed in Table 17.

Table 17: Wear Stages of L-1079 *Pantolambda bathmodon* teeth

Specimen Number (NMMNH)	Tooth	Wear Stage
P-15400	Lp4	2
P-19540	Rm1	2
P-19541	Lm1	2
P-19541	Lm2	1+
P-19544	LP2-P5	1-1+
P-19545	LM2	2
P-19545	LM?1	2+
P-19546	RM3	3
P-19608	M?	2+
P-19612	c?	3
P-19617	Rp5	2
P-19625	RM1	3+
P-19654	Lp2, p5-m1, Rm2-m3	3
P-19662	Rm3	2
P-19663	Lm2-m3	2
P-21561	Lm2	3
P-41514	LM2	3
P-57814	RM2	2+
P-69889	Rp2	1
P-69890	Lp5	1+
P-69918	i?	2+
P-69919	Lp1	3
P-69920	Lp4	2
P-69921	Lm3	1
P-69922	Lc	1
P-69923	I?	2
P-69924	C?	2
Uncat	RM3	1

Two teeth at Wear Stage 3 (NMMNH P-19625 and NMMNH P-19546) in this sample are particularly notable when it comes to MNI estimates. These teeth can be reasonably grouped together (the RM1 of NMMNH P-19625 is more worn than the RM3 of NMMNH P-19546 as would be expected), but could not belong to another individual with less worn lower molars or premolars. Essentially, since the M3 is the least worn tooth in complete posterior dentitions, the extreme wear on the M3 is not consistent with less wear than in other animals.

Since the MNI was, in part, determined based on Lm3, where the three teeth were at a lower wear stage than the Wear Stage 3 M3, another individual must be included in the assemblage even if a conservative estimate of the repeating elements would tabulate these differently. Thus there are at least 3 individuals that contributed teeth to the MNI count *and* an additional individual with a much more highly worn dentition in the assemblage.

By examining the relative wear of teeth at different positions, the dental MNI of *Pantolambda bathmodon* at L-1079 can be increased from three individuals (determined by counting repeating elements) to four individuals (by taking into account what teeth can reasonably be expected to derive from the same individual). This dental estimate further corroborates the MNI ascertained from the postcrania.

Further Nuance on MNI of Pantolambda bathmodon: Histological Sectioning

Histological sections made of selected teeth from the L-1079 quarry provide a final avenue for investigating the MNI of *Pantolambda bathmodon*. Ten specimens of *Pantolambda bathmodon* teeth were sectioned (Table 18) and the results incorporated into a study of the life history of *Pantolambda* (Funston et al., 2022; Appendix III).

Table 18: L-1079 Specimens Sectioned for Paleohistology

Specimen (NMMNH)	Elements Sampled
P-19541	Lm1 trigonid, Lm2 trigonid
P-19604	Rm? trigonid, Canine
P-19612	Canine
P-19625	RM1, Root of lower molar
P-41514	Maxilla with M1–3
P-69892	Lm3 talonid
P-69918	Lower Incisor
P-69919	Lp1
P-69923	Upper Incisor
P-69925	Canine

The sectioned specimens were selected on the basis of several factors including: (a) simplicity of the tooth structure (with a selection preference initially given to single-rooted teeth from the anterior portion of the dentition), (b) preservation of portions of both the crown and the root, and (c) capturing a variety of tooth row positions and wear stages. Ultimately, in selecting these specimens, a balance between the resulting data loss from destructive histological sampling and the potential gains for the histology study. The protocol for making the thin sections can be found in Funston et al., (2022).

The primary way in which these sections can nuance the MNI estimate of *Pantolambda bathmodon* is through providing evidence of adults of different ages in the pantodont assemblage at L-1079 through cementum annulations. Cementum is a mineralized tissue that forms the outer layer of tooth roots and supports the attachment of the periodontal ligament (Berkovitz and Shellis, 2018). Cementum is laid down seasonally in alternating light and dark bands (annulations) (Wittwer-Backofen et al., 2004). These annulations thus are a faithful record of time with

each light-dark couplet representing an annual cycle (Klevezal, 1996; Wittwer-Backofen et al., 2004; Berkovitz and Shellis, 2018).

The cementum annulations of a complete molar series of *Pantolambda bathmodon* (NMMNH P-41514) results in 0.5 fewer cementum annulations being present in M2 and M3 than in M1. This result shows that the posterior two teeth erupted later than M1, but that shows that all of the teeth give the same signal for the age of the animal. This pattern indicates that the entirety of the permanent dentition of *Pantolambda bathmodon* erupted within its first year of life (Funston et al., 2022). Applying this insight to the L-1079 assemblage, estimates of the age of the individuals in the assemblage can be made (Fig. 36; Table 19).

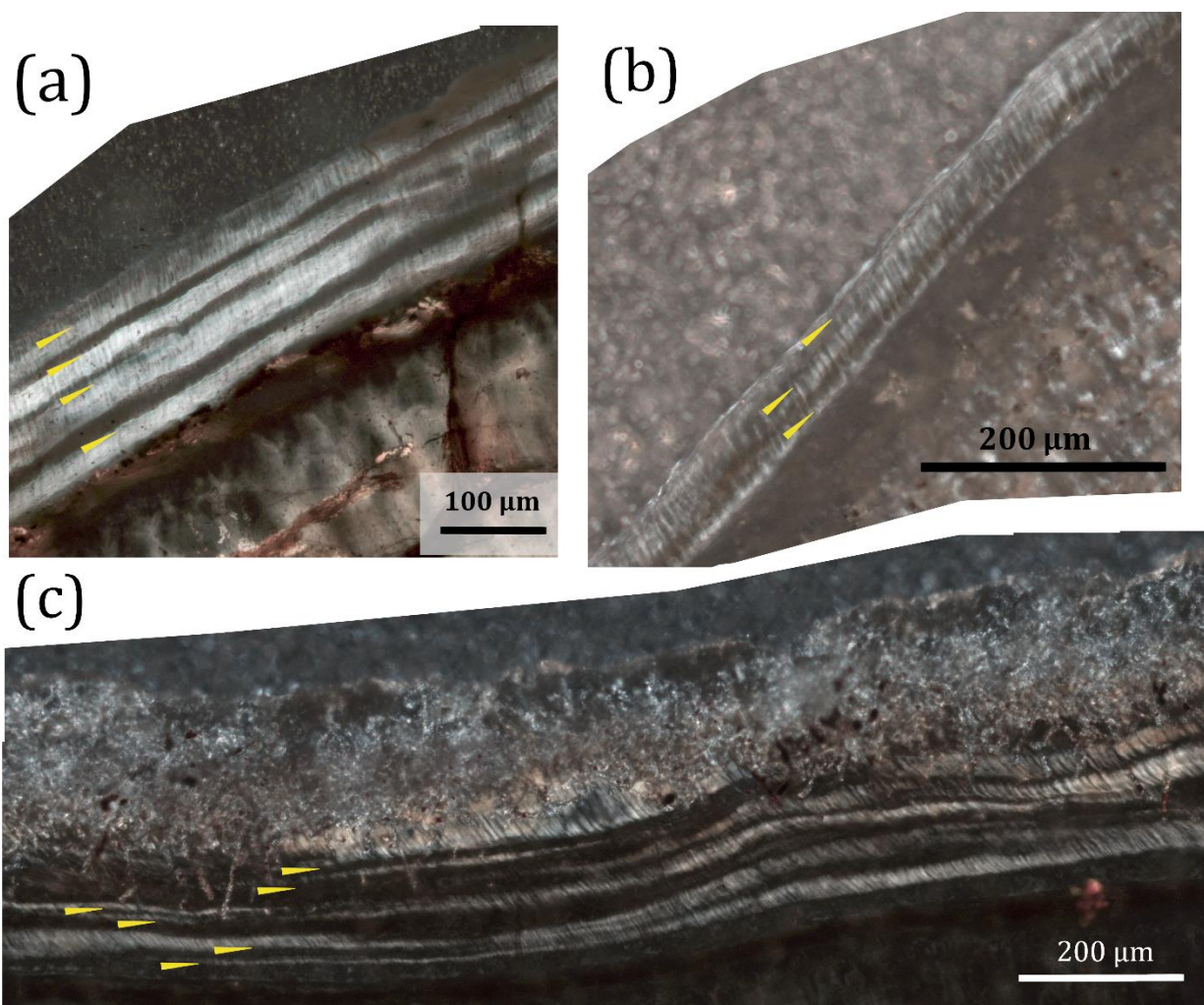


Figure 36: The different ages of individuals within the quarry can be evidenced through cementum annulations. In (a), the root of NMMNH P-69919 (Lp1) shows four white-black couplets. Three white-black couplets are evidenced in NMMNH P-69892 (Lm3) and six couplets are present in (c) NMMNH P-19625's lower molar root in longitudinal section. Yellow arrows placed across the center of the cementum couplets. An unannotated version of this figure is available in the appendix (Fig. A.14) so that the annulations can be seen more clearly. Images are taken under cross-polarized light and provided by Greg Funston.

Table 19: Ages of L-1079 Specimens Based on Cementum Annulations

Specimen (NMMNH)	Estimated Age (Years)
P-19541	3
P-19612	3
P-19625 (M1)	5
P-41514	3
P-69892	3
P-69918	2
P-69919	4
P-69923	4
P-69925	5
P-19625 (lower molar root)	11

Some caution is needed in assessing the results of cementum annulations because of later reworking of the layers in certain specimens. For example, in the lower molar root of specimen NMMNH P-19625 (Fig. 36c), the outer layers of cementum were disrupted by the invasion of ?plants/fungi. This rendered the outer, couplets indiscernible. The estimated age of 11 years was arrived at by examining the average thickness of the previous cementum couplets and extrapolating outwards through the disrupted material. Even though the total age is an estimate, six cementum annulations are visible in this specimen. This absolute minimum age of six years distinguishes NMMNH P-19625 from the other specimens and establishes it as the oldest among the palaeohistological sample.

All together, we have evidence of individuals of *Pantolambda bathmodon* who were two, three, four, five, and ~eleven years old at time of death at L-1079. Thus, the cementum annulations of the histological sections further corroborate the less conservative MNI estimate of 5 and indicate that many of the *Pantolambda bathmodon* individuals in this study were different ages.

A further interesting insight into the MNI arises from one particular individual where a large portion of the dentition appears to be preserved. Among the typically, dark brown enamel of the *Pantolambda* specimens of the quarry (e.g. NMMNH P-19663, Fig 35d, e), an assortment of teeth with lighter-colored enamel are present. The enamel of these teeth is golden honey-brown in color and are typically still set in fragments of either the dentary or the maxilla. The bone fragments are all similar color (light tan brown) with black weathering scratches and an overall smooth outer

surface. The broken edges of the dentary and maxilla fragments all expose a light tan to medium brown interior color. Additionally, the teeth exhibit wear ranging from Wear Stage 1 to Wear Stage 2 that is consistent with the patterns seen in other specimens. Essentially, the molars exhibit higher wear stages than the premolars in this subsample. This pattern of wear is consistent with what is observed in more complete specimens (e.g. AMNH 16663) and expected because the first molars erupt before the premolars are replaced (Funston et al., 2022).

Most critically, the specimens that exhibit this pattern of golden-brown enamel and other similar features all are non-overlapping elements (Table 20; Fig. 37-38).

Table 20: Teeth Hypothesized to Belong to A Single Individual

Specimen (NMMNH)	Element	Location in Mouth
P-69889	Rp2	Right Lower
P-19540	Rm1	Right Lower
P-15400	Lp2 (root) and Lp4 (set in dentary)	Left Lower
P-69890	Lp5	Left Lower
P-19541	Lm1 (trigonid)	Left Lower
P-19541	Lm2 (trigonid)	Left Lower
P-69892	Lm3 (talonid)	Left Lower
P-19544	LM2-LM4	Left Upper
P-19545	LM?1 (protocone)	Left Upper
P-19545	LM2 (paracone and metacone)	Left Upper

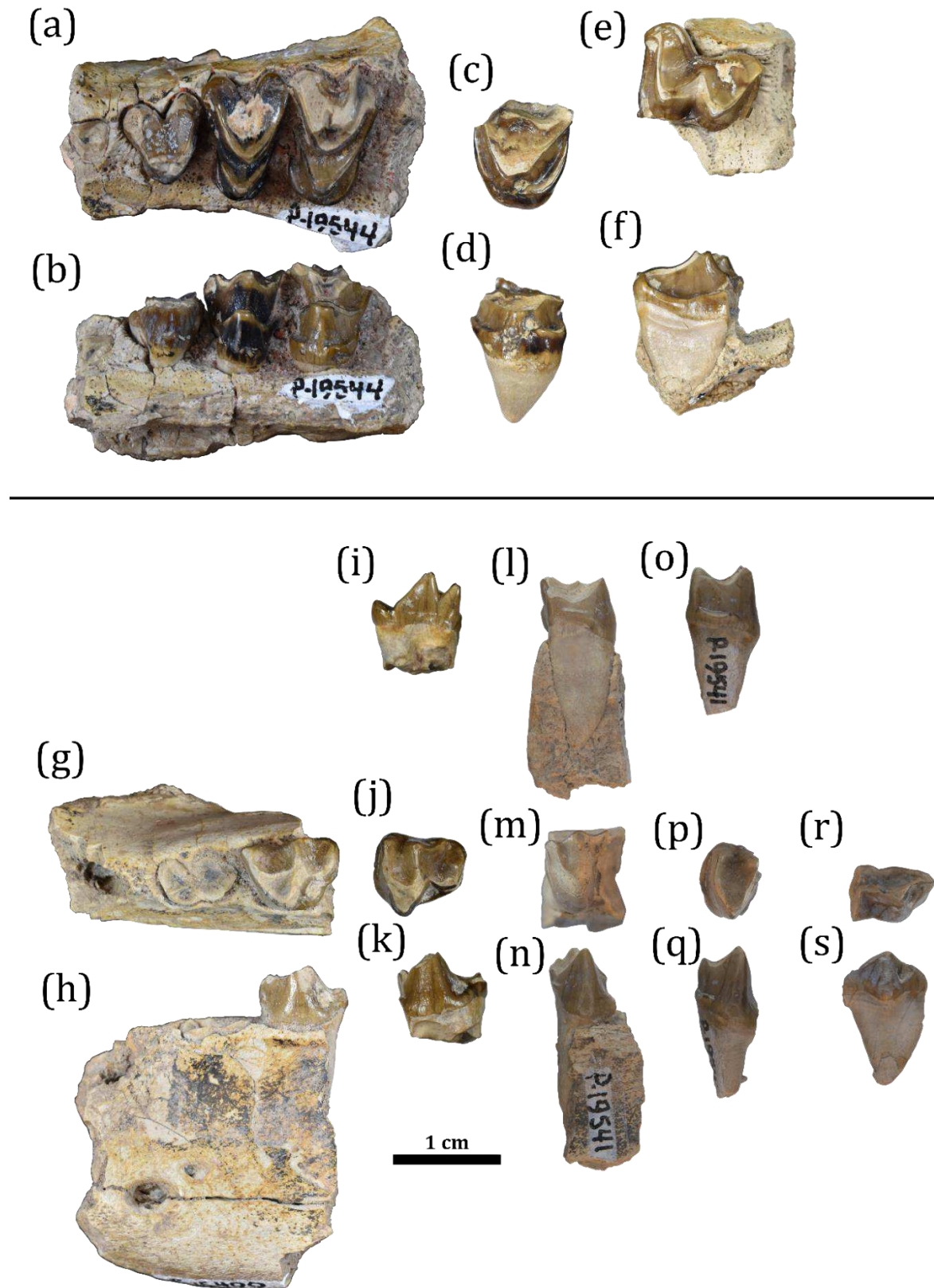


Figure 37: Teeth belonging to the left side of the mouth of the single individual with (a-f) deriving from the upper dentition and (g-s) from the lower dentition. The upper dentition consists of NMMNH P-19544's premolars in (a) occlusal and (b) lingual views; NMMNH P-19545's M?1 protocone in (c) occlusal and (d) lingual views and M2 in (e) occlusal and (f) anterior views. The lower dentition consists of a Lp4 of NMMNH P-15400 in (g) occlusal and (h) buccal views; NMMNH P-69890's Lp5 in (i) lingual, (j) occlusal, and (k) buccal views; NMMNH P-19541's Lm1 and Lm2 trigonids in (l, o) anterior, (m, p) occlusal, and (n, q) buccal views; and NMMNH P-69892's Lm3 talonid in (r) occlusal and (s) buccal views. Photos (l-s) taken by Greg Funston.

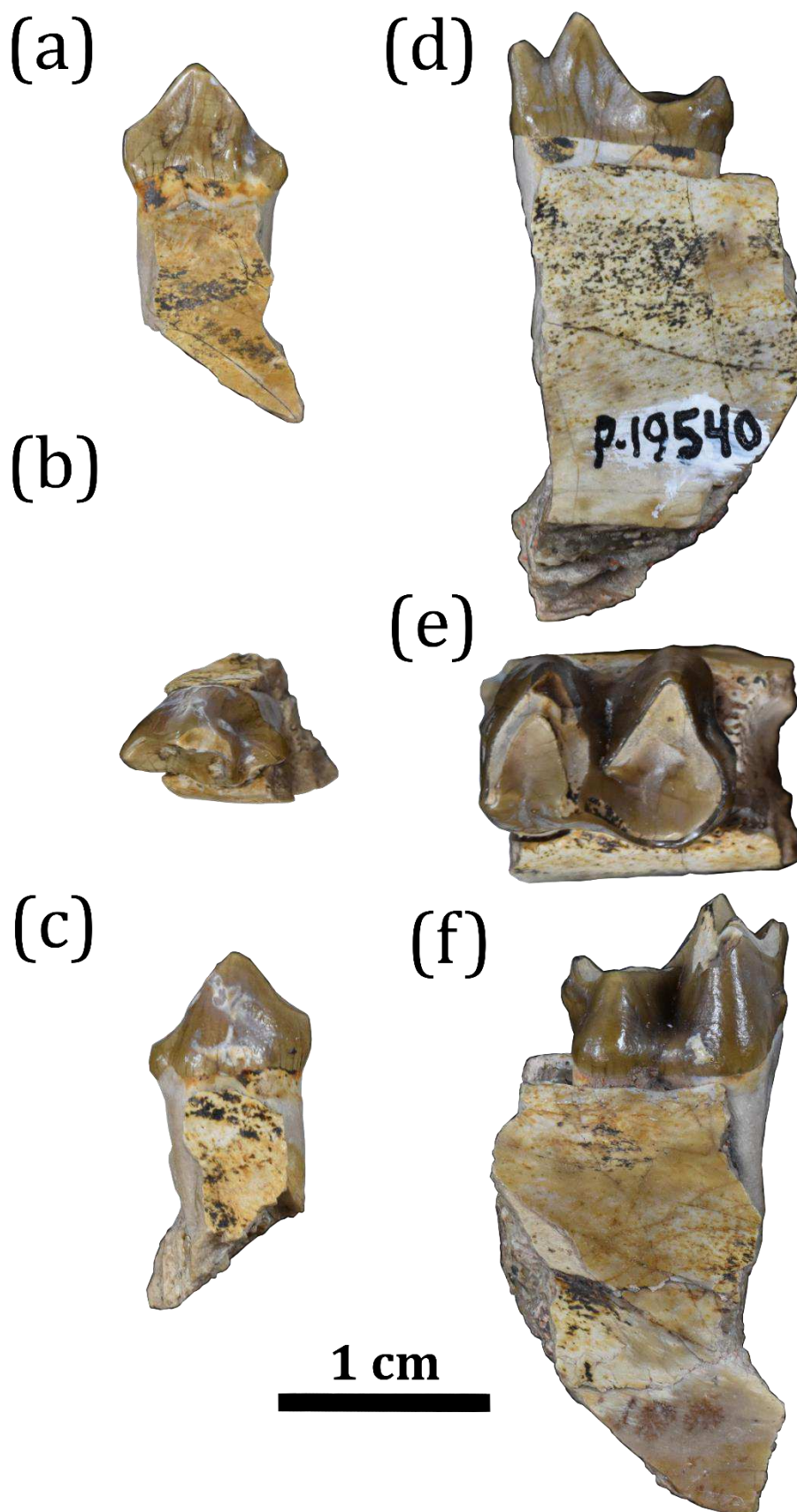


Figure 38: Teeth belonging to the right side of the mouth of the single individual with NMMNH P-69889's Rp2 in (a) lingual, (b) occlusal, and (c) buccal views and NMMNH P-19540's Rm1 in (d) lingual, (e) occlusal, and (f) buccal views.

This pattern of similarity is further born out with nuances of the palaeohistology. The sectioned teeth that belonged to this individual all preserve three couplets of cementum annulations. Most strikingly, the number of cross-striations between three accentuated lines in the enamel was consistent between these two specimens (Funston et al., 2022). Additionally, these teeth exhibit striae of Retzius separated by a single cross-striation (Retzius periodicity = 2). These striae that reach to the surface of the tooth as perikymata. Perikymata were rare within the L-1079 sample, but were observed on several other (unsectioned) teeth within the grouping hypothesized to belong to the same individual. Altogether, the balance of evidence favors these teeth being derived from the same individual. This individual was three years old at time of death as indicated by the cementum annulations of P-19541 and P-69892.

The presence of an LM2 (P-19545) among the 'same individual' specimens is exciting because a second LM2 was part of the sampled specimen, NMMNH P-41514 (Fig 39). Cementum annulations indicate that NMMNH P-41514 was also 3 years old at time of death. Operating under the assumption that the 'same individual' specimens are indeed from a single animal, these repeating elements indicate that are at least 2 3-year old individuals in the assemblage. Taking on board that realization, the pantodont MNI from cementum annulations (five individuals) can be increased to a MNI of six individuals.

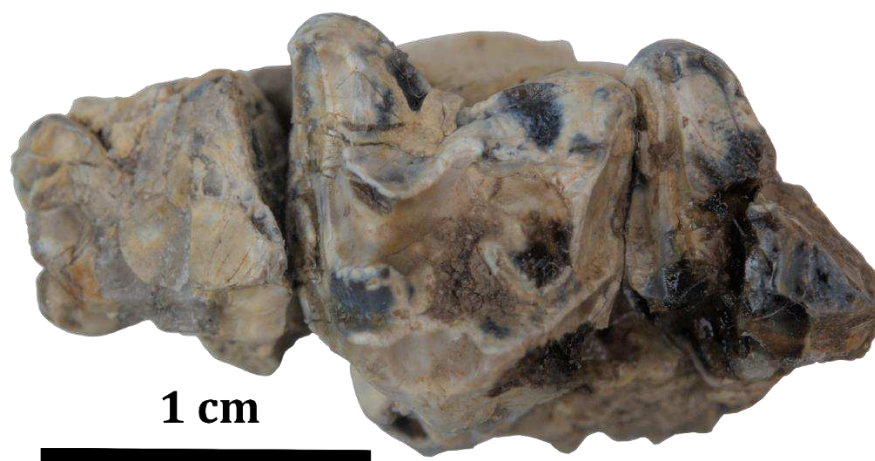


Figure 39: The fragmentary maxilla of NMMNH P-41514 illustrating the LM2 with an estimated age of three years. Photo credit: Greg Funston

Thus an interesting demography of *Pantolambda bathmodon* for the quarry arises from this analysis of ages. It is likely that *Pantolambda bathmodon* reached sexual maturity before it was year old (Funston et al., 2022). The L-1079 assemblage shows a mix of adults that clustered around a few years old (2-4 years) with several, older individuals (5 and 11 years). There is the potential that the assemblage contains at least two 3-year old individuals on the basis of repeating elements of the dentition. All told, this analysis of the MNI of *Pantolambda bathmodon* demonstrates that there were about a half-dozen pantodont adults grouped in this assemblage.

In further analyses of the L-1079 assemblage, both the 'strict', postcrania-based MNI (4 individuals) and the less conservative, 'holistic' MNI arising from integrating palaeohistology (6 individuals) will be used. The selection of which MNI value will be presented in the main text will be guided by whether an 'over' or 'underestimate' would result in a more cautious analysis. The alternative MNI for each analysis will then be presented in Appendix II.

Comparison of the L-1079 Assemblage with Broader Biostratigraphic Zone Patterns

Based on its stratigraphic position towards the top of the Ojo Encino Member and taxa present, this site belongs to the *Mixodectes pungens* biostratigraphic zone (M zone), the youngest within the Nacimiento Formation. However, the relative abundances of the taxa at this site are not congruent with those of the overall M zone (Fig. 21, Williamson, 1996). Within the M zone, most abundant taxon sampled is *Tetraclaenodon puercensis* (~30%) followed by *Mimotricentes subtrigonus* (~15%) (Williamson, 1996). *Pantolambda bathmodon* makes up about 5% of the specimens sampled from the M zone (Williamson, 1996).

At L-1079, *Pantolambda bathmodon* makes up 16% of the assemblage while *Tetraclaenodon puercensis* and *Mimotricentes subtrigonus* make up 20% and 8% of the assemblage respectively (Fig. 40).

