Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Are talonids more evolvable than trigonids? Evidence from North American Paleogene primates

John P. Hunter^{1,*}, Naava Schottenstein² & Jukka Jernvall^{3,4}

- ¹⁾ Department of Evolution, Ecology and Organismal Biology, The Ohio State University at Newark, 1179 University Drive, Newark, OH 43055, USA (*corresponding author's e-mail: hunter.360@ osu.edu)
- ²⁾ Department of Biological and Physical Sciences, Columbus State Community College, 550 East Spring Street, Columbus, OH 43215, USA
- ³⁾ Institute of Biotechnology, P.O. Box 56, FI-00014 University of Helsinki, Finland
- ⁴⁾ Department of Geosciences and Geography, P.O. Box 64, FI-00014 University of Helsinki, Finland

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Upper molar crown types, characterized by the number, location, and shape of the main cusps alongside the presence and the orientation of cutting edges, facilitate rapid classification of basic morphotypes. This enables broad taxonomic and temporal sampling efficiently. Our research extends the application of crown types to lower molars and premolars of Paleogene primates in North America to categorize the variety of lower premolars and molars that arose among early primates and that likely played a key role in their diversification. We further took advantage of the natural division of lower cheek teeth into a higher (i.e., earlier developing) trigonid and a lower (i.e., later developing) talonid to test evolutionary hypotheses arising from differences in developmental timing. We tested whether the talonid evolved greater diversity in shape than the trigonid, and we assessed the relative contributions of the trigonid and the talonid to the temporal pattern of dental diversification in early primates. In our data, crown type richness generally varied with species sampling. Disparity measures, such as city block distance or total range, may be more independent of species richness, but values were also largely uniform through the p3-m2 series, showed little difference between trigonids and talonids, and were sensitive to the effects of an unusually diverse structure restricted to a single family (i.e., the multi-cusped, bladed premolars of carpolestid plesiadapiforms). Remaining comparisons therefore focused on diversity, rather than disparity of crown types. In p3, the number of talonid crown types outnumbered trigonid crown types by more than two to one. In p4–m2, the number of trigonid and talonid crown types are similar, but species distributions across crown types differed markedly. Species were distributed highly unevenly across trigonid crown type such that at each tooth locus one trigonid crown type tended to dominate whereas others were represented by just one or a few species. Species were somewhat more evenly distributed across talonid crown types. Temporal trends during the Paleogene primate radiation revealed that, overall, crown type richness paralleled species richness. However, separating the trends into

trigonid and talonid components revealed a distinct temporal difference between talonid and trigonid diversification. Initially, during a Paleocene phase of the radiation, talonid crown type richness exceeded trigonid crown type richness in p3 and p4, and peaked earlier than trigonid crown type richness in m1 and m2. Later, during the Eocene, trigonid crown type richness either met (p3) or somewhat exceeded (p4–m2) talonid crown type richness. Talonid evolution probably played a greater role than trigonid evolution during the Paleocene phase of the primate radiation, which occurred among plesiadapiform lineages starting from an ancestral condition with a much lower talonid than trigonid. Talonid and trigonid richness trends were more similar during the Eocene phase, which occurred among euprimate and some plesiadapiform lineages where the talonid approached the trigonid in height. This finding underscores the prominent role that highly variable structures play during the early phase of an adaptive radiation.

Introduction

"The point is that quite elementary statistical procedures, applied with imagination and understanding, will go a long way to solving many problems."

"We have many tools. Some of them are trendy just now; but we need them all. Flying altitude should be adapted to the problem at hand."

