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# A tooth crown morphology framework for interpreting the diversity of primate dentitions

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## Abstract

Variation in tooth crown morphology plays a crucial role in species diagnoses, phylogenetic inference, and the reconstruction of the evolutionary history of the primate clade. While a growing number of studies have identified developmental mechanisms linked to tooth size and cusp patterning in mammalian crown morphology, it is unclear (1) to what degree these are applicable across primates and (2) which additional developmental mechanisms should be recognized as playing important roles in odontogenesis. From detailed observations of lower molar enamel–dentine junction morphology from taxa representing the major primate clades, we outline multiple phylogenetic and developmental components responsible for crown patterning, and formulate a tooth crown morphology framework for the holistic interpretation of primate crown morphology. We suggest that adopting this framework is crucial for the characterization of tooth morphology in studies of dental development, discrete trait analysis, and systematics.

**KEYWORDS**
amelogenesis, cusp patterning, dental anthropology, odontogenesis, tooth crown

## 1 | INTRODUCTION

Teeth are the most durable part of the skeletal system and therefore represent a significant portion of the primate fossil record. As such, variation in tooth crown morphology plays a crucial role in species diagnoses, phylogenetic inference, and in the reconstruction of the evolutionary history of the primate clade. However, the use of tooth shape variability in studies of primate systematics and taxonomy deserves renewed consideration as a growing number of studies have shed light on important developmental mechanisms (not just phylogenetic and evolutionary trends) that contribute to the diversity seen in mammalian crown morphology.[1–8] These various studies have highlighted a complex relationship between the genotype and phenotype of the mammalian dentition,[9,10] and provide new and revised ways to interpret morphological variation. In particular, these studies have demonstrated how small changes in the developmental parameters of growth can have a significant impact on variation in the morphology of molars.[8,11–13]

The two most recognized developmental models that have arisen from evolutionary developmental studies of murine dentitions and comparative studies of mammalian dentitions are the patterning cascade model (PCM) of cusp development[3,7,8,11,14,15] and the inhibitory cascade model of tooth size variation.[12] While a number of studies have found support for these models to explain variation in primate tooth crown morphology and metameric size variation, they cannot account for a number of aspects of primate tooth crown morphology. For example, there are several patterns of cusp expression in primates that appear to suggest an added level of developmental complexity not yet widely acknowledged.[16,17] Additionally, these studies provide little insight into the complex patterning of *crest* morphology present among primate molar crowns. Thus, our understanding of the phylogenetic and developmental processes underlying the dental morphology used in primate systematics is incomplete and leads to ambiguity regarding the interpretation of dental variation in primate systematics. More fundamentally, it challenges the current presumed homology of

many crown traits among primates and raises concerns regarding the suitability of the current nomenclature system used to identify and name these dental features.

Despite a growing understanding of the developmental mechanisms underlying tooth formation in mouse molars, it has been difficult to confidently attribute these same mechanisms to the growth and development of primate teeth. While this partially reflects an inability to conduct experimental research on human and nonhuman primates, this issue has often been confounded by observations of final tooth forms that are limited to the outer enamel surface (OES). In part, this is because such studies are limited in their ability to determine the precise morphology and developmental origin of many dental crown structures. High-resolution imaging of the dentine surface (or enamel–dentine junction) has made it possible to study the primary developmental structures of tooth crowns in sufficient detail to extract novel morphological data that can be used to resolve some of these issues. The dentine surface preserves the morphology of the basement membrane of the developing tooth germ before mineralization,[18,19] and therefore represents the first stage of crown development in which many morphological features of the tooth crown appear. The value of the dentine surface for understanding the developmental basis of crown morphology has already been demonstrated by a number of previous studies.[16,18,20–27] Utilizing a vast database of micro-computed tomography scanned primate dentitions, we conduct qualitative observations of the dentine surface from a taxonomically broad sample of primate lower molars to assess the suitability of the current phylogenetic and developmental processes traditionally implicated as being responsible for tooth crown patterning. To what degree can diversity in primate tooth morphology be confidently attributed to phylogenetic inheritance? Are the current developmental models responsible for crown variation in nonprimate mammals also applicable to primate teeth, and can they explain all the types of variation present? From these extensive observations, and a review of the current anthropological and developmental literature, we address these concerns and introduce a new developmental framework for the holistic interpretation and application of tooth crown diversity in primates (Figure 1). Below, we introduce each component of the framework, including some previously unrecognized aspects of growth, and provide examples of how they manifest themselves in various primate dentitions and how each contributes to the ontogenetic process of tooth crown growth and patterning.

## 2 | CLADE AND TOOTH CLASS-SPECIFIC TOOTH FORM

The first component of the framework is the developmental mechanisms responsible for the clade-specific morphologies seen in the primate dentition. While clearly an important source of variation for the patterning of primate teeth itself, this combined package of genetic mechanisms establish the class-specific (e.g., incisors, canines, premolars, and molars), and clade-specific tooth shape that many of the other components of the framework are linked to. By

understanding the mechanisms responsible for dental variation at this genetic level, the timing of these events relative to the other components of the framework, and the perceived limitations or constraints of these processes, considerations of other elements of the framework can be made and deviations from expected morphologies appropriately considered.

Early theories for interpreting dental diversity and the underlying mechanisms involved in the development of specific tooth types focused on explaining the graded sequence of tooth shape in mammals. Based on early observed correlations between tooth position and shape across a wide range of mammals, Butler[28] proposed the "regional field" theory to explain the development of different tooth types along the dental axis. This theory suggested that all tooth primordia were initially equivalent and that tooth shape was controlled by varying gradients of signaling molecules along the first branchial arch. This model, therefore, suggested that tooth type was determined by extrinsic factors. Much later, Osborn[29] proposed the "dental clone" theory to explain serial differences in tooth patterning, suggesting that teeth develop from a single clone of cranial neural crest-derived mesenchymal cells. As these initial cells were nonequivalent for incisor, canine, and molar tooth categories, they were able to form these differently shaped dental series. Unlike the "regional field" model, the clone theory suggested that tooth type was intrinsically determined. More recent progress on the mechanisms responsible for tooth patterning at the genetic level has shown temporal and spatial patterns of region-specific gene expression in the branchial arch mesenchyme that appears to specify tooth type.[30,31] These genes are activated and inhibited by gradients of bone morphogenetic protein (BMP) and fibroblast growth factor signaling molecules along the anterioposterior axis of the epithelium. The expression of these genes in the neural crest-derived cells is thought to define different dental clone cell populations, which contribute to the formation of new group-specific tooth types.[32,33]

