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Evidence of Dietary Differentiation Among Late Paleocene–Early Eocene Plesiadapids (Mammalia, Primates)

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ABSTRACT *Plesiadapis cookei* is an extinct relative of extant euarchontans (primates, dermopterans; scandentians), which lived in North America during the late Paleocene. *P. cookei* body mass has been estimated to be ~2.2 kg, making it large compared with other species of its genus from North America, but similar to some from Europe. In particular, size as well as dental form similarities to *P. russelli* have been noted. However, it is thought that *P. russelli* evolved from *P. tricuspidens*, and into *Platychoerops daubrei*. Dental similarities among *P. cookei*, *P. russelli*, and *P. daubrei* have been hypothesized to reflect a more folivorous diet than utilized by *P. tricuspidens*. Here we test the hypothesis that *P. cookei* is more dietarily specialized than *P. tricuspidens* by quantifying functionally significant aspects of molar, premolar, and incisor forms. Casts of M_2s and P_4s of *P. tricuspidens, P. cookei*, and *P. daubrei* were microCT-scanned. We measured the relief index and/or the complexity from surface reconstructions of scans. Results show that *P. cookei* has higher M_2 relief and complexity than *P. tricuspidens*; *P. daubrei* exhibits the highest relief and complexity. Similarly, *P. cookei* has a more complex P_4 than *P. tricuspidens*, whereas that of *P. daubrei* exhibits the highest complexity. Finally, the I^1 of *P. cookei* resembles more the incisor of *P. daubrei* than that of *P. tricuspidens*. Because high relief and complexity of dentitions are related to fibrous plant diets in living mammals, these findings support the hypothesis that previously identified similarities among *P. cookei*, *P. russelli* and *P. daubrei* reflect a folivorous diet. Am J Phys Anthropol 142:194–210, 2010. © 2009 Wiley-Liss, Inc.

Cheek teeth, typically the molars and premolars, of mammals represent an appropriate system to study in order to address questions of dietary ecology in extinct taxa because they have a limited number of functional demands. Cheek teeth are predominately used to chew and fragment food in preparation for swallowing and further digestion. Therefore, diversity in functional demands on molar teeth is roughly equivalent to diversity in material properties of different food items processed (e.g., Kay, 1975; Lucas, 2004), the jaw movements used to process those items (e.g., Butler, 1972; Kay and Hiemae, 1974), and possibly energy requirements or life history (e.g., Lanyon and Sanson, 1986; Lucas, 2004; Veiberg et al., 2007). Variance in cheek tooth morphology does appear to have a strong functional basis as demonstrated by countless studies of extant and fossil forms (e.g., Simpson, 1936; Szalay, 1968; Gingerich, 1974; Kay, 1975; Lucas, 1979; Strait, 1993; Evans and Sanson, 2003; Evans et al., 2007a; Boyer, 2008). This is in contrast to incisor teeth (e.g., Rose, 1981a; Cuozzo and Yamashita, 2006) or canines (e.g., Leutenegger and Kelly, 1977) [but see the study by Ungar (1994)], which may also have functional demands related to grooming and/or social displays.

Gingerich (1976) provided an example of how morphology of cheek teeth can contribute evidence for a detailed reconstruction of diet and evolutionary diet change in the fossil record. He showed that qualitative changes in upper fourth premolar (P^4) morphology were consistent with an hypothesized incremental transition from a generalized omnivorous diet to a specialized folivorous diet in a lineage of European fossil primate relatives (e.g., Bloch et al., 2007), going from late Paleocene *Plesiadapis tricuspidens* to earliest Eocene *P. russelli* to early Eocene *Platychoerops daubrei*.[1] Gingerich (1974, 1976) and other researchers (e.g., Jepsen, 1930; Russell et al., 1967) noted that the teeth of these taxa showed interspecific differences in the strength of development of enamel crests: in Gingerich's (1976) hypothesized lineage, the molar teeth exhibit a morphocline from bunodont (having blunt occlusal surfaces) in *P. tricuspidens* to a taller crown (due to pronounced crest development) in *P. daubrei*. Gingerich (1976) also described other points of incremental evolutionary morphological change in the incisors of this lineage in greater detail than had been

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[1] "… *P. russelli* … links *Platychoerops daubrei* directly to the ancestral species *Ples. tricuspidens*." (Gingerich, 1976, p 40).

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done previously, but such changes are less easily linked to specific dietary changes.