Kurtén (1988: xii)

Crown types then and now

Björn Kurtén did not invent crown types, but his pragmatic approach to solving scientific questions, sometimes relying on simple methods in preference to complicated ones, certainly inspired those who did. Crown types are a simple way to summarize the shape of mammalian teeth, originally upper molars, and are based on the number, placement, and shape of the main cusps and the cutting blades linking them. Crown types followed an even simpler morphotyping scheme based on the presence or absence of a single cusp, the hypocone, a feature that initially has a small impact on dietary ecology, allowing a greater variety of foods to be consumed, but eventually underlies the diversification of herbivorous groups of mammals (Hunter & Jernvall 1995). Jernvall (1995) first used crown types in a study of development and dental diversity in extant mammals, building a morphospace based on upper molar shape and inferring the effect of constraints, developmental and functional, in the pattern of its occupied and unoccupied regions. Jernvall *et al.* (1996, 2000) applied crown types to the problem of detecting trends in the morphological diversity and evolution of herbivorous mammals over the 66-million-year span of the Cenozoic Era. Jernvall and Wright (1998) used crown types in combination with endangerment status to predict the likely impact of future extinctions on the ecological diversity of primates. A variation on the crown typing approach focused on functional traits in the teeth of derived herbivores found strong associations of dental traits with climate and vegetation (Žliobaitė *et al.* 2016).

The crown typing approach, like any method, entails both advantages and disadvantages. The main strengths of crown typing lie in its simplicity and speed. Crown types are basic morphotypes that knowledgeable researchers can recognize in actual teeth and then classify those teeth rapidly. Crown typing requires no special equipment other than perhaps a hand lens or a stereomicroscope to view the very smallest teeth. Crown types are of course repeatable by the same or a different researcher and are therefore replicable. Crown typing does require some judgement to apply consistently. For novices undertaking a crown typing study of a novel group, Jernvall et al. (2000) provide the most detailed account of the method and offer much practical advice. One acknowledged feature of crown typing is that its resolution is coarse. Crown typing is not the tool of choice to detect subtle differences between teeth that are difficult to see visually and do not result in changes in the crown type variables. However, when teeth vary in the number and arrangement of cusps or crests, or when multiple

trophic levels are involved, then crown typing is an effective means to summarize variety across a group. We recommend that crown typing be included in every dental morphologist's toolkit. Jernvall *et al.* (2000) advised that crown typing should be done on actual specimens or high-resolution casts as opposed to 2D figures in published literature. This basic advice still applies, but advances in 3D scanning and computed tomography along with publicly available databases of 3D images of teeth have established a new potential resource for future crown typing studies (e.g., MorphoSource, www.morphosource.org).

One reason for undertaking this study was to reveal the broad pattern of morphological evolution in Paleogene North American primates. Comparable data sets of upper molar crown types at fine taxonomic resolution (i.e., at the species level) exist for extant primates globally (Jernvall & Wright 1998) and extinct condylarths, artiodactyls, and perissodactyls of the northern continents (Jernvall et al. 1996, 2000). An early dataset at a somewhat coarser taxonomic resolution (i.e., at the family level) consisting of upper molar crown types, body size, and crown height categories spans extant marsupial and placental mammals, including extant primates (Jernvall 1995). A distinct but related scheme based on features thought to reflect the durability, strength, or cutting ability of herbivore teeth as produced by wear, has been applied to a variety of derived herbivorous mammals including some primates (Žliobaitė et al. 2016). All these studies, however, focused on the upper molars. Because of our questions, see below, we extend crown types for the first time to lower cheek teeth, including premolars and molars.

We chose to focus on lower cheek teeth to utilize the natural division of lower cheek teeth into discrete parts, the trigonid located mesially and the talonid located distally. By treating the trigonid and talonid separately, we decrease the coarseness of the crown typing approach (i.e., we increase structural resolution) with the ability to specify where in the lower teeth — the trigonid, the talonid, or both — changes in morphology or morphological diversity occur. Functionally speaking, the trigonid and talonid overlap in their capabilities and contribution to breaking down food, especially in more derived forms (e.g., Kay 1975). However, in most mammals with tribosphenic dentitions or little derived from the tribosphenic condition, the talonid acts primarily as a crushing or grinding basin, forming a mortar-and-pestle arrangement with the upper molar protocone, whereas the trigonid supports the main shearing blades (Davis 2011 and references therein). These generalizations make it possible to infer likely functional associations, either causes or consequences, of observed evolutionary change in morphology or changes in morphological diversity based simply on which parts of the lower teeth are involved.