The implications of this for the dental morphologist are that we should expect to see, within a particular clade, similar crown morphology from one tooth to the next in the same regional zone, with the potential for slight variation as the developmental signal is passed along the tooth row. Importantly, when we observe significant deviations from the morphologies predicted by the field and clone theories, this allows us to either return to and perhaps challenge the suitability of these models for primate dentitions, or allows us to hypothesize how other developmental factors or components of the framework may interact with these basic morphologies to create the variation observed. For the sake of simplicity here, we focus on the four patterns of morphology seen in primate lower molars (Figure 2). While this clearly represents an incomplete representation of the diversity of basic crown morphology in primates, particularly when considering the variation in tooth form within the strepsirrhine clade, this does provide the basic expectation of tooth shape and patterning for each group that later components of the framework can interact with to create the variation we see in each taxon.
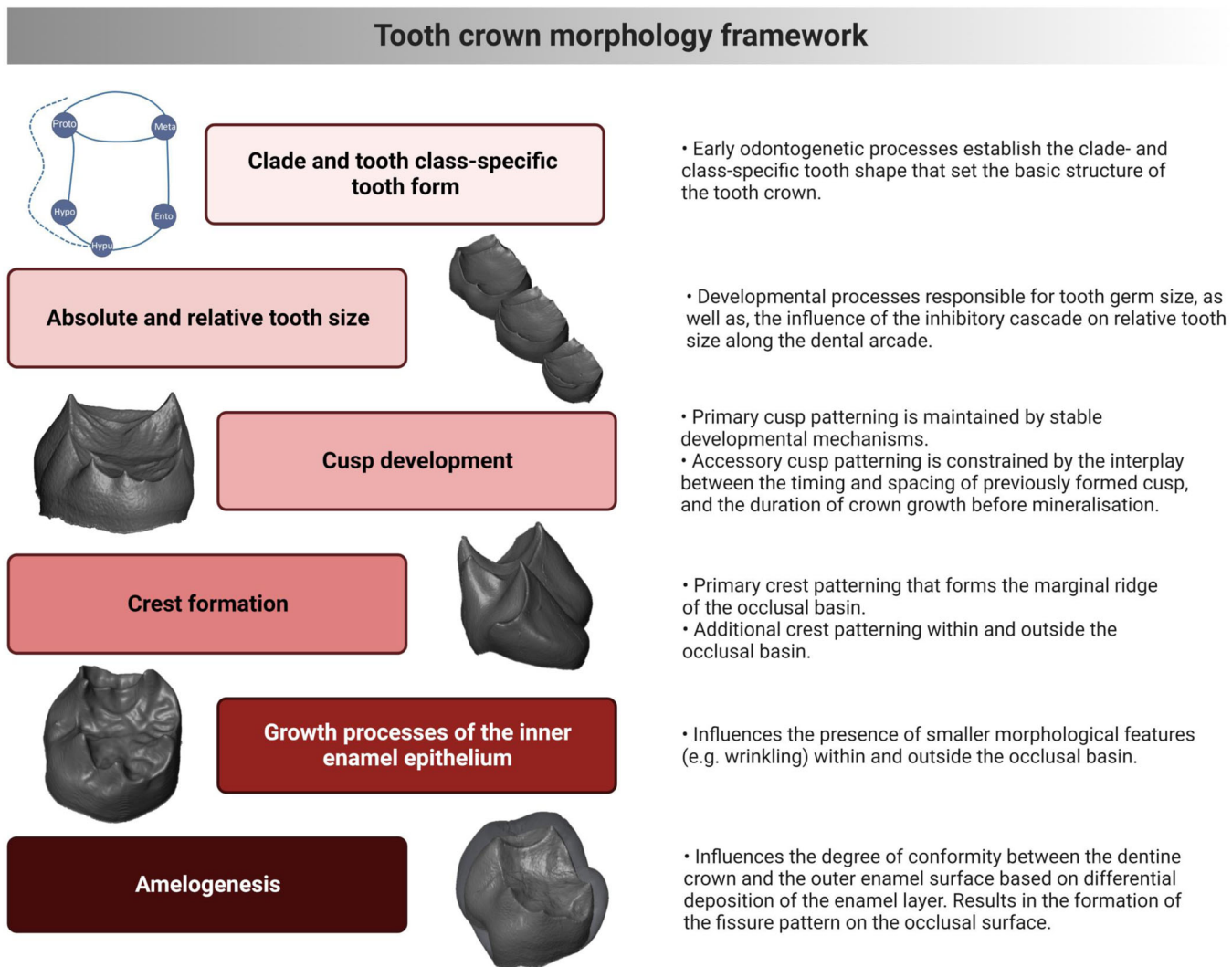
**Tooth crown morphology framework**

**Clade and tooth class-specific tooth form**

• Early odontogenetic processes establish the clade- and class-specific tooth shape that set the basic structure of the tooth crown.

**Absolute and relative tooth size**

• Developmental processes responsible for tooth germ size, as well as, the influence of the inhibitory cascade on relative tooth size along the dental arcade.

**Cusp development**

• Primary cusp patterning is maintained by stable developmental mechanisms.
• Accessory cusp patterning is constrained by the interplay between the timing and spacing of previously formed cusp, and the duration of crown growth before mineralisation.

**Crest formation**

• Primary crest patterning that forms the marginal ridge of the occlusal basin.
• Additional crest patterning within and outside the occlusal basin.

**Growth processes of the inner enamel epithelium**

• Influences the presence of smaller morphological features (e.g. wrinkling) within and outside the occlusal basin.

**Amelogenesis**

• Influences the degree of conformity between the dentine crown and the outer enamel surface based on differential deposition of the enamel layer. Results in the formation of the fissure pattern on the occlusal surface.

**FIGURE 1** Schematic diagram summarizing the main components of the proposed tooth crown morphology framework. Created with BioRender.com.

## 3 | ABSOLUTE AND RELATIVE TOOTH SIZE

The second component of the framework is tooth size. The overall size of the mammalian dentition is undoubtedly maintained by a relatively stable genetic/phylogenetic program. Numerous studies of nonhuman primate dentitions have yielded estimates of heritability and genetic pleiotropy for various odontometric variables,[34–38] as well as patterns of genetic integration between antimeres, isomers, metameres, and among tooth classes.[39,40] At the same time, developmental models have been proposed for how the modification of dynamic developmental pathways may have influenced the evolutionary trends in postcanine tooth size seen within the mammalian dentition. In 2007, Kavanagh, Evans, and Jernvall proposed an inhibitory cascade model of tooth development based on experimental studies of mouse molars in culture. During these experiments, they found that when mouse molars were isolated from their posterior tail in vitro, the rate of initiation of the

succeeding molars in the sequence was increased and resulted in larger teeth. From this, Kavanagh et al.[12] hypothesized that relative dental proportions in mammals are established by the net balance between the level of genetic activation signaling from the mesenchyme, and molar-derived inhibitory signaling from the previously formed tooth. A key feature of the inhibitory cascade is that the changes in these competing activator/inhibitor signals should be cumulative. The model, therefore, predicts that the size of the second molar should account for approximately one-third of the area of the molar row and that the size of the first and third molar should follow a predictable relationship that results in either a small-to-large gradient, large-to-small pattern, or a sequence of molars of equal size. Billet and Bardin[41] recently demonstrated in a large sample of placental species that the directionality of these molar size proportions covary with the absolute size of the molar field; large-sized species follow a small-to-large gradient from anterior to posterior, while small-sized species follow a large-to-small gradient from anterior to posterior.
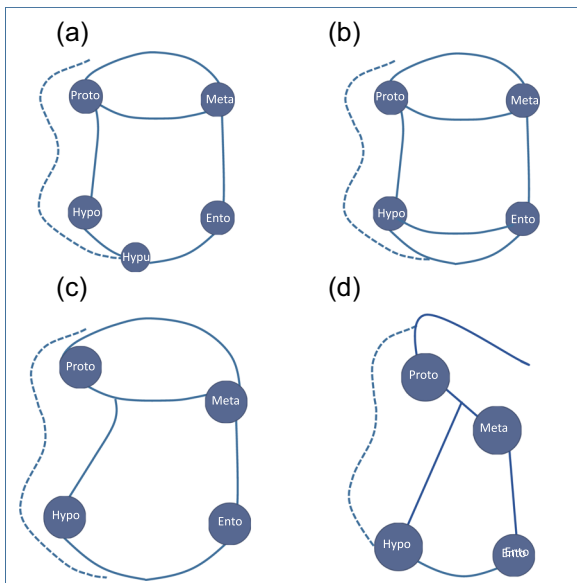
**FIGURE 2** The basic form of molar in each clade. (a) The Y-5 molar pattern of hominoids, (b) the bilophodont pattern of cercopithecoids, (c) the four-cusped pattern of platyrrhines, and (d) tribosphenic pattern of the strepsirrhines.