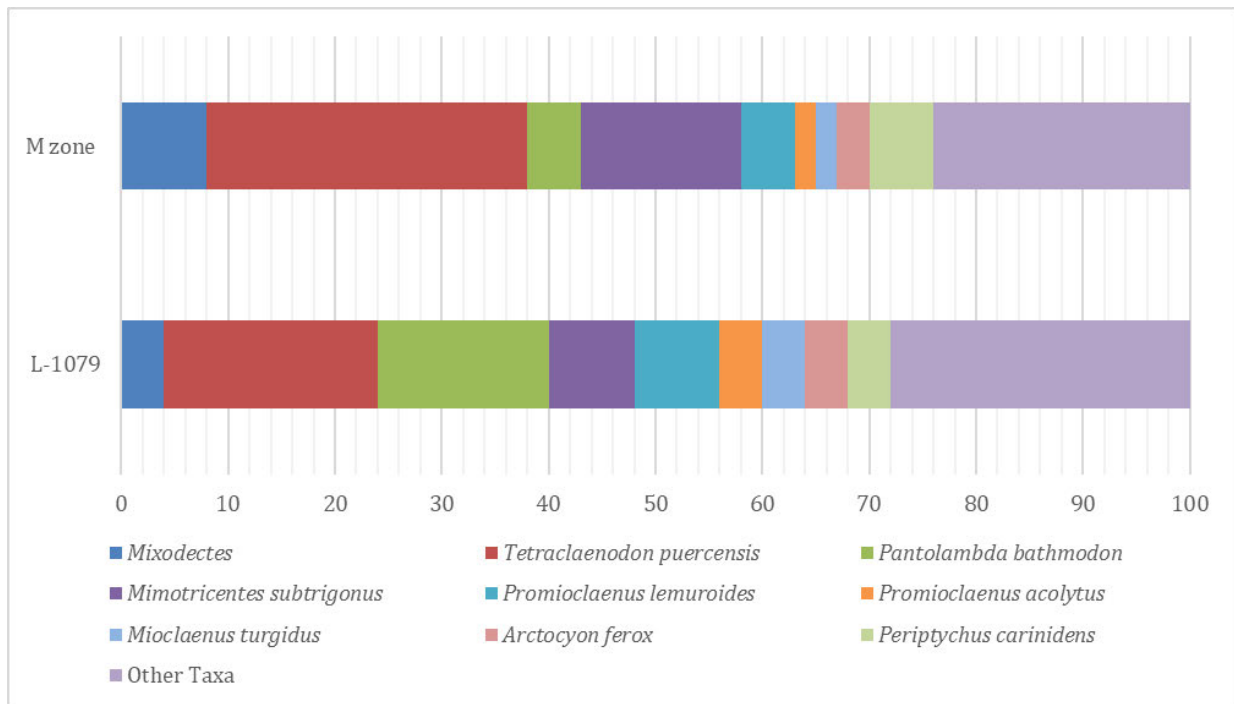


Figure 40: Relative taxonomic abundances of the overall *Mixodectes pungens* (M) zone of the San Juan compared with the abundances of taxa from L-1079 (using strict pantodont MNI). *Pantolambda bathmodon* (dark green) is overrepresented in the L-1079 assemblage particularly relative to *Tetraclaenodon puericensis* (dark red) and *Mimotricentes subtrigonus* (dark purple).

P. bathmodon is about three times as abundant at L-1079 as would be expected from the baseline relative abundances of the M zone with the abundances of *T. puericensis* and *M. subtrigonus* both substantially reduced as a result. Thus, *Pantolambda bathmodon* is overrepresented in the L-1079 assemblage while taxa like *T. puericensis* and *M. subtrigonus* are underrepresented.

The strict L-079 pantodont MNI was used in making this assessment. Even when using the lower number of individuals, the number of pantodonts seems elevated in the assemblage. The pattern of overrepresentation of *P. bathmodon* is even more pronounced when the holistic MNI is taken into account (Fig. A15).

Pantolambda bathmodon occurs rarely within the M zone (Escavada Wash and East and West Flanks of Torreon Wash; Williamson, 1996). Williamson (1996) previously suggested that the occurrence of several individuals of *P. bathmodon* (the L-1079 specimens treated in this current analysis) might indicate gregariousness within the taxon. This notation evidences that the L-1079 taxa were included in the overall M zone abundance calculations in this study. If this locality was excluded from an M zone abundance calculation, it is likely that *Pantolambda bathmodon* would encompass an even smaller percentage of the overall M zone fauna. Thus, their

abundance at L-1079 becomes even more noteworthy. This observation raises the question of what might have caused the concentration of pantodonts at this particular site.

Taphonomy of L-1079

The L-1079 pan collects fossils from several meters of stratigraphy. Thus, the assemblage, while spatially constrained, is time-averaged and can be regarded as mixed. However, the abundant teeth and postcranial bones of *Pantolambda bathmodon* at L-1079 originate from a <1 m thick horizon ~0.82-1.25 m above the pan. The abundance of diagnostic postcranial elements of this particular taxon make possible an assessment of the taphonomic processes acting upon these individuals.

The postcrania of *Pantolambda bathmodon* are highly fragmentary and fractured. However, the breaks between these pieces are clean and tend to refit precisely (Fig. 41). When bones like the nearly complete left femur of NMMNH P-19669 are pieced back together, they are revealed as undeformed. These bones do not show evidence of crushing, abrasion, or bite marks prior to their fossilisation. Thus, the highly fragmentary nature of the postcrania is inferred to result from modern erosion from the cliff face prior to collecting in the pan. Essentially, as these bones are exposed on the surface, they are more likely to fracture incrementally and wash into the pan rather than remaining intact.



Figure 41: A nearly complete left femur from NMMNH P-19669 (a) lateral, (b) anterior, and (c) medial views. The pieces precisely refit and reveal an undeformed element. This observation indicates that the bones are broken by modern erosive processes rather than broken in transport before being fossilised.

The abundance of *Pantolambda bathmodon* in the spatially constrained area of L-1079 could indicate either a behavioural (e.g. that the animals were herding and died in a group) or taphonomic (e.g. that the pantodont bones were transported and concentrated post-mortem) signal. A way to investigate whether (and how extensively) a concentration of bones has been transported is to assess which

Voorhies group is most represented (Voorhies, 1969; Behrensmeyer, 1975; Coombs and Coombs, 1997; Zunino et al., 2012).

Flume studies have been used to assess the susceptibility of different skeletal elements to fluvial transport with the most easily transported elements assigned to Group I and the elements most resistant to transport assigned to Group III (Voorhies, 1969; Table 9). Group I elements can be transported under normal flow conditions while Group II and Group III elements typically are transported under flood conditions (Behrensmeyer, 1975). The proportion of different Voorhies groups can indicate the degree of sorting resulting from fluvial processes and, thus, act as a proxy for determining the extent of post-mortem transport on a fossil assemblage. Although Voorhies Group analysis cannot be easily performed on mixed assemblages because homologous elements in the skeletons of different animals may have different susceptibility to transport (Behrensmeyer, 1975), this assessment is an appropriate technique to employ at L-1079 because the vast majority of the identifiable postcranial material in the quarry belongs to *P. bathmodon*. Additionally, while the majority of the material recovered from L-1079 is from terrestrial animals, gar scales have also been found and indicate some fluvial influence on the assemblage. Thus, the amount to which the fluvial system affected the L-1079 pantodonts can be unpacked.

The definitive pantodont material from the L-1079 site was tabulated by skeletal elements and details of these tabulations can be found in Table A.7.i-iii. The elements count estimated for *Pantolambda bathmodon* and the resulting element numbers expected from the MNI of this assemblage are found in Table A8. The expected elements on the basis of the MNI were then compared to number of elements observed at L-1079 (Fig. 42-43). The fragment counts for larger elements like humeri, pelves, and femora were consistent with those predicted under the strict MNI.

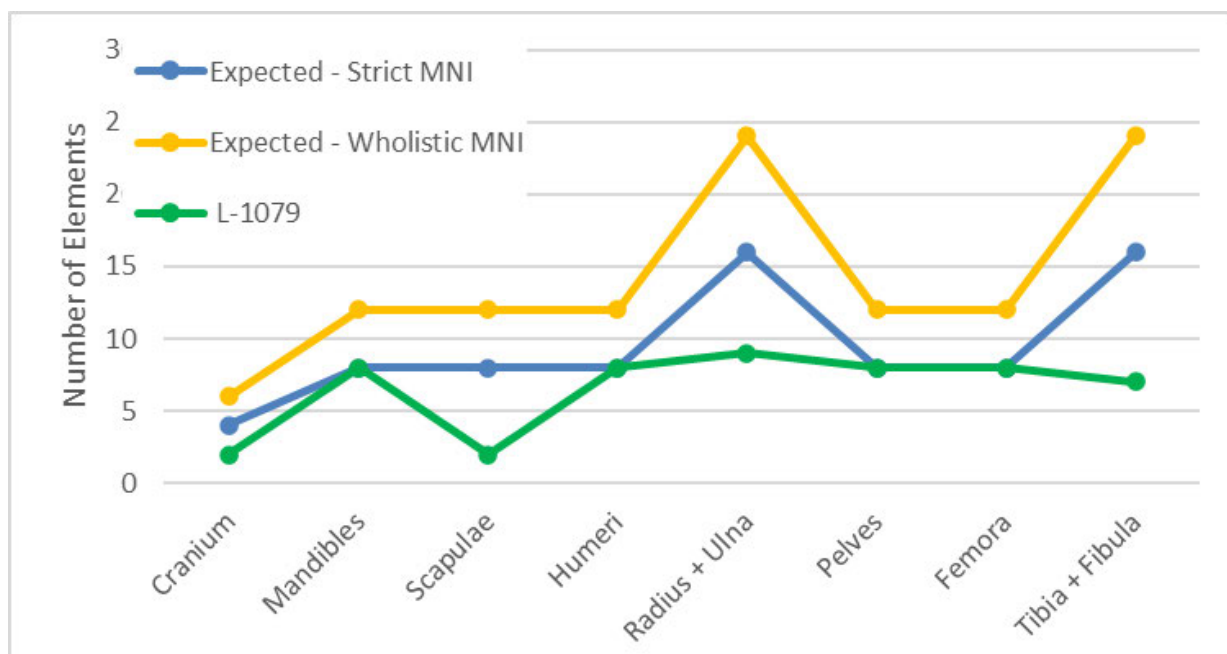


Figure 42: A comparison of the number of L-1079 cranial and proximal appendicular elements with that expected from both the strict and the wholistic MNI. Notably, the number of mandibles, humeri, pelves, and femora by fragments were consistent with the strict MNI estimate.

Smaller and lighter elements like metapodials, phalanges, and ribs (Fig. 43) were less represented in the quarry assemblage than would be expected from the MNI estimates.

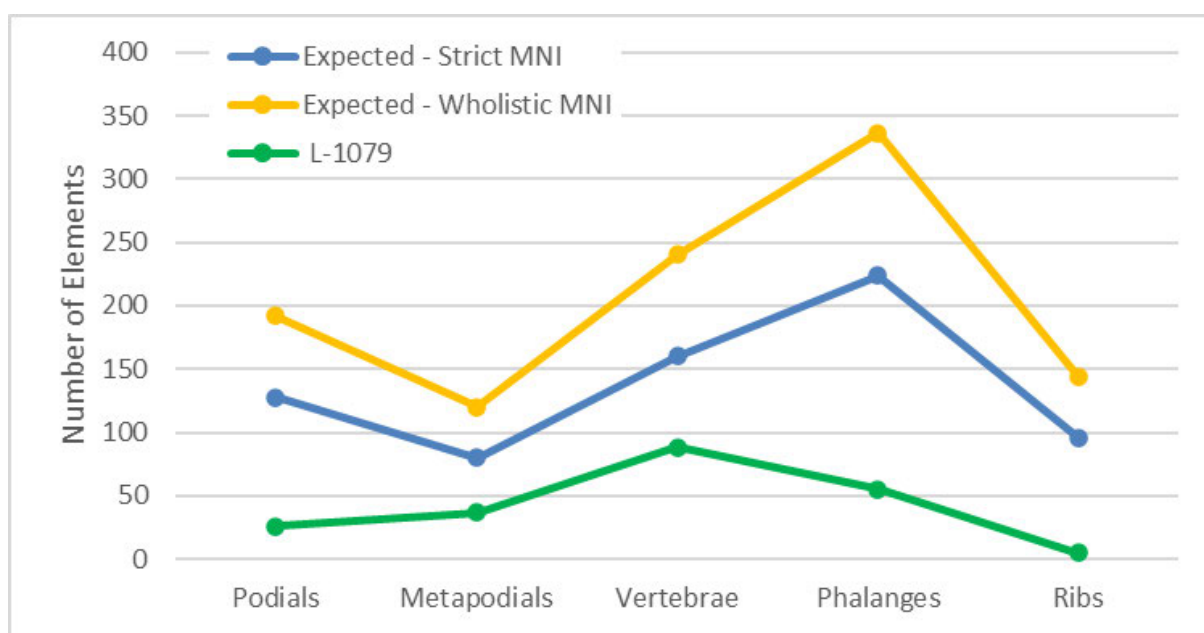


Figure 43: A comparison of the number of small axial and distal appendicular L-1079 elements with that expected from both the strict and wholistic MNI estimates. The greatest discrepancies between observed and predicted elements occurs in the case of the phalanges and ribs.

Overall, the percentages of elements present compared to that expected (Fig. 44) reveals a higher percentage of all larger elements (except scapulae) than that of smaller elements like vertebrae, ribs, and distal limb elements.

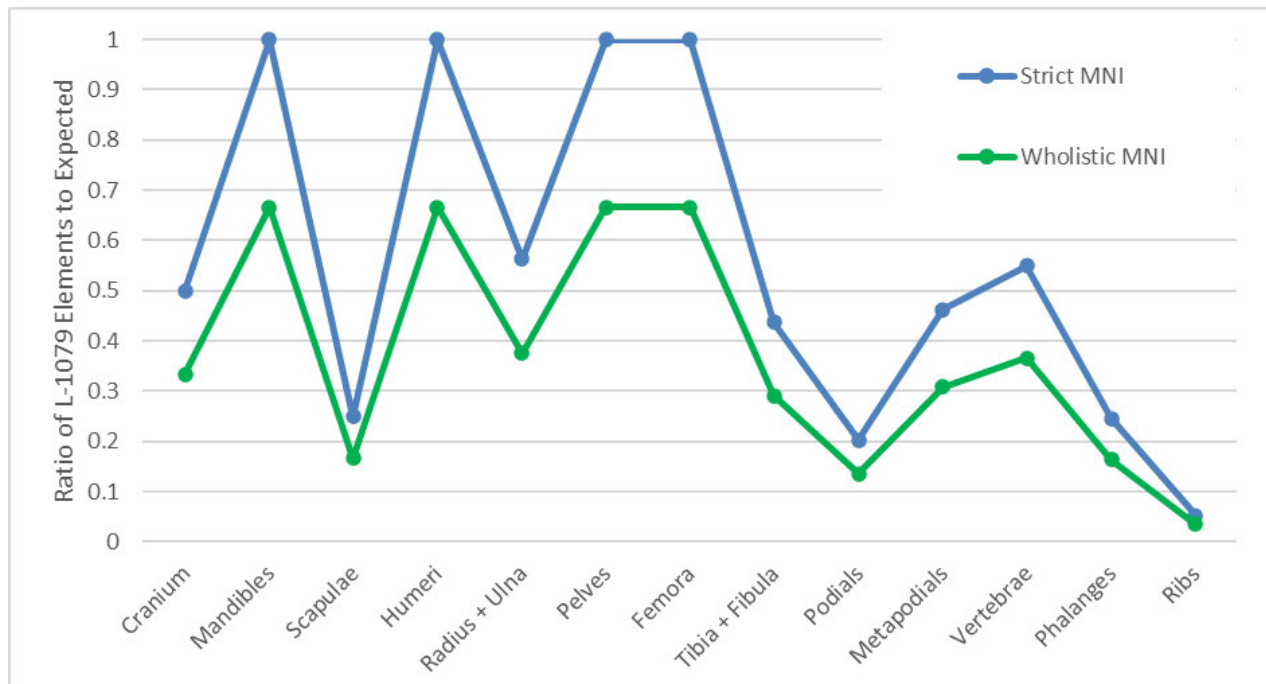


Figure 44: Ratios of the elements counted for the L-1079 quarry with those expected from the MNI estimates. These ratios range from a 100% correspondence for large bones like humeri and femora to 3-5% for ribs.

These element counts were consolidated into Voorhies Groups (Voorhies, 1969; Behrensmeyer, 1975) and the ratios between the elements observed at L-1079 and those expected from the MNI were calculated (Table 21).

Table 21: Number of Elements from Different Transport Groups

Voorhies Group	I	II	III	I + II	II+II I
Expected Number of Elements (Strict MNI)	256	136	12	232	8
Expected Number of Elements (Holistic MNI)	384	204	18	348	12
Number of Elements Present at L-1079	93	77	10	57	8
L-1079/ Expected (Strict MNI)	0.36	0.57	0.83	0.25	1
L-1079/ Expected (Holistic MNI)	0.24	0.38	0.56	0.16	0.67

Although heavily fragmented by modern erosive process, postcrania from *P. bathmodon* belonging to all Voorhies Groups I, II, and III (Voorhies, 1969; Behrensmeyer, 1975). Under the strict MNI estimate (four individuals), Groups I, II,

and III show between 36%-83% of the elements expected (Fig 45). The high number of Group III elements and the 100% representation of Group II+III elements arises because both of these groups capture a low number of elements and the number of mandibles/rami in the L-1079 sample was consistent with (and indeed, contributed to) the MNI estimate.

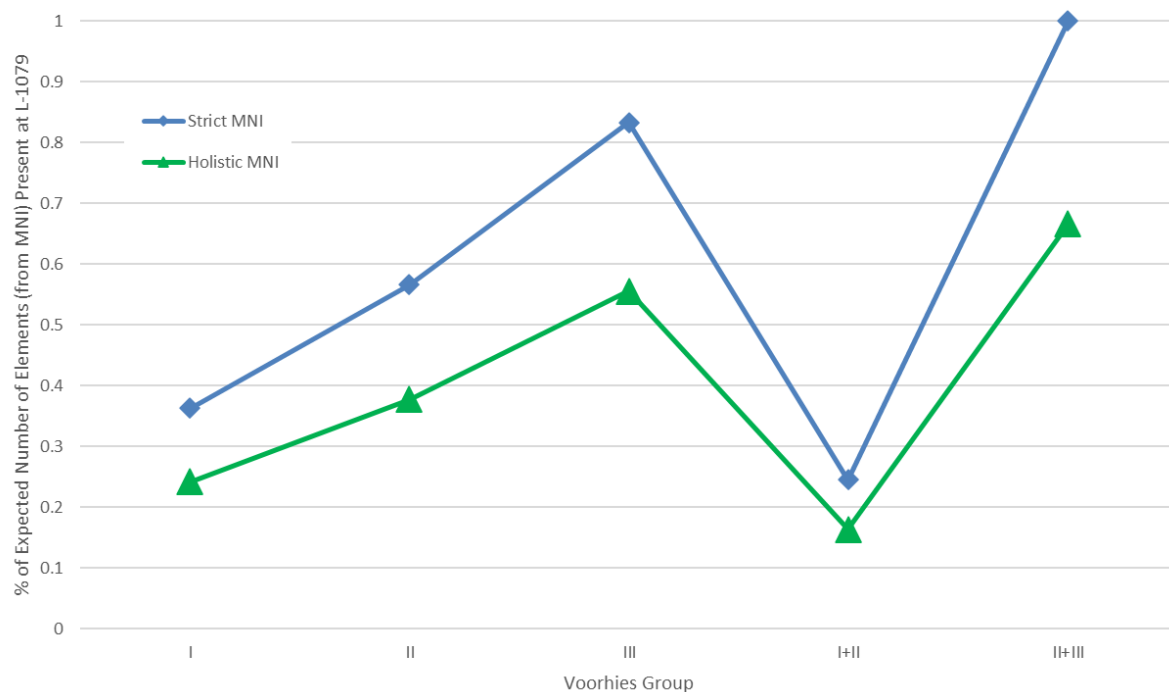


Figure 45: The percentage of the Voorhies Groups predicted by MNI seen at L-1079. Elements belonging to Groups III and II+III are well-represented while elements from Group I and I+II are poorly represented in the assemblage.

Groups I and I+II have the a lowest percentage of elements present. These low numbers result from the underrepresentation of both ribs and phalanges in the assemblage. Elements from these groups are susceptible to transport under normal flow conditions and could potentially have been winnowed from the bones in this deposit prior to burial. It is possible that this preferential winnowing could speak to the conditions in which these animals decomposed. Animal limbs tend to disarticulate roughly proximo-distally in dry environments while they disarticulate from the extremities in wet environments (Hill, 1979). It's possible that the decomposition of these animals in a fluvial system would have led to the freeing of bones like the phalanges and podials from the carcass first. The prevalence of these loose bones would then support their winnowing away by the current.

The overall mixed balance of Voorhies groupings and the consistency between large elements and the MNI indicates that the pantodonts in the L-1079 assemblage were not transported a large distance by water. Similarly, this pattern of Voorhies groups (abundant Group II in addition to Group III) indicates the pantodonts at this quarry are not likely resulting from a lag deposit.

It appears that minimal transport processes acted on these animals after their death. Therefore, it seems less likely that these pantodonts were concentrated post-mortem than that they were associated in a group prior to their deaths.

Interestingly, when compared to taphonomic studies of contemporary animals in the Serengeti, the patterns of elements in this quarry give a speculative framework for how these animals might have died. In the case of modern drownings in wildebeest populations, the resulting skeletal assemblage is characterized by (1) the predominance of adults and variable representation of juveniles, (2) presence of intact elements from all skeletal groups, and (3) assemblages dominated by axial elements and long bones (Capaldo and Peters, 1995). These patterns are strikingly similar to those observed at L-1079. Speculatively, the L-1079 pantodonts could have experienced a catastrophic event – a mass drowning – that led to this remarkable assemblage.

In summary, the balance of evidence at L-1079 suggests the following taphonomic sequence: (1) these pantodonts, all adults at varying ages, die in a group– possibly as a result of a mass drowning – and (2) the carcasses are not transported far downstream. These animals (3) decompose in a wet setting and (4) there is subsequent minimal sorting of skeletal elements likely through winnowing away of smaller bones. Then, (5) the bones experience final burial in the fluvial setting until (6) modern erosion from cliff face which results in bone fracture.

Comparison with Other Pantodont and Paleocene Mammal Bonebeds

The L-1079 assemblage gives evidence of a pantodont bonebed¹⁷. While this locality marks the first bonebed with so many individuals of *Pantolambda*, several other pantodont genera preserve mass death assemblages. Multiple quarries of *Coryphodon* have been reported including the Roehlers *Coryphodon* Catastrophe Quarry (RCCQ; McGee, 2001, McGee, 2002), the Deardorff Quarry (McGee and Turnbull, 2010), and AMNH 242 in the San Juan Basin (Lucas, 1984a). Additionally, a myriad of individuals of *Alcidedorbignya* with abundant juvenile material has been recovered from Tiupampa in Bolivia (Muizon et al., 2015, Muizon and Billet, 2022). The age composition of that is suggested to result from proximity to a breeding ground (Muizon and Billet, 2022).

The key difference between L-1079 and these other pantodont bonebeds lies in its lack of exposure of the pantodont-bearing bed. RCCQ, Deardorff, and AMNH 242 all were excavated along the bedding plane to reveal multiple articulated or partially articulated individuals. This excavations allowed for more sophisticated reflections on the orientations of the bones in context of the depositional environment. In contrast, at L-1079, the material has been collected after it has eroded from the bone-bearing layer. This collection strategy means that any spatial context for these bones has been lost and introduces an additional step to the taphonomic processes acting upon the L-1079 material. Notably, even in a sample collected in 2019, a pantodont tooth (Fig. A13) was recovered. This observation indicates that pantodonts are *still* actively weathering out of the site and that this current analysis represents a snapshot in time rather than a comprehensive assessment of the full potential of this locality.

Although collection strategies and exposure are very different, the element distribution at L-1079 exhibits a striking similarity to the assemblage at RCCQ (McGee, 2001). As seen at RCCQ, the proximal limb elements are more represented in the assemblage than the distal limb elements at L-1079. Juveniles are underrepresented (or absent) in both assemblages. Speculatively, these similarities

¹⁷ A bonebed is here conceptualized as a “‘relative concentration’ of vertebrate hardparts preserved in a localized area or stratigraphically limited sedimentary unit (e.g. a bed, horizon, stratum) and derived from more than one individual” (Rogers and Kidwell, 2007).

of patterns might indicate that pantodonts were susceptible to mass death events in fluvial settings.

Herding behaviour results in animals being more likely to form mass death assemblages (Behrensmeyer and Hook, 1992). As seen in pantodonts, multiple mass death assemblages are known for the condylarth, *Meniscotherium*, (Williamson, 2001). It is suggested in the study of *Meniscotherium* that predisposition towards these en-masse burials likely resulted from its living in large groupings. The existence of multiple pantodont mass death assemblages can be leveraged to make similar inferences for the behavior of these animals.

Indeed, the demography of the L-1079 assemblage further supports this inference of a large group. The range of adult ages within the assemblage (two to eleven years old) indicates that this pantodont group likely represents more than an immediate family (i.e. parents and offspring). Thus, while not as visually striking and evocative as localities like Roehler's *Coryphodon* Catastrophe Quarry and Tiupampa, the pantodont bonebed at L-1079 allows for further reflections on gregariousness within this clade.

Gregariousness within Pantodonta

The herd behaviour inferred for the L-1079 assemblage can be placed into conversation with other pantodont assemblages. In addition to the iconic *Coryphodon* quarries (Lucas, 1984a; McGee, 2001; McGee, 2002; McGee and Turnbull, 2010), there are hints from other localities of pantodonts exhibiting grouping behaviours. During early study in the Plateau Valley, three articulated skeletons of *Barylambda faberi* were collected from the same locality (Patterson, 1935). Similarly, at Hannold Hill, Texas, a *Coryphodon molestus* locality yielded three adults and one juvenile in association (Lucas, 1989). It seems that, when one finds a single pantodont in the field, others might be expected to be lurking nearby.

Gregariousness within pantodonts is further supported by ancillary evidence from footprints. Most notably, a Late Paleocene exposure preserves parallel trackways from *Coryphodon* that indicate herding behaviour (Wroblewski and Gulas-Wroblewski, 2021). Further, footprints laid down by herds of larger mammals (either

pantodonts or dinoceratans) are known from the Eocene of the western United States and Iran (Mustoe, 2002 and Abbassi and Lockley, 2004).

Altogether, it seems that gregariousness represents a baseline behaviour for this enigmatic group of mammals across all body sizes. The L-1079 assemblage indicates that, similar to other pantodonts, *Pantolambda bathmodon* was similarly gregarious.

The Life History of *Pantolambda bathmodon*

The paleohistological data that underpinned the further reflection on pantodont MNI within the L-1079 assemblage and the implications for the group's demography underpinned life history reflections for *Pantolambda bathmodon* derived from a jointly-authored paper (Funston et al., 2022; Appendix III). Here I aim to set the findings from this study in more detailed conversation with previous work on juveniles of other pantodonts and to speculate about their broader implications.

Pantolambda bathmodon has a placental-like reproductive strategy with a long gestation period (~7 months), rapid dental development (with the majority of the premolars erupted at or prior to birth), and a short suckling period (~1-2 months) (Funston et al., 2022). This animal was likely extremely precocial and grew and developed quickly reaching both sexual maturity and close to adult body size within its first year of life (Funston et al., 2022).