In addition, there are differences in developmental timing between the trigonid and talonid that may have long-term evolutionary implications. The talonid is lower than the trigonid ancestrally in tribosphenic dentitions, including in the teeth of many early primates. Because tooth crown shape becomes established from the top down during the ontogeny of a developing tooth, the relative height of cusps indicates the sequence in which they form, with the tallest cusps forming earlier and lower cusps later (Jernvall 1995). Later development, inferred from observed lower height, generally entails greater variability (Jernvall 2000, Hunter et al. 2010, Winchester 2016) and perhaps greater evolvability as well (Jernvall & Jung 2000, Harjunmaa et al. 2014, Ortiz et al. 2018, Selig 2024). When low cusps occur close to the base of the crown, they might not even form at all if they fail to initiate before crown morphogenesis ceases and root formation begins. Because natural selection requires heritable variation on which to operate and because there may be more such variation associated with the talonid than with the trigonid, then the long-term evolutionary potential of the talonid may be greater than that of the trigonid, for at least while the talonid is lower (i.e., develops later) than the trigonid. We predict that greater evolutionary potential of the talonid is manifest as greater morphological variety in the talonid over evolutionary history. Although this study focuses on primates, its specific results are generalizable across mammals that derive from an ancestry with tribosphenic teeth. In its most general principles, however, exploring the relationship between developmental variation and evolutionary diversity, its applicability may extend still further.

Why primates? A primer on Paleogene primates of North America

North American primates offer an opportunity to document evolutionary patterns and phenotypic diversity that is independent of the diversification of ungulates previously studied by Jernvall et al. (1996, 2000) using upper molar crown types. However, these radiations overlap in time and geography, and were likely subject to many of the same intrinsic and extrinsic influences (e.g., long-term climatic trends). North American primates include two main groups, the plesiadapiforms and the euprimates. Extensive diversification within plesiadapiforms, particularly in dental traits, underscores the broad range of dietary habits and ecological roles attained in the group (Szalay 1968, Rose 1981, Silcox et al. 2017). Plesiadapiforms were diverse in numbers of species and varied in morphology during the Paleocene and into the Eocene, occurring on all northern continents. Their dentitions include both inferred generalized and specialized forms, thought to be adapted to a range of diets ranging from insects to fruit and even sap (Russell 1964, Beard & Wang 1995, Silcox & Gunnell 2008, Silcox et al. 2017). In just one example, the bladed (i.e., plagiaulacoid) premolars of carpolestid plesiadapiforms likely served to concentrate occlusal stress during a slicing-crushing cycle, shattering hard, brittle food items such as nuts, seeds, and invertebrates (Biknevicius 1986). Because adaptations in the premolars seem just as conspicuous as in molars, and perhaps just as important, we further extended the crown typing approach to include premolars as well as molars.

The appearance of the first euprimates occurred close in time in North America, Europe, and Asia, coinciding with a major global warming event, the Paleocene–Eocene Thermal Maximum, 56 million years ago. The fossils of Eocene euprimates exhibit distinctive primate traits such as postorbital bars, nails on digits, and adaptations for arboreal locomotion (Rose 1995, Ni *et al.* 2013). Fossil euprimates, like plesiadapiforms, show a range of dental morphologies correlating with different dietary adaptations (Kay 1975, Lucas 2004, Boyer 2008). Taken together, Paleogene plesiadapiforms and euprimates con-

tribute significantly to our understanding of the phylogenetics, paleoenvironments, and biogeography of early primates. Their dental morphologies, which differ somewhat from those of extant primates, offer a rich record of evolutionary sequences, convergence, and parallelism in early primate evolution (Rasmussen 2007).