**FIGURE 3** Tooth size gradients in (a) *Macaca mulatta* specimen (M1 < M2 < M3) and (b) *Chiropotes satanas* specimen (M1 > M2 > M3). Both absolute and relative tooth size can interact with other components of the framework to influence tooth crown morphology. Images are not to scale.

In general, observations of relative molar proportions in mammalian tooth rows tend to match the predictions of the inhibitory cascade model. In an analysis of 35 mammals, including several marsupials and extinct taxa, the model matched the predictions for all but a few outliers.[42] These predictions have also been matched in a sample of Rodentia,[43] a sample of South American ungulates,[44] and a large sample of Mesozoic and Cenozoic mammaliaforms.[45] In primates specifically, studies show that most taxa conform to the inhibitory cascade model,[42,45] and demonstrate a linear change in size with tooth position. In platyrrhines, Bernal et al.[46] demonstrated that relative occlusal areas were not significantly different from the size gradients predicted by the model when phylogeny was taken into account, while Schoer and Wood[47] report similar findings among all but *Papio* from their cercopithecoid sample. Figure 3 provides examples of contrasting size gradients that are consistent with the inhibitory cascade in the lower molars of *Macaca mulatta* (cercopithecoid) and *Chiropotes satanas* (platyrrhine).

While observations of relative molar proportions in mammalian teeth tend to match the predictions of the inhibitory cascade model (ICM), it should be noted that some studies have reported strong deviations from the predictions of the model. For example, while Roseman and Delezene[48] found that molar proportions in a sample of anthropoid primates were generally consistent with the inhibitory cascade, their hominoid and cercopithecin samples showed a significant divergence from the predictions of the model. By considering deciduous premolars, however, Evans et al.[49] showed that hominoids do actually meet the expectations of the ICM. Bernal et al.[46] point out that while their platyrrhine molars were generally consistent with the model, it could not explain the loss of the third molar in callitrichines. Finally, studies have suggested that the
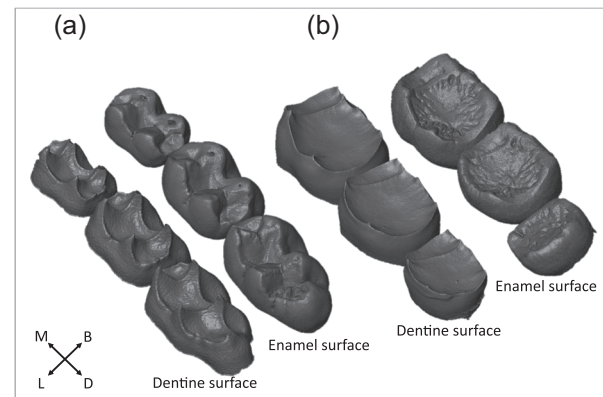
inhibitory cascade model may be limited in its ability to predict intraspecies molar size variation,[50] overpredicting aspects of within-species covariation by substantial margins.[51,52] Boughner et al.[53] also found no predictable patterns of molar size ratios among a sample of human molars. Ultimately, while the ICM likely represents a useful model for understanding molar proportions in mammals, it is important to acknowledge that other sources of variation may exist that allow selection to influence tooth size along the tooth row. For example, while Navarro and Maga[54] successfully mapped quantitative trait locus (QTL) in mice associated with the predictions of the ICM, another single QTL was found that only influenced the M3. Whether these specific deviations can commonly be explained by modifications in the ratios of activator/inhibitor signals at certain stages of growth, or represent a unique and independent contribution to molar size covariation, the ICM model appears to be relevant for the majority of studied mammalian groups and therefore is likely to be a fundamental developmental process in the development of primate dentitions. A more recent study has also demonstrated in a sample of extant euarchontans that molar complexity may also conform to the ICM, following a linear, morphogenetic gradient along the molar row.[55] As such, inclusion of these processes and concepts are a key component of the tooth crown morphology framework and the holistic description and interpretation of primate crown size and patterning.

## 4 | CUSP DEVELOPMENT

Much of what is known about the development of multicuspid teeth comes from research in experimental genetics, evolutionary morphology, and embryology, and has led to the development of models through which variability in tooth crown morphology can be interpreted. In particular, studies of developing murine teeth,[3,7,11,14,15] and computational modeling of mammalian tooth

germs,[7,8] have shown that the mechanisms responsible for the patterning of multicuspid tooth crowns involve the punctuated and iterative appearance of embryonic signaling centers known as enamel knots. These enamel knots are thought to be equivalent to the signaling centers responsible for the epithelial appendage patterning of scales, feathers, limb buds, and hair follicles.[56–58]

In these examples, pattern formation is regulated and controlled by the spatial distribution of the signaling centers, and a Turing-type reaction–diffusion system that involves the interaction between differentially diffusing activatory and inhibitory morphogens. While these signalling centres have been implicated in the control of cell proliferation and folding of the inner enamel epithelium, which determines the shape and size of the tooth, they also produce proteins that inhibit the formation of new enamel knots nearby, creating a temporospatial zone of inhibition. As such, new signalling centres can only form outside the zones of inhibition of previously formed enamel knots. The primary enamel knot appears in the tooth germ at the tip of the first cusp and induces the appearance of secondary enamel knots. These secondary enamel knots appear along the inner enamel epithelium at the sites of the future cusps and, in turn, influence the potential expression of further cusps through an interplay between the timing and spacing of enamel knot initiation, and the duration of growth before the late bell stage of odontogenesis where appositional growth begins. This morphodynamic iterative process, which has been called the PCM of cusp development, suggests that the patterning of cusps is not predetermined. Instead, the size, spacing, and timing of initiation of previously formed cusps influences the potential presence of later-forming cusps.

Originally, the PCM was used to examine variation in cusp number and patterning among Lake Ladoga ringed seals,[11] and as developmental programs associated with tooth formation are likely to have evolved early in mammalian evolutionary history, this model may also explain cusp patterning in other mammal clades. In primates, the vast majority of work has been conducted on hominid molars, and in general report findings consistent with predictions made by the PCM. In humans, Kondo and Townsend[59] and Harris[60] showed that the presence of an accessory cusp on the mesiolingual aspect of the upper molars was more likely to be present on larger molars, presumably due to the reduced spatial constraint of the secondary enamel knots. Similarly, studying the dentine surface of chimpanzee lower molars, Skinner and Gunz[61] report the presence of accessory cusps on the distal margin of the tooth crown that were generally consistent with PCM predictions. More recently, Ortiz et al.[62] conducted similar research at the dentine surface of 17 living and fossil hominoid species, and reported that most of the diversity in accessory cusp expression in this sample could be explained by the PCM. Monson[63] and Winchester[64] noted some discordance between certain aspects of their observed morphology and a PCM-predicted morphology in cercopithecine molars, but this has yet to be formally and extensively studied. Extensive research in other primate clades is currently lacking.