Similar to *Pantolambda*, *Alcidedorbignya* appears to have been highly precocial with all of its deciduous teeth erupted at birth (Muizon and Billet, 2022). Extant animals that seem to correspond to the mineralization patterns observed in *Alcidedorbignya* include Reeves muntjac and fallow deer (Muizon and Billet, 2022). Based on the appearance of wear facets on its deciduous premolars, *Alcidedorbignya* appears to have begun weaning later with regard to dental eruption than these extant analogues (Muizon and Billet, 2022). This observation possible represents a departure from *Pantolambda* which evidences the beginning of a weaning transition period around 30 days after birth (Funston et al., 2022). The exceptional assemblage of juvenile material available for *Alcidedorbignya* presents a great opportunity for future work in applying palaeohistology sectioning and trace

elements geochemistry to the question of precise timings of their life history. This strategy would allow for precise comparisons between *Pantolambda* and *Alcidedorbignya*.

A decent sample of juvenile material also exists for *Coryphodon* that provides some insight into its growth and development. As seen in *Pantolambda*, the deciduous cheek teeth of *Coryphodon* erupted prior to the full fusion of both cranial sutures and long bone epiphyses (Lucas and Schoch, 1990). Similarly, it has been suggested that *Coryphodon* grew rapidly and approached near adult proportions prior to the loss of its deciduous dentition or the fusion of its long bones (Lucas and Schoch, 1990). This pattern is reminiscent of the rapid pace of early life displayed by *Pantolambda*. Another point of resonance between these taxa arises from the hypothesis that *Coryphodon* gave birth to singleton offspring (Lucas, 1984a). However, *Coryphodon* and other coryphodontids appear to depart from the life history exhibited by *Pantolambda* in terms of their overall lifespan. Lucas (1984a) suggests that *Coryphodon* might have lived up to 30-50 years. Similarly, in a histological study of Asian coryphodontids, life histories comparable to *Hippopotamus amphibius* or slower were hypothesized within the clade (Mao et al., 2014).

An important nuance on the rapid pace of life inferred for *Pantolambda* is important to raise here. Since the majority of the sample derived from the L-1079 quarry where the individuals may have died catastrophically and prematurely rather than reaching their expected lifespan. While we potentially have a younger snapshot than would be expected of animals passing after senescence, other animals in the sample give support that the inference of a rapid pace of life within this taxon holds. More critically, NMMNH P-22012 bears extremely worn teeth similar to that of NMMNH P-19625 with both animals evidencing a lifespan between seven and eleven years. This age of death of these individuals with less functional dentition still supports the rapid pace of life for *Pantolambda* because the animals are living less than half the time expected for their body size when compared to modern animals.

More speculatively, the rapid pace of life evidenced by *Pantolambda bathmodon* might hint at how pantodonts might have achieved large body sizes so quickly in the post-extinction evolutionary landscape of the Paleocene. The possibility exists that their ability to give birth to large, well-developed young that quickly weaned provided the physiological underpinning of that achievement. The rapid pace of life and achievement of sexual maturity within the first year of life indicates that these animals would have had short generation times despite their relatively large body sizes. These short generation times could translate to a quicker rate evolution (particularly when the characteristic of body size is considered). The achievement of large body sizes in pantodonts after the K-Pg extinction might have been underpinned by this growth and development strategy and the underlying physiology that supported it.

Chapter Summary:

In this chapter, I have explored the palaeobiology of *Pantolambda bathmodon* through reflections body size estimates within pantodonts and a taphonomic analysis of an interesting locality from the eastern flank of Torreon Wash. Pantodonts are among the first mammals to achieve large body sizes after the K-Pg extinction, but quantitative estimates of their mass have remained sparse. Long-bone body size estimates in *Pantolambda* and *Barylambda* are systematically higher than those derived from both the dental measurements and occipital condyle widths. In contrast, long bone estimates for *Coryphodon* are more consistent with dental estimates. It is possible that this mismatch in estimates reflects the very small cranium of pantolambdids and barylambdids relative to their body size. Due to the unusual body proportions of this group of extinct animals, the question of what proxies might be most appropriate to use in estimating the body size of pantodonts remains open. Further investigation of this question might be productively resolved by convex hull analysis of mounted skeletons.

Although the analysis is limited by the mixed nature of the assemblage (the pan samples several meters of stratigraphy) and the collection protocols employed at the site over the last 50 years, the taphonomy of NMMNH L-1079 gives insight into the

social structure and behavior of *Pantolambda bathmodon*. The presence of at least four adult pantodont individuals (and, more realistically at least six) of a variety of ages and the abundance of long bones supports the inference that the assemblage captures a group of pantodonts that died together and underwent minimal transport post-mortem. This pattern of bones in the assemblage indicates that these animals more likely experienced a catastrophic event like a mass drowning rather than accumulating more slowly due to attrition. Thus, *Pantolambda bathmodon* likely exhibited grouping behavior and was potentially gregarious. This behaviour is consistent with broader trends observed across Pantodonta from small-bodied *Alcidedorbignya* to large-bodied *Coryphodon*.

Finally, the life history of *Pantolambda bathmodon* is elucidated through palaeohistological analysis. Overall, *Pantolambda bathmodon* experienced a rapid pace of life. It gave birth to large, well-developed precocious young that likely reached sexual maturity in their first year of life. *Pantolambda bathmodon's* mortality clusters at around half the age that would be predicted from body mass in extant mammals (although this inference must be nuanced by the majority of the palaeohistology sample coming from the L-1079 quarry). This speedy growth and development of this animal might provide the physiological foundation with which pantodonts quickly achieved large both sizes in the wake of the K-Pg extinction.

Chapter 4:

Conclusions and Future Steps



West Flank of Torreon Wash, San Juan Basin, New Mexico (taken May 2018)

“Just because you’ve written a book about something, doesn’t mean you’re done thinking about it.”

-Ursula K. Le Guin

Conclusions:

In addition to being intrinsically interesting animals in their own right, pantodonts hold the potential to be a natural laboratory for understanding body size evolution in early mammals. A systematic review of the clade demonstrates that pantodonts are interesting among Paleocene mammals for having an excellent fossil record with multiple genera known from nearly complete skeletons and for experiencing endemic radiations in both North America and Asia. Although they have been recognized more broadly as being the largest animals in Paleocene ecosystems, many aspects of their paleobiology remain currently in the realm of speculation. The time is ripe for revisiting these iconic Paleocene mammals with an eye to fully explicating their anatomy and reflecting on its implications for their functional morphology.

Even as prior work represents a treasure trove of potential data, the pantodont fossil record is being further enriched by new finds from the San Juan Basin in New Mexico. A juvenile skeleton of *Pantolambda bathmodon* preserves the first deciduous dentition for the genus. This dentition is broadly consistent with the juvenile dentitions of other pantodonts across a range of body sizes. This juvenile skeleton also provides insight into ontogeny with clear evidence that *Pantolambda* erupted its first molar before the fusion of its cranial sutures and long bone epiphyses.

The deciduous dentition of *Pantolambda bathmodon* (a definitive pantodont) provides additional insight into the phylogenetic affinities of the cyriacotheriids, a group of putative pantodonts. To wit, the way that *P. bathmodon*'s deciduous premolars exhibit textured enamel and that the ectoloph on the dP5 develops with a more buccally directed preparacrista resulting in a narrower ectoloph 'v' than in the adult molars is reminiscent of characteristics of *Cyriacotherium*. Additionally, the mesostyle of the permanent molars of *Pantolambda* is variably located along the buccal slopes of the major cusps. Some dentitions preserve this cusp nearly abutting the buccal margin which is similar to how the mesostyle of *Cyriacotherium* sits adjacent to the buccal cingulum. In each of these cases, *Presbytherium* represents a further structural analog or intermediate between the deciduous premolars of *Pantolambda* and the more derived *Cyriacotherium*. These anatomical observations

corroborate the phylogenetic analyses of Zack (2009) and Scott (2010) but challenge the results of Lucas (1998) and Halliday (2017). These further anatomical observations of *Pantolambda bathmodon* underscore the value of working towards an in-group phylogeny for the clade that tests the hypothesis of the affinity of the cyriacotheriids further through incorporating characters to capture these features (e.g. the location of the mesostyle).

Additionally, the new San Juan Basin material has taxonomic value for further understanding the variation within and between species of *Pantolambda*. Newly described material of *Pantolambda intermedium* from the San Juan Basin reinforces that this animal, although known from scrappy material, is indeed a distinct species from *P. bathmodon* and *P. cavirictum*. Additionally, a skeleton of *Pantolambda cavirictum* with extensive postcrania shows broad similarities with *P. bathmodon* in how the manus is constructed. This skeleton will be the framework for further analysis of whether the largest species can reasonably be kept in this genus.

Pantolambda as a genus spans encompasses species that differ by a factor of ~ 1.5 in terms of their linear measurements. *P. bathmodon*'s bones are roughly the size of a wolverine while *P. cavirictum* approaches the size of the tapir. Later pantodonts became even larger than *P. cavirictum*. Overall, pantodonts appear to have spanned three orders of magnitude of size with tiny *Alcidedorbignya* weighing in at around ~ 1.5 kg and *Barylambda* and the Asian coryphodontids potentially tipping the scales at > 1000 kg.

However, the odd proportions of the skulls and postcrania within the clade mean that determining reasonable quantitative estimates of pantodont body size remains elusive. In investigating limb bone and dental proxies for body size, a mismatch between pantolambdid/barylambdid estimates and those for coryphodontids was recognized. This mismatch likely results from differences in head-body proportions within the clade. Essentially, coryphodontids have a larger heads in proportion to their body size (particularly the robusticity of their limb bones) than other pantodonts. This realization suggests that individual metrics must be sought for different subgroups within the broader umbrella of Pantodonta and that what metric

might be most appropriate in each case is still an open question. An appropriate body size proxy is particularly important to resolve for the largest North American pantodont, *Barylambda*, because of its appearance in the mid-Paleocene (Tiffanian). Thus, *Barylambda* is critical for understanding the early steps of this group into the largest sizes it achieved.

Finally, a taphonomic analysis of the L-1079 quarry in the San Juan Basin of New Mexico using minimum number of individuals estimates from repeated elements, relative wear, and palaeohistology gives insight into the social structure and behaviour of *Pantolambda bathmodon*. A group of at least 4-6 adults were found at this locality with abundant postscrania indicating that their bones had not been transported very far. The balance of evidence favors these animals being associated in life as well as in death and suffering from a catastrophic fate (potentially a mass drowning). The L-1079 assemblage, therefore, provides compelling evidence that, like most other members of the clade for which data are available, *Pantolambda bathmodon* was likely gregarious. A paleohistological study of the material from the L-1079 quarry showed that *Pantolambda* exhibited a rapid pace of life with well-developed young weaning early and reaching sexual maturity within the first year of life. *Pantolambda* appears to have lived for less than half the time expected from modern mammals at a similar body size. The resulting inference of short generation times underpins the speculation that this unique life history might have supported pantodonts in achieving large body sizes so quickly after the K-Pg extinction.

Future Directions

I see the importance of this thesis as lying less in the individual threads presented and more in creating the framework for future research priorities.

Some interesting avenues for pantodont research:

- 1) The single most important thing to support work on pantodonts and an immediate research priority is the creation of a resolved in-group phylogeny for the group. The phylogeny of these animals is in part stymied from long-standing taxonomic problems within several genera, particularly *Coryphodon*.

In the short term, one way to step around the taxonomic issues of *Coryphodon* and incorporate it into an in-group phylogeny is to adopt a 'single individual' scoring strategy. In the context of large-scale datasets that focus on understanding broader mammal relationships and more targeted datasets focused on clarifying the relationships within Pantodonta, *Coryphodon* is likely best treated at the level of an individual specimen rather than using a composite of multiple individuals for scoring. The assumption underlying this suggestion is that all species of *Coryphodon* (whatever they might ultimately be) are more closely related to each other than to other pantodonts and mammals more broadly. By scoring a single specimen, we can hypothesize where *Coryphodon* as a genus sits in the mammal family tree. Key specimens that may be suitable for scoring include the nearly complete skeleton of *Coryphodon molestus*, AMNH 48163. This individual, if needed, could be supplemented by other individuals from the same quarry (AMNH 242) which can reasonably be assumed to be a population.

The limitations of this adopted scoring strategy lie within determining what the intraspecific relationships are of *Coryphodon* itself. However, such limitations are necessary when remaining agnostic about which species of *Coryphodon* are valid. This short term strategy would allow for traction on the bigger question of pantodont in-group relationships.

- 2) Additional anatomical investigations, particularly into historic genera described before the 1930s would be useful for clarifying anatomy for scoring and would allow for an understanding of these animals under the modern synthesis of paleontology. In particular, a full revision of the genus *Pantolambda* is overdue, particularly in light of the more extensive postcrania of *Pantolambda cavirictum* now available. I aim to use my work on new specimens from the San Juan Basin to kickstart that systematic work. Other opportunities for anatomical descriptions lie in the excellent collection of barylambdid pantodonts (*Barylambda*, *Haplolambda*, and *Leptolambda*) at the Field Museum.

- 3) The body sizes of pantodonts could be further investigated by taking advantage of existing mounted skeletons. Using volume-based estimation methods like convex hulls as a way of estimating body mass would allow with a holistic view of the entire skeleton and allow for the challenges of unique proportions within the clade to be sidestepped.
- 4) The abundance of juvenile material of pantodonts and new tactics of examining that material (e.g. Funston et al., 2022; Muizon and Billet, 2022) invite further work on pantodont life history, growth and development. In particular, using paleohistology to constrain the specific milestones of gestation period, weaning period, and life span would greatly expand our understanding of pantodonts as living animals.

Life history traits derived from paleohistological work could subsequently be plotted onto an in-group phylogeny for pantodonts to answer questions like 'did specific life history traits arise more than one within Pantodonta?' Additionally, the rates of evolution of both life history and body size could be estimated with the aid of an in-group phylogeny.

Finally (and speculatively), while the inhibitory cascade model has been nuanced and critiqued in recent years, this model could potentially could speak to subtle variations in the size of molars within the clade (sensu the spider diagrams presented in Simons, 1960) and the subsequently be put into conversation with the developmental insights provided by paleohistology.

In summary, we can see that that there are many potential avenues for future study of pantodonts. Onwards to the next adventure! :-)

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Appendix I:

On Becoming A Plague Doctor:

A Reflective Practice Account of Pursuing a Doctorate During the COVID-19 Pandemic



(Image Source: Screenshot of "Scary Creepy Plague" GIF:
<https://giphy.com/gifs/creepy-scary-plague-IJJDeKvvG8m9W>)

"But what is true of the ills of this world is also true of the plague. It may serve to make some people great. However, when you see the suffering and pain that it brings, you have to be mad, blind, or a coward to resign yourself to the plague."

- Albert Camus, *The Plague*, Pt. 2, pg. 96

2023:

Reflection on our experiences is important. Putting the things that we do, that happen to us, that happen around us into perspective helps us learn. Reflection helps us think about how to do better in our future endeavours.

Reflective practice accounts (RPAs) are one way of concretely engaging in that reflection. They are used in such diverse fields as medicine and teaching, but are less common in the natural sciences. I learned about RPAs when I was working on a teaching certification and found the act of writing useful for looking back. It felt a natural extension from my journalling. This particular reflective practice account departs from the norm because it's been written piecemeal over years. I take the liberty now in November 2023 of organizing the information narratively. The act of writing is for me. The experience of reading is for you.

~

2020:

An excerpt from my research notebook (February 13):

"Pantodont Work Plan for Next Few Months...create goals for future museum visits (particularly AMNH and FMNH) b/c not possible to go to China right now [maybe next year]"

An excerpt from my journal (March 6)

"It's a nervous time to be a human and I am feeling anxious. I didn't realize how uncomfortable the paleo meeting at Brewdog would make me feel yesterday. I am nervous of the people still and had a panic at work later that day."

An excerpt from my research notebook (March 17)

"The world is changing quickly – the coronavirus (COVID-19) from Wuhan, China has reached the level of pandemic around the world. I went into the department this morning briefly to grab my desk plants and a few reference books. Now I am working from home, pretty much indefinitely to respect social distancing protocols.

Steve is also social distancing. It's weird to think how the next few weeks might go. I'm starting to get scared, not losing my head panicked, but cautious and properly wary."

An excerpt from my research notebook (March 23)

"The UK is now in lockdown. I am not okay."

An excerpt from my research notebook (March 24)

"Steve's suggested some things I can work on at home. Expand literature review into a proper systematic review of pantodonts."

An excerpt from my journal (April 15)

"How am I supposed to do this doctorate if I can't look at fossils?"

~

2023

Gibbs (1988) outlines an iterative, six step cycle for supporting reflection on experience that begins with (1) a description of the experience and (2) a recording of one's feelings and thoughts about the experience. I spent the late spring of 2020 feeling out of control and alone. The loss of the routine of going to the campus destabilized me. I had not fully realized how much I as an autistic person needed that structure. The loss of routine and day-to-day conversations with my supervisor brought my less productive tendencies to the forefront.

~

"Pestilence is in fact very common, but we find it hard to believe in a pestilence when it descends upon us. There have been as many plagues in the world as there have been wars, yet plagues and wars always find people equally unprepared."

(Albert Camus, *The Plague*, Pt. 1 pg. 30)

~

2021

December 8: The day I started writing this reflective practice account

In the present moment I am writing this reflection, with the Omicron variant beginning to again set the world on fire and with continued uncertainty around travel and access to workspaces, it may make very little sense to spend words talking about COVID-19. After all, everyone alive today is well-familiar with the various ways this pandemic has impinged on our professional, social, and ethical lives. However, there will come a time when this pandemic exists mainly in the memories of those of us alive today...making our way through it...when a younger generation will maybe roll their eyes at the COVID stories and joke about how their elders certainly get strange about wearing face masks in supermarkets and on public transit.

Science is a beautifully human endeavour that cannot be separated from the lived context of the researchers performing it. And, in so many ways, this PhD. thesis is a product of the pandemic in which it is written.

My objectives in this piece are to reflect on events that happened in the world that have strongly influenced my own research practice and my thoughts around performing science. My hope is that this reflective practice account will provide a glimpse into the mind of myself as a researcher.

~

"A pestilence does not have human dimensions, so people tell themselves that it is unreal, that it is a bad dream which will end. But it does not always end and, from one bad dream to the next, it is people who end..." (Albert Camus, *The Plague*, Pt. 1, pg. 30)

~

2022

Email from Judy Galkin, AMNH (January 4)

"Due to the current surge in Covid 19, we are cancelling all scheduled visits to the research collections for the months of January and February and are not scheduling any visits for the month of March at this time."

Email from myself to Judy Galkin, AMNH (January 5)

"Hi Judy, Thank you for letting me know about the visit being cancelled. I acknowledge receipt of the email and I understand that my visit has been cancelled. I appreciate having enough lead time on the decision to revise my travel plans.

I understand the need for the visit cancellation given the current virus surge, but am honestly pretty crushed at the moment. I will definitely be in touch in a few months time to try to reschedule the visit."

Excerpt from my journal (January 5)

"I can't stop crying."

~

"They considered themselves free and no one will ever be free as long as there is plague, pestilence, and famine." (Albert Camus, *The Plague*, Pt. 1, pg. 31)

~

2022

An excerpt from my research notebook (February 28)

"Observation for the reflective practice account – I photograph every specimen I look at now. I don't know when or if I will see them again. I don't take return visits to collections for granted anymore. Ancillary – I want to figure everything for others as well. What if they aren't able to go to museums? This is what I have learned during the pandemic. Figure everything. That is what I will do for my thesis."

2023

Step (4) of Gibbs (1988) invites analysis to make sense of the situation. I am a completionist. I want to look at and digest all of the information before starting to come to conclusions. I want others to have similar access to information. My initial response to several years of having extremely limited information was idealistic. I wanted to create the ultimate pantodont resource. Every bone would be figured for others.

I am a slow, deliberate worker. I need to spend time staring at the wall. And, now as I sit here needing to finish up writing in a huge hurry, unsure if I will make a deadline imposed by an opportunity to teach...I have to let go of that pandemic response of wanting to FIGURE ALL THE BONES. I now worry there won't be enough figures in this thesis. Future readers, I am so sorry if that's the case.

The pandemic broke me and rebuilt me with a framework of idealism. This thesis has tempered me and retaught me pragmatism.

~

2020

An excerpt from my journal (May 16)

"What are the ethics of working with fossils from native lands?"

~

2022

Excerpt from my research notebook (March 30)

"Notes for RPA:

(1) Collaborators and colleagues at the institutions I work with; people are the most critical things for the science.

(2) I've become more circumscribed in my hypothesis formulation. I want my work to be data production and to focus on making solid, small building blocks. I want to hew foundation stones that others can then build on. Chasing more sweeping insights into evolution can come later."

~

2023

Step (3) of Gibbs (1988) asks for an evaluation of the experience both good and bad. In this present moment, I find it difficult to value the things that have happened to me during these studies, both pandemic-related and otherwise. I think a better framing is value-neutral. What sense can I make of these experiences? How to I resolve the myriad of thoughts and ideas into an somewhat coherent whole? Where am I at the end of all this?

I started this doctorate riding a wave of idealism. I was going to make a pantodont phylogeny. I was going to do some math with that phylogeny and reflect on rates of body size evolution within this clade. I was going figure out form and function of pantodonts, to become a world-expert on these animals. And, if you're here at this point in the thesis, you'll see that...none of those ideas made it into this writing.

How has my science changed as a result of becoming a plague doctor? I started a specimen-focused worker and I remain such. However, sitting down with my friend and colleague, Greg Funston, in 2020 and trying to draw ever more information out of the scrappy, scrappy bones of the L-1079 quarry helped me to dig deeper into a set of fragments than I ever would have imagined. I learned how to frame hypotheses carefully so that, even if my information is limited, I can hopefully arrive at meaningful insights.

A fundamental thing that I have learned as a plague doctor is how to science in an information-poor environment. As a paleontologist, I am used to incomplete data. There's a lot of peace in knowing that 'nobody knows about this bone because it hasn't been found yet' and a lot of excitement that arises from the idea of future discovery. I didn't anticipate the huge challenge I'd find in having the knowledge

that a fossil exists that can answer my question...in a museum on the other side of the world...with no access or images or opportunity. The data existing and being out of reach locked me up in the most profound way during these studies...particularly during the early years of the pandemic. This current work is the lesser for that drive towards perfectionism. I held still for so long. But my future work will be the better. I have learned to my core the value of working with the incomplete. There is a great humility in beginning. I have learned to my core the value of collaborations and colleagues. They are where the science lies. I have learned, again and again, the value of compassion through the compassion shown to me.

I think that, even before the plague, I was careful of other people. I have always wanted to be kind. The pandemic helped me realize our interconnectedness as people in a completely different way though. I've found my work becoming increasingly person-centered over the last few years. Even as I work on these esoteric topics, I find the work driven by sharing with others. The 'end' of what I am doing now isn't this abstract sense of 'finding a deep truth about nature'. Now, the end has become the communication. The science, the knowing, arises from the information we are able to share. And seeing others, listening to others, valuing others perspectives...all of these things make for more effective sharing of the learning.

Completing a PhD. under the best of circumstances is an extended exercise in experiential learning (Gibbs, 1998). The only way to tackle research and learn is to get properly stuck in to doing the work. For many reasons, I wish I could have just become a pantodont doctor rather than also a plague doctor. And the plague was just one facet of an incredibly difficult experience. Since 2018, I have broken an arm, negotiated...difficult interpersonal dynamics...with peers, needed to take time out for mental health, studied during a pandemic, developed an anemia, experienced concussion. Becoming a plague doctor, it has forced me to conceptualize myself as a whole person rather than just a brain on legs.

When I look at the sum of my experiences during these studies, I see that my science has become the better for it. The good and the bad. It gives me the

neutrality of the now. As I take a break from frantically making last-minute figures for this thesis. That is due in three day's time. It is always an adventure.

Gibbs (1998)'s last step of reflective practice before the cycle iterates is an actional plan for how to deal with a similar situation. After all, the end of a reflection is refining one's practice. My actional plan for future research is simply to be gentle with myself. To do what I can when I can rather than waiting for the perfect moment. To start working with incomplete information and build outwards from there. To be kind. I hope in this learning there is the framework of a successful lifetime as a scientist, as a plague doctor, as a person.

- Paige dePolo, completed November 27, 2023

~

Note: All quotations from *The Plague* taken from the Penguin Modern Classic edition translated by Robin Buss (2001).

Appendix II: Panto-Parts

Supplemental *Pantolambda* Figures and Fine Details of L-1079 Taphonomy



Pantolambda Grooming by Taliesin Coleman

"Universal law is for lackeys. Context is for kings."

– Captain Lorca, Star Trek Discovery (S1E3)

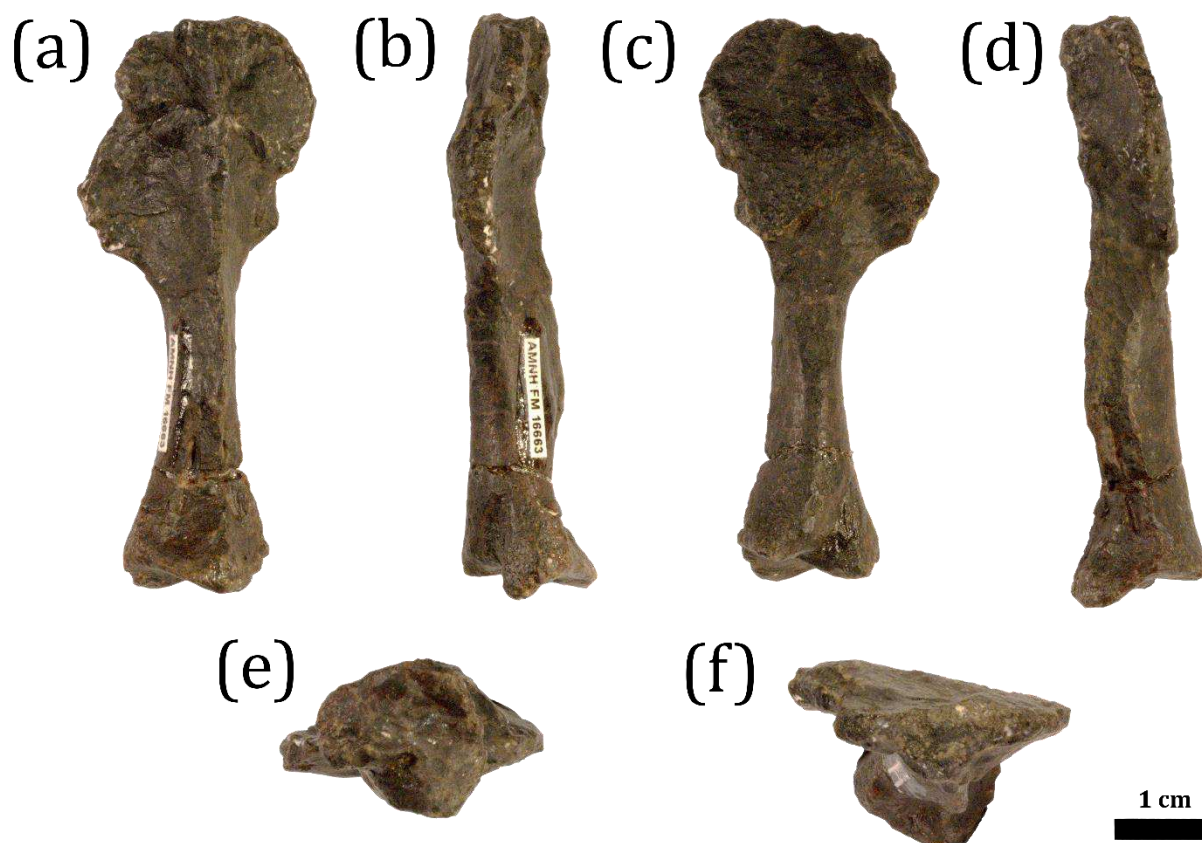


Figure A1: The manubrium of *Pantolambda bathmodon* (AMNH 16663) in (a) ventral, (b) left lateral, (c) dorsal, (d) right lateral, (e) posterior, and (f) anterior views.