The Paleogene radiation of plesiadapiforms and euprimates in North America, where the record is most complete, offers some commonalities with the radiation of northern hemisphere ungulates over the same time frame (Jernvall et al. 1996, 2000). Both radiations involve the transition from faunivory to herbivory and probably involved a broad range of mixed diets bridging these extremes. Both radiations began with mammals possessing basically tribosphenic teeth. Both departed from the tribosphenic pattern with the convergent evolution of an upper molar hypocone with reduction and eventual loss of the lower molar paraconid (Hunter & Jernvall 1995). Both evolved a range of derived dental forms with the adoption of new herbivore diets. The major differences are in the specific groups involved (primates versus ungulates) and in locomotor adaptations. Paleogene primates were predominantly arboreal (Bloch & Boyer 2002, Chester et al. 2015), whereas Paleogene ungulates were largely terrestrial (Argot 2013, Gould & Rose 2014, Gould 2017). Differences between these groups in locomotor morphology suggest that Paleogene primates and contemporaneous ungulates probably spent time and foraged at different heights of vertically tiered forest communities, potentially lessening competition between members of the groups.

Materials and methods

Data collection

The data for North American Paleogene primate species were obtained from the Paleobiology Database (PBDB, https://paleobiodb.org/). The downloaded information included taxon name, family, and first and last appearance in the fossil record. Our study encompassed 13 primate families, 10 plesiadapiform and three euprimate (Table 1). The temporal scope of our samples extended from the Puercan to the Duchesnean North American land mammal ages. We studied temporal trends at the level of land mammal ages, which are variable in duration but average about 3 million years each. We categorized each species as present or absent in these respective time intervals.

Collection visits

To classify crown types, we visited several notable collections. Preference was given to fossil teeth over casts; however, we utilized casts in the absence of available fossils. The collections that we accessed were located at the National Museum of Natural History, the University of Michigan Museum of Paleontology, the University of Toronto, and Johns Hopkins University.

Methodology for crown typing

Our approach for crown typing of lower teeth was adapted from Jernvall *et al.* (1996, 2000) originally developed for upper molars. We selected teeth with minimal damage and wear to ensure accurate identification of landmarks. The focus was on the morphological types of lower third and fourth premolars and first and

second lower molars. We defined six variables to characterize the crown types, following the nomenclature of L00410 or S00100. The first letter represents cusp shape, which can be round (R), sharp (S), or lophed (L, indicating a bladelike shape), but S and L were combined before analysis to avoid redundancy on loph count variables. The subsequent three numbers correspond to the count of buccal, lingual, and central cusps, respectively. We introduced a variable for the number of central cusps to accommodate a centrally placed paraconid or hypoconulid if they occur. The final two numbers denote the number of longitudinal and transverse blades, either lophs or crests. We recorded crown types separately for complete teeth, trigonids, and talonids wherever it was possible to do so. This practice enabled us to include many incomplete specimens in which only the trigonid or the talonid remains

Results

Sampling, crown type and species richness, and disparity measures

The initial download from the PBDB included taxon records for 198 species of North American Paleogene primates (Table 1). We characterized

Higher taxon	Family	Number of species in	Number of species sampled sampled for crown types at each tooth locus				
		PBDB	p3	p4	m1	m2	
Plesiadapiformes	Carpolestidae	15	0	5	5	7	
•	Micromomyidae	10	2	2	2	2	
	Palaechthonidae	8	5	7	5	0	
	Paromomyidae	17	1	11	11	12	
	Picrodontidae	7	1	1	1	1	
	Plesiadapidae	19	8	9	8	13	
	Purgatoriidae	1	1	1	1	0	
	Saxonellidae	1	1	1	1	1	
	Picromomyidae	7	0	1	1	0	
	Microsyopidae	21	2	5	6	5	
Euprimates	Omomyidae	73	15	19	19	21	
	Notharctidae	20	9	11	12	13	
	Adapidae	2	0	1	1	1	
Total		198	45	74	73	76	

Table 1. Taxa included in this study. PBDB = Paleobiology Database (https://paleobiodb.org/).



Fig. 1. Number of crown types plotted against the number of species crown-typed for North American primate families at tooth loci p3–m2. Outliers that are less rich in crown types than expected are identified and indicated by arrows.

a subset of these species with crown types, with sampling ranging from 23% complete for p3 (45 out of 198 species) to 38% complete for m2 (76 out of 198 species). Sampling of p4 (74 out of 198 species) and m1 (73 out of 198 species) was similar at approximately 37% and only slightly lower than sampling of m2. However, we sampled all 13 families at least once for p4 and m1 crown types, but only 10 families each for p3 (all except Carpolestidae, Picromyidae, and Adapidae) and m2 (all except Palaeochthonidae, Purgatoriidae, and Picromyidae).