Figure 4 provides examples of accessory dentine horns at the dentine surface from a variety of primate taxa whose presence and size
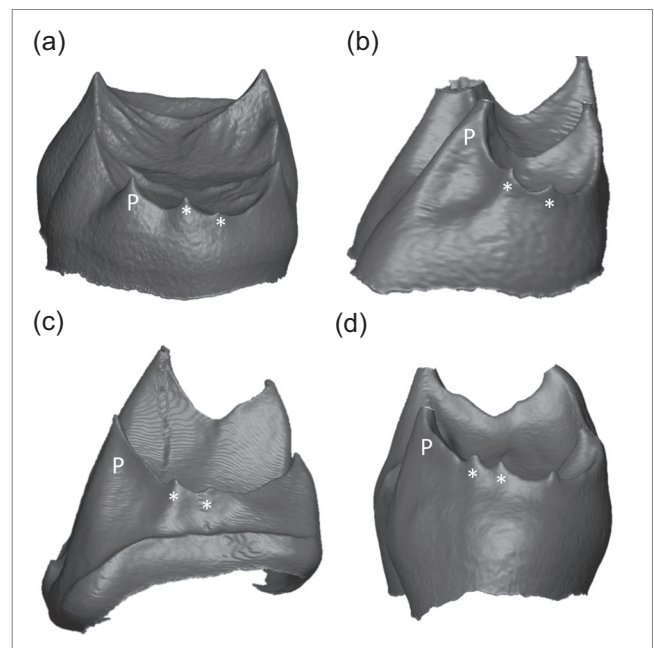


**FIGURE 4** Examples of accessory dentine horns at the enamel–dentine junction from a variety of primate taxa, whose presence and size are consistent with the iterative patterning inherent in the patterning cascade model. Accessory dentine horns (*) form in association with a primary dentine horn (P). All represent lower second molars. Distal view. Images are not to scale.

could be consistent with the iterative patterning inherent in the PCM. In these examples, the positioning of the taller accessory dentine horn tip corresponds to the location of a previously present enamel knot and subsequent temporospatial zone of inhibition. Due to the size of the cusp, and the relative position on the marginal ridge, this allows the initiation of a new enamel knot on the marginal ridge, and subsequent dentine horn. Despite these observations, support for the PCM explaining variation in accessory cusp presence in primates tends to continuously focus on particular regions of the tooth crown. For example, the distal marginal ridge of mandibular molars (i.e., the location of a cusp 6) or the mesiolingual corner of maxillary molars (i.e., the location of Carabelli's trait). Significantly less attention has been drawn to the *lack* of accessory cusp presence in other regions of the tooth crown. Recently, Bermudez de Castro et al.[65] demonstrated that while molar size decreases in *Homo sapiens* from anterior to posterior, the absolute and relative size of the protoconid (the first cusp to appear in the developmental sequence) increases from M1 to M3. They suggest that the comparatively large zones of inhibition associated with the protoconid on the M3 may be responsible for the common reduction or disappearance of the cusps of the talonid in humans.

While this study provides evidence in primates of how the components of the PCM may restrict or inhibit cusp formation, there are several examples of morphological patterns of expression where dentine horns are almost never observed. In 2008, Skinner et al.[16] described variations in the position of dentine horns on the distal and lingual ridge of extant and fossil hominoid molars, and identified

several distinct patterns of expression. On the distal margin, accessory dentine horns were found on the distal slope of the hypoconulid, the distal slope of the entoconid and/or in the fovea between the hypoconulid and entoconid. Similarly, on the lingual margin, Skinner et al.[16] report the variable presence of accessory dentine horns both within the fovea between the metaconid and entoconid, and on the distal slope of the metaconid. However, accessory dentine horns are rarely seen on the mesial and distal slopes of other primary dentine horns as might be predicted under the PCM. For example, from our observations, accessory dentine horns on the mesial slope of the entoconid, the mesial slope of the hypoconid, or the distal slope of the protoconid are extremely rare. These observations remain consistent across the primate taxa in our sample despite significant variations in the height, shape, and position of the relevant primary dentine horn, and overall tooth size.

More generally, based on the assumption that secondary enamel knot zones of inhibition are the only constraining factor in cusp formation, it should be expected that cusps would form in the wide occlusal space of the trigonid and talonid basins. However, cusps are almost never observed in these locations. Thus, there must be additional, currently unidentified, factors present in the developing tooth germ that influence where cusps (and particularly small accessory cusps) can form. We suggest that one of these factors is a developmental link between what manifests as the marginal ridge at the dentine surface and iteratively initiated enamel knots. While the marginal ridge of a tooth may display multiple closely spaced accessory cusps between two primary cusps, only a few observations of dentine horns within the occlusal basin have been made (and crucially these are often associated with abnormalities in crest patterning). Skinner et al.[16] suggest this could be related to a highly conserved pattern of expression of inhibitory proteins such as Sostdc1 (ectodin), which have been implicated in cusp patterning in mice.[15] Another influencing factor in accessory cusp expression that warrants further research relates to the shape of individual cusps. Evans et al.[66] recently proposed the "power cascade model" to explain the growth and shape of unicuspid teeth and individual cusps. As individual cusp shape varies significantly between primate groups, cusp shape may have some influence on the variable presence of accessory cusps in these taxa. A developmental link between cusps and crests (see also crest section below) also needs further testing in primates. It is crucial to acknowledge the hypothesized constraint on where cusps can form on the tooth crown when assessing cusp number variation linked to taxonomy, discrete dental trait variation (e.g., the concept of a "double" cusp six also discussed below), and patterns of cusp variation that could provide a functional advantage during mastication and confer fitness advantages.

## 5 | CREST FORMATION

While the mechanisms responsible for overall tooth shape and cusp formation have received considerable attention from developmental biologists and anthropologists, the mechanisms driving crest formation have received comparatively little attention. We expect that this has been due to a focus on the enamel surface, in which enamel deposition often removes or minimizes the expression of crests, and the associated difficulty in imaging the dentine surface, where crests are predominant. Current genetic research has implicated Ectodysplasin (Eda) signalling in the regulation of crests in mouse dentitions.[67] The vast majority of work from dental morphologists and anthropologists has focused on specific, prominent, and often unique crest morphologies in certain primate groups that were thought to convey phylogenetic information. This includes variation in the positioning and direction of the cristid obliqua in some platyrrhine and strepsirrhine clades,[68] the presence or absence of a lingual marginal ridge connecting the metaconid and entoconid in some strepsirrhine groups,[69] and the presence, expression, and variation seen in trigonid crest morphology in hominoids[68] and middle Pleistocene hominins.[70,71] Unfortunately, while these observations at the enamel surface have been useful in gathering a broad understanding of crest morphology in primates, they are limited in their ability to assess subtle morphological variation in these features and develop hypotheses on how developmental processes or patterns of covariation may also influence the expression of these features in some clades. Based on our examination of mandibular molar dentine surface morphology, we suggest that (1) primary crest patterning does not necessitate the presence of cusps and that (2) there is a meaningful developmental distinction between primary crests (those that form the marginal ridge of the crown) and additional crest patterning (those found within the occlusal basin or beyond the marginal ridge) during odontogenesis.

## 5.1 | Primary crest patterning does not necessitate the presence of cusps

Historically, the study of crests on molar crowns was based on observations at the enamel surface. In the case of thick-enameled primates, such as humans and all fossil hominins, the marginal ridge crest that runs between dentine horns is all but invisible. This has resulted in a focus on cusps and cusp patterning. Examination of the dentine surface reveals that in all primate clades, there is a primary pattern of crests on the molar crown (although it is of course, visible in the many thin-enameled primates). Our examination across a broad sample of primate taxa demonstrates that crest patterning may not require the presence of cusps, such that within a species there can be instances of primary crests that are (and are not) interrupted, or associated with a primary cusp. Figure 5 presents molar rows of a fossil *H. sapiens* individual (Sidi Abderrahman 2) and a *Cheirogaleus major* individual (MfN 35352). In humans, the first and second molars have entoconid dentine horns on the distolingual crest, while the third molar of this individual has the crest but no entoconid. Similarly, the *C. major* molars have a prominent marginal crest that circumscribes the crown, but no distal dentine horns. We suggest this is clear
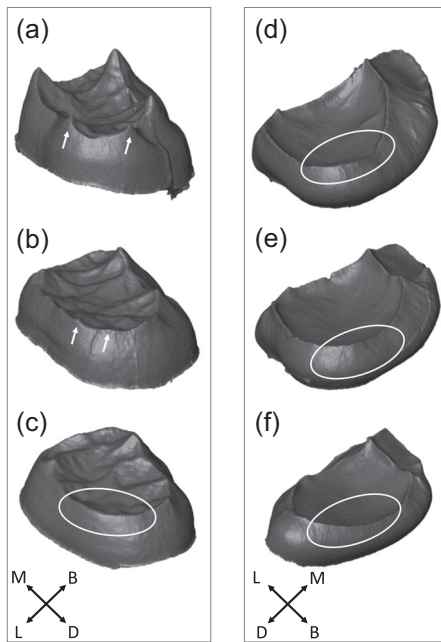
**FIGURE 5** First (top), second (middle), and third (bottom) molars of a fossil *Homo sapiens* individual (left) and a *Cheirogaleus major* individual (right). While some primary dentine horns are present, both specimens exhibit marginal crests (white circles) without a corresponding primary cusp (white arrows). This suggests that the processes of primary crest development may not necessitate the presence of cusps. Images are not to scale.