Figure A2: The sternum of *Pantolambda bathmodon* in (a) dorsal and (b) ventral view.

Table A 1.iii: Dental Measurements Used in Pantodont Body Size Estimations

Taxon	Specimen Number	p5 Length (mm)	p5 Width (mm)	m1 Length (mm)	m1 AW (mm)	m1 PW (mm)	m1 avg. width	m1 avg area
<i>Pantolambda bathmodon</i>	AMNH 16663	8.1	7.6	9.2	9.4	9.3	9.35	86.02
<i>Barylambda faberi</i>	AMNH 32511	21.7	19	25.5	20.3	20.1	20.2	515.1
<i>Titanoides primaevus</i>	FMNH P-15520	17.3	16.2	19.6	15.3	13.3	14.3	280.28
<i>Coryphodon armatus</i>	UM 21691	18.7	18	21.7	18	17.6	17.8	386.26
<i>Coryphodon molestus</i>	AMNH 48163	15.6	14	21.3	17.3	18	17.65	375.945
<i>Alcidedorbignya inopinata</i>	MHNC 8372	4.26	3.12	4.5	3.83	3	3.415	15.3675

Table A1.ii: Dental Measurements Used in Pantodont Body Size Estimations

Taxon	Specimen Number	m2 Length (mm)	m2 AW (mm)	m2 PW (mm)	m3 Length (mm)	m3 AW (mm)	m3 PW (mm)
<i>P. bathmodon</i>	AMNH 16663	10.4	10.2	9.4	12.9	10.7	7.7
<i>B. faberi</i>	AMNH 32511	26.8	20.6	20.1	32	20.2	16.5
<i>T. primaevus</i>	FMNH P-15520	24	17.6	15.3	31	19.7	16.2
<i>C. armatus</i>	UM 21691	28.3	22.6	17.4	34.8	24.8	20.6
<i>C. molestus</i>	AMNH 48163	28.1	22.8	23.7	34.1	24.2	21.2
<i>A. inopinata</i>	MHNC 8372	5.51	4.75	3.69	6.39	4.55	3.03

Table A1.iii: Dental Measurements Used in Pantodont Body Size Estimations

Taxon	Specimen Number	m1-m3 length	p5-m2 length
<i>Pantolambda bathmodon</i>	AMNH 16663	32.5	27.7
<i>Barylambda faberi</i>	AMNH 32511	84.3	74
<i>Titanoides primaevus</i>	FMNH P-15520	74.6	60.9
<i>Coryphodon armatus</i>	UM 21691	84.8	68.7
<i>Coryphodon molestus</i>	AMNH 48163	83.5	65
<i>Alcidedorbignya inopinata</i>	MHNC 8372	16.4	14.27

Table A2: Pantodont Occipital Condyle Widths (OCW)

Taxon	Specimen Number	OCW (mm)
<i>Pantolambda bathmodon</i>	AMNH 16663	36.39
<i>Hypercoryphodon thompsoni</i>	AMNH 26384	145.1
<i>Pantolambda bathmodon</i>	AMNH 2549	39.8
<i>Eudinoceras kholobolchiensis</i>	AMNH 21744	162
<i>Barylambda faberi</i>	AMNH 32511	103
<i>Pantolambda cavirostrum</i>	AMNH 965	57.2
<i>Coryphodon molestus</i>	AMNH 48164	74.5

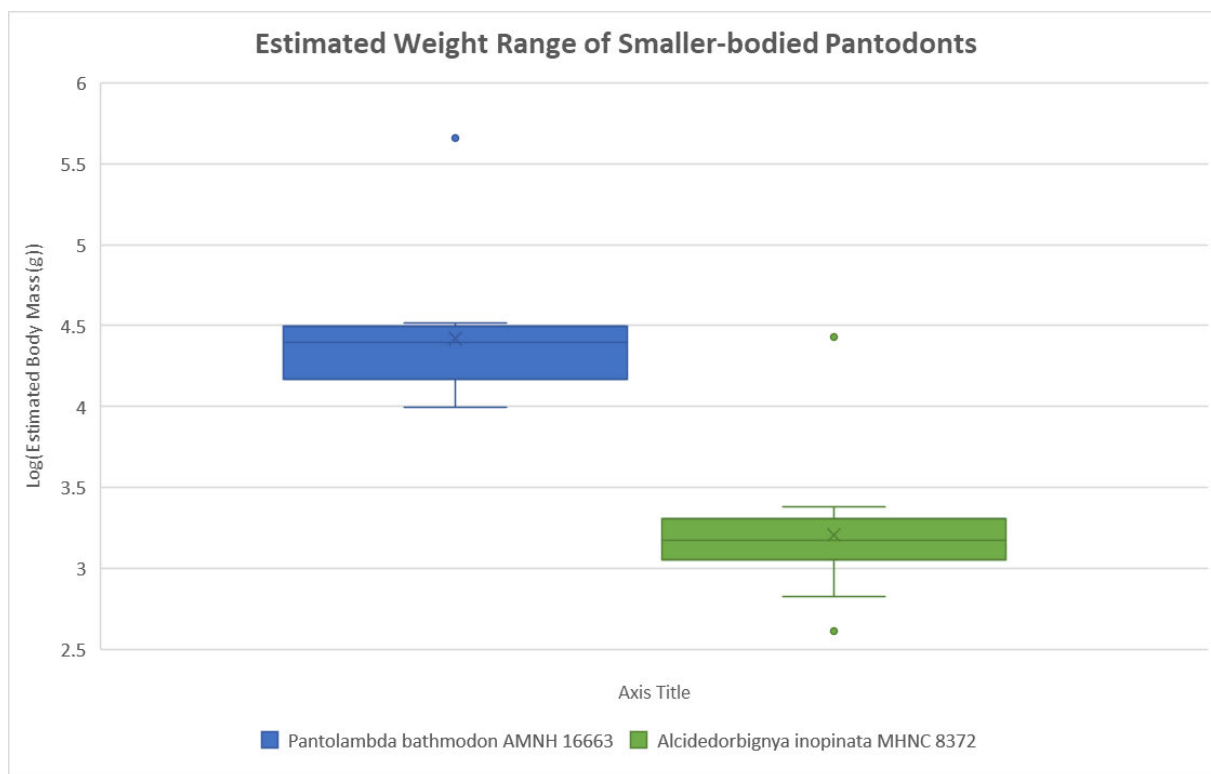


Figure A3: Box and whisker plots showing the range of body mass estimates of *Pantolambda bathmodon* and *Alcidedorbignya inopinata*.

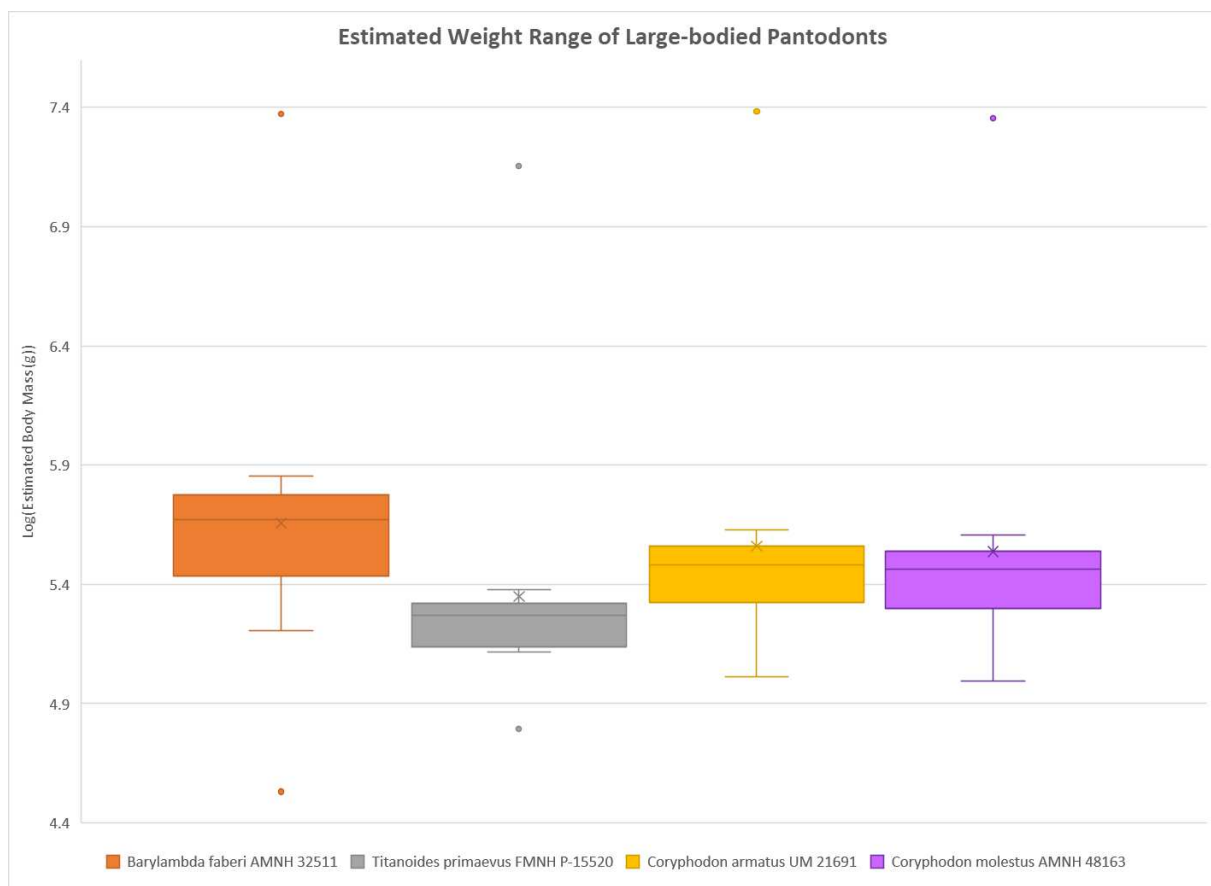


Figure A4: A box and whisker plot showing the range of body mass estimates of *Barylambda faberi*, *Titanoides primaevus*, *Coryphodon armatus*, and *C. molestus*.

The measured section (Fig. 31; Table A3) through L-1079 was taken between two clear marker beds to aid in placing it within the existing, basin-wide stratigraphy. The marker beds are paleosols that range in color from dark-grey to black (Leslie et al., 2018) and appear in the field as fairly fine-grained mudstones. Starting at UTM 13S 0294362/3986352, the section was measured along a bearing of roughly 250°. Although the bedding has a very slight dip, for this short section, the correction would be negligible. Thus, the assumption of flat bedding (0° dip) was made. Due to topography, Unit 10 and 11 were difficult to access safely and observations made were limited as a result. The total amount of section measured was 28.77 m.

Table A3: Details of Measured Section through L-1079

Unit	Description	Thickness (m)
Base of Black Mudstone ("Upper Black")		
11	Patchy gray mudstone with some sandy lenses	4.45
10	Reddish mudstone with patches of white and gray	1.45
9	Light grey to white mudstone; top of unit capped by boulder bed (clasts subrounded to rounded, > 1.4 m in long axis but not much more than 1.75 m); localized in layer, but no clear evidence of imbrication, long axis of boulders subparallel to bedding); boulders composed of medium to coarse-grained, gray-white sandstone	1.25
8	Mottled, red and white mudstone; red coloration dominates unit while white portions are patchy and not laterally continuous; clear popcorn weathering	2.10
7	Gray, fine-grained mudstone; no clear sedimentary structures; popcorn weathering towards top of the unit; 'cliff-forming' above L-1079 pan	2.90
6	White, medium to coarse grained sandstone; predominantly quartz and feldspar; resistant to weathering and top of unit forms L-1079 pan	1.50
5	Mudstone to fine grained sandstone distinctive for colored (white, dark grey-black) banding. Rusty red banding also observed in adjacent portions of wash. Bands within measured section were: medium gray (1.04 m thick), light white (0.48 m thick), light gray (2.92 m). Light white band composed of coarser grains than grey bands.	3.44
4	Light gray mudstone but with some sandy component (medium, angular grains present). More 'cliff-forming' with similar concretions to underlying unit. Distinguished from underlying unit by slope break and some grey and white banding	4.53
3	Medium gray mudstone, abundant concretions (rusted, chocolate brown color) litter the slopes. Note the slope change is useful in distinguishing the unit.	4.20
2	Light gray (some red-weathering patches; patchy yellow coloration at base of unit); fine-medium grained sand, subangular, poor to medium sorting; quartz (~50%), feldspar (both plagioclase + ksp; 30%), abundant lithic fragments (20%)). No clear bedding or other sedimentary features. Forms higher grade slope (more 'resistant'); some popcorn weathering, but limited to finer grain areas	1.43
1	Medium gray, fine-grained mudstone; forms low relief slope; popcorn weathering indicative of fairly high clay content	1.52
Top of Black Mudstone ("Middle Black")		

Table A4: *Pantolambda bathmodon* Tooth Fragment Tallies:

Specimen Number (NMMNH)	Specimen Identification	Number of Fragments
P-15400	Lp2(root)-p4(crown) (set in dentary)	-
P-19540	Rm1	1
P-19541	Lm1 (partial), Lm2 (partial)	2
P-19543	Maxilla with root of LP5	1
P-19544	LP2-P5 (in maxilla)	1
P-19545	LM2 (partial – paracone + metacone); LM?1 (partial – protocone)	2
P-19546	RM3 (isolated)	1
P-19604	Rm? trigonid; isolated canine	2
P-19608	M? (isolated protocone)	1
P-19612	Canine fragment (isolated)	1
P-19617	Rp5	1
P-19625	RM1; lower molar root	2
P-19653	6 tooth bearing fragments: (1) portion of mandibular symphysis with Ri1, Ri2, and Li1 roots; (2) root of canine; (3) portion of Rm3; (4) portion of dentary with roots of ?left premolars; (5) LMx; (6) LP2 (broken), set in maxilla	-
P-19654	Dentary with Lp2, p5-m1, Rm2-m3 ¹⁸	4
P-19662	Rm3 in dentary	1
P-19663	Lm2-m3	1
P-19681	Dentary with root of Lp4 and partial Lp5	-
P-21561	Lm2	1
P-41514	LM1-M3 (partial)	1
P-57814	RM2 (partial -paracone + metacone)	1
P-69889	Rp2	1
P-69890	Lp5	1
P-69892	Lm3 (partial; talonid)	1
P-69918	i? ¹⁹	1
P-69919	Lp1	1
P-69920	Lp4	1
P-69921	Lm3	1
P-69922	Lc	1
P-69923	I?	1
P-69924	pt C?	1
P-69925	c?	1
Uncatalogued	RM3	1
P-19623	Misc. Tooth Fragments	1*
P-19665	Isolated Tooth Fragments	1*
P-19682	Tooth Fragments	1*
P-57815	Lmx (partial)	1*
Total		40

Notes: '-' indicates fragment is tabulated in Table A.6 so that it is not double-counted. * indicates specimens not loaned to the University of Edinburgh during the project and, therefore, were not examined directly or included in further analysis.

¹⁸ Roots of lower incisors (Li1, Li2, and Ri1-3) tabulated in tooth count.

¹⁹ This tooth was tallied as an i? for caution's sake. On comparison with AMNH 16663, it is likely an i3.

The total number of *Pantolambda bathmodon* dental fragments considered in this study was 40.

Table A5: *Tetraclaenodon puercensis* Tooth Fragment Tallies

Specimen Number (NMMNH)	Specimen Identification	Number of Fragments
P-15399	Rp5	1
P-15624	Rm3	1
P-15626	Lm3	1
P-19505	RM2 (isolated)	1
P-19507	LM? (isolated)	1
P-19508	LM? (isolated)	1
P-19510	Rm? (isolated)	1
P-19512	LP5 (isolated)	1
P-19514	Rdp5 (isolated)	1
P-19515	Lm?	1
P-19516	P? (isolated)	1
P-19518	LM2 (isolated)	1
P-19519	RM3 (isolated)	1
P-19524	Rm? (isolated)	1
P-19525	P? (isolated)	1
P-19533	RM? (isolated)	1
P-19535	Rp5 (isolated)	1
P-19537	Rp?, m3 (isolated)	2
P-19549	Lm2	1
P-19603	Lm? (isolated)	1
P-19607	Rp5-m3	1
P-19610	m? (partial)	1
P-19613	Tooth fragments	1*
P-19618	RM3, tooth fragments	2*
P-19620	Rm1 + tooth fragment	2
P-19622	Rm2-m3 (isolated)	1
P-19624	LM2-M3; upper tooth fragments	2*
P-19626	Rm1-m3, Lm1-partial, P5, tooth frags (isolated)	4*
P-19627	Rm? (isolated)	1
P-19628	Rm? (isolated)	1
P-19629	Rm? (isolated)	1
P-19630	Rm1, m2, m2? dentary fragment	3
P-19631	LM3 (isolated)	1
P-19632	RM?, tooth fragments (isolated)	2*
P-19633	RM1, LM2, tooth fragments (isolated)	3*
P-19634	RP4-M3, LP4-M1 partial, M3, canine (isolated)	4
P-21560	Lm2, m1, p5 partial (isolated)	3
P-57816	Lp5	1
P-69882	Lm?	1
P-69891	Tooth fragments	1*
P-69893	M? frags	1*
P-77378	LM3	1

Total		59
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Table Notes: * indicates that this is a minimum estimate for the number of fragments contained in the sample (used when exact number is not clear from the data table)

The total number of *Tetraclaenodon puerensis* dental fragments considered in this study was (at minimum) 59.

Table A6: Bone Fragment Tallies:

Specimen Number (NMMNH)	Specimen Label (<i>P. bathmodon</i>)	Total Fragments	Identifiable
P-15400	Lp4 and bone fragments	106	No (but yes, to element/taxon occasionally)
P-19542	Ungual phalanges	5	Yes, to the element and taxon
P-19653	Mandible Fragments	15	No (but yes, to element/taxon occasionally)
P-19655	Ulna fragments	15	Yes, to the element, sometimes taxon
P-19656	Astragali	2	Yes, to the element and taxon
P-19657	Vertebrae	90	Yes, to the element and taxon
P-19658	Ribs	81	Yes, to the element
P-19659	Tibia Fragments	9	Yes, to the element and taxon
P-19668	Pelvis Fragments	14	No (but yes, to element/taxon occasionally)
P-19669	Femur Fragments	17	Yes, to the element and taxon
P-19672	Patellae	5	Yes, to the element and taxon
P-19674	Humerus Fragments	12	Yes, to the element (sometimes taxon)
P-19675	Foot bones	118	Yes, to the element (sometimes taxon)
P-19676	Scapula Fragments	2	Yes, to the element and taxon
P-19677	Skull Roof	2	Yes, to the element and taxon
P-19679	Radial Fragments	6	Yes, to the element and taxon
P-19680	Calcanea	9	Yes, to the element and taxon
P-19681	Bone Fragments	67	No (but yes, to element occasionally)
P-19691	Bone Fragments	961	No (but yes, to element/taxon occasionally)
P-21562	Bone Fragments	117	No (but yes, to element occasionally)
P-69883	Unciform	1	Yes to the element and taxon
Uncatalogued	Bone Fragments	407	No (but yes, to element/taxon occasionally)
Total		2061	

The total number of bone fragments examined in this study was 2,061.

At least 52 fragments are known from other mammals and (an underestimate) 11 fragments of other vertebrates. Thus, the total number of vertebrate fragments (tooth and bone) incorporated in for this study was 2223.

Further Commentary on Pantolambda Specimens:

- P-15400: This specimen consists of predominantly indeterminate bone fragments (93 total) partially comprised of short sections of long bones. At least 2 dorsoventrally crushed, fragmentary vertebral centra are present along with 7 rib fragments (ranging from 1-2.5 cm). An ectocuneiform and another indeterminate podial (?tarsal) are present along with an indeterminate articular surface. Most notably, a dentary fragment with a Lp4 and root of Lp2 is present that likely belongs to the 'same individual' (see Fig. 34 g,h). A small, slightly bulbous (weathered spiral?) coprolite is also present, but was not tabulated in the bone fragment total.
- P-19653: This specimen consists of fragments of mandibles (and tooth-bearing pieces). Six fragments bear teeth or roots: (1) portion of mandibular symphysis with Ri1, Ri2, Li1; (2) root of canine (C?); (3) portion of right dentary with root of Rm3; (4) dentary with left (?) premolars (tabulated as Lp?, Lp?); (5) left Mx; and (6) LP2 (broken) still set in maxilla. Four poorly preserved fragments bear indeterminate teeth/roots that are not tabulated in the MNI calculation. Five pieces (2 condyloid processes, 1 vertebral centra, a fragment of the lower margin of the dentary, and a chunk of bone with two large alveoli) don't bear teeth.
- P-19655: This specimen consists of fragmentary ulnae. Ten fragments are consistent in size and morphology with *Pantolambda bathmodon*'s ulna – three with trochlear notches, one midshaft, four fragments of the olecranon, and two distal ends (Fig. A6) . Two olecranon fragments are from a left ulna and two are from a right ulna. Thus, four ulnae of *P. bathmodon* are represented within this sample. Two smaller fragments with trochlear notches do not belong to *P. bathmodon*. There are also three small pieces that are not from pantodonts – one ?navicular (~1.2 cm), a small ?calcaneum fragment, and a rib tubercle.
- P-19657: This specimen consists primarily of vertebral centra in varying stages of completeness with very few neural arches or zygapophyses preserved. Most thoracic or lumbar, but some smaller caudal centra present. Many pieces are dorsoventrally compressed. The majority of these centra (71) are consistent in size and overall morphology with *Pantolambda bathmodon*. However, a notable subset (15) came from a much smaller animal and are not tabulated in the subsequent Voorhies groups analysis. There were also 4 indeterminate bone fragments in this bag.
- P-19658: This specimen consists of rib fragments ranging in length from 5 to 25 cm. A rough tally of the combined length of all the rib fragments is 108.6 cm. Of the 81 fragments organized under this specimen number, only six of them seem to be a large enough diameter to be reasonably referred to *Pantolambda bathmodon* (Fig. A7). The combined length of these larger rib fragments (13.7 cm) is less than the length of two average (incomplete) ribs of AMNH 16663. This observation indicates that pantodont ribs are underrepresented in the L-1079 sample. There is no evidence of bone modifications (e.g. bite marks, crushing, fungal invasion) visible to the naked eye and evidence of flattening within some rib fragments likely resulting from fossilization. While the ribs are extremely fragmentary, the edges of these breaks are sharp and unworn. The breakage appears to be the result of modern erosion processes when the material eroded out of the bluff about L-1079 rather than the result of extensive fluvial transport.
- P-19659: This specimen consists of tibia fragments (Fig. A8). One fragment is a complete proximal end of a left tibia preserving both condyles. Two other proximal end fragments (mirrors of each other) are more incomplete, lacking condyles. Five distal tibia fragments (3 right and 2 left) are present with a pronounced medial malleolus consistent in morphology with *Pantolambda bathmodon*. This sample captures a minimum of 5 pantodont tibiae. One additional, chalky white distal tibia is not consistent with *P. bathmodon* both morphologically and in terms of size.