Crown type richness of families (Table 2) and the number of species crown-typed per family (Table 1) were positively associated with each other at all tooth loci p3–m2 (Fig. 1). Certain families were less rich in crown types than expected given the number of species sampled and represent outliers to the general positive trend. These were notharctids at p3 and p4, plesiadapids at

Tab	ble	2.	Num	ber	of	crown	types	per	family	/ at	р3-	-m2
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Higher taxon	Family	р3	p4	m1	m2
Plesiadapiformes	Carpolestidae	0	5	5	6
· · · · · · · · · · · ·	Micromomyidae	2	2	1	2
	Palaechthonidae	4	6	5	0
	Paromomyidae	1	5	6	5
	Picrodontidae	1	1	1	1
	Plesiadapidae	5	5	7	9
	Purgatoriidae	1	1	1	0
	Saxonellidae	1	1	1	1
	Picromomyidae	0	1	1	0
	Microsyopidae	2	5	4	4
Euprimates	Omomyidae	9	12	10	11
	Notharctidae	2	9	7	6
	Adapidae	0	1	1	1

p4 and m2, and paromomyids at m2. No outliers were apparent at m1. At the level of partial crown types of molars, there was a similar sampling effect as the number of talonid crown types was associated with the species richness sampled within each trigonid crown type (Fig. 2).

We applied two commonly used measures of disparity appropriate for count-based data, average city block distance and total range, to determine whether trigonids and talonids differed in disparity and whether there were trends through the cheek tooth row (Table 3). These disparity measures revealed only minor differences between trigonids and talonids of p3, m1, and m2. The exception was an anomalously high disparity among p4 trigonids in the sample, but this result was entirely due to the inclusion of carpolestids, which had a particularly diverse range in their bladed (plagiaulacoid) lower p4. Removing carpolestids reduced p4 trigonid disparity to levels comparable to that of the rest of the dentition. Similarly, there was little variation through the cheek tooth series, especially after we removed the carpolestids. Average city block distance was slightly lower at the extreme mesial (p3 trigonid) and distal (m2 talonid) ends of the series than in the middle of the series, total range at p3 was lower than at the other tooth loci, and trigonids slightly exceed talonids in both disparity measures at p4-m2. However, all differences were small.

Richness in crown types and evenness in species distribution among crown types

At p3, the number of talonid crown types was more than double the number of trigonid crown types (Table 4). At p4–m2, the number of trigonid and talonid crown types were more like each other, with trigonid crown type richness slightly exceeding talonid crown type richness by two or three crown types or about 10%. Species were not uniformly distributed across trigonid and talonid crown types. There were few common crown types at each locus known from three or more species, but there were many rare crown types known from just one or two species (Fig. 3 and Table 4). Further, species were highly unevenly distributed across trigonid crown types at



Fig. 2. Percentages of m1 and m2 talonid crown types plotted against number of species sampled within trigonid crown types; 10 and 8 single-species trigonid crown types were observed for m1 and m2, respectively (large dots).

p4–m2 such that one very common crown type dominates in number of species. Species were less unevenly distributed across talonid crown types at p4–m2.

Temporal trends

Because of a paucity of crown type data after the Uintan land mammal age, we restricted temporal trends to the Puercan (early Paleocene) through Uintan (middle Eocene) land mammal ages. Species and crown type richness at p4–m2 loci rose and fell together through the Paleogene, with peaks in the Tiffanian (late Paleocene) and Wasatchian (early Eocene) land mammal ages (Fig. 4). There was a parallel drop in species and

Table 3. Crown type disparity measures applied to trigonid and talonid crown types of p3–m2; asterisk (*) indicates removal of carpolestids.