As a component of his study of plesiadapid dental evolution, Gingerich (1976) hypothesized that *P. cookei*, a late Paleocene plesiadapid from North America, was more specialized for a folivorous diet than earlier occurring *P. tricuspidens*, but less specialized than other later occurring *P. daubrei*. This is the major hypothesis we test in this study. He described its upper fourth premolar morphology as representing an intermediate stage in the dietary transition he hypothesized for the European species. Gingerich (1976) also stated that *P. cookei* is dentally very similar to *P. russelli*, and even used this similarity as evidence for temporal correlation between European and North American localities preserving these two taxa.[2]

Because Gingerich (1976) focused mainly on the dietary significance of P^4 and because the molar changes he cited have never been quantified, his hypotheses of a dietary transition in which *P. cookei* represents an intermediate stage (i.e., in which it is more folivorous than *P. tricuspidens*) are susceptible to refutation by studies of other aspects of the dentition and quantitative analysis of molar shape. Specifically, Gingerich's dietary and phylogenetic hypotheses generate the prediction that *P. cookei*, like *P. russelli,* should be distinct from *P. tricuspidens* in the direction of *P. daubrei* in quantifiable tooth features reflecting dietary preference [i.e., relative size of the molars in proportion to body size—greater in folivores (Kay, 1975); development of shearing area on the molars—greater in folivores (e.g., Kay, 1975); complexity of molar and premolar teeth—greater in folivores and fibrous food eaters (Evans et al. 2007a)]. *P. russelli* is currently known from only two I^1s, one I^2, P^3, P^4, P_3, and two fragmentary M_3s; thus, there is not enough of a sample to statistically test whether it meets these predictions. However, samples for *P. tricuspidens*, *P. cookei*, and *P. daubrei* are better represented and can be used to evaluate some of the predictions of Gingerich's hypothesis. In this study, we test the hypotheses of Gingerich (1974, 1976) using various quantitative features of lower molars and premolars, new samples of lower premolars, and caliper-measured quantifications of incisor shape.

Even using cheek teeth, the dietary ecology of extinct mammals can be difficult to reconstruct. Determination of the relative size of teeth in proportion to body size is rarely accessible in fossils because their anatomy is typically too incompletely known; such determination requires generating a meaningful quantification of skull, skeleton, or postcranial element (e.g., femur) size that can be contrasted with the teeth (e.g., Gingerich and Gunnell, 2005). Furthermore, phylogenetically based morphologic disparity often drastically separates fossils from living forms, obscuring any relationship between form and function. For example, a quantification of total tooth crown shearing area may accurately reflect the relative reliance on leaf matter, compared with fruits, tubers, or seeds in one group of mammals but not in another (see discussion in Boyer, 2008).

This study overcomes these difficulties of inferring relative tooth size and inferring aspects of tooth function from tooth form. First, because of an unusual abundance of craniodental material (for a Paleogene mammal taxon), the tooth size relative to skull and dentary size can be confidently determined for two of the plesiadapid species studied here (*P. tricuspidens* and *P. cookei*). Second, we quantify tooth shape using digital tooth models. This facilitates examination of the aspects of shape that reflect how well teeth can fracture foods with different material properties, somewhat independent of the presence of phylogenetically unique features such as particular cusps and crests. Occlusal relief (M'Kirera and Ungar, 2003; Boyer, 2008) and complexity (Evans et al., 2007a) of teeth and tooth rows are potentially independent, functionally informative aspects of tooth form. We use these variables as well as others to assess the presence of functionally significant differences in molar teeth of plesiadapids.

If plesiadapids shifted their ecological niche substantially near or across the Paleocene–Eocene boundary, it would be useful to document quantitatively because such a shift may reflect a response to climatic changes and other environmental changes occurring at this time (Gingerich, 1976; Maas et al., 1988; Zachos et al., 2001). A better understanding of the nature of changes in plesiadapids could help explain modifications in other components of late Paleocene and early Eocene faunas as well (Gingerich, 1989).

Institutional and specimen number abbreviations

AMNH, American Museum of Natural History, New York; MNHN, Muséum Nationale d'Histoire Naturelle, Paris; UM, University of Michigan Museum of Paleontology, Ann Arbor; USNM, United States National Museum of Natural History, Smithsonian, Washington D.C.; YPM-PU, Yale Peabody Museum–Princeton University collection, New Haven.

AL, catalogue number prefix indicating a specimen is part of the Lemoine's "Ageian" collection (Russell et al., 1967) now housed at the MNHN; Av, Avenay; Br, Berru; Cr, Cernay Les Reims.