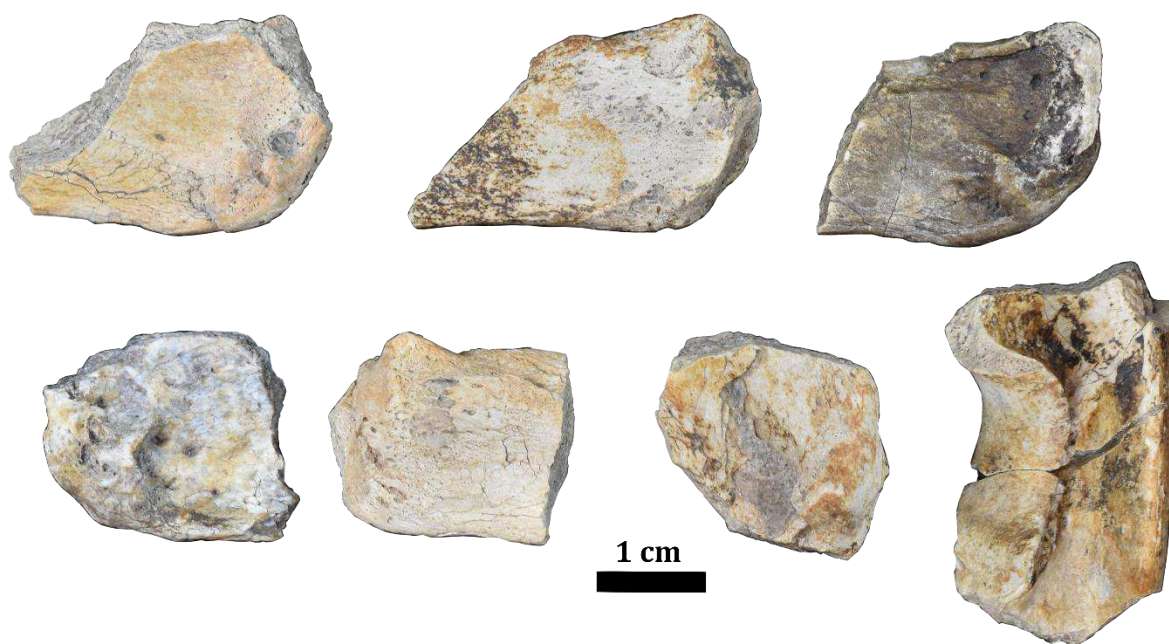
- P-19668: This specimen consists of pelvis fragments. Eight fragments contain smooth curving surfaces that are likely the acetabular fossa and five, flatter/more platelike fragments lack evidence of the fossa. Additionally, there is also one worn fragmentary tooth crown.
- P-19669: This specimen consists of fragmentary femurs. The largest piece is a nearly complete left femur pieced together from fragments preserving about 2/3 of the shaft and the distal end with the lateral condyle (Fig. 38). 4 additional fragments preserve portions of the distal end of the femur and none of these could overlap. One fragment preserves the midshaft as it flares towards the third trochanter. Eight humeral heads are preserved and in these, where the proximal surface is preserved, a deep fovea capitis is present. The morphology of these pieces is broadly consistent with that of *Pantolambda bathmodon*. A final three fragments appear to be battered pieces of the greater tubercle. Altogether, this specimen is composed of fragments of at least 8 femurs (based on the number of heads present).
- P-19672: This specimen consists of five patellae, four of which belong to *Pantolambda bathmodon* (Fig. A9). They are identified as such because of their sharply slanting distal margins (opposite the apex) and overall triangular shape. A fifth, much smaller patella does not belong to a pantodont. The right *Pantolambda* patellae are complete and the more robust of the left patellae is as well. The second of the left patellae is more antero-posteriorly thin than the other patellae and exhibits recent breakage.
- P-19674: This specimen consists of twelve fragments. Three fragments are clear humeral heads with the most complete (a chocolate brown color) preserving both greater and lesser tubercle (e.g. Fig. A10). Additionally, five fragments are portions of the scroll of the capitulum (the two chalky white ones might be part of the same, large humerus). Two of the capitulum fragments are likely derive from a different, smaller taxon to *Pantolambda bathmodon*. One further fragment is likely a chunk of the greater tubercle. The additional three fragments seem to be definitively portions of the humerus, but their specific placement within the bone is difficult to determine. Their size and general bulk support them being referred to *P. bathmodon*.
- P-19675: This specimen consists of a series of manus and pes bones. There are six clear carpal elements (2 scaphoids, 2 cuneiforms, 1 unciform, 1 lunar), seven clear tarsal elements (1 navicular, 2 cuboids, 2 endocuneiforms, 1 ectocuneiform, 1 mesocuneiform), and three podial elements [I'm not confident in their identifications; 2 ?scaphoids, 1 ?navicular]. There metapodials are fragmentary and preserve primarily ends rather than shafts. There are 30 proximal and 21 distal metapodials with an additional 6 metapodial fragments where the orientation was less clear. There are 40 pantodont phalanges (1 additional from another animal – on basis of smaller and more proximo-distally elongated) with a mixture of proximal and intermediate and 3 unguals. Additionally, there is a distal radius fragment included in this bag.
- P-19677: This specimen consists of two skull roofs with the posterior portions of the frontals and the anterior portions of the parietals preserved along the midline. These skull roofs can be assigned to *Pantolambda bathmodon* on the basis of the development of a weak sagittal crest and the shape of the midline contact between the frontals and parietals (Fig. A11). The larger of the two skull roofs was pieced together from multiple fragments that precisely refit which illustrates the broader observation within the L-1079 assemblage that the majority of the breakage of the pantodont postcrania was caused by modern erosion as bones became exposed in the cliff face.
- P-19679: This specimen consists of six radius fragments (Fig. A12). Two fragments preserve the distal end of the radius (one left and one right). Four fragments preserve the proximal end of the radius (radial head). The siding of the proximal ends of the radius is one right, 3 left. At least 4 radiae from 3 individuals are preserved in this sample.

- P-19681: This specimen consists of an assortment of bone fragments that are variably identifiable. There are three fragments belong to the neural arches of vertebrae, three fragments come from calcanea (none of which are pantodont), three rib fragments, two partial metapodials, and a ?radius fragment. Additionally, there are three fragmentary phalanges and a ?cuboid that are consistent in size with *Pantolambda bathmodon*. There are several pieces of teeth including the very worn crown of a ?bunodont upper molar and another fragment. Two canines (one with portions of the crown; one preserving the uppermost part of the root) are consistent with the size of *Pantolambda bathmodon* but not confidently referred to that taxon. The canine fragments are therefore not tabulated in the dental MNI estimate. A fragment of maxilla bearing the root of a Lp4 and lowermost part of the crown of a Lp5 is present and included in tooth tallies for MNI estimates. There is one fragmentary osteoderm. Finally, 44 indeterminate bone chunks were included in the specimen bag.
- P-19691: This specimen consists of an assortment of bone fragments that are variably identifiable. The majority of the larger indeterminate limb bone fragments were bulky enough to be referable to *Pantolambda bathmodon*. Among the recognizable elements are pieces of vertebrae (both centra and neural arches), short sections of ribs, the fragmentary trochlea of an ulna, some fragmentary ?podials, a partial crocodile osteoderm and a tiny alligatorid tooth. Seven humerus fragments (4 midshaft, 2 capitulum, 1 head) can be referred to *P. bathmodon* on the basis of size, the triangular cross-section of the midshaft, and the well-developed, ridge-like deltopectoral region and sweeping epicondylar crest. All bone fragments larger than 1 mm along the long axis were tabulated for this specimen.
- P-21562: This specimen consists of an assortment of bone fragments that are variably identifiable. In this sample, was a small, simple peg-like tooth (incisor or anterior premolar) that did not belong to *Pantolambda* and another indeterminate tooth fragment. The broken end of a humeral head was present that was roughly consistent with the size of *Pantolambda bathmodon* but lacked other diagnostic features. Other identifiable long bone fragments included the distal end of a femur (mediolaterally compressed), a fragment of the capitulum of a humerus, and eroded fragment of distal ?fibula. Eight fragmentary vertebral centra are present and one clear chunk of a neural arch. Of these centra (all of which are dorsoventrally compressed), at least 5 of them are around the size expected for *Pantolambda bathmodon* but lack strictly diagnostic features. These 5 centra were included in the pantodont tally for Voorhies group analysis. Eight rib fragments were present in the sample along with one fragmentary metapodial, three indeterminate long bone shafts, and 5 fragmentary articular surfaces, but none of these pieces was identifiable to the taxon level. Finally 82 indeterminate bone chunks were also included in the specimen bag. One fragment of crocodile osteoderm was present. In addition to the bone fragments, two spiral coprolites and three small (<1.5 cm) pieces of radially growing barite crystals were present.
- Uncatalogued Specimens: This specimen consists of an assortment of bone and tooth fragments that are variably identifiable. Notably, there is a RM3 of *Pantolambda bathmodon* (Fig A12), two sets of non-pantodont teeth (*Torrejonia*, *Mimotricentes*) (Fig 30a, b), and two *Periptychus* lower premolars (Fig 30c). Poscrania included two ulna fragments (one pantodont olecranon, one distal end from another taxon), one pantodont patella, two partial astragali from other taxa, a radial head and distal tibia (both from *Pantolambda bathmodon*), and seven vertebral centra. There were also four distal metapodials, one ?cuboid, three phalanges, and one ungual that are consistent in morphology with pantodonts. Additionally, a gar scale and alligator tooth were recovered. Finally, there were several hundred tooth and bone fragments.



1cm

Figure A5: NMMNH P-19543 preserves the root of a left ultimate upper premolar (LP5). This fragment was originally labeled as the root of an upper molar, but the more mesiodistally-shortened outline of the tooth (resulting in a triangular rather than a quadrate outline indicates that it is a premolar instead.



1 cm

Figure A6: NMMNH P-19655 Assortment of ulna fragments to illustrate level of completeness for this element



Figure A7: Selected rib fragments from NMMNH P-19658 that are consistent in circumference and morphology with those of *Pantolambda bathmodon*. These fragments illustrate the typical level of completeness of ribs observed in the L-1079 assemblage.



Figure A8: Tibia fragments from NMMNH P-19659 illustrating one proximal ends and five distal ends.

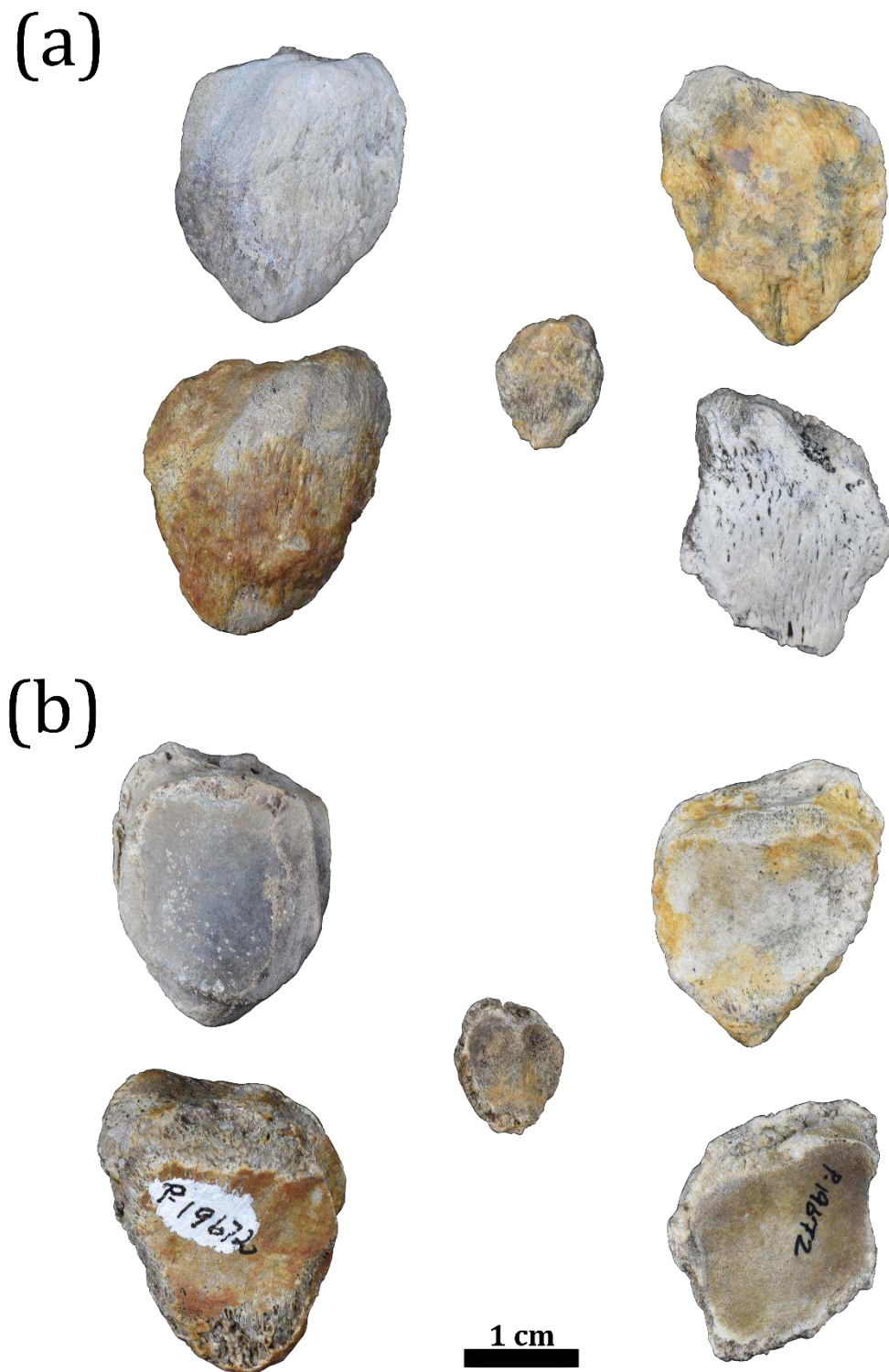


Figure A9: Patellae of P-19672 in (a) anterior and (b) posterior view exhibiting four patellae with a shape and size consistent with *Pantolambda bathmodon*. An additional, smaller patella (center) from a different taxon is also present.

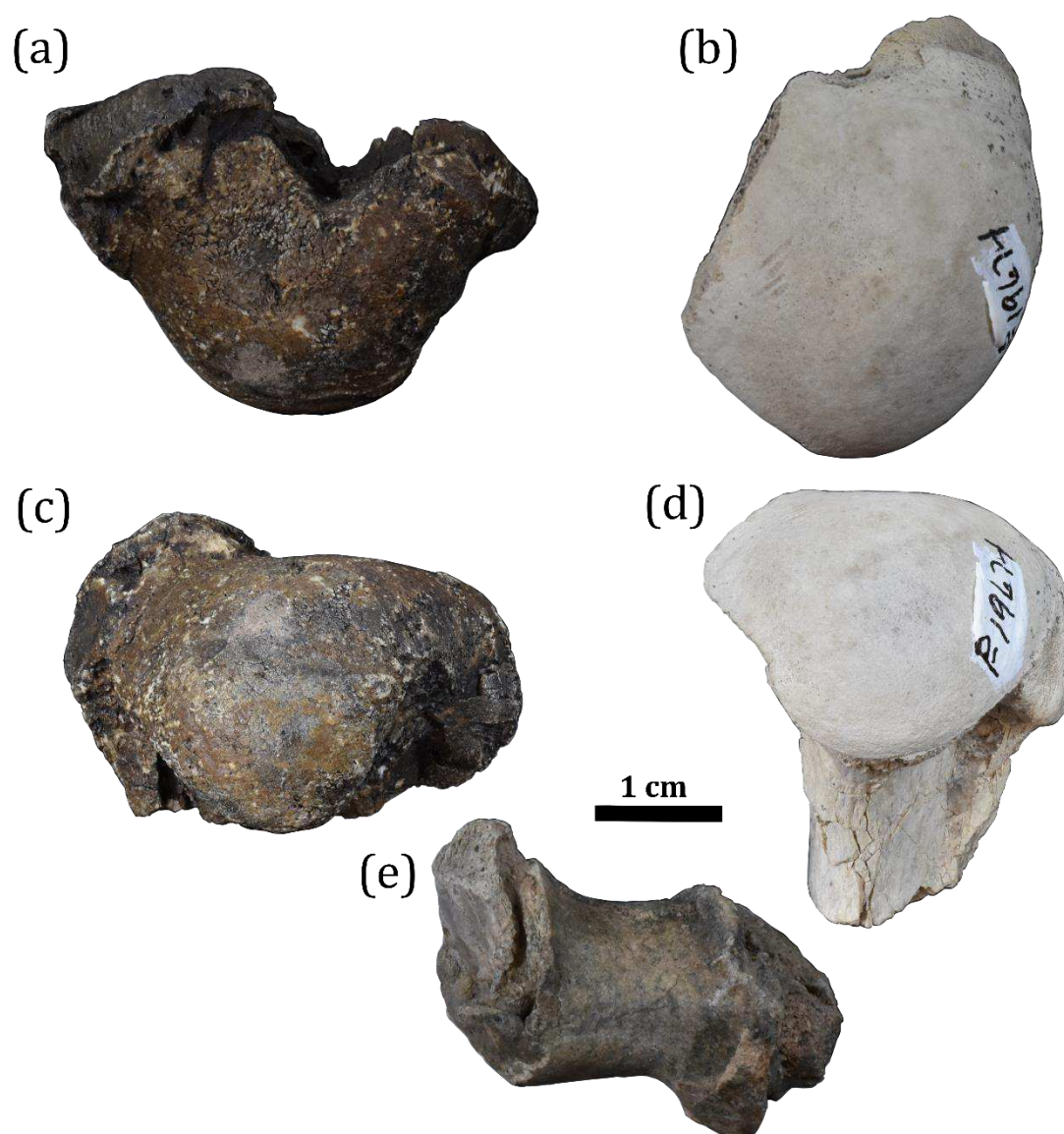


Figure A10: Humerus fragments of NMMNH P-19674 with two humeral heads (a, b) in proximal view, (c, d), in anterior view and (e) illustrating a fairly complete capitulum.

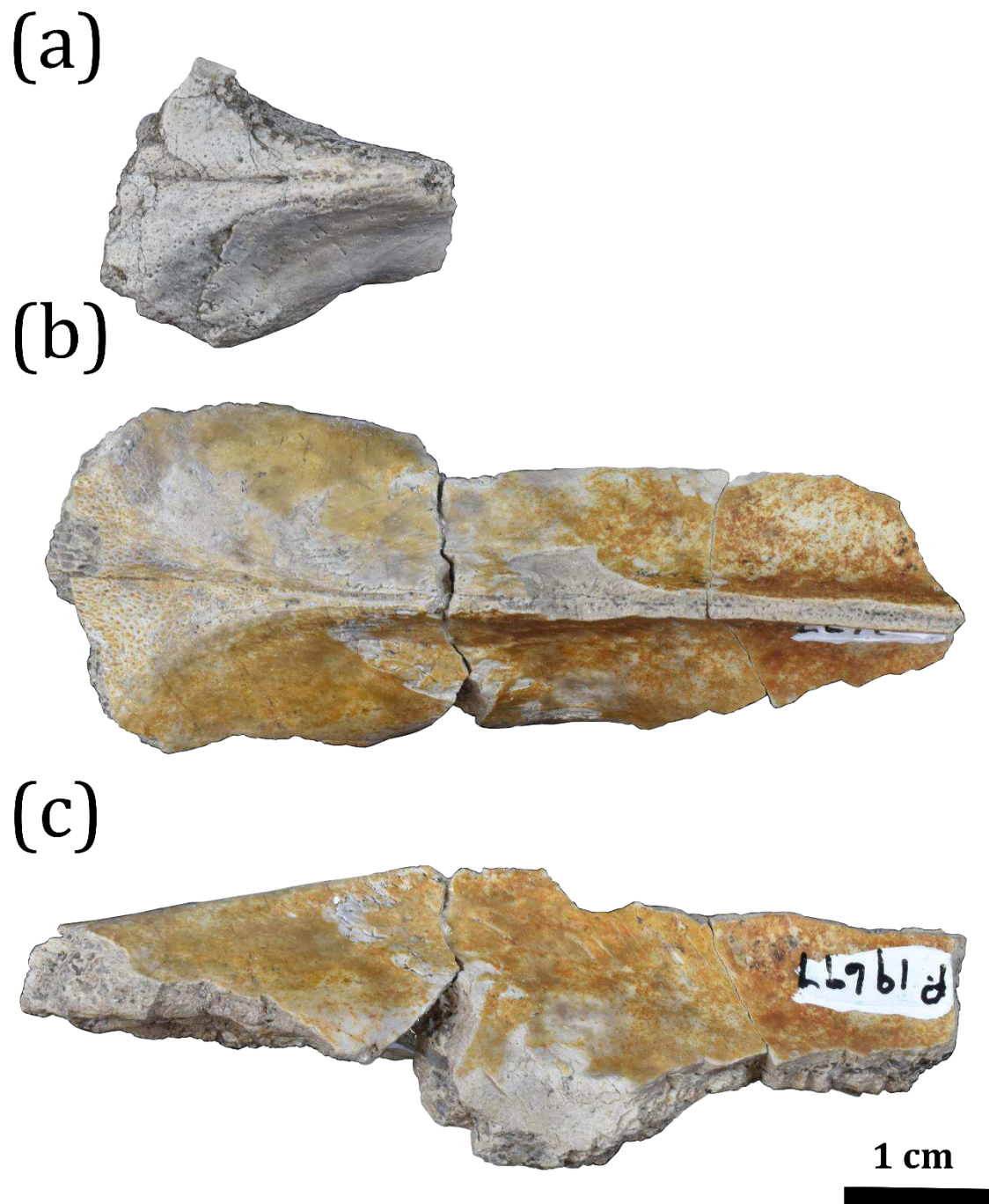


Figure A11: Skull roofs of P-19677 with one small piece (a) preserving the frontal-parietal suture along the midline of the skull and a second individual showing more of the parietal in (b) dorsal and (c) right lateral view. Both pieces are oriented so that the anterior part of the skull is oriented towards the left of the page.



Figure A12: Radius fragments (NMMNH P-19679) of *Pantolambda bathmodon* consisting of both proximal and distal ends. At least three individuals are present in the assemblage on the basis of the radius.

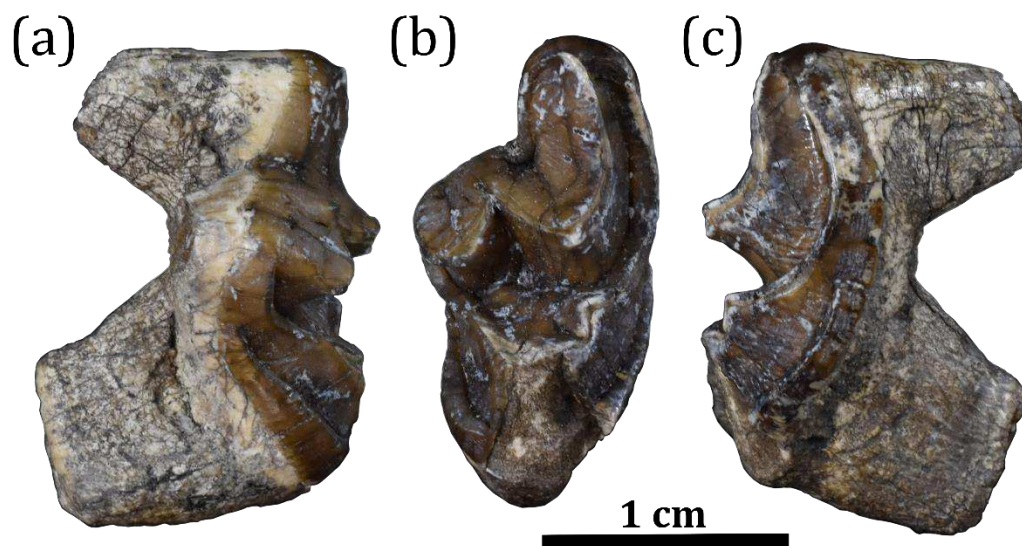


Figure A13: Uncatalogued RM3 in (a) posterior, (b) occlusal, and (c) anterior views. This tooth belongs to Wear Stage 1 with the enamel of the cristae preserving its narrow edge and the apices of the cusps preserved. Notably, this tooth was collected in 2019 and gives evidence that pantodont material was still eroding out of the cliff side when this study was commenced.

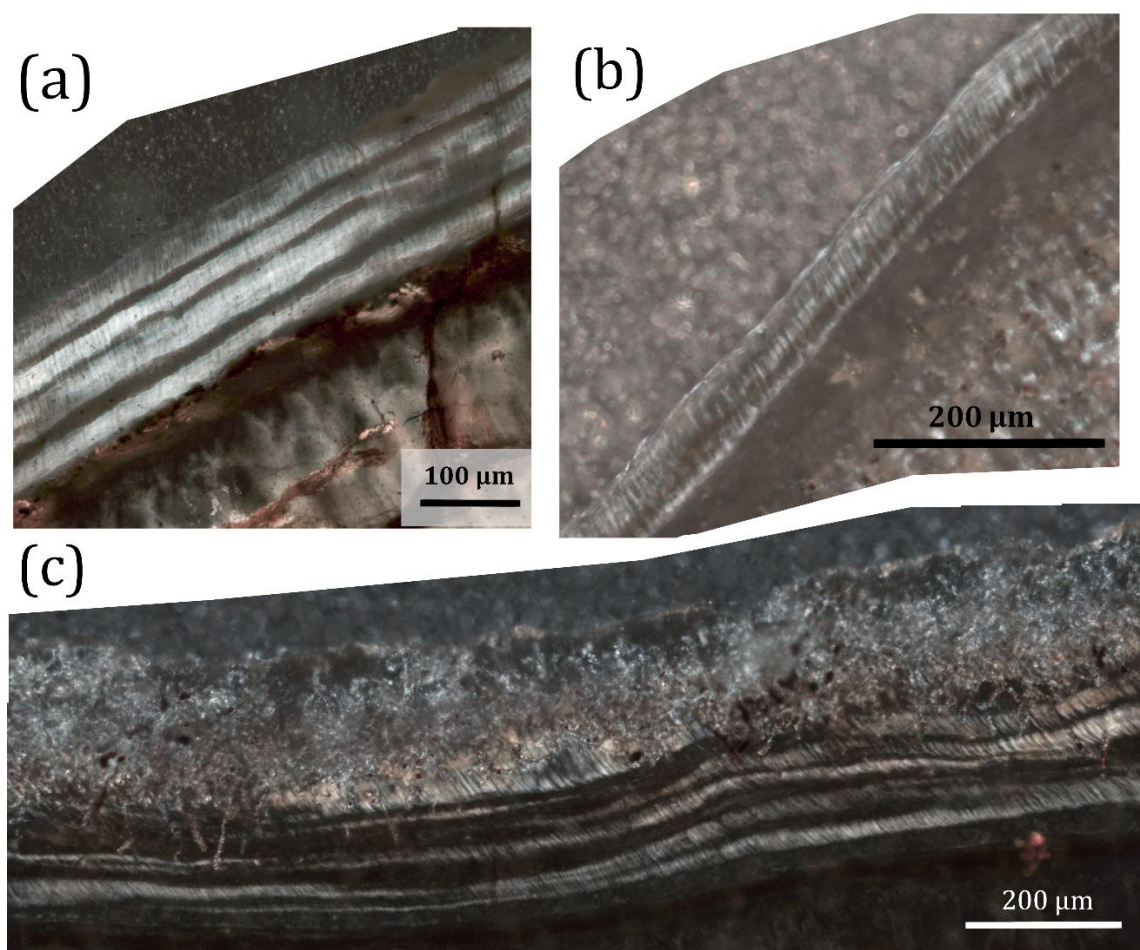


Figure A14: The different ages of individuals within the quarry can be evidenced through cementum annulations. In (a), the root of NMMNH P-69919 (Lp1) shows four white-black couplets. Three white-black couplets are evidenced in NMMNH P-69892 (Lm3) and six couplets are present in (c) NMMNH P-19625's lower molar root in longitudinal section. Images are taken under cross-polarized light and provided by Greg Funston.

Comparison of the L-1079 Assemblage with Broader Biostratigraphic Zone Patterns with 'Holistic' MNI

Using the holistic MNI of six individuals at L-1079, *Pantolambda bathmodon* makes up 22% of the assemblage while *Tetraclaenodon puercensis* and *Mimotricentes subtrigonus* make up 19% and 7% of the assemblage respectively (Fig. A.15).