Tooth locus	Part	Mean city block distance	Total range
р3	trigonid	2.0	4
	talonid	2.4	5
p4	trigonid	4.1	13
•	trigonid*	2.9	7
	talonid	2.7	6
m1	trigonid	3.0	8
	talonid	2.4	7
m2	trigonid	2.6	6
	talonid	2.3	7

crown type richness in the Clarkforkian (late Paleocene) land mammal age. Primate families tended to be either bottom-heavy with peaks in richness of both species and crown types during the Torrejonian (middle Paleocene) or Tiffanian, or top-heavy with a peak in richness in species and crown types during the Wasatchian or Bridgerian (early-to-middle Eocene; see Fig. 5). All bottom-heavy families were plesiadapiforms, whereas top-heavy families were euprimates and few plesiadapiform groups such as microsyopids. At p3, diversification in talonid crown types outstripped trigonid diversification early on. Greater richness in talonid crown types persisted through both the Torrejonian and Wasatchean peaks, only converging with trigonid richness in the Bridgerian. At p4, talonid diversification similarly outpaced trigonid diversification initially, but trigonid diversification exceeded talonid diversification somewhat by the Wasatchian. At m1, talonid diversification exceeded trigonid diversification until the Tiffanian after which trigonid diversification somewhat exceeded talonids. At m2, trigonid and talonid diversification was more evenly matched than at the other tooth loci, with talonid richness slightly exceeding trigonid richness in the Tiffanian and trigonid richness exceeding talonid richness in the Bridgerian. In all cases, talonid diversification either began earlier or outpaced trigonid diversification early on during the Paleocene phase, whereas trigonid diversification became more important during the Eocene phase.

Discussion

Crown typing of Paleogene primates is ongoing, and this contribution must be viewed as a

Table 4. Number of crown types, common crown types, and the number of species representing them. Common crown types are observed in more than just one or two species.

Tooth locus	Part	Number of crown types	Common crown types (in rank order)	Number of species
p3	Trigonid	4	S00100	33
	0		R00100	4
	Talonid	10	R00100	26
			R10000	6
p4	Trigonid	20	S00100	37
	-		S01100	4
	Talonid	18	R00100	19
			R11000	13
			R01100	5
			R11100	4
			S00100	3
			R10000	3
m1	Trigonid	16	R12000	36
	-		S12000	12
			R12010	3
			R11111	3
	Talonid	13	R11010	22
			R11110	18
			R11000	14
			R11100	13
m2	Trigonid	12	R12000	23
			R11000	8
			S12000	5
			R12010	4
			R11100	3
	Talonid	10	R11010	23
			R11000	20
			R11110	17
			R11100	16



Fig. 3. Species richness of trigonid and talonid crown types at p4–m2 in decreasing rank order, that is, the number of species is plotted against decreasing crown type rank order beginning with the most common crown types on the left and ending with the least common crown types on the right. For species richness and codes of the most common crown types *see* Table 4.



Fig. 4. Species richness and crown type richness at p4–m2 plotted against a time series of North American land mammal ages. Pu = Puercan, To = Torrejonian, Ti = Tiffanian, Cl = Clarkforkian, Wa = Wasatchian, Br = Bridgerian, Ui = Uintan.

preliminary report of a work-in-progress. Our sampling of known species of this group for crown types currently ranges from 23% to 38% complete depending on the tooth locus. Incomplete sampling at this stage may be at least partly due to incomplete preservation because p3–m2 are not uniformly preserved in all species. In addition, we have not yet accessed all collections of North American Paleogene primates. So far, we have assigned crown types only after exam-



Fig. 5. Crown type richness of six representative primate families p4–m2 plotted against time. Bottom-heavy families are on the left, and top-heavy families are on the right. All of the bottom-heavy families are plesiadapiforms, whereas top-heavy families include all the euprimates and some plesiadapiforms, for example, the microsyopids. For North American land mammal age abbreviations *see* Fig. 4 caption.

ining actual fossils or casts first-hand. Additional crown type assignments may be possible after examination of 3D images or even from the literature where it can be done unambiguously. For now, gaps persist in our data especially among the later Eocene (post-Uintan) primates.