evidence that the processes of the primary crest and secondary enamel knot development are somewhat independent (acknowledging the constraint the former may have on the latter discussed above). This is a similar phenomenon to the expanded talonid on, for example, hominoid mandibular fourth premolars that present a prominent distal marginal ridge at the dentine surface but no distal dentine horns.

Marginal ridge crest formation in primate molars is, we suggest, an unrecognized, but important developmental process that can interact with other components of the framework to create variation in crown morphology. We find further evidence of this in the case of incompletely formed marginal crests (Figure 6). This concept would also be consistent with incompletely formed marginal ridges on mandibular premolars.[72] In addition to the marginal crests that circumscribe the crown, we also recognize the trigonid crest connecting the two mesial cusps as the result of the same primary crest patterning mechanism in most primate groups (see Section 8 for exceptions). As seen in the *Chiropotes* specimen in Figure 7, a prominent middle trigonid crest separates the trigonid and talonid basin despite the comparatively small size of the mesial dentine horns. We consider it extremely unlikely that such a well-pronounced ridge represents a passive structure produced simply by cusp-induced tensions of the epithelium. Furthermore, the trigonid crest of the *Chiropotes* specimen appears to join the buccal marginal ridge distal to the protoconid, further suggesting the independent nature of these features.
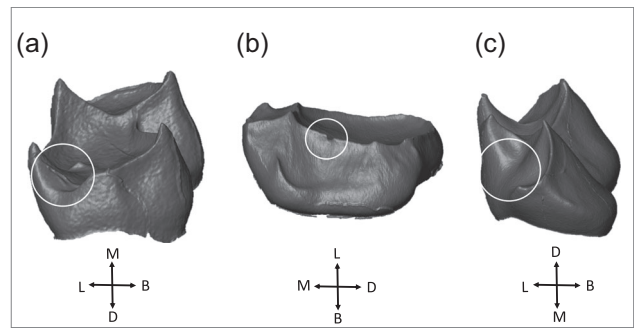


**FIGURE 6** Three examples (white circles) of incomplete crest patterning: (a) *Alouatta seniculus* on the distal marginal ridge, (b) *Chiropotes satanas* on the buccal marginal ridge, and (c) *Indri indri* on the mesial marginal ridge. These images suggest that crests between primary cusps do not simply behave as passive structures produced by cusp-induced tensions of the epithelium. Images are not to scale.
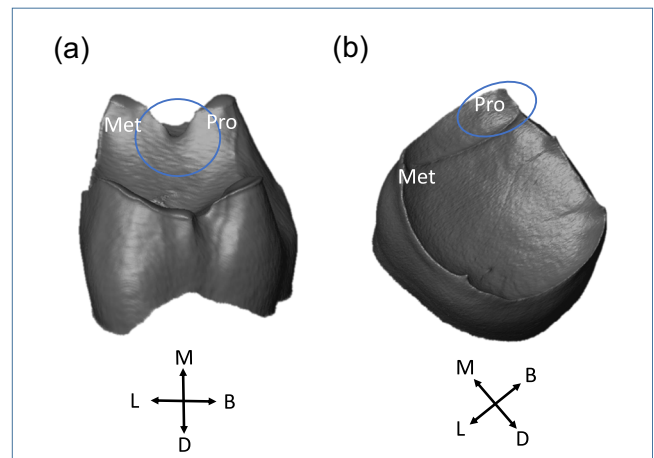


**FIGURE 7** Two examples (blue circles) suggesting that trigonid crest morphology is under a primary crest patterning mechanism that does not necessitate cusp presence. The trigonid crest of the *Callithrix jacchus* specimen (a) displays a discontinuous crest, while the *Chiropotes satanas* specimen (b) demonstrates the presence of a trigonid crest that appears independent of the protoconid (i.e., forming distal to the dentine horn). Met, metaconid; Pro, protoconid. Images are not to scale.

## 5.2 | Trigonid and talonid crest patterning in hominoids

While generally categorizing trigonid crest expression in primates to what we have termed "primary crest patterning," specific mention needs to be made of the variable expression of these features in hominoids. Unlike the stable expression of trigonid crests seen in the previous examples, extant hominoids such as *Pan*[16] and middle Pleistocene hominins[70,71,72] can exhibit complex and variable patterns of trigonid crest expression that have been discussed in relation to their potential taxonomic and phylogenetic significance. Some of these studies have established graded scales or typologies of observed variation to allow for the comparison of trait frequency

among groups. In some cases, these have resulted in the description of up to 14 different morphological crest variants in the mesial half of *Homo* mandibular molars.[71] These vary from well-pronounced and continuous single crests, to specimens with weakly pronounced, incomplete, and/or multiple ridge patterned morphologies. While some of these may represent "true" trigonid crests, we encourage the consideration of other developmental factors in the variable expression of these features. For example, in the trigonid crest variants presented, there was also significant variation in cusp arrangement, tooth size, and tooth shape within their sample. As we have discussed previously, cusp patterning and tooth size appear to have a significant influence on discrete dental trait expression, and we suggest the same for trigonid crest patterning in hominoids. Furthermore, it is also possible that some variants of this trait may represent or be further influenced by the growth processes of the inner enamel epithelium (IEE) discussed below. Importantly, however, these features appear to be highly variable and their taxonomic and phylogenetic and/or functional significance remains to be tested. We thus recommend exercising caution when using these features for phylogenetic analysis until an improved understanding of their developmental origin is discovered.

## 5.3 | Additional crest patterning

In addition to what we identify above as the primary crests that form the marginal ridge at the dentine surface, there are numerous examples of additional crests that develop inside, or outside, the occlusal basin. The most commonly cited example of these additional crests in primate dental morphology is the protostylid.[74–78] The protostylid has traditionally been viewed as an accessory cusp or crest on the buccal surface of the protoconid, and a remnant of the primitive buccal cingulum.[79] In Skinner et al.'s[80] analysis of protostylid expression in early hominin taxa, they expanded this definition to include the presence of crest features along the anterior, middle, and distal portion of the buccal face of the tooth, arguing that they appear to be the result of the same developmental process. In this study, we extend these observations to nonhominoid primate molars and report findings that agree with those of Skinner et al.[77] While in many strepsirrhine clades, a complete cingulum crest is observed along the buccal surface of the tooth, variably expressed and often incomplete crests were observed in several Old World and New World monkey taxa. Skinner et al.[80] suggested that the presence and expression of protostylid crests in hominoids is influenced by the size, shape, and spacing of the dentine horns, and the overall size of the tooth. Additionally, it is also possible that the size of the tooth germ, the slope of the cusp surface, and the direction of the dentine horn tip play a role in producing additional crest variation. Our observations of protostylid expression in nonhominoid primates are consistent with this suggestion, and thus we distinguish these features from the primary crest patterning discussed above. Unlike the developmental mechanisms responsible for primary crest patterning, additional crest formation appears to

reflect many of the same constraints as those imposed by secondary cusp development.