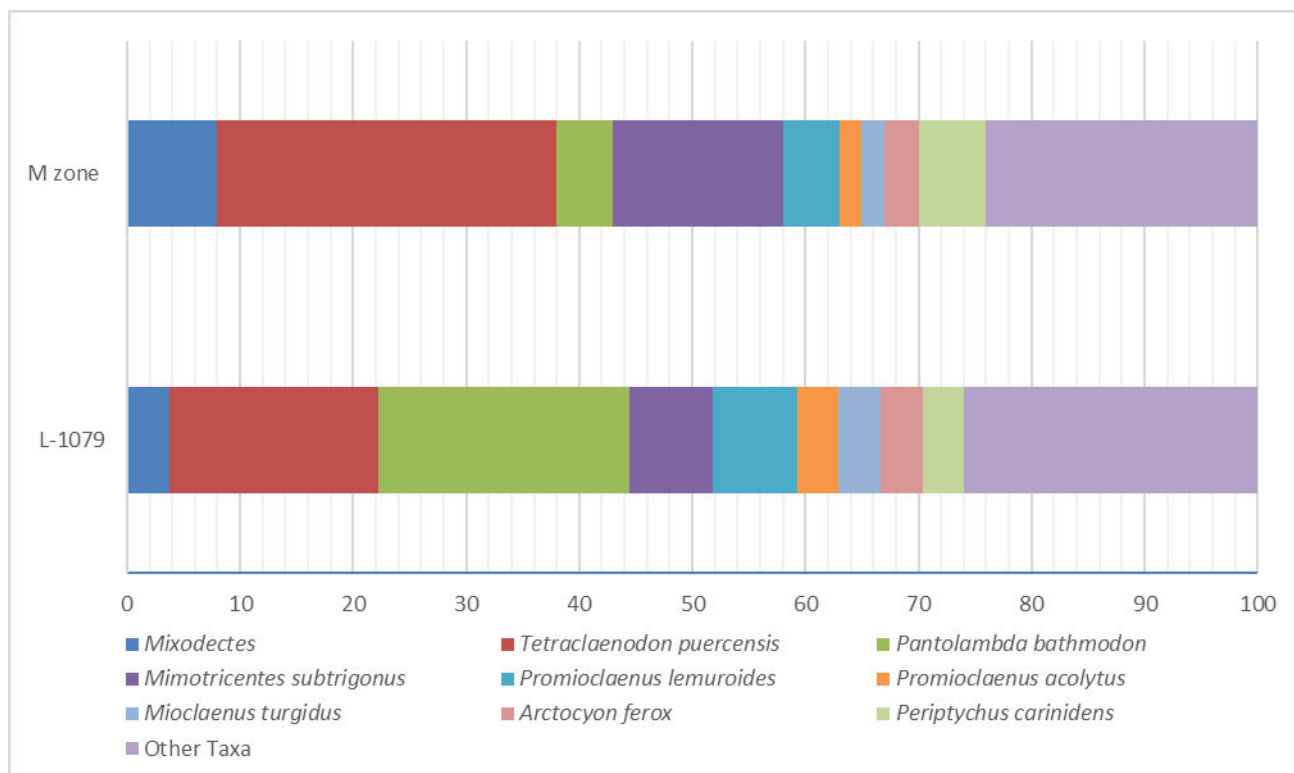


Figure A15: Relative taxa abundances of the overall *Mixodectes pungens* (M) zone of the San Juan compared with the abundances of taxa from L-1079 (using holistic pantodont MNI). *Pantolambda bathmodon* (dark green) is overrepresented in the L-1079 assemblage particularly relative to *Tetraclaenodon puercensis* (dark red) and *Mimotricentes subtrigonus* (dark purple).

In this less conservative analysis, *P. bathmodon* is about four times as abundant at L-1079 as would be expected from the baseline relative abundances of the M zone. Indeed, notably, it exceeds the abundance of very common M zone taxon *Tetraclaenodon puercensis* within assemblage.

Table A7.i: Voorhies Group Tabulations

	P-15400	P-19542	P-19653	P-19655	P-19656	P-19657	P-19658	P-19659
Cranium								
Mandibles ^a			2					
Vertebrae	2					71		
Ribs	1						2 ^b	
Scapulae								
Humeri								
Radius								
Ulna				4				
Pelves								
Femora								
Tibia								5
Fibula								
Podials	2				2			
Metapodials								
Phalanges		5						
Patellae								

^aLeft and right rami tabulated as separate in this analysis. The expected number of 'mandibles' for a pantodont is two.

^bEstimate made based on conservative assessment of which rib fragments belong to *Pantolambda*

Table A7.ii: Voorhies Group Tabulations (continued)

	P-19668	P-19669	P-19672	P-19674	P-19675	P-19676	P-19677	P-19679
Cranium							2	
Mandibles								
Vertebrae								
Ribs								
Scapulae						2		
Humeri				3				
Radius								4
Ulna								
Pelves	8							
Femora		8						
Tibia								
Fibula								
Podials					16			
Metapodials					30			
Phalanges					43			
Patellae			4					

Table A7.iii: Voorhies Group Tabulations (continued)

	P-19680	P-19681	P-19691	P-21562	P-69883	Uncatalogued	Tooth Fragments ^a	Total
Cranium								2
Mandibles							6	8
Vertebrae			3	5		7		88
Ribs			1	1				5
Scapulae								2
Humeri			4	1				8
Radius								4
Ulna						1		5
Pelves								8
Femora								8
Tibia						1		6
Fibula				1				1
Podials	6	1				1		26
Metapodials		2			1	4		37
Phalanges		3				4		55
Patellae						1		5

^aThe tabulation consolidates the tooth fragments shown in Table XX. Six mandibles tabulated because the MNI estimates resulted in 3 unique teeth from each side of the jaw (Rm3, Lm2, Lm3).

Table A8.i: Pantodont Anatomy Elements Summary

Cranium	Mandibles	Scapulae	Humeri	Radius + Ulna	Carpals ^a	Metacarpals	Pelves ^b	Femora
1	2	2	2	4	18	10	2	2
Expected Number of Elements (Strict MNI = 4)								
4	8	8	8	16	72	40	8	8
Expected Number of Elements (Wholistic MNI = 8)								
6	12	12	12	24	108	60	12	12

Notes: ^aAssumed the presence of a centrale in the carpals estimate because the shape of the manus supports the presence of that bone (Simons, 1960). ^bPelves tabulated as right and left innominates because identifications made on basis of acetabulum.

Table A8.ii: Pantodont Anatomy Elements Summary

Tibia + Fibula	Tarsals	Metatarsals	Vertebrae ^a	Phalanges	Ribs ^b
4	14	10	40	56	24
Expected Number of Elements (Strict MNI = 4)					
16	56	40	160	224	96
Expected Number of Elements (Wholistic MNI = 8)					
24	84	60	240	336	144

Notes: ^aVertebrae estimate for *Pantolambda* = 7 cervical, 12 thoracic, 5 lumbar (*Pantolambda*, Simons, 1960), 15 caudal (from Alcidedorbignya; near relative). ^bNumber of ribs derived from thoracic vertebrae.

Table A9: Measurements of *Pantolambda bathmodon* Teeth from L-1079 Quarry

	Upper Dentition			
Specimen Number	Tooth Position	Length (mm)	Width (mm)	
P-19543	LP5	7.7*	13.9*	
P-19544	LP2	6.3	8.1	
P-19544	LP4	7.4	12.0	
P-19544	LP5	7.6	12.5	
P-19545	LM2	10.7	-	
P-19546	RM3	9.3	17.9	
P-19653	LP2	6.8	8.8	
P-57814	RM2	11.3	-	
	Lower Dentition			
Specimen Number	Tooth Position	Length (mm)	AW (mm)	PW (mm)
P-15400	Lp4	8.0	5.9	
P-19540	Rm1	10.6	7.2	8.5
P-19617	Rp5	8.4	7.0	4.4
P-19654	Lp2	7.5	5.0	
P-19654	Lp5	8.6	7.9	5.8
P-19654	Lm1	10.5	8.1	8.8
P-19654	Rm1	10.4	8.2	9.1
P-19654	Rm3	14.4	7.7	7.1
P-19662	Rm3	12.6	6.9	6.4
P-19663	Lm2	8.9	7.1	7.8
P-19663	Lm3	12.3	7.1	6.8
P-19681	Lp3*	6.7	4.6	5.6
P-19681	Lp5*	6.5	6.0	6.1
P-21561	Lm2	10.8	8.5	9.1
P-69890	Lp5	8.2	7.10	4.5
P-69889	Rp2	7.3	4.5	
P-69920	Lp4	7.9	6.3	
P-69921	Lm3	14.0	7.8	6.7
P-69922	Lc	8.2	8.0	

Notes: AW = Anterior Width (measured transversely across trigonid); PW = Posterior Width (measured transversely across the talonid); * indicates measured at alveolar margin because tooth crown broken (in the case of P-19681, the AW and the PW reflect the widths of the anterior and posterior tooth roots)

Appendix III:

The origin of placental mammal life histories



A lower molar trigonid of *Pantolambda bathmodon* (right) paired with its histological section and geochemical analysis of the enamel (left). Image Credit: Greg Funston

"I'm not the smartest fellow in the world, but I sure can pick smart colleagues."
– Franklin D. Roosevelt

The origin of placental mammal life histories

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After the end-Cretaceous extinction, placental mammals quickly diversified¹, occupied key ecological niches^{2,3} and increased in size^{4,5}, but this last was not true of other therians⁶. The uniquely extended gestation of placental young⁷ may have factored into their success and size increase⁸, but reproduction style in early placentals remains unknown. Here we present the earliest record of a placental life history using palaeohistology and geochemistry, in a 62 million-year-old pantodont, the clade including the first mammals to achieve truly large body sizes. We extend the application of dental trace element mapping^{9,10} by 60 million years, identifying chemical markers of birth and weaning, and calibrate these to a daily record of growth in the dentition. A long gestation (approximately 7 months), rapid dental development and short suckling interval (approximately 30–75 days) show that *Pantolambda bathmodon* was highly precocial, unlike non-placental mammals and known Mesozoic precursors. These results demonstrate that *P. bathmodon* reproduced like a placental and lived at a fast pace for its body size. Assuming that *P. bathmodon* reflects close placental relatives, our findings suggest that the ability to produce well-developed, precocial young was established early in placental evolution, and that larger neonate sizes were a possible mechanism for rapid size increase in early placentals.

Placentals are the most diverse group of mammals, comprising more than 6,000 extant species¹¹ and the largest animals ever. Their success may relate to their derived life history^{8,12}, with maternal investment shifted prenatally through extended gestation^{7,13}. This adaptation allows placentals the unique capability among mammals to produce highly precocial young: typically single offspring born at larger masses with well-developed dentition, fur and open eyes^{13,14}. Extended gestation may have released placentals from developmental constraints associated with prolonged lactation in other mammals^{8,15,16}, enabling experimentation with new locomotor modes and habitats^{17,18}. However, when extended gestation evolved in mammals remains unclear; Mesozoic eutherians (mammals more closely related to placentals than marsupials) did not grow like living placentals^{19–21} and it has been hypothesized that ancestral placentals gave birth to altricial young²¹. Nonetheless, immediately after the end-Cretaceous extinction, early Palaeocene placentals emerged from a 100 million years ago (Ma) lineage of small-bodied ancestors and quickly achieved much greater masses as they diversified into various niches⁴. Thus, the early Palaeocene was probably an important interval in the eutherian transition to placental-like growth strategies, but the life histories of these mammals remain unknown.

Among early placental clades, the Palaeocene–Eocene Pantodonta are a key group, because they were among the first large mammalian herbivores, becoming the largest mammals ever up to that point in time²². The early Palaeocene (approximately 62 Ma) *P. bathmodon* (approximately 42 kg) is represented by multiple skeletons representing most of its ontogeny, including a small juvenile with deciduous dentition and unfused epiphyses (New Mexico Museum of Natural

History and Science (NMMNH) P-27844; approximately 17 kg at death). As one of the largest mammals in its ecosystem²³, its life history might provide insight into the relationship between life history and body size in Palaeocene eutherians.

Life histories of extinct animals can be reconstructed using incremental growth features of mineralized tissues such as bones and teeth^{24–26}. Bones preserve evidence of stress and annual cycles^{27,28}, and they accurately reflect growth rate throughout life^{29,30}, including changes associated with maturity³¹. In teeth, daily incremental lines in the dentine and enamel allow for precise chronologies and faithful recording of life history events including birth and nutritional stress such as that experienced during weaning^{32,33}, whereas cementum preserves annual growth cycles^{24,34}. Chemical signals of birth and early-life diet are recorded in the developing teeth by the abundances of certain trace elements, such as zinc (Zn), which is enriched at birth^{35,36}, and barium (Ba), which varies according to bioavailability in the diet²⁶. When integrated with daily growth increments, trace element maps can reveal birth and the timing of weaning, a technique applied to primates up to 2.6 million years of age^{9,10,26}, but with unrealized potential in other fossil mammals.

Here we combine palaeohistological and geochemical evidence to reconstruct the life history of *P. bathmodon* on a daily scale and evaluate the physiology of a key group in the rise of mammals following the end-Cretaceous mass extinction. These data provide unprecedented insight into the life history of a fossil mammal, revealing that characteristic placental reproductive strategies were established early in their evolution.

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Dental development, birth and weaning

Incremental growth features are well preserved in the teeth, especially the enamel, and are clearly visible in histological thin sections (Fig. 1b–g and Extended Data Fig. 1). Daily laminations in the dentine and enamel³⁷ (Fig. 1b,c,e) track the successive growth of the tooth crown (Extended Data Table 1). High-resolution trace element mapping of several teeth (Extended Data Table 1 and Supplementary Figs. 1–7) reveals patterns in Zn and Ba that correspond to these incremental growth patterns and provide evidence of birth and weaning in *P. bathmodon* (Fig. 2), extending the viable window for dietary trace element mapping by roughly 60 million years compared with previous studies¹⁰. The most complete record of early life comes from a second lower molar of an adult individual (NMMNH P-19541), in which both the neonatal event and the weaning transition are preserved (Fig. 2).

Birth is recorded in the enamel by a prominent neonatal line (Figs. 1g and 2b), a discontinuity in the enamel prisms reflecting developmental disruptions in response to the physiological stress of birth³⁸. The neonatal line is Zn-enriched (Fig. 2b and Extended Data Fig. 2), as observed in modern teeth, in which this results from changing levels of Zn in serum over the birth interval and the ingestion of Zn-rich colostrum^{35,36}. The neonatal line is Zn-enriched in multiple cusps of the tooth, and no other accentuated lines in the enamel of this or other teeth are Zn-enriched (Fig. 2b; see Supplementary Information). This suggests that analysis of Zn may be useful as an independent criterion for distinguishing neonatal lines from other accentuated lines in fossil mammals³⁶.

Concentrations of Ba in the enamel were elevated postnatally, but decrease sharply after a short period (Fig. 2c). This pattern is present in both the protoconid and the paraconid of the second lower molar, as well as in the first lower molar of the same individual (Fig. 2d), indicating

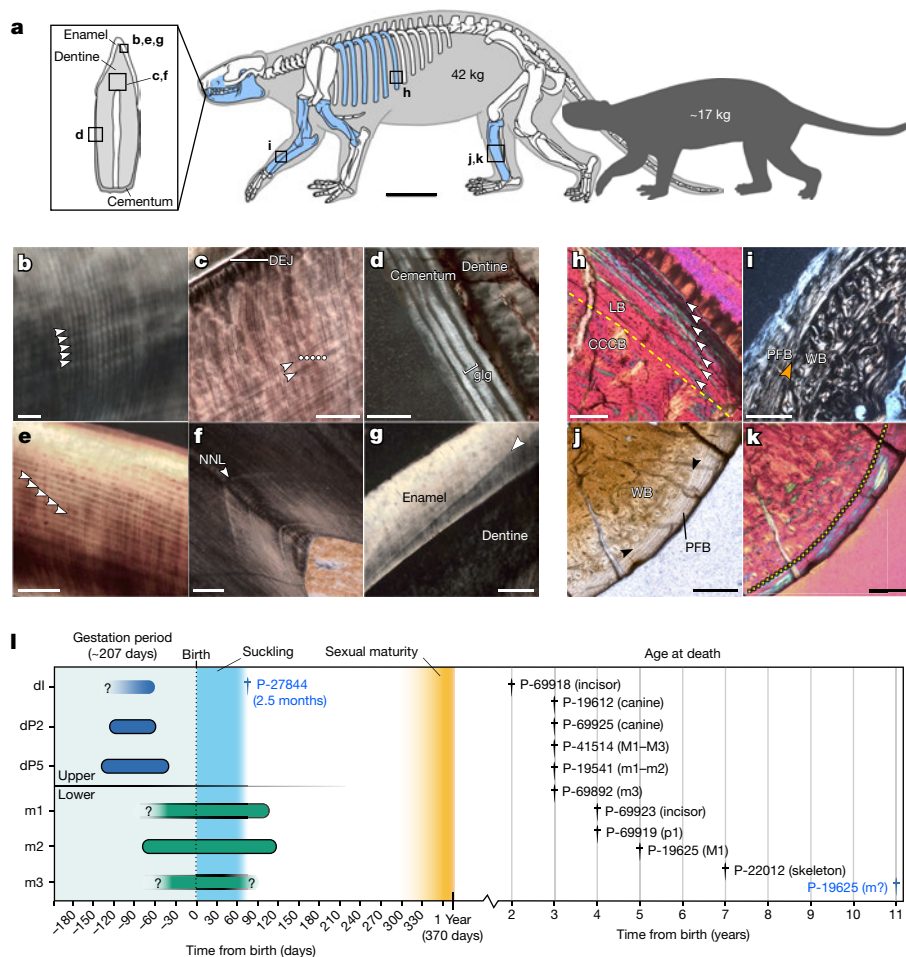


Fig. 1 | Palaeohistology of *P. bathmodon*. **a**, Skeletal reconstruction of adult, with sampled elements in blue. The boxes show the representative locations of palaeohistological images, and the silhouette shows the relative size of juvenile NMMNH P-27844. **b–g**, Dental features used for reconstruction of life history (all coronal sections): enamel cross-striations (arrowheads) in the second lower molar of NMMNH P-19541 (**b**); lines of von Ebner in the deciduous ultimate upper premolar of NMMNH P-27844 (the white dots mark five lines and the arrowheads show the orientation of the lines) (**c**); cementum annulations (one light and one dark band) in the first lower premolar of NMMNH P-69919 (**d**); daily laminations (arrowheads) in the lower incisor of NMMNH P-69918 (**e**); the neonatal line (NNL; arrowhead) in the dentine of the deciduous ultimate upper premolar of NMMNH P-27844 (**f**); and the NNL (arrowhead) in the enamel of the second lower molar of NMMNH P-19541 (**g**). **h–k**, Osteohistological features used for reconstruction of life history (all transverse midshaft diaphysis sections): the lines of arrested growth (arrowheads) in the outer cortex of the rib of NMMNH

P-22012; dashed yellow line indicates boundary between compact coarse cancellous bone (CCCB) and primary lamellar bone (LB) (**h**); the annulus (orange arrowhead) at weaning transition in the radius of NMMNH P-27844 (**i**); weaning transition (arrowheads and yellow dotted line) in the outer cortex of the tibia of NMMNH P-27844 under plane polarized light (**j**) and cross-polarized light with a lambda filter (**k**). Images in **b–g**, **i** are under cross-polarized light, and the image in **h** is under cross-polarized light with a lambda filter. **l**, Life history chronology of *P. bathmodon* showing crown formation times for deciduous (blue) and adult (green) teeth, life history events and mortality. Daggers indicate ages at death; youngest and oldest specimens are in blue. Scale bars, 10 cm (**a**), 25 μ m (**b**), 50 μ m (**e**), 100 μ m (**c**, **d**), 200 μ m (**f–h**) and 500 μ m (**i–k**). CCCB, compact coarse cancellous bone; DEJ, dentinoenamel junction; dI, deciduous incisor; dP2, deciduous upper second premolar; glg, growth layer group; LB, lamellar bone; m1, lower first molar; M1, upper first molar; PFB, parallel-fibred bone; p1, lower first premolar; WB, woven-fibred bone.

that it represents a consistent biogenic signal. Temporary postnatal Ba enrichment in *P. bathmodon* is identical to that reported in modern and fossil primates^{9,10,26}, in which it reflects the increased bioavailability of Ba in breastmilk²⁶. The decreased levels in Ba presumably mark the onset of weaning and indicate a minimum suckling period of about 31–56 days in *P. bathmodon*. Further independent evidence for a short suckling period also comes from mesowear and microwear in the dentition of a young juvenile (NMMNH P-27844; Extended Data Fig. 3), where growth increments in the dentine of the deciduous teeth are exceptionally well preserved (Fig. 1c and Extended Data Fig. 1). Like in the enamel, a birth signature appears to be recorded in the dentine by a neonatal line, and in this individual, the postnatal dentine is Zn-enriched (Extended Data Fig. 4). Dentine continues to infill the pulp cavity throughout life, providing a record of growth both before and after eruption of the tooth and allowing precise estimation of age at death²⁴. Approximately 75 daily growth increments separate the neonatal line and the pulp cavity in each tooth of this juvenile skeleton, indicating an age at death of approximately 2.5 months for this individual. Despite its young age, the presence of dental mesowear and microwear³⁹ (Extended Data Fig. 3) in this individual shows that solid foods (not only milk) were being ingested, providing an upper constraint of 75 days on the onset of weaning.

Aligning daily growth records in the teeth based on the neonatal lines enabled the reconstruction of a dental chronology (Fig. 1l). Crown formation times in the teeth were rapid, ranging from 68 to 183 days (approximately 2–6 months; Extended Data Table 1). All of the deciduous teeth were complete and began erupting before birth, and the first and second adult molars had begun mineralizing. The adult molar crowns were completed within 4 months after birth and would have begun erupting in the first year. On the basis of the eruption sequences in other pantodonts^{40–42}, in which the third molar erupts last, it is therefore likely that all of the adult teeth of *P. bathmodon* erupted within the first year (see Supplementary Information).

In the permanent teeth of mammals, age at death can be estimated from annual bands in the cementum that anchors the tooth to the jaw^{24,34}. Cementum annulations were clearly present in the acellular cementum of most teeth in our sample (Fig. 1d). Most individuals had between two and four annual pairs (Extended Data Table 1), but three individuals with highly worn dentitions compared with other Palaeocene pantodonts had five, seven and possibly as many as 11 pairs, respectively (Extended Data Fig. 5; see Supplementary Information).

Skeletal growth

The bone microstructure of the juvenile skeleton (NMMNH P-27844) exhibits densely vascularized fibrolamellar bone, indicating relatively rapid growth (Fig. 1i–k). No annual growth marks are present, consistent with its dental age of approximately 2.5 months, but a band of more organized, slowly growing parallel-fibred bone occurs towards the outer surface of the radius and tibia (Fig. 1i and Extended Data Fig. 6), at an estimated mass of 9 kg (see Supplementary Information). External to this band, the bone shows reduced vascularity and relatively slower growth, on the basis of a higher proportion of parallel-fibred matrix (Fig. 1j,k), although laminations in this tissue are not as well developed as in the lamellar bone of the adult individual. This transition probably corresponds to changes in growth rate associated with weaning, as in living ungulates, a similar transition occurs in some individuals over this interval⁴³ (see Supplementary Information). The position of this transition partway through the cortex provides evidence for weaning in this individual before death at 2.5 months of age, supporting the 1–2 month suckling period suggested by dental trace elements and tooth wear.

In a skeletally mature adult (NMMNH P-22012), seven annual growth marks were discernible in the exterior cortical bone, matching the number of cementum annulations in its teeth and demonstrating that it was 7 years of age when it died. The exterior cortex is formed

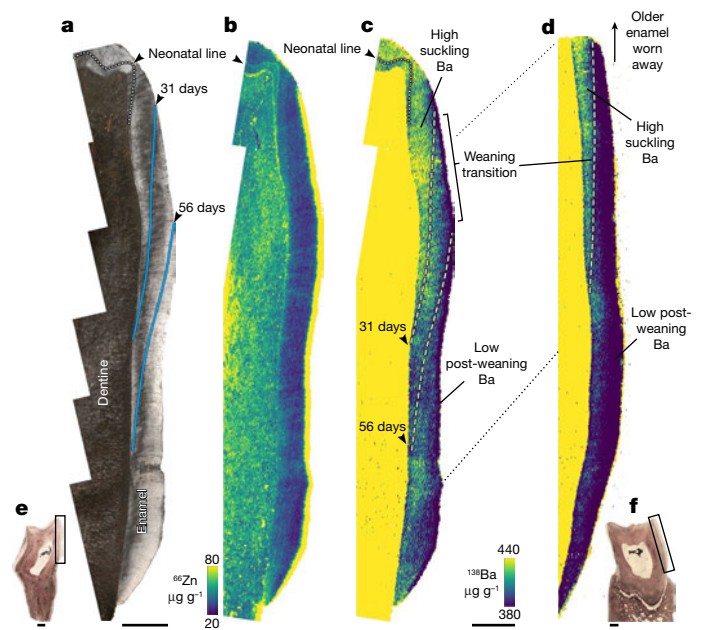


Fig. 2 | Trace element distributions in the enamel of the first and second lower molars (NMMNH P-19541). **a**, Thin section under cross-polarized light shows clear daily laminations and the neonatal line (dotted line) in the enamel of the paraconid of the second lower molar. **b**, Trace element map of Zn shows enrichment at the neonatal line. **c**, Ba is enriched in early postnatal enamel (also see Supplementary Fig. 8), but decreases gradually between 31 and 56 days after birth (dashed lines). **d**, The transition between high and low levels of Ba is clearer in the paraconid of the first lower molar of the same individual, where older enamel including the neonatal line has been worn away. **e, f**, Overview images showing the position of images within the first (**f**) and second (**e**) lower molars. Scale bars, 500 μm (**a–d**) and 1 mm (**e, f**). See also Supplementary Figs. 1–3.

of highly organized lamellar bone, indicating slow growth (Fig. 1h). The earliest annual growth mark is within the slowly growing exterior cortex (Extended Data Fig. 7), indicating that growth rate decreased substantially before the end of the first year of life. This probably corresponds to the achievement of sexual maturity³¹, suggesting that *P. bathmodon* probably reached sexual maturity and approached maximum body size in its first year.