Observed association between numbers of crown types and the number of species sampled within a family (Fig. 1) suggests that we are at the early stages of sampling morphological diversity of primates by this approach. By analogy to collector's curves in ecology, as sampling improves, one should see diversity increase rapidly at first, but then increase more slowly, eventually levelling off to approach an asymptotic limit represented by actual diversity. Because no levelling off is evident in the number of crown types at any of the tooth loci examined and only the slightest suggestion of a slowing down (Fig. 1), more sampling is needed to determine whether an asymptote is being approached. Alternatively, it is also possible that species richness and crown type richness overlap in information-content as they measure different aspects of the same biological quantity, the shape of teeth. Crown type richness explicitly arises out of variation in specific dental variables that we have chosen because of their structural, functional, and developmental significance. Species richness - especially when taxonomists diagnose species largely on dental characters and such is the case in Paleogene mammals generally - summarizes dental variation in ways that are useful for recognizing discrete species distinct from other species. Similarly, molar talonid crown type richness also increases with the species sampling of the trigonids associated with them (Fig. 2). If variation in talonid shape were completely reducible to variation in trigonid shape, then additional sampling of species within trigonid crown types would be unlikely to yield additional talonid crown types. In contrast, we found that talonid crown type richness varies directly with species-sampling within trigonids, suggesting that talonids vary in their own ways quite apart from variation among trigonids. This is basically also what experiments on developing mouse molars have shown; the later developing talonid shows much higher range of variation than the earlier developing trigonid (Harjunmaa et al. 2014). Yet, functional demands are likely to limit evolutionary variation of talonid (and trigonid) as the number of talonid crown types (Table 4) and their disparity (Table 3), though similar, can be lower than in the trigonid depending on the tooth locus.

For exploratory purposes, we calculated some disparity measures on trigonid and talonid crown types to gain perspective on the magnitude of differences between crown types beyond what simple counts can provide (Table 3). In general, differences in disparity between trigonid and talonid crown types are small, as are the differences along the cheek tooth series. The major exception to this general pattern is the great disparity among p4 trigonids, more than double the total range in crown type variables compared to other trigonids and talonids through the series. However, this pattern only holds when we include the carpolestids and disappears when we exclude them. Identifying interesting patterns of morphological diversification in one structure and restricted to a single taxonomic group might be an important new use for crown types and similar approaches in the future. This ability might be fruitfully employed, for example, to identify potential key innovations, especially unique ones as opposed to iterative ones that have evolved multiple times (Hunter & Jernvall 1995, Hunter 1998). Nevertheless, our current goals lie elsewhere. One potential pattern that may deserve further scrutiny is the slightly higher disparity observed in the middle of the p3–m2 series than at its mesial and distal ends (Table 3). For now, because trigonids and talonids at the same tooth loci do not differ greatly from each other in disparity in our sample of Paleogene primates, except for the carpolestid p4, we focus here on crown type richness and evenness in their species distribution.

Overall, talonids seem to be more diverse than trigonids but in different ways depending on the tooth locus. At p3, with only four trigonid crown types and 10 talonid crown types (Table 4), there is no question that p3 talonids are richer in crown types and more diverse than p3 trigonids. At p4-m2, the situation becomes less clear because the number of crown types is more similar between the trigonid and talonid, and trigonid crown type richness even exceeds talonid richness to a small degree (10%-20%). However, the distribution of species across trigonid crown types is best described as one of low evenness or high dominance with a highly uneven distribution of species across crown types and dominance by one crown type in the number of species. The distribution of species across talonid crown types at p4-m2, while far from uniform, is observably more even (with less dominance by one crown type) than across trigonid crown types (Fig. 3). In fact, the evenness observed in the distribution of species across talonid crown types is not dissimilar to the rank species-abundance profiles of modern ecological communities where both the richness and evenness components of diversity are relatively high (Magurran 1988). By analogy to the measurement of diversity in ecology, we see talonids in our sample as more diverse than trigonids at p4-m2 by virtue of the more even distribution of species across them despite similar levels of crown type richness.