## 6 | GROWTH PROCESSES OF THE INNER ENAMEL EPITHELIUM

A final point of discussion regarding crown complexity at the dentine surface points to the phenomenon of wrinkling within the occlusal basin. Unlike the primary and additional crest patterning described in the previous sections, this form of occlusal complexity is exclusively found in extant and fossil hominoid molars, and varies significantly in presence and patterning both within and between species. Figure 8 demonstrates the presence of primary crests, additional crests, and growth processes of the inner enamel epithelium within several individuals. Currently, it is unknown what developmental processes are responsible for the phenomenon of wrinkling within the occlusal basin. Kraus and Oka[81] observed wrinkles on the dentine surface of fetal molars germs in a small sample of hominoids and suggested that they may result from rapid cell division in the inner enamel epithelium. Why rapid cell division would occur only in the occlusal basin and not on the outer surfaces of the crown is a problem worthy of consideration. It is also conceivable that the mineralization of enamel and dentine could influence the IEE and introduce the subtle wrinkling seen in some hominoid molars; however, this hypothesis may also struggle to account for the localization of wrinkling within the occlusal basin. Butler[82] suggested that ridges were "produced by tensions set up in the epithelium by the relative movement of cusps, owing to unequal growth or to changes in the shape of the follicle." While this theory may account for the localization of wrinkling within the occlusal basin, as tensions could only be established between cusps, it struggles to account for why this phenomenon is only observed in some hominoid molars and no other primate clades. While it is still unclear how these features occur, it is important to differentiate them from the primary and additional crest patterning discussed above.

## 7 | AMELOGENESIS

The majority of studies that have examined both the dentine surface and enamel crown of the same teeth have concluded that occlusal crown features at the OES are visible at the dentine surface,[18,20–24,27] and that the process of enamel deposition appears to only modify the expression of crown features, instead of eliminating or producing them.[16] In 2010, Skinner et al. identified several different patterns (similar to those first identified by Nager[18]) of contribution from dentine surface shape and enamel deposition to final external morphology. In the first pattern, enamel disposition did not appear to add or remove features observed at the dentine surface. Enamel deposition did, however, alter the surface slope of certain traits, creating broad convex cusps from much thinner dentine horns. In the second pattern, enamel deposition appeared to accentuate features
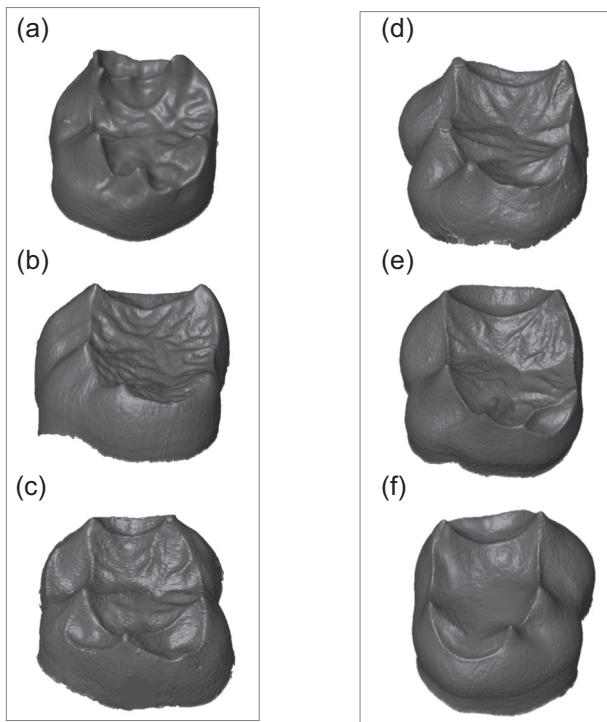
**FIGURE 8** Examples of occlusal basin wrinkling in hominoid molars. (a) *Homo neanderthalensis*, (b) *Pongo pygmaeus*, and (c) *Paranthropus robustus* specimens with complex patterns of occlusal wrinkling that are likely attributed to specific growth processes of the inner enamel epithelium. The *Pan troglodytes* specimens (c–e) demonstrate within-species variation present in occlusal wrinkling. Images are not to scale.

already present at the dentine surface, although new features were not observed along areas of the OES that corresponded with smooth, low-complexity locations of the dentine surface. The third pattern, initially reported in one *Chiropotes* specimen but since commonly observed in this study in several Pitheciidae species, demonstrated a crenulated OES that was independent of the comparatively smooth underlying dentine surface. Importantly, Skinner et al.[83] considered this third observation to represent a developmentally distinct process from the enamel contributions of the previous patterns.

More recently, Häkkinen et al.[84] explored the mechanisms that could be responsible for the uneven enamel distributions overlying smooth dentine surfaces. Using horizontal micro-CT sections of pig molar as the starting point of their simulations, Häkkinen et al.[84] modeled enamel matrix secretion on to reconstructed dentine surface outline as a diffusion-limited free boundary problem and as a simple geometric extrapolation. While the geometric extrapolation model assumes an excess availability of nutrients along the advancing ameloblast layer during the secretory stage of amelogenesis, a diffusion-limited secretion process model assumes an environment in which concave surfaces become increasingly exaggerated as these features extending into the nutrient-rich domain receive progressively more nutrients than the concavities. These simulations showed that diffusion-limited processes of matrix secretion accurately

predicted the enamel deposition patterns observed in real pig molars, successfully reproducing the thickened enamel observed above dentine surface ridges and the deep enamel fissures on the concave sides of the cusps. In contrast, these features were lost when enamel deposition was geometrically extrapolated. Importantly, similar results were also found when simulating enamel deposition in *Homo* and *Pongo* molars, and showed how subtle features present at the dentine surface in hominoids could translate into exaggerated forms at the OES. In relation to the crenulated enamel pattern observed in several *Pitheciidae* species, Häkkinen et al.[84] showed that reducing interfacial tension in their simulations increased small undulations in the ameloblast moving front, suggesting that lowered stiffness of the ameloblast layer may be responsible for the crenulated enamel seen in some taxa. While further research is needed to uncover the precise mechanisms responsible for producing crenulated enamel in certain primate taxa, the results of this simulation are consistent with previous suggestions that crenulated enamel is the result of a distinct developmental process (Figure 9).

Currently, the model of diffusion-limited enamel deposition proposed by Häkkinen et al.[84] represents the best mechanical explanation for how small features observed at the dentine surface in primates can transform into the altered, and often exaggerated, traits observed at the OES in primates. Collectively, both the observations made from this study and from computational modeling demonstrate that the OES is not simply an extrapolation of the dentine surface and that the process of amelogenesis can significantly enhance, and in rare cases introduce, variation in final tooth
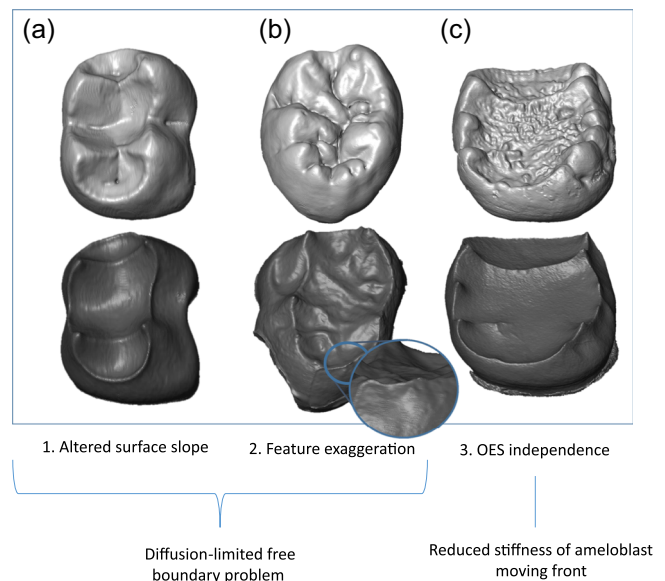


1. Altered surface slope     2. Feature exaggeration     3. OES independence

Diffusion-limited free boundary problem       Reduced stiffness of ameloblast moving front

**FIGURE 9** Examples of three patterns of outer enamel surface morphology that differ from the initial shape and patterning of the dentine crown. While variation between the dentine surface and outer enamel surface (OES) in the (a) *Cercopithecus mitis* and (b) *Paranthropus robustus* specimens can be attributed to a diffusion-limited free boundary mechanism, the (c) *Cacajao calvus* deposition pattern may be related to a reduced stiffness of the ameloblast moving front during amelogenesis. Images are not to scale.

form. This has important implications for the identification and scoring of discrete dental traits at the OES, and the homology of tooth crown features across primates. For example, our observations show that, in some cases, crest features present at the dentine surface may resemble cusp-like structures at the OES due to corresponding localized thickening of enamel above these crests.