MATERIALS AND METHODS

Specimens

This study examines cranial, mandibular, and dental material attributable to *P. tricuspidens* from the Berru locality near the village of Cernay Les Reims, France; *P. cookei* from various localities in northwestern Wyoming (United States), and *Platychoerops daubrei* from French localities of Mutigny and Avenay, as well as from Lemoine's "Ageian" collection from various deposits near Reims (Gingerich, 1976). Some isolated *Plesiadapis* teeth from Berru were lacking species identifications. Those analyzed here were identified as *P. tricuspidens* by having length and width dimensions in the range of those measured by Gingerich (1976, table A-16).

Cranial specimens examined include the following:

1. MNHN Cr 125 is the first known and most complete skull of *P. tricuspidens* (Russell, 1959, 1964; Gingerich, 1976) from Berru. It represents an older individual with heavily worn teeth.
2. The Pellouin skull of *P. tricuspidens* resides in the private Berru locality collection of M. Pellouin. It is preserved in a manner similar to MNHN Cr 125, but appears slightly younger. It is less complete than MNHN

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[2] "Moreover, in closely resembling the contemporaneous *Ples. cookei* from North America, the European *Ples. russelli* further demonstrates the very close relationship of the faunas of the two continents..." (Gingerich, 1976, p 40). New paleontologic and geochronologic evidence (Gradstein et al., 2004) now demonstrates that *P. cookei* is from older deposits than *P. russelli*.

Cr 125 in missing the nasal bones and premaxillae (Gingerich, 1975, 1976; MacPhee and Cartmill, 1986).

3. UM 87990 is a skull and skeleton of *P. cookei* from locality Sand Coulee-117 (sc-117) in the strata of the Willwood Formation, dated to the middle Clarkforkian (Cf) (late Paleocene biochron Cf-2) in the Clarks Fork Basin, Wyoming (Gingerich and Gunnell, 2005). The specimen has not yet been comprehensively described, but this work is in progress. Descriptions of cranial measurements are given in Table A1. Cranial measurements are given in Table A2.

Dentary specimens and measurements are given in Tables A3 and A4.

Tooth positions studied here include M_2, P_4, and I^1. All M_2 and P_4 exhibit minimal wear. Tables A5 and A6 list M_2 and P_4 specimens available for this study, along with various measurements and calculated variables discussed below. These fossils were converted to digital surface models using the methods described by Boyer (2008). Briefly, fossil teeth were molded using a President Jet Polyvinylsiloxane dispenser gun loaded with light body molding material. Casts were made from these molds using EPO-TEK 301 epoxy, colored with gray pigment. Casts were ground using a dremel tool until only the tooth of interest remained. M_2s and P_4s were mounted on 36-mm discs and microCT-scanned at 18 μm resolution using a Scanco Medical brand machine (model μCT 40) set to between 55 and 70 keV, and 145 and 114 μAmp.

Tooth scans were segmented using Scanco software and exported as DICOM image stacks. In the program Amira, tooth surface reconstructions were generated from DICOM image stacks of segmented tooth scans and were cropped in a standard way to eliminate surfaces that were not part of the tooth crown's enamel (e.g., tooth roots and dentary) as described and illustrated by Boyer (2008).

Table A7 is a list of *P. cookei* specimens that preserve P_4. Table A8 is a list of I^1s and various caliper measurements and indices. These metrics are described in Table A1.

Measurements and analysis

Data on skull size and dentary depth (as proxies for body size) were necessary to evaluate whether proportional differences in molar size exist among taxa and specimens sampled. Skull size in the available specimens was compared via 39 measurements of particular cranial bones (Fig. 1; Tables A1 and A2). These measurements were used in two different ways: 1) Overall skull size of *P. cookei* was expressed as the antilogged average of 39 natural log ratios of its cranial measurements to those of *P. tricuspidens*. In other words, its measurements are expressed as an average of 39 direct comparisons to measurements on *P. tricuspidens*. The overall skull size of *P. cookei* could then be given as a percentage of that of *P. tricuspidens.* 2) The geometric means of these 39 measurements for each specimen were also calculated and used to make a less direct comparison between the three fossil skulls.

Because of the small sample size of skulls (n = 1 for *P. cookei*), body size was also evaluated using dentary dorsoventral depth (DD) at M_2 (Fig. 1; Tables A3 and A4) following Gingerich (1976). Interspecific differences in natural log dentary depth were examined using Student's t-test and nonparametric Mann–Whitney U test. The program PAST was used for statistical analyses.