Life history in *P. bathmodon*

Correcting for the onset of tooth mineralization partway through fetal development (see Supplementary Information), the prenatal growth record in the deciduous teeth indicates a gestation period of roughly 207 days or 29.5 weeks. This is an order of magnitude longer than in marsupials or monotremes, but falls close to extant placentals of similar body size (Fig. 3b). Within placentals, gestation length is dichotomous between species that give birth to single or multiple young in each litter⁴⁴ (Fig. 3c). The long gestation period in *P. bathmodon* suggests that it was likely (posterior probability = 0.96) to have given birth to singleton offspring (see Supplementary Information).

Multiple independent lines of evidence from two individuals indicate the onset of weaning between 1 and 2 months after birth in *P. bathmodon*. Postnatal enrichment in enamel Ba for 1–2 months after birth in an adult individual (Fig. 2c,d) is consistent with the development of abrasive microwear and mesowear on the dentition of the juvenile 2.5 months of age (Extended Data Fig. 3) and with the transition recorded in its limb bones (Extended Data Fig. 6), identical to weaning transitions recently described on the basis of fluorescent labelling⁴³. Together, these lines of evidence constrain weaning in *P. bathmodon* to between 31 and 75 days after birth, with the weight of evidence supporting cessation of suckling by 2 months after birth. The age (31–75 days) and mass (9 kg) at

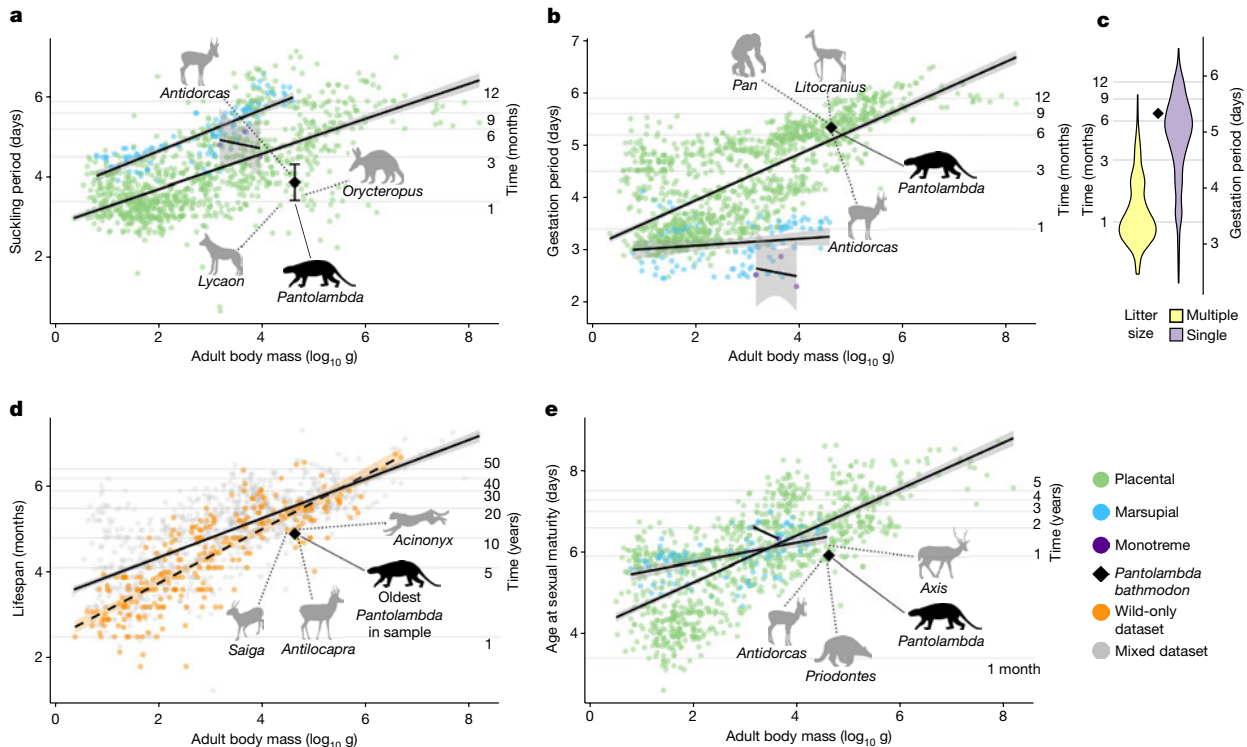


Fig. 3 | Comparison of the reconstructed life history of *P. bathmodon* to extant mammals using the PanTHERIA dataset⁵⁰. **a**, Suckling period showing the range (31–75 days; error bars) estimated for *P. bathmodon* based on dental trace elements, bone histology and dental wear. **b**, Gestation period. **c**, Violin plot of the gestation period sorted by litter size. **d**, Maximum lifespan showing data from PanTHERIA (grey solid line) and from the wild-only lifespan dataset of Newham et al.³⁴ (orange dashed regression line). **e**, Age at sexual maturity for living mammals (placentals, marsupials and monotremes) plotted against adult body mass (log₁₀ mass in grams). Trend lines show generalized linear model regressions for placentals, marsupials and monotremes, with 95% confidence intervals for the regression indicated by shaded envelopes. Horizontal lines show untransformed values. Silhouettes for each panel show living taxa similar in the reconstructed parameter to the estimate for *P. bathmodon*. The silhouette of *P. bathmodon* was created by S.L.S. The silhouettes of *Acinonyx*, *Antilocapra*, *Lycaon*, *Orycteropus*, *Pan* and *Prionotus* were adapted from Phylopic images (CC0 1.0; <https://creativecommons.org/publicdomain/zero/1.0/>). The silhouette of *Litocranius* was original artwork by G.F.F. All other silhouettes were generated from public domain images (CC0 1.0; <https://creativecommons.org/publicdomain/zero/1.0/>).

weaning in *P. bathmodon* were shorter and smaller than expected for a placental of its adult body mass, but its gestation period (207 days) was slightly longer (Fig. 3a,b). This indicates greater prenatal than postnatal investment in the young, characteristic of placental mammals⁷, but also suggests a distinct life history for these early Palaeocene placentals, consistent with other unusual aspects of their biology⁴⁵.

Most individuals within our sample died between 2 and 5 years of age (Fig. 11), suggesting high mortality in young animals. The oldest specimen in our sample (estimated to be approximately 11 years of age) lived only half the expected lifespan for a mammal of its body mass (20 years; Fig. 3d). This high mortality, in conjunction with its short suckling period and rapid onset of sexual maturity (Fig. 3a,e), suggests a fast pace of life in *P. bathmodon*, despite its relatively large size (42 kg).

Combined with its rapid dental and skeletal development, these life history parameters indicate a highly precocial lifestyle in *P. bathmodon*, comparable with the most precocial extant mammals (for example, deer, giraffes and sheep), which give birth to young with hair and open eyes^{13,14}. After a long gestation—the hallmark of the typical placental reproductive mode—a mother *P. bathmodon* probably gave birth to a single, haired offspring with open eyes and well-developed dentition, which was nursed for 1–2 months. At approximately 62 Ma, this constitutes the earliest example of a placentalian-grade physiology in the fossil record.

Growth in early placentals

The growth pattern and rate of *P. bathmodon* differs from those of both Mesozoic mammaliaforms^{19,34} and other Cenozoic mammals^{46,47}. The

confidence intervals for the regression indicated by shaded envelopes. Horizontal lines show untransformed values. Silhouettes for each panel show living taxa similar in the reconstructed parameter to the estimate for *P. bathmodon*. The silhouette of *P. bathmodon* was created by S.L.S. The silhouettes of *Acinonyx*, *Antilocapra*, *Lycaon*, *Orycteropus*, *Pan* and *Prionotus* were adapted from Phylopic images (CC0 1.0; <https://creativecommons.org/publicdomain/zero/1.0/>). The silhouette of *Litocranius* was original artwork by G.F.F. All other silhouettes were generated from public domain images (CC0 1.0; <https://creativecommons.org/publicdomain/zero/1.0/>).

mammaliaform *Morganucodon* grew at a much slower rate and for a longer period, evidence of a protracted life history more like that of reptiles than of mammals^{19,34}. Late Cretaceous multituberculates and some eutherians had faster growth rates than *Morganucodon*, but these were still not as rapid as extant mammals¹⁹. By contrast, *P. bathmodon* exhibits fast growth rates and a rapid developmental schedule, more similar to living precocial placentals. Nonetheless, *P. bathmodon* lived and died faster than expected for a mammal of its body size, outpacing extant mammals and even other extinct mammals from later in the Cenozoic^{46,47}. The closest living analogues for *Pantolambda*, independent of mass (Extended Data Fig. 8a), are small antelope, such as the neotragines *Madoqua* (Dik-dik) and *Raphicerus* (Steenbok). However, when adult body mass is considered, *Pantolambda* is unique among terrestrial mammals (Extended Data Fig. 8b). This life history strategy would have enabled *P. bathmodon* to proliferate at a rapid rate for an animal of its size, which may have been advantageous in the recovering ecosystems of the Palaeocene. Perhaps, as was the case with locomotion⁴⁵ and brain size⁴⁸, placental life history strategies became limited to their modern range later, as ecosystems saturated.

In contrast to its distinctly rapid pace of life, the gestation period of *P. bathmodon* is remarkably similar to living placentals of its body mass (Fig. 3b and Extended Data Fig. 8), suggesting a more constrained relationship between size and gestation. Indeed, neonate weight and adult body mass are more tightly correlated than other life history parameters in extant placentals (Extended Data Fig. 9), suggesting that neonate weight drives and/or is constrained by adult body mass. As longer gestation enables the larger neonate sizes required for larger

adults (Extended Data Fig. 9c), extended gestation periods such as that in *P. bathmodon* may have contributed to the rapid increase in body mass in early Palaeocene placentals. The option of extended gestation may have reduced developmental constraints on body size and allowed placentals to expand into vacant niches after the extinction of the non-avian dinosaurs, reaching larger sizes than any Mesozoic mammal²² and culminating in the largest animals ever⁴⁹.

The excellent preservation of daily incremental structures and dietary trace element signatures in a fossil approximately 62 million years of age unlock a new perspective for studying the life history of extinct mammals. Our results suggest that biogenic trace element signals can be retained much longer than previously realized, providing new tools for inferring birth and early-life diet in ancient fossil mammals. Rather than being a limitation for studying reproduction, the abundantly preserved isolated teeth of Mesozoic mammals may enable combined palaeohistological and geochemical approaches to directly address the evolution of reproduction in mammals, including its role in their survival at the end-Cretaceous extinction and their radiation thereafter. Indeed, the highly precocial life history of *P. bathmodon* shows that the physiology of at least some close placental relatives had diverged from other mammals by at least the Palaeocene, early in their evolutionary history²¹, and suggests that the capacity to increase body size had a role in their ascent from humble Mesozoic beginnings to the dominant role they have in global ecosystems today.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-022-05150-w>.

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Methods

We prepared thin sections (see Supplementary Information) of the teeth and bones of 12 specimens of *P. bathmodon*, including two partial skeletons and totalling 45 elements (23 bones and 22 teeth), collected from the Torrejonian NALMA of the Nacimiento Formation in the San Juan Basin of New Mexico, USA⁵¹. The specimens were selected to represent as much of the skeleton and as many tooth positions as possible and to capture varying degrees of dental wear, presumably attributable to individuals of different ages. No statistical method was used to determine sample size and specimen analysis was not randomized or blinded. The minimum number of individuals based on skeletal overlap a priori was three, but age variation indicated a minimum of seven individuals in our palaeohistological sample.

Incremental marks in the cementum, dentine and enamel were counted from thin sections to assess the timing and pace of tooth development. Cementum annulations, lines of von Ebner in the dentine and cross-striations in the enamel were each clearly visible under cross-polarized light. Pairs of one light and one dark band in the acellular extrinsic fibre cementum near the cervix of the tooth were counted as growth layer groups representing annual growth cycles^{24,52,53}. Lines of von Ebner in the dentine, clearly distinct from more broadly spaced Andresen lines^{24,54}, were counted from high-magnification photomontages as daily increments of growth. Likewise, cross-striations in the enamel were interpreted as daily increments of growth^{54,55}. In every specimen, enamel cross-striations were aligned into clearly visible growth laminations, which have a daily periodicity^{37,56}. The neonatal line in the enamel was identified as a prominent, Zn-enriched³⁵ accentuated line formed by discontinuities in the enamel prisms. In the dentine of the deciduous teeth, the earliest accentuated stress line was identified as the neonatal line²⁴, which was supported by consistent changes in Zn concentration across the neonatal boundary^{35,57} (Extended Data Fig. 4). The neonatal line was used to demarcate prenatal and postnatal developmental periods, and to align sequences from different tooth positions within and between individuals. Daily growth increments in the enamel were traced from high-resolution photomontages to create temporal maps of daily dental development for each tooth. Enamel secretion, crown extension and crown formation rates were estimated using previously published methods⁴⁷.

Dietary trace element concentrations were assessed using laser ablation inductively coupled plasma mass spectroscopy (LA-ICP-MS) at the University of Edinburgh and the University of St Andrews Isotope Geochemistry (STaIG) laboratory. After pilot runs using an ATECH-I-LR Analyte Excite 193 nm ArF excimer coupled to an Attom ICPMS, Nu Instrument at the University of Edinburgh, to assess the suitability of the material for analysis, a broad array of trace element concentrations (¹¹B, ²³Na, ²⁵Mg, ²⁷Al, ³¹P, ⁴³Ca, ⁴⁶Ca, ⁵⁵Mn, ⁵⁹Co, ⁶⁰Ni, ⁶³Cu, ⁶⁶Zn, ⁸⁸Sr, ⁸⁹Y, ¹³⁸Ba, ²⁰⁸Pb and ²³⁸U) in the enamel and dentine of six teeth were mapped using LA-ICP-MS on an Agilent 8900-QQQ at the STaIG laboratory. Entire enamel sequences of three teeth (the paraconid of a lower first molar (NMMNH P-19541), the protoconid of a lower second molar (NMMNH P-19541) and the labial enamel of an incisor (NMMNH P-69918)) were scanned at high resolution (20- μ m spot size, 10 μ m s⁻¹ scanning speed and inductively coupled plasma cycle time of 0.2889 s), with an effective pixel size of 60 μ m² (Supplementary Figs. 1–4). Small regions of interest in the deciduous teeth (NMMNH P-27844) were also scanned at high resolution (38- μ m spot size and 38 μ m s⁻¹ scanning speed; Supplementary Figs. 5–7). LA-ICP-MS data were processed and rasterized in Iolite v4.5.5.4 (ref. ⁵⁸). Concentrations were normalized to and drift-corrected by a National Institute of Standards and Technology 612 glass standard after gas blank subtraction, and standardized to approximately 40% Ca. Elemental maps and transects were registered to temporal maps of dental development to evaluate daily changes in diet.

Dental microwear was evaluated using scanning electron microscopy using a Carl Zeiss SIGMA DH VP field emission scanning electron microscope at the University of Edinburgh operated at 15 kV for secondary electron imaging of the fine-scale features of the occlusal surface of the first upper molar of NMMNH P-27844.

Reconstructed life history parameters for *P. bathmodon* were plotted alongside data from the PanTHERIA dataset⁵⁰ for comparison. Because the PanTHERIA dataset includes mostly captive individuals, which are likely to have greater maximum lifespans than wild individuals, the estimated maximum lifespan of *P. bathmodon* was also compared with a recent wild-only dataset of mammal maximum lifespan³⁴. Relative importance of life history parameters for predicting body size was evaluated using multiple regression, and litter size was predicted using linear discriminant analysis based on gestation period. Principal components analysis was used to identify the closest living analogues of *P. bathmodon*.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Fossil specimens in this study are housed at the NMMNH, and the palaeohistological thin sections underlying the analyses are accessioned at the University of Edinburgh but will be returned to the NMMNH for permanent curation upon completion of our research. The living mammal datasets are available from Jones et al.⁵⁰ (<https://doi.org/10.6084/m9.figshare.c.3301274.v1>) and Newham et al.³⁴ (<https://www.nature.com/articles/s41467-020-18898-4#Sec18>). Overview images of palaeohistological slides and LA-ICP-MS data are deposited at Figshare (<https://doi.org/10.6084/m9.figshare.20272737>). Source data are provided with this paper.

Code availability

No custom code or software was used in the study.

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Author contributions G.F.F. designed the study, made the thin sections, conducted the histological, life history and statistical analyses, prepared the figures and wrote the manuscript. P.E.d. contributed to the study design, identification of the material, morphological analyses and drafting the manuscript. J.T.S. and M.D. conducted the LA-ICP-MS analyses at STaIG and contributed to figures and drafting the manuscript. S.L.S. created the skeletal reconstruction

of *P. bathmodon* and contributed to discussion and drafting the manuscript. L.E.P. conducted the LA-ICP-MS analyses at the University of Edinburgh and contributed to drafting the manuscript. N.J.C. conducted the scanning electron microscopy analyses. J.R.W. contributed to drafting the manuscript. T.E.W. oversaw the collection and curation of the material, provided stratigraphic data and contributed to drafting the manuscript. J.W.B.R. supervised the LA-ICP-MS analyses. S.L.B. coordinated the project and contributed to study design and drafting the manuscript.

Competing interests The authors declare no competing interests.

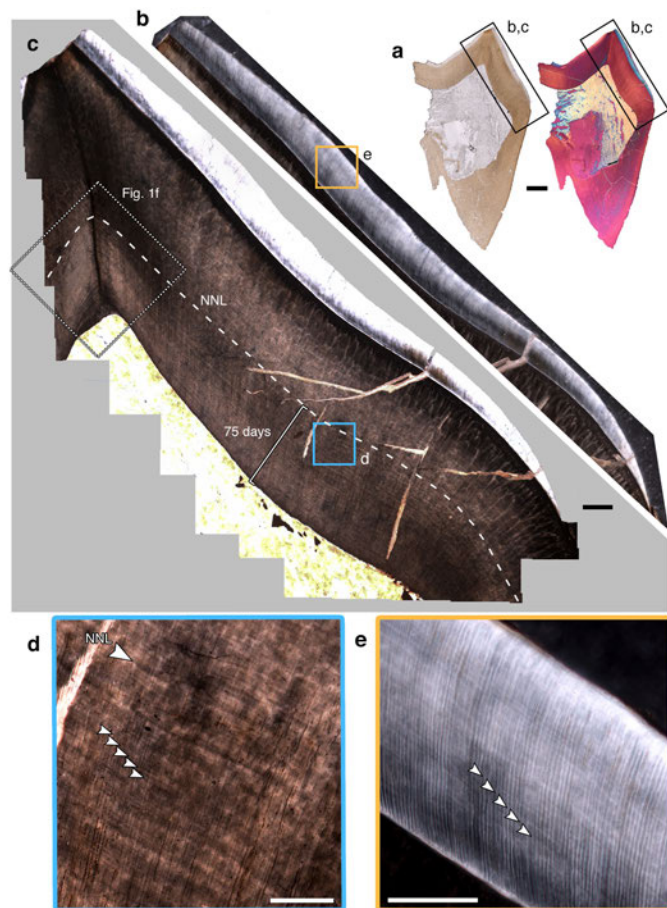
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-022-05150-w>.

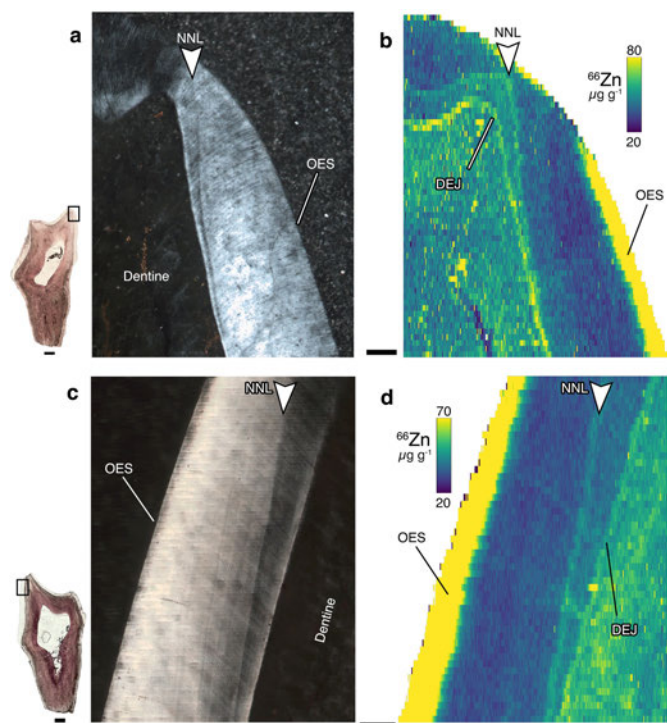
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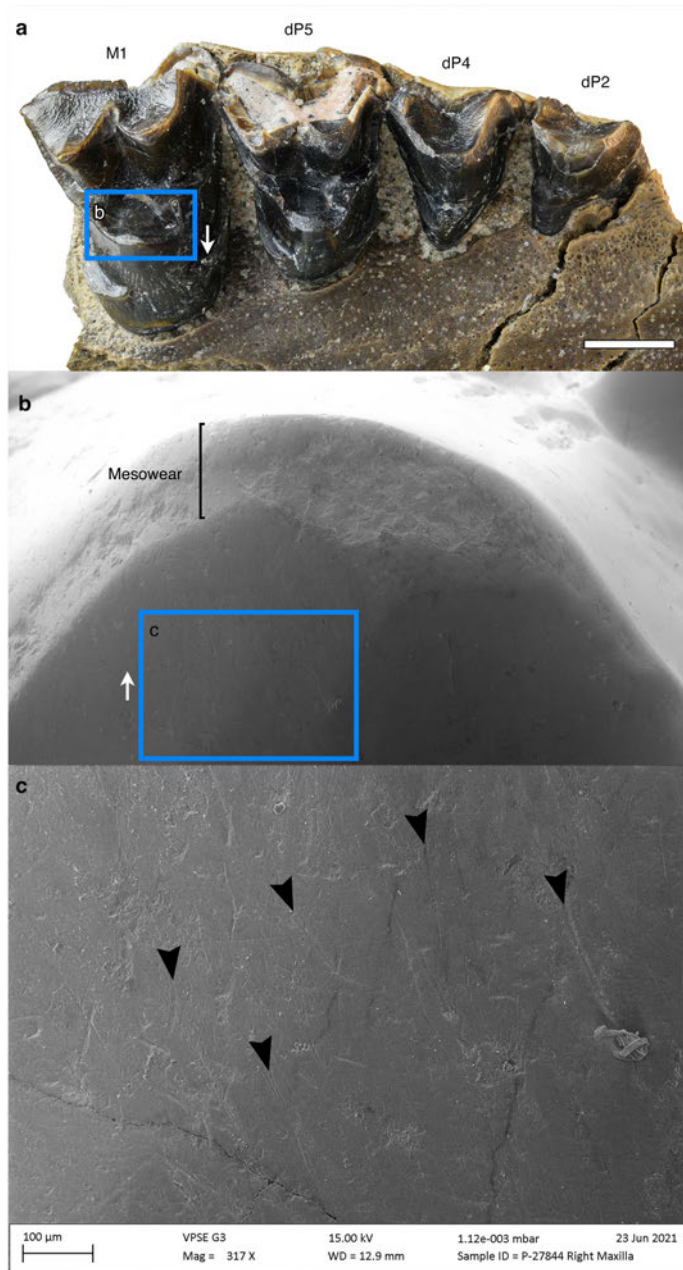
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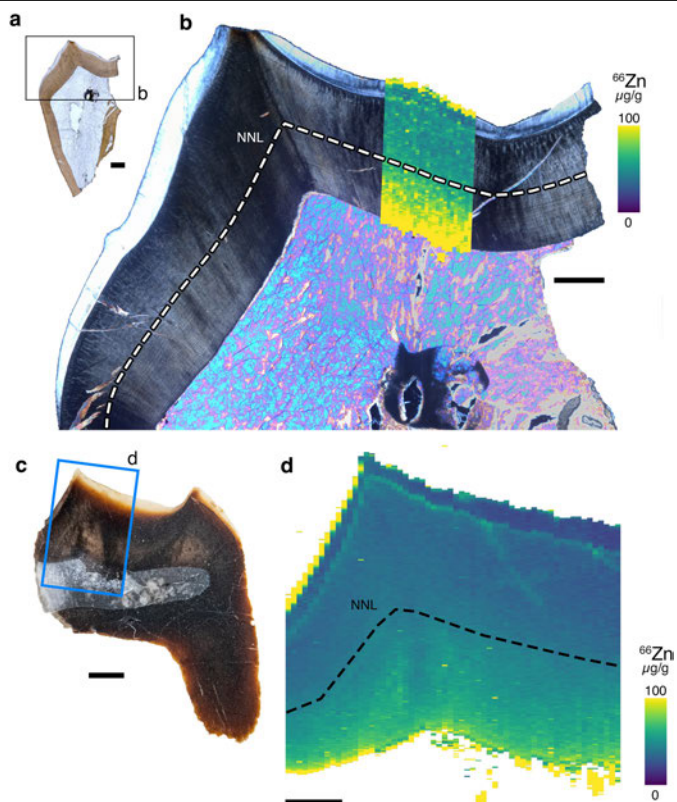
Extended Data Fig. 1 | Incremental features of the teeth of *Pantolambda bathmodon*. (a) Overview of coronal section of deciduous ultimate upper premolar of NMMNHP-27844 under plane-polarized light (left) and cross-polarized light with a lambda filter (right), showing locations of inset images. (b,c) Photomontages of the protocone exposed for the enamel (b) and the dentine (c), showing excellent preservation of incremental features, neonatal line (dashed line), and locations of close-up images. (d) Contrast-enhanced close-up of lines of von Ebner preserved in the dentine (arrows), extending parallel to the dentinoenamel junction and perpendicular to dentine tubules, and neonatal line (large arrow). (e) Contrast-enhanced close-up of enamel cross-striations and daily laminations (arrows) in the enamel, extending sub-parallel to the dentinoenamel junction and perpendicular to the enamel prisms. Images in b–e are under cross-polarized light. **Abbreviations:** NNL, neonatal line. Scale bars: 1 mm (a), 200 μm (b, c), 100 μm (d, e).