While these studies further our understanding of the potential mechanisms responsible for morphological alterations and exaggerations of the dentine surface at the OES, one final observation that deserves discussion in this section is the presence of uneven enamel deposition and subsequent cuspal growth in the *absence* of a discernible corresponding dentine horn. As seen on the distal marginal ridge of the *Paranthropus robustus* specimen in Figure 9, cuspules may appear at the OES without an obvious corresponding dentine horn at the dentine surface that could account for the tubercles present at the enamel surface. Although it is possible that the scan resolution of these images may hinder the visualization of very small, but present, dentine horns in these examples, it is also worth considering whether other anatomical or developmental mechanisms may be responsible for this phenomenon. Studies examining the gross anatomy and microstructure of tooth enamel using scanning electron microscopy and histology have demonstrated numerous differences in the orientation of the enamel rods between the enamel deposited over the dentine horn and the surrounding cervical enamel.[85,86] Such variation suggests the potential for differences in localized ameloblast signalling, and as the enamel knot is the primary signalling centre of dental development, may indicate that ameloblasts over the location of previously formed enamel knots are receiving specific growth instructions relative to the surrounding tissue. If developmental mechanisms linked to enamel knot formation and apoptosis are responsible for subsequent variation in ameloblast behavior along the EDJ, it may be possible that they also have the potential to provide unique cuspal growth instructions that are capable of creating cuspules at the OES without a dentine component in the form of a horn. While this provides a tentative hypothesis for the presence of OES cuspules in these specimens, a further requirement of this suggestion would be evidence of a lack of IEE folding in the presence of an enamel knot. Although many of these suggestions remain to be tested, recognition of these features in some primate taxa does provide early insights into the complex relationship between enamel knot signalling and cusp expression in the primate dentition.

In summary, we are proposing this framework as a means to understand and interpret crown variation based on six components: clade-specific tooth form, relative tooth size, cusp patterning, crest patterning, growth processes of the IEE, and amelogenesis. Importantly, while the framework currently acknowledges the six components described, we consider it possible that an increased understanding of the processes responsible for tooth development may reveal factors that warrant the inclusion of additional components within the framework. Currently, however, we consider the components of the framework useful in understanding and describing the morphological diversity seen in primates. We suggest that adopting this framework is beneficial for the holistic interpretation of tooth crown morphology in studies of dental development, discrete trait analysis, odontometrics, and systematics. Furthermore, the framework contributes to a focus on understanding some of the developmental processes that natural selection can act upon to create the phenotypic variation seen in mammals.[87–89] In addition to discussions regarding the presence of morphological features at the crown surface, the current developmental hypotheses for their variable expression, and how these match with current observations at the dentine surface, the framework also formally acknowledges distinctive patterns of morphological *absence* in primates; the lack of morphological features where they should be expected based on the current theories of development. The tooth crown morphology framework has a number of implications for important aspects of dental morphology that are discussed below.

## 8 | DISCUSSION

### 8.1 | The tooth crown morphology framework and crown nomenclature

The tooth crown morphology framework contributes to an understanding of how phylogenetic and developmental mechanisms, and the interplay between these factors, contribute to tooth crown patterning in primates. Despite studies highlighting the important influence of signalling interactions and developmental processes on cusp expression, the presence and topography of primary cusps likely reflect a highly canalized process that carries a strong phylogenetic signal. Alternatively, growing evidence suggests that accessory cusp expression is based on a morphodynamic process related to the timing, spacing, and size of earlier forming cusps. Thus, it is unlikely that the expression of accessory cusps in primates relates to the phylogenetic inheritance and conservation of a specific ancestral gene coded for a particular cuspule. The relatively predictable presence and expression of accessory cusps in certain primate clades likely reflects the phylogenetic influence of some of the contributory factors responsible for accessory cusp expression (i.e., tooth size and primary cusp size and position relative to the overall tooth germ). As patterning of these genetically determined contributory factors is shared among closely related primate clades, they also then share similar constraints on accessory cusp formation, resulting in predictable trends of accessory cusp expression both within and between species.

Recognizing that accessory cusps may be of limited phylogenetic value raises important considerations regarding the suitability of the current nomenclature system used to identify these dental structures (including small crests). The most widely used and established system of nomenclature for studying mammalian molars was introduced by Cope[90] and Osborn,[91] and was based on interpretations of the origins of tritubercular mammalian molar patterns. This involved modeling the evolution of the mammalian dentition from a simple cone-shaped tooth, through the more complex forms that involved

the budding and rotation of several structures along the crown surface over time. Individual cusps and associated structures were thus named in this system based on their presumed origins and relations to the original primitive tooth cone. Unfortunately, despite being intended to denote evolutionary processes and historical homology, fundamental errors associated implicit in this terminology have since been recognized, resulting in what Hershkovitz[92] describes as the "corruption of dental evolutionary thought through the use of similar terms for non-homologous upper and lower dental elements, and dissimilar terms for the homologous element (s)." Despite the early realization of fundamental flaws in this system, the majority of these terms are still widely used today.

Other researchers have proposed alternative systems of nomenclature, such as those of Vandebroek[93] and Gregory.[94] The benefits associated with using these alternative terms may have related to a perceived better representation and the corresponding description of the feature in question, a perceived form of homology associated with that term, or represented an attempt to communicate a structure in a way that is free of any developmental implication. However, rarely are the systems of nomenclature from which they are borrowed used in their entirety, resulting in a mosaic, interchangeable, and highly inconsistent nomenclature. While we agree that the names for the primary cusps of mammalian molars are likely too entrenched in the discipline to change,[95] we suggest caution in naming accessory cusps and using them for systematics wherein there is an implicit assumption of homology between distantly related taxa. As Skinner and Gunz[61] and Davies et al.[96] have previously suggested, the commonly used terms "double C6" and "double C7" to describe the presence of two cusps on the distal or lingual marginal ridges of lower molars also appear to be invalid and misrepresent the developmental processes that underlie the formation of these cusps. That is, under an iterative pattern it is not correct to consider additional accessory dentine horns as being a "double" of the previously formed dentine horn (nb. we do acknowledge the formation of "twinned" dentine horns as noted by Martin et al.[17] whose etiology remains poorly understood).