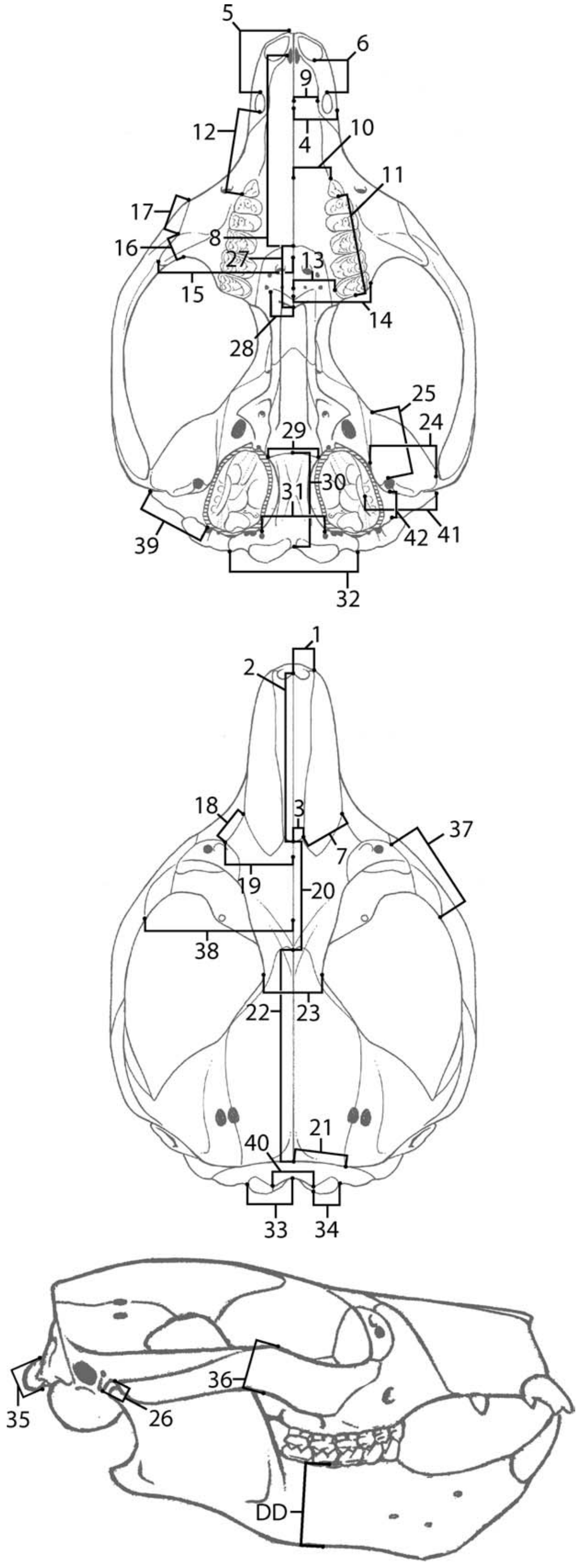


Fig. 1. Cranial measurements used to compare the size and shape of skulls of *Plesiadapis tricuspidens* (MNHN Cr 125, and the Pellouin skull) and *Plesiadapis cookei* (UM 87990). See Table A1 for description of numbered measurements. See Table A2 for values. See Table 1 for the results of proportional comparisons.

Three different dietarily relevant metrics were calculated from M_2 microCT scans and statistically compared between the three fossil species examined. Two of these metrics were also calculated on P_4s. Interspecific differences in these metrics were examined using ANOVA and nonparametric Kruskal–Wallis test, followed by post-hoc comparisons of species' means using Tukey's honestly significant differences (HSD) method and Bonferroni-corrected Mann–Whitney *U* test. The measurements are presented in Tables A5 and A6.

Metrics computed and compared include the following:

1. Two-dimensional M_2 and P_4 crown areas (*2da*) were calculated by exporting occlusal view silhouettes of surface scans from Amira to Sigma Scan Pro 5.0 and using area-measuring functions. These data were natural log transformed and compared between the three species to assess interspecific differences in tooth size.
2. *2da* and three-dimensional tooth crown surface area (*3da*) measurements from M_2s were used to calculate relief indices (RFIs) as described by Boyer (2008). Briefly, surface reconstructions of teeth were smoothed using 100 iterations and defaults (Lambda = 0.6) in Amira. Three-dimensional surface area of the tooth crown was then calculated using functions in Amira. RFI then equals the following:

   $$\mathrm{RFI} = \ln[(\sqrt{3da})/(\sqrt{2da})]$$

   Boyer (2008) has shown that, across prosimian primates and nonprimate euarchontans, taxa that eat more leaves and less fruit have M_2s with significantly greater relief than taxa with more generalized or frugivorous proclivities. Teeth with higher RFI in these comparisons can be qualitatively described as more "cresty," or more hypsodont.
3. The complexity of the occlusal surfaces of M_2 and P_4 were represented via a metric called an orientation patch count (OPC) (Evans et al., 2007a). Unsmoothed tooth scans saved as Amira ".surf" files were loaded into the program Surfer Manipulator (http://users.monash.edu.au/~arevans/software.html). Functions available in the "File Converter" window were used to remove undercuts from the tooth surface image (i.e., transform the surface from full 3D to 2.5-D) and to "blank" the image. Blanking refers to the process of removing any elevation data from outside the margins of the tooth. The teeth were then interpolated into ".grid" files. Using features available in the "Surfer Functions" window, grid files were replotted at a standard resolution of 50 rows of points from the mesial to the distal end of each tooth (Evans et al., 2007a; Zohdy et al., 2008). GIS tools available in the "CSV viewer" window of Surfer Manipulator were then used to break the surface into patches that face the same direction for eight cardinal directions (e.g., North, Northeast, East) The number of patches (consisting of 3 or more pixels) needed to represent each tooth was then counted; the resulting count for each specimen is its OPC. Evans et al. (2007a) have shown that rodents and carnivorans with similar diets are similar in OPC of the occlusal surface of the entire cheek tooth row, and that taxa with more folivorous, fibrous diets have more complex teeth (or a higher OPC).

Molarization of premolars represents another way of increasing complexity of the overall tooth row. Gingerich (1976) noted incipient molarization of P^4 in *P. cookei*, but described P_4 as simple, like that of *P. tricuspidens*. It seems surprising that the upper premolar would exhibit molarization without any changes in the corresponding mandibular tooth. Therefore, we surveyed the morphology of previously studied and newly recovered P_4 specimens of *P. cookei* from the YPM and UM and noted whether there was any molarization via development of a trigonid basin, or paraconid cusp (Table A7).

Finally, although previous authors have argued convincingly that *P. cookei* has an upper central incisor that is more simplified and more similar to that of *P. russelli* and *P. daubrei* than to that of *P. tricuspidens*, no attempt has ever been made to quantify these differences. Therefore, we took a series of six measurements to quantify the previously discussed qualitative differences between these taxa (Tables A1 and A8). Gingerich (1976) described the posterocone as relatively reduced in *P. cookei* and *P. daubrei* when compared with *P. tricuspidens*. We quantified posterocone projection relative to the area of the incisor crown base (Tables A1 and A8, index 1). Two other apparent differences that we quantified are the incisor crown girth (Tables A1 and A8, index 2) and incisor crown length (or occlusal projection; Tables A1 and A8, index 3) relative to the crown base. Finally, Gingerich (1976) provided drawings illustrating a reduction in the laterocone relative to the anterocone in *P. cookei* when compared with *P. tricuspidens*. We quantified laterocone prominence as the ratio of the distance between the tips of the anterocone and laterocone to the distance between the anterocone and posterocone (Tables A1 and A8, index 4). *P. daubrei* completely lacks an laterocone and cannot be represented using index 4. These metrics are compared using the statistical tests discussed earlier.

RESULTS

Skull and dentary size as reflectors of body size

Though it is clear that both *P. cookei* and *P. tricuspidens* were absolutely large among plesiadapids generally, the relative body size in these two species has remained ambiguous. A more precise quantification of relative body size is important because it will help reveal whether the molar teeth are of proportionally similar or different sizes. Data from previous studies revealed that *P. cookei* has molar teeth with occlusal areas that are 140% (M^1), 127% (M^2), and 119% (M^3) larger than those of *P. tricuspidens* [data from Gingerich (1976, table A-16) for *P. tricuspidens* and from Rose (1981b, table 14) for *P. cookei*]. These data lead to the hypothesis that *P. cookei* was a bigger animal than *P. tricuspidens* (Fleagle, 1999). However, side-by-side comparison of the UM 87990 cranium and MNHN Cr 125 (as well as the Pellouin skull) in dorsal or ventral view shows that the *P. tricuspidens* specimens dwarf *P. cookei*, the opposite of what tooth size differences would lead one to predict (see Fig. 2).