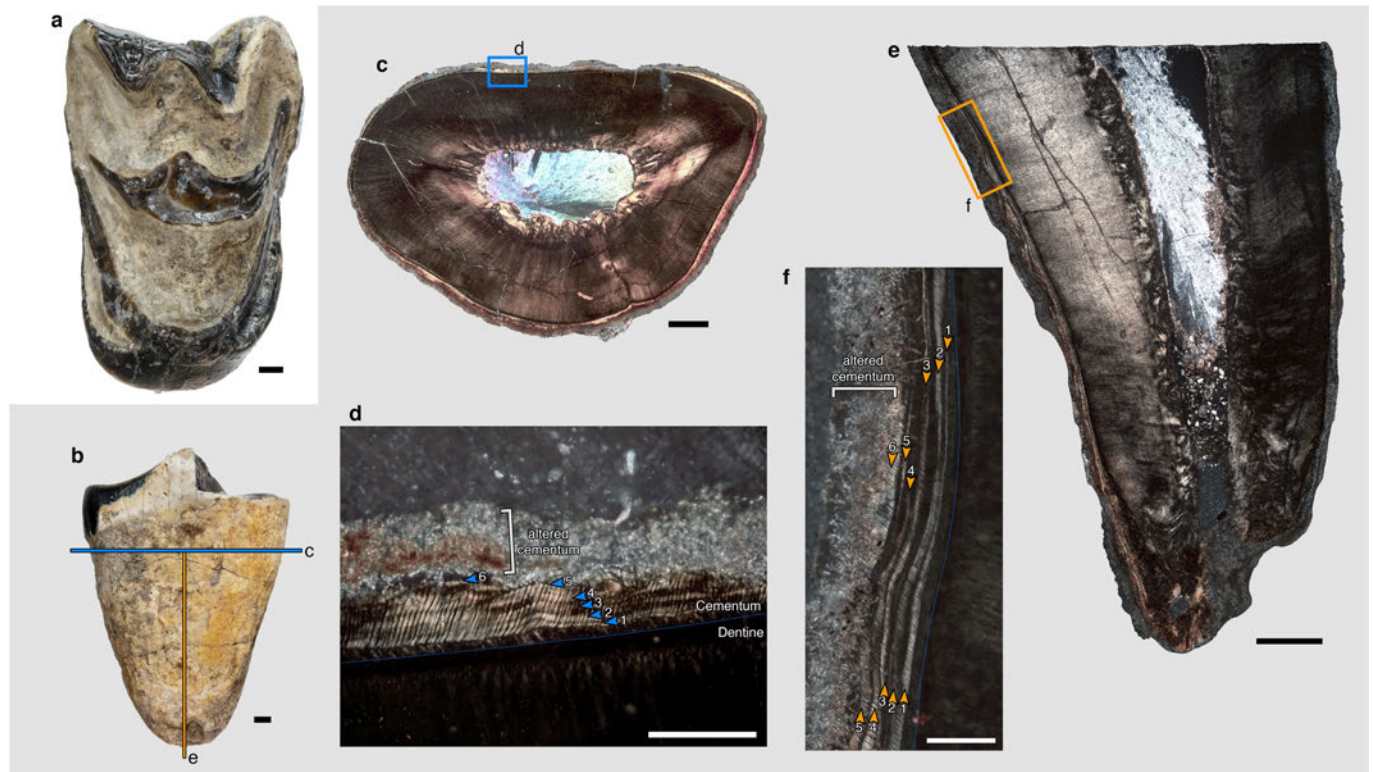
Extended Data Fig. 2 | Zn-enrichment of the neonatal line in the enamel of lower second molar of NMMNH P-19541. (a, c) coronal sections of enamel of paraconid (a) and protoconid (c) under cross-polarized light. Insets show location on coronal sections of entire tooth. (b, d), LA-ICP-MS trace element maps, showing higher concentrations of Zn in discrete areas corresponding to the neonatal line (white arrows). **Abbreviations:** DEJ, dentinoenamel junction; **NNL**, neonatal line; **OES**, outer enamel surface. Scale bars: 1 mm (insets), 100 µm (a–d).



Extended Data Fig. 3 | Microwear on the dentition of NMMNH P-27844. (a) Right maxilla with three deciduous premolars and adult first molar in occlusal view, showing location of scanning electron microscopy (SEM) scan. (b) Overview secondary electron (SE) image of protocone of adult first molar, showing development of mesowear and location of close-up image. (c) Close-up SE image of scratches and gouges attributable to abrasive microwear; black arrows highlight curved scratches resulting from chewing motion. White arrows highlight curved scratches resulting from chewing motion. White arrows in (a) and (b) indicate lingual direction. **Abbreviations:** **d**, deciduous; **M**, upper molar; **P**, upper premolar.

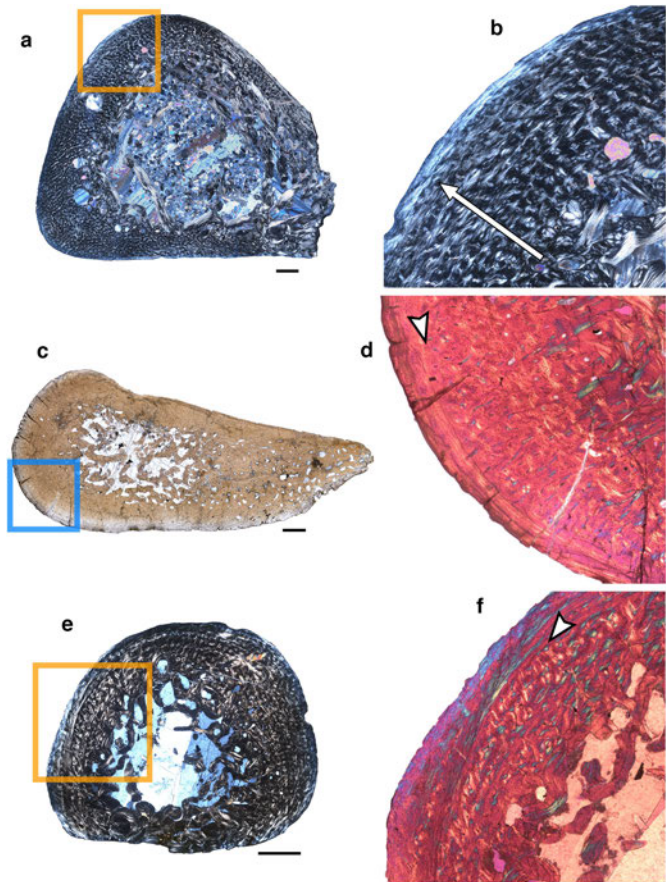


Extended Data Fig. 4 | Changes in zinc associated with birth in the deciduous upper premolars of NMMNHP-27844. Postnatal dentine is enriched in Zn in the deciduous upper ultimate premolar (a, b) and the deciduous upper second premolar (c, d). (a) Overview of thin section showing location of close-up image. (b) Mosaic image showing protocone in cross-polarized light, with trace element map overlain, showing change at histologically-inferred neonatal line (dashed line; NNL). (c) Overview image of embedded block showing location of trace element map. (d) Trace element map showing increased postnatal Zn. Scale bars: 1 mm (a, c), 500 μm (b, d). **Abbreviations:** NNL, neonatal line.

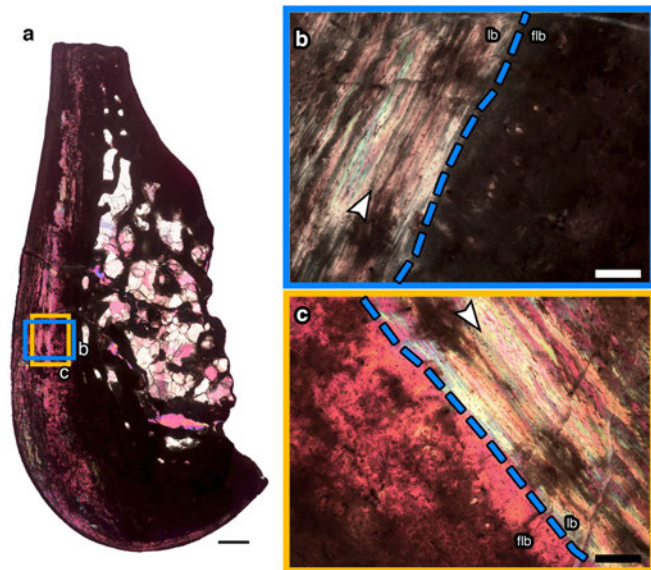


Extended Data Fig. 5 | Dental wear, cementum annulations, and maximum lifespan in the oldest sampled individuals. (a) Right first upper molar of NMMNH P-19625, showing extensive wear and erosion of enamel in most areas of the crown. (b) Anterior root of lower molar (tooth position unknown) from another individual of NMMNH P-19625, showing the location of the thin sections. (c) Overview transverse section of cervical root area, showing clear demarcation of cementum and dentine, and location of close-up. (d) Close-up of acellular extrinsic-fiber cementum in transverse section, showing six pairs

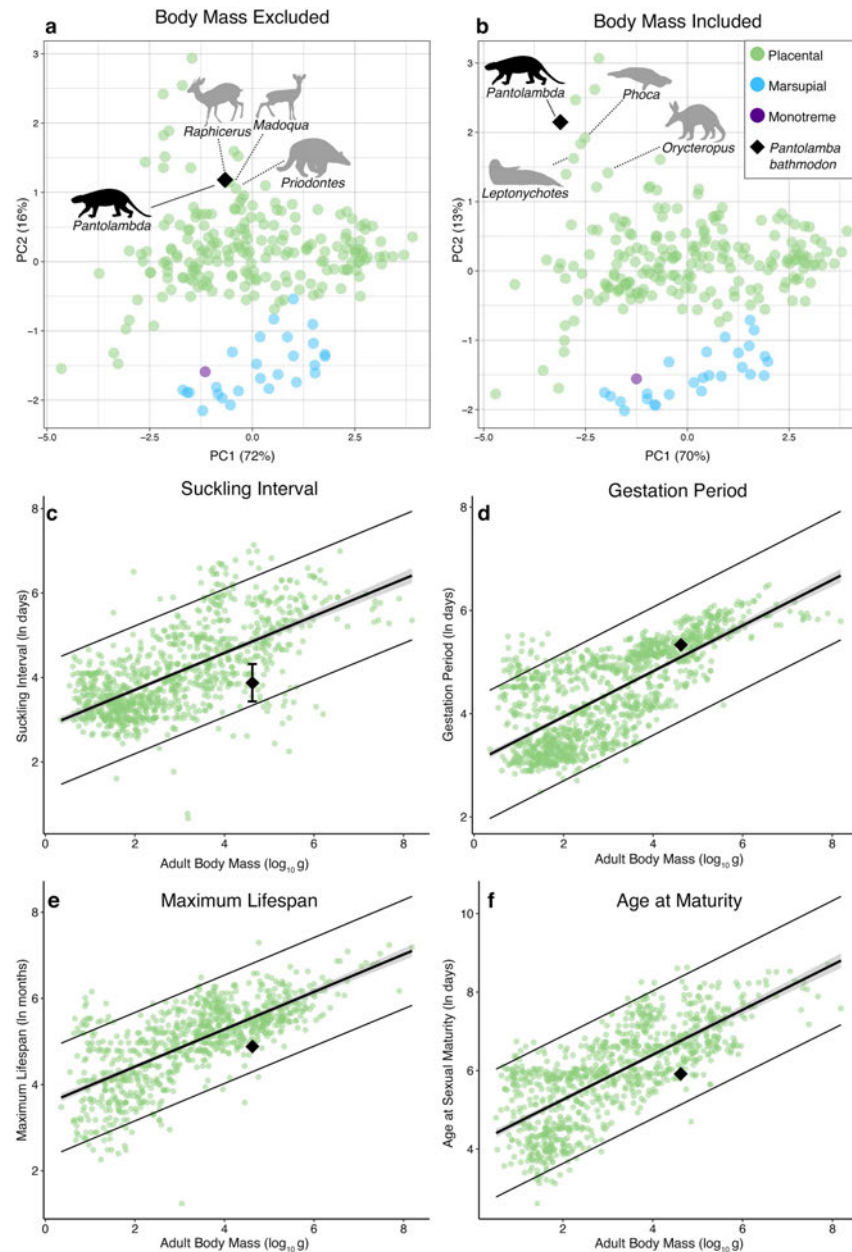
of dark and bright bands comprising annual growth layer groups and alteration of external cementum; bright bands indicated with blue arrows. (e) longitudinal section of the same tooth, showing thick external layer of cementum, continuity of growth layer groups, and location of close-up. (f) close-up image of acellular extrinsic-fiber cementum in longitudinal section, showing six annual growth layer groups and alteration of external cementum; bright bands indicated with orange arrows. Images c-f under cross-polarized light. Scale bars: 1 mm (a-c, e), 200 μ m (d, f).



Extended Data Fig. 6 | Weaning transition recorded in the postcranial bones of NMMNH P-27844. (a) Transverse section of right humerus diaphysis under cross-polarized light, showing arrangement of tissues and large medullary cavity and location of close-up image. (b) Close-up of cortex of right humerus under cross-polarized light, showing increase in proportion of parallel-fibered bone (brighter tissues) later in growth (arrow), indicative of a decrease in growth rate. (c) Transverse section of right tibia diaphysis under plane polarized light, showing location of close-up image. (d) Close-up of cortex of right tibia under cross-polarized light with a lambda filter, showing transition (arrow) from highly-vascularized fibrolamellar bone with a high proportion of woven-fibered matrix (upper right) to more slowly-growing parallel-fibered bone with reduced vascularity (lower left). (e) Transverse section of right radius diaphysis under cross-polarized light, showing location of close-up image. (f) Close-up image of cortex of right radius under cross-polarized light with a lambda filter, showing annulus of parallel-fibered bone (arrow) separating region of highly-vascularized fibrolamellar bone (lower right) from region of less-vascularized fibrolamellar bone with a higher proportion of parallel-fibered bone (upper left). Scale bars: 1 mm (a, c, e), 500 μ m (b, d, f).

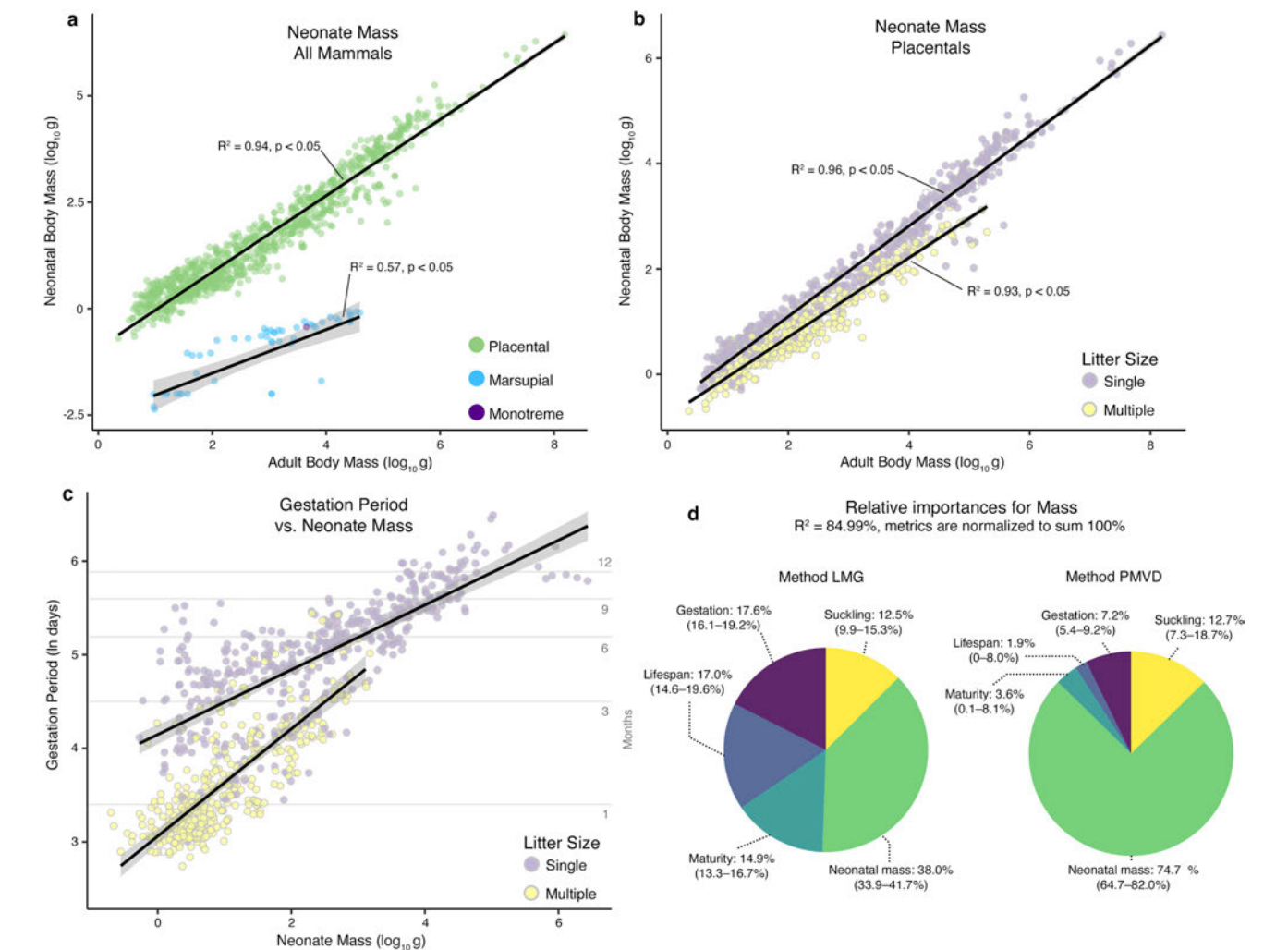


Extended Data Fig. 7 | Transition to slower growth likely reflecting sexual maturity. (a) Coronal section of posterior dentary of NMMNHP-22012 under cross-polarized light with a lambda filter, showing locations of close-up images. Dark regions have been diagenetically altered by the deposition of opaque minerals. (b, c) Close-up of transition (dashed line) between faster-growing fibrolamellar bone (flb) and slower-growing lamellar bone (lb), indicative of sexual maturity, under cross-polarized light (b) and cross-polarized light with a lambda filter (c). Arrows indicate first line of arrested growth, deposited after the transition to slower growth. Scale bars: 1 mm (a), 200 μ m (b, c).



Extended Data Fig. 8 | Life history of *P. bathmodon* compared to living mammals. (a, b) principal components analyses using the PanTHERIA dataset (placentals, green; marsupials, blue; monotremes, purple) incorporating suckling interval, gestation period, maximum lifespan, and age at sexual maturity, with adult body mass excluded (a) or included (b) as a variable; close living analogues to *P. bathmodon* indicated by silhouettes. (c–f) regressions of life history variables in placental mammals with 95% confidence intervals (thin black lines) centred on the generalized linear model regression trendline for suckling interval (c), gestation period (d), maximum lifespan (e), and age at

sexual maturity (f), showing that *P. bathmodon* is within the 95% confidence interval of placentals in all parameters. Silhouette of *Pantolambda bathmodon* created by SLS. Silhouettes of *Orycteropus* and *Prionotus* adapted from Phylopic images (CC0 1.0 <https://creativecommons.org/publicdomain/zero/1.0/>), silhouette of *Leptonychotes* is original artwork by GFF, silhouette of *Phoca* was generated from a photograph taken by GFF, and all others were generated from public domain images (CC0 1.0 <https://creativecommons.org/publicdomain/zero/1.0/>).



Extended Data Fig. 9 | Relationship between neonate mass and adult body mass in extant mammals. (a) Generalized linear model regression of neonate body mass against adult body mass for all species in the PanTheria dataset, showing clear separation of placental mammals (green, p -value $< 2.2 \times 10^{-16}$) from non-placental mammals (p -value: 4.07×10^{-6}); 95% confidence interval for regression slope shown as shaded envelope. (b) Neonate body mass plotted against adult body mass for placental species, showing tight correlations of neonate mass and adult mass (p values both $< 2.2 \times 10^{-16}$); 95% confidence

interval for generalized linear model regression slope shown as shaded envelope. (c) Gestation period plotted against neonate body mass; 95% confidence interval for generalized linear regression slope shown as shaded envelope. (d) Relative importance of multiple regression of adult body mass against neonate weight, gestation period, maximum lifespan, time to sexual maturity, and suckling period, showing relative contribution of factors to adult body mass; confidence intervals derived from 1000 replicates of bootstrapping.

Extended Data Table 1 | Quantitative dental histological data for *Pantolambda bathmodon*

Specimen (NMMNH)	Element	Retzius Periodicity	Enamel Secretion Rate (µm/d)	Lamination Angle	Crown Extension Rate (µm/d)	Prenatal Formation Time (d)	Crown Formation Time (d)	Cementum Annulations [§]	Trace Element Analysis
P-19541	Lm1	2	9.3	4.4°	93.5	-	154	3	Protoconid
	Lm2	2	9.9 [†]	7.2°	78 [†]	78	195	2.5	Protoconid and Paraconid
P-19612	C	1	9.3	5.0°	89	-	-	3	-
P-19625	M1	1	-	-	-	-	-	5	-
	Root	-	-	-	-	-	-	11*	-
P-22012	P4	-	-	-	-	-	-	7	-
	LdP2	1	9.2 [†]	4.1°	114 [†]	116	68	0.5	Paracone
P-27844	LdP4	1	-	-	-	-	-	-	Paracone
	LdP5	1	9.75 [†]	5.0°	142 [†]	138	98	0.5	Protocone
P-41514	LM1	1	-	-	-	-	-	3	-
	LM2	1	-	-	-	-	-	3	-
	LM3	1	-	-	-	-	-	2.5	-
P-69892	Lm3	2	9.1	9.4	71	-	-	2.5	Pilot transect
P-69918	i	1	7.4	6.4°	70	-	121	3	Labial enamel
P-69919	Lp1	1	10.4	6.1°	78	-	115	4	-
P-69923	I	1	7.0	5.65°	49	-	126	4	-
P-69925	C	1	-	-	-	-	-	3	-

Note: *estimate, see Supplementary Information for further details. For teeth with a neonatal line, [†] prenatal, [‡] postnatal. [§] counted as a pair of light and dark bands; - inapplicable or not available

Reporting Summary

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Software and code

Policy information about [availability of computer code](#)

Data collection Photoshop CC 2021 was used to process image data and to assemble microscopy images into photomontages. Microsoft Excel was used for compiling data including histological measurements, LA-ICP-MS pilot data, and the PanTheria dataset. ImageJ 1.52q was used to take histological measurements.

Data analysis Iolite v4.5.5.4 software was used to process LA-ICP-MS data. RStudio v3.6.1 was used for all statistical analyses. Packages used include ggplot2, ggplotify, ggpubr, ggsci, gridExtra, MASS, MPSEM, relaimpo, and tidyverse. No custom code was used for data analysis.

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Fossil specimens (in this study are housed at the New Mexico Museum of Natural History and Science, and the palaeohistological thin sections underlying the analyses are accessioned at the University of Edinburgh but will be returned to the NMMNH for permanent curation upon completion of our research. The living mammal datasets are available from Jones et al. (ref 51; <https://doi.org/10.6084/m9.figshare.c.3301274.v1>) and Newham et al. (ref 35; <https://www.nature.com/>)

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Ecological, evolutionary & environmental sciences study design

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Study description	The study included the production of palaeohistological thin sections from fossil material, analysis of incremental structures within the thin sections, LA-ICP-MS analysis of trace element distributions in the thin sections, and comparison of these results to a previously-published life history dataset of extant mammals. Quantitative data were not separated into experimental groups nor treated in any way.
Research sample	The research sample included fossil specimens of <i>Pantolambda bathmodon</i> accessioned at the New Mexico Museum of Natural History and Science, and on loan to the University of Edinburgh for morphological analyses. We chose to use specimens from this collection because it is the largest collection of <i>Pantolambda bathmodon</i> available, each specimen has associated locality data, and the specimens were available for consumptive histological sampling. Sampled elements were chosen to represent as many tooth positions as possible, and to represent a variety of ontogenetic stages, based on degrees of skeletal fusion, size, and dental wear. All specimens were collected from the Nacimiento Formation in the San Juan Basin of New Mexico. We used two publicly available datasets for comparison (PanTheria and Newham et al.). The PanTheria dataset was chosen because it is the largest life history dataset of mammals currently available, and it contains data for a wider range of clades and each of the life history variables of interest. We chose the Newham et al. dataset because it is the largest available lifespan dataset for which values derived from wild and captive animals are separate.
Sampling strategy	The sample was chosen based on availability and suitability for destructive sampling. For geochemical sampling, specimens which showed clear incremental growth marks and a distinct neonatal line were selected. LA-ICP-MS scans were created for entire enamel sequences of either the protoconid or paraconid of three teeth, supplemented by targeted sampling of small areas of other teeth. The sampling areas for LA-ICP-MS were chosen because they included pre- and post-natal regions of enamel and dentine as well as the neonatal line. No predetermination of sample size was done, and samples were chosen on availability of material and suitability for consumptive sampling.
Data collection	Growth increments in the enamel and dentine were manually traced and counted from high-resolution digital photomontages produced using the automated "photomerge" feature of Adobe Photoshop CC 2021. Traces and counts were performed by GFF. LA-ICP-MS data was collected automatically, using an ATLEX-I-LR Analyte Excite 193nm ArF excimer coupled to an Attom ICPMS, Nu Instrument operated by LEP at the University of Edinburgh, and a Laurin Technic S155 2-volume ablation cell featuring a 193 nm ASI Resolution ArF excimer laser coupled to an Agilent 8900 Triple Quadrupole ICP-MS operated by JTS and MD at the University of St. Andrews.
Timing and spatial scale	Histological data was collected between June 2020 and April 2022. LA-ICP-MS data was collected between June 30, 2021, and February 15, 2022. Sampling was not periodic or organized into cohorts.
Data exclusions	Pilot LA-ICP-MS transects were collected to evaluate the suitability of the material for more comprehensive analysis. Pilot transects were not rigorously controlled with respect to orientation, direction, or spot size, and therefore do not reflect biological signals. For these reasons, these transects were not considered in our final analyses.
Reproducibility	Replication is not applicable to the study because there were no experimental groups.
Randomization	Randomization was not applied because there were no experimental groups.
Blinding	Blinding was not used because there were no experimental groups.
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☐	☒ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology and Archaeology

Specimen provenance	Nacimiento Formation, San Juan Basin, New Mexico, USA. Specimens collected under US BLM Paleontological Use Permit # NMMNH 8270-RS-8C. Permission for destructive analysis was provided by the New Mexico Museum of Natural History and Science February 25, 2022.
Specimen deposition	New Mexico Museum of Natural History
Dating methods	No new dates are provided
☒ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.	
Ethics oversight	Fieldwork permits were granted by the Bureau of Land Management of the United States of America (US BLM Paleontological Use Permit # NMMNH 8270-RS-8C). No other ethical approval or guidance required for the study.

Note that full information on the approval of the study protocol must also be provided in the manuscript.