Because species richness and crown type richness are associated in our data, it is unsurprising that these two estimates of diversity rise and fall together through the Paleogene primate radiation (Fig. 4). The appearance of two peaks one during the Tiffanian (late Paleocene) and



Fig. 6. Trigonid and talonid crown type richness plotted against time at p3–m2. For North American land mammal age abbreviations see Fig. 4 caption.

another during the Wasatchian (early Eocene) land mammal ages suggests the presence of two waves of diversification. The decline in diversity of species and crown types during the intervening Clarkforkian land mammal age (late Paleocene) may be at least partly artifactual as Clarkforkian is not as well sampled as either the Tiffanian or Wasatchian. Nevertheless, it is possible that at least some of the observed Clarkforkian decline in species and crown types is real, reflecting a transitional time after a decline of certain plesiadapiform families but before the radiation of euprimates (Fig. 5). A similar transitory dip in crown type richness occurs among nonlophodont ungulates (i.e., "condylarths") during the latest Paleocene (i.e., Clarkforkian) in North America (Jernvall et al. 2000: fig. 19.5) before the appearance of new lophodont crown types among ungulates (mainly among perissodactyls and artiodactyls) in the early Eocene. Because nonlophodont ungulates are likely to have overlapped contemporaneous primates in diet to some extent, at least more so than lophodont ungulates, it is tempting to speculate that both groups experienced simultaneous decline

for similar reasons. The overall trajectory of taxonomic and morphological diversification and decline in primates observed here (Fig. 4) generally parallels that of nonlophodont (Jernvall *et al.* 2000) or bunodont ungulates (Janis 2000) over the same time. This correspondence suggests that the two groups responded in similar ways to environmental pressures during the Paleogene, despite differences between the groups in locomotor adaptations and, likely, use of the forest canopy (primates) versus floor (ungulates).

Talonid and trigonid diversification patterns are different from each other, with talonid diversification being relatively more important early on during the Paleocene phase of the primate radiation (Fig. 6). Talonid diversification outpaces trigonid diversification in the premolars or precedes trigonid diversification in the case of the molars during the Paleocene phase. Trigonid diversification becomes more important during the Eocene phase eventually matching talonid diversification at p3 or surpassing it at p4–m2.

In these results, it is possible to see the effects of two interacting factors. First, we expect talonids to be more variable because of their later development, which is inferred from the lower height of the talonid cusps relative to trigonid cusps in combination with current understanding of dental morphogenesis. Second, there is an evolutionary trend through plesiadapiforms and early euprimates for the talonid to become higher, that is to develop earlier, reducing the height difference between the trigonid and the talonid. These trends culminate in derived primates with enlargement of upper molar hypocone, squaring of the upper teeth, reduction of the lower molar paraconid, and enlargement of matching upper and lower occlusal surfaces (Kay 1975). Ancestrally, the talonid of tribosphenic molars is relatively low on the tooth crown, and this condition has been inherited by the plesiadapiforms. Talonid evolutionary diversification appears to be most pronounced among these Paleocene plesiadapiforms, where the talonid was lowest and presumably developed latest. In the Eocene, especially among euprimates where the height difference between the trigonid and talonid is less, and the talonid began to develop soon after the trigonid, talonid evolutionary diversification is more modest. The talonid effect (high variation and evolutionary potential when it develops late) during the Paleocene phase is even more striking in premolars, in keeping with the extremely low talonids on premolars compared with molars.

Conclusions

Crown types are a simple approach for making a quick assessment of the shape of the major features of mammalian teeth. The method is not just for upper molars anymore, and it can be applied much more broadly than it has to date across teeth or perhaps even other structures and taxa. Crown types are amenable to studies of several different components of diversity from simple richness to disparity or differences in shape among crown types (less useful here as it turns out), to the evenness with which species are distributed across crown types (a novelty of this study). Coupled with a little "imagination and understanding" (Kurtén 1988) of how teeth function and develop, crown types become a powerful means to test hypotheses, including those

linking development with evolution such as the talonid effect tested here. Morphogenesis certainly constrains evolution but also provides the path by which meaningful evolutionary change occurs. We hope that our work will inspire further exploration of the interconnectedness of morphogenesis with morphological and ecological diversity realized over evolutionary time.

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