It is possible that MNHN Cr 125 represents an exceptionally large individual for its species, whereas UM 87990 represents an exceptionally small individual. However, the teeth preserved in the maxillae of these two specimens suggest against this possibility. The only teeth preserved in MNHN Cr 125 are M^3s. Measurements of this tooth position reveal that it is 4.17 mm in mesiodistal length, shorter than the average of 4.83 mm in the Br sample of *P. tricuspidens* M^3s measured by

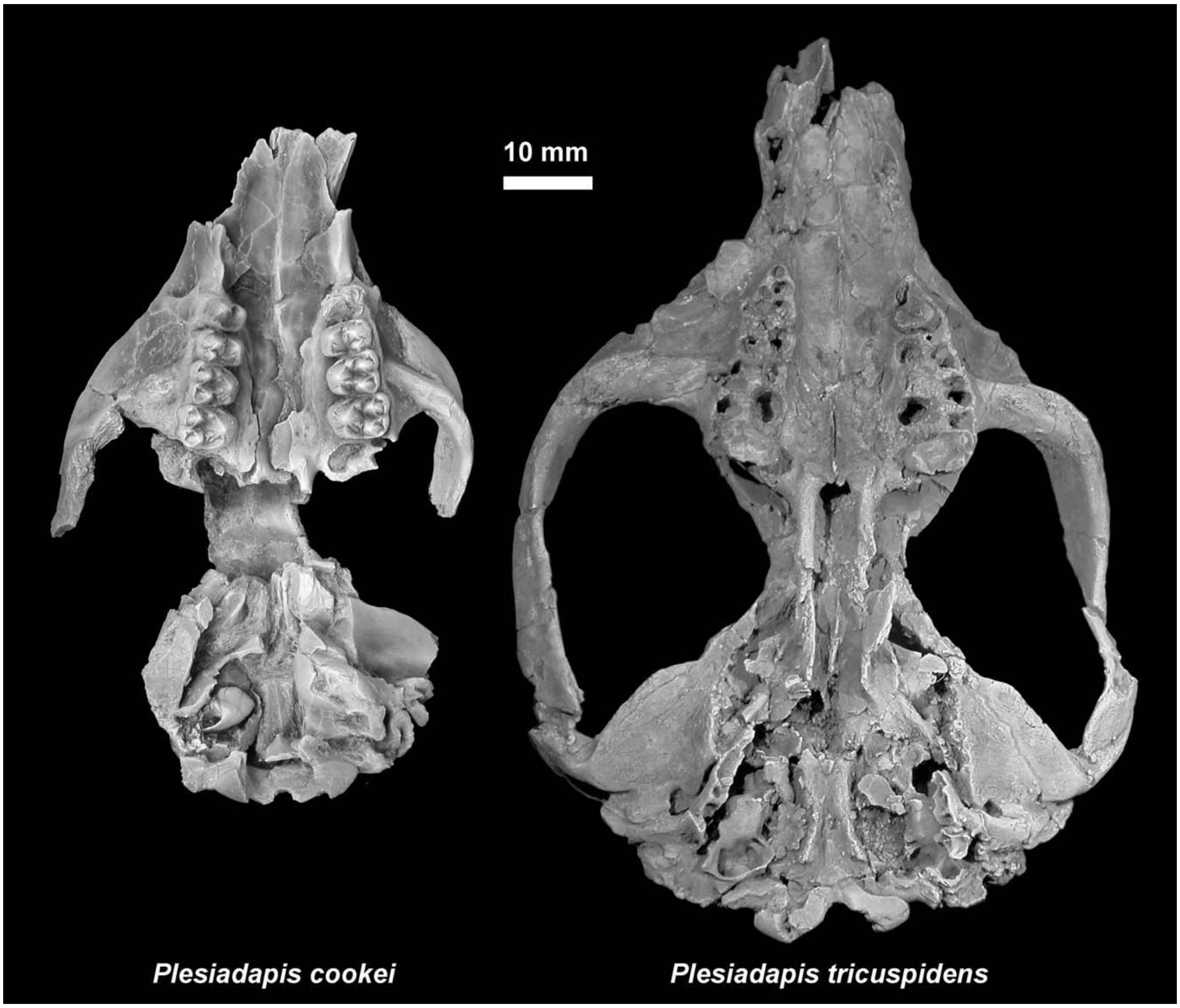


Fig. 2. Skulls of plesiadapids in ventral view at the same scale. *Plesiadapis cookei* (UM 87990) on left; *Plesiadapis tricuspidens* on right (MNHN Cr 125). The apparently drastic size difference between the two is mainly an artifact of different modes of brittle distortion. The geometric mean of 39 measurements of the cranium (see Fig. 1) is 10.7 for *P. cookei*, and 10.6 for *P. tricuspidens*.

Gingerich (1976, table A-16). Furthermore, the M^1 and M^2 of UM 87990 are 5.11 and 5.27 mm in length, respectively—much greater than the maximum of 4.70 and 5.10 mm measured by Gingerich (1976, table A-16) for these teeth in the sample of *P. tricuspidens*. Thus the teeth of these two individuals suggest the same pattern of size differences as locality samples of teeth.

Close inspection reveals that the contradiction between skulls and teeth is partly due to differential patterns of deformation among the different skulls. UM 87990 is compressed anteroposteriorly and mediolaterally, so that it is now smaller in these dimensions than it was in life, whereas the *P. tricuspidens* specimens are compressed dorsoventrally, so that they probably still retain their transverse plane dimensions. The deformation of these skulls appears to have been largely a brittle process. Therefore, the degree to which size differences have been accentuated is revealed by a series of 39 measurements on undeformed parts of individual cranial bones (Table 1; Fig. 1; Tables A1 and A2). This exercise shows that the skulls of *P. cookei* and *P. tricuspidens* are almost identical in the size of almost every feature measured except for the glenoid fossae, which are distinctly larger in the two *P. tricuspidens* specimens. Specifically, measurements from all regions of the *P. cookei* skull (UM 87990) are, on average, 99% the size of those of the skulls of *P. tricuspidens* (MNHN Cr 125 and the Pellouin skull). As discussed in the Methods section, the value “99%” is literally the antilogged average of 39 natural log ratios of *P. cookei* to *P. tricuspidens* cranial measurements. In other words, it is an average of 39 direct comparisons. A less direct comparison using a geometric mean of these 39 measurements yields a slightly different but comparable result. The geometric mean of the *P. cookei* measurements is 10.7, and that of MNHN Cr 125 is 10.6, suggesting that, instead, the *P. tricuspidens* skull is 99% the size of that of *P. cookei* (Table 2).

Unfortunately, no statistical significance can be assigned to results of skull comparisons as they involve

TABLE 1. Size comparison among plesiadapid skulls

(1) Reference specimen	(2) Comparison specimen	*N*	Mean ratio of (2):(1)	Cranial length est. for (1)
P. cookei UM 87990	*P. tricuspidens* A	39	1.005	105.8 mm[a]
P. tricuspidens B	*P. tricuspidens* A	30	0.995	106.9 mm[a]
P. tricuspidens A	*P. cookei* UM 87990	39	0.995	106.5 mm[b]
P. tricuspidens B	*P. cookei* UM 87990	30	0.994	106.3 mm[b]

est., estimate; *N*, number of measurements compared between two specimens; *P. tricuspidens* A, MNHN Cr 125; *P. tricuspidens* B, Pelluoin skull.

[a] Cranial estimates based on a measured length of 106.36 mm for MNHN Cr 125.

[b] Cranial estimates based on a estimated length of 105.83 mm for UM 87990.

TABLE 2. Summary measurements

Measurement	Taxon	*N*	*x*	*R*	SD	CV
Craniomandibular						
Skull geomean	*P. tricuspidens*	2	10.44	10.28–10.60	na	na
	P. cookei	1	10.71	na	na	na
	P. daubrei	na	na	na	na	na
Dentary depth	*P. tricuspidens*	37	15.89	12.35–20.32	1.97	12.00
	P. cookei	17	16.50	13.25–19.70	1.97	12.00
	P. daubrei	3	12.89	11.77–14.38	1.34	10.00
Second mandibular molar						
M_2 2da	*P. tricuspidens*	15	17.75	15.81–22.97	1.97	11.12
	P. cookei	20	29.32	23.38–34.53	3.16	10.77
	P. daubrei	9	19.76	15.57–22.74	2.29	11.58
M_2 3da	*P. tricuspidens*	15	44.13	38.66–59.73	5.48	12.15
	P. cookei	20	77.93	61.26–94.08	7.59	9.74
	P. daubrei	9	56.68	42.56–70.12	8.26	14.57
M_2 RFI	*P. tricuspidens*	15	0.47	0.40–0.50	0.02	na
	P. cookei	20	0.49	0.47–0.53	0.02	na
	P. daubrei	9	0.52	0.50–0.56	0.02	na
M_2 OPC	*P. tricuspidens*	15	56.52	45.13–66.6	6.51	11.52
	P. cookei	20	63.42	53.38–74.13	5.33	8.41
	P. daubrei	9	73.08	68.00–88.00	4.91	6.72
Fourth mandibular premolar						
P_4 2da	*P. tricuspidens*	5	11.10	10.09–12.08	0.92	8.29
	P. cookei	5	16.28	14.24–19.05	2.15	13.19
	P. daubrei	4	17.83	15.22–19.91	1.96	11.01
P_4 OPC	*P. tricuspidens*	5	30.15	23.13–34.75	4.82	16.00
	P. cookei	5	38.58	33.63–42.75	3.70	9.58
	P. daubrei	4	62.25	57.85–67.50	4.53	7.28
Premaxillary central incisor						
I^1 2da	*P. tricuspidens*	7	15.98	11.69–21.57	3.33	20.81
	P. cookei	6	29.09	26.50–32.53	2.92	10.04
	P. daubrei	5	25.59	19.00–30.15	4.27	16.67
I^1 index 1	*P. tricuspidens*	6	1.56	1.46–1.62	0.06	na
	P. cookei	6	1.41	1.26–1.52	0.10	na
	P. daubrei	5	1.17	1.11–1.23	0.05	na
I^1 index 2	*P. tricuspidens*	6	0.89	0.78–0.98	0.07	na
	P. cookei	7	1.04	0.94–1.14	0.06	na
	P. daubrei	5	1.02	0.95–1.07	0.04	na
I^1 index 3	*P. tricuspidens*	4	1.68	1.55–1.75	0.09	na
	P. cookei	4	2.07	1.83–2.33	0.20	na
	P. daubrei	5	1.95	1.81–2.06	0.09	na
I^1 index 4	*P. tricuspidens*	5	0.32	0.28–0.35	0.04	na
	P. cookei	4	0.25	0.24–0.27	0.02	na
	P. daubrei	na	na	na	na	na

N, sample size; *x*, mean; *R*, range; SD, standard deviation; CV, coefficient of variation; na, not available or not applicable.

just three specimens. Therefore, a comparison of 17 dentaries of *P. cookei* and 37 dentaries of *P. tricuspidens* was made (Table 2; Fig. 3). The two samples are not significantly different (*t*-test: $t = 1.08$, $P = 0.28$; Mann–Whitney $U = 272$, $P = 0.28$). On the other hand, three *P. daubrei* dentaries (not included in the statistical analysis because of small sample size) are smaller than the average of both *Plesiadapis* samples (Table 2; Fig. 3; Tables A3 and A4). Similarity in absolute sizes of the skulls and dentaries is taken as strong evidence that *P. cookei* and *P. tricuspidens* are of equivalent body size, despite differences in tooth sizes.

Molar size revisited

M_2 occlusal areas are summarized in Table 2: comparisons among species using Kruskal–Wallis test and ANOVA reconfirm the finding of previous authors that

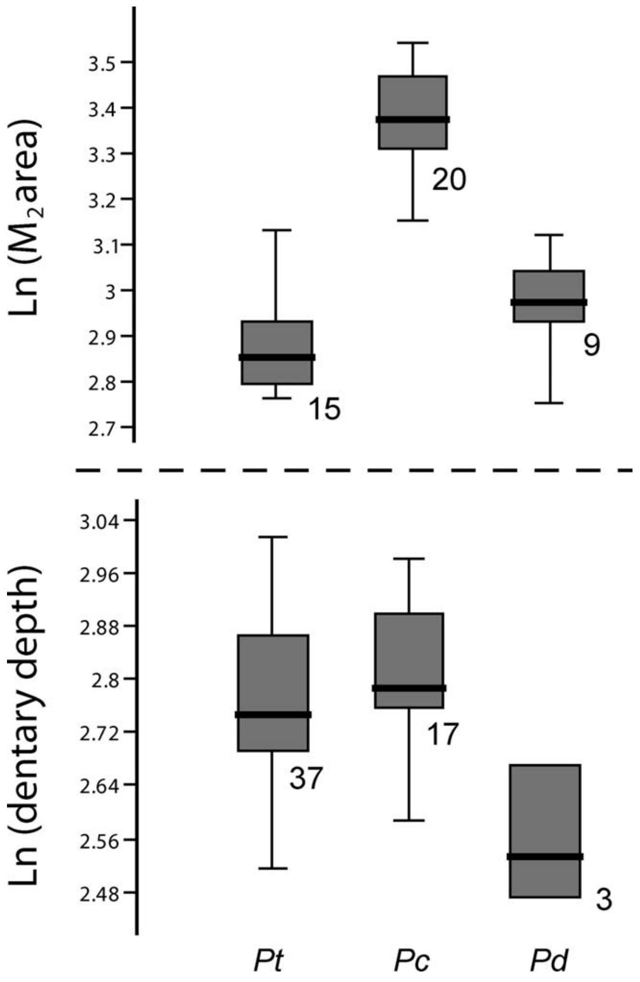


Fig. 3. Box plots of natural log dentary depth at level of M_2 (bottom) and M_2 *2da* (top). Heavy horizontal lines in boxes are positioned at median value. Boxes encompass 50% of data points; wiskers encompass 95%. Data points outside of the 95% brackets are shown as single point outliers. Numbers