While Skinner and Gunz[61] drew their conclusions from observations of hominoid molars (and specifically *Pan troglodytes*), we extend these concerns to several additional primate groups, and to other examples of "double" and "triple" cusp expression in the literature.[17,97] Of equal importance is the acknowledgment that in some primate clades, accessory cusps are extremely stable in their expression and thus appear developmentally distinct from cusps found in the same location of the crown in other primate groups. For example, while the majority of cusps found on the mesial marginal ridge of primate lower molars represent true accessory cusps (in that they are variable within species and reflect differences in primary cusp patterning and tooth germ size), the presence of a cusp mesial to the protoconid in Pitheciinae was consistently expressed in this clade in our sample. This may warrant the introduction of new terms for these features that distinguish them from traditional accessory cusps found in other taxa. Based on the current recommendations within this framework, Chapple and Skinner[98] have expanded on a

nomenclature by Davies et al.[96] that introduces cusps within a conservative, nonhomologous naming scheme that focuses on simple location-based categorizations, thereby avoiding some of the current issues relating to taxonomic and phylogenetic analysis. Overall, we believe the tooth crown morphology framework will continue to be ideally suited to readdressing the issues of nomenclature that are still present in the discipline.

## 8.2 | Discrete dental traits under the tooth crown morphology framework

Discrete dental trait analysis is a longstanding and useful tool for assessing evolutionary relationships among modern humans (Scott and Turner[99] and references therein), fossil hominins,[73,75–77,100,101] and living nonhuman primates.[102–104] Skinner et al.[16] previously highlighted the importance of using dentine surface morphology to elucidate developmental processes responsible for the presence and variable manifestation of dental traits. We would suggest that the framework proposed here is also crucial to properly defining discrete dental traits, creating appropriate scoring procedures, and using them in systematics. As noted previously, Skinner and Gunz[61] highlighted the likely link between the PCM and cusp 6 expression in chimpanzee and bonobo molars. Similarly, Skinner et al.[80] noted that variation in protostylid expression between *Australopithecus africanus* and *P. robustus* was related to (a) the relative placement of the protoconid (cusp patterning) and (b) the expression and location of buccal crests (crest patterning). Shovel-shaped incisors are clearly associated with variation in crest development, while the Carabelli's cusp trait appears to be linked to the placement of the protocone (cusp spacing) relative to the crown base (tooth size).

Importantly, while we aim to draw attention to the developmental factors responsible for discrete dental trait expression in primates, we are not suggesting that these features carry no heritable or genetic component, or are of no use for inferring genetic relatedness within or between closely related species. Numerous studies have successfully used discrete dental traits as a means of documenting biological relationships among human populations,[99,105,106] demonstrating some level of genetic influence in their expression. Rather than these features simply representing the phenotypic expression of a specific gene, however, it is likely that, for many dental traits, population trends may also reflect regional differences in cusp patterning and tooth size, which themselves carry some genetic component. As such, while some phylogenetic signal may still be present within each of those variables in some form, it may not be comparable to the development of a genetically programmed cusp. This is a challenging problem as each dental feature within each species and/or population may have a differing contribution of genetic and nongenetic factors responsible for its presence and expression. Ultimately, we emphasize that traits should be carefully considered within the components of this framework, and that

caution is advised when interpreting trait expression patterns at higher taxonomic levels. Acknowledging the developmental factors responsible for discrete dental trait expression will improve the identification and scoring of these features in many cases, while in others may inform their incorporation into future phylogenetic investigations.

## 8.3 | Relevance of the tooth crown morphology framework to other tooth types

While we have formulated and presented this framework with a focus on mandibular molars, we would suggest that it is also consistent with the developmental mechanisms responsible for all other tooth types of the primate dentition. For example, at the dentine surface, incisor morphology is created by a strong single crest and often a varying number of mamelons, which we would suggest are more accurately described as dentine horns or primary and secondary enamel knots. Canines tend to be formed by a large primary cusp with mesial and distal crests, although in some taxa (e.g., lemurs) they have been incorporated into the incisor row and are incisor-like in shape. Premolars are particularly relevant for evaluating the applicability of the framework as they can be both canine-like and molar-like in their morphology. Indeed, the phenotypic similarity between the premolars and molars of some primate clades suggests similarities in genetic control (perhaps due to overlapping/extending gradient fields in the dental arch) and thus similarities in the contributions of various components in the framework. Examples of this include transverse crests between mesial cusps of mandibular premolars that are likely developmentally similar to trigonid crests in mandibular molars, or distal accessory cusps on the talonid that are similar to distal dentine horns of mandibular molars. Additionally, evidence of integrative modules in dentitions of hominoids[107] and baboons[38] suggests links between premolar and molar development. It is appropriate to consider variations in the morphology of each tooth type and similarities in morphology between tooth types within the context of the framework we have outlined.

## 8.4 | Relevance of the tooth crown morphology framework beyond primates

It is worth considering the degree to which many (if not all) aspects of this framework are relevant to the study of nonprimate mammalian dentitions. Multicuspid teeth have evolved in many vertebrate species, the processes responsible for the development of tooth patterning appear to be highly conserved. For example, a defining feature of tooth crown patterning in mammalian dentitions appears to be the presence and expression of secondary enamel knots, and these molecular structures have been reported in mouse, vole, shrew, and ferret dentitions.[4,108–110] Perhaps, most significantly, however, observations of secondary enamel knots in a species of marsupial

(*Monodelphis domestica*)[111] suggest that all mammalian dentitions may share the same regulatory mechanisms. Furthermore, as previously discussed, the inhibitory cascade model has been generally supported in widely disparate phylogenetic clades, as well as a phylogenetically broad sample of extant and extinct mammals, suggesting that this developmental mechanism may have been established early in mammalian evolution. Importantly though, many of the studies that investigated the predictions of the PCM in tribosphenic molars also report that the model did not *consistently* explain accessory cusp expression in their entire sample, suggesting slightly different developmental pathways or additional unknown parameters in these taxa.[112] Whether these developmental deviations relate to the similar unknown factors responsible for unpredictable cusp expression in primate molars (and in particular the lack of accessory cusps surrounding the entoconid) remains to be determined.

## 8.5 | Spatial Constraints on the tooth germ

One developmental phenomenon that is not currently included in the framework is physical pressure that can be put on the developing tooth germ to influence its morphological development. It is possible that pressure could be applied by a number of anatomical structures such as large blood vessels, the cortical bone of the mandible or maxilla, or an adjacent developing tooth crown. Previous authors have hypothesized how the amount of available space in a jaw may contribute to increased tooth crown variability in third molars.[113,114] Skinner and Skinner[115] hypothesized that a defect on the maxillary lateral incisor of an orangutan was caused by direct contact, via a fenestration in the tooth crypt, with the maxillary central incisor. The much larger and more developmentally advanced central incisor creates an indentation on the lateral incisor crown and this close-packing of tooth germs could be caused by undergrowth of the face in orangutans. In 2017, Renvoisé et al.[116] demonstrated from both computational modeling and cultured tooth explants that cusp positioning in mouse and vole molars may be significantly dependent on the support of the developing jaw. The vole molars in culture, which would normally display an offset cusp pattern in vivo, lost their offset arrangement. Conversely, in the mouse molars, an unnatural cusp offset pattern was achieved in the cultured molars when attached with artificial lateral constraints[116] While these findings have yet to be tested in primate dentitions, these studies do point to the role of surrounding tissue in the regulation of tooth shape and patterning.

## 9 | CONCLUSION

From extensive qualitative observations from a broad sample of primate lower molars, we assessed developmental processes that underlie tooth crown patterning. In addition to currently recognized processes, we identify several additional aspects of dental tissue

development and discuss them within a tooth crown morphology framework. We recommend this framework be used to understand and interpret variations in primate tooth crown morphology. While the precise developmental mechanisms responsible for several components of the framework are still unknown, the acknowledgment of each component and their phylogenetic and developmental basis is crucial for the holistic interpretation of tooth crown morphology in future studies of dental development, discrete trait analysis, odontometrics, and systematics.

## DATA AVAILABILITY STATEMENT

Data are available on request from the authors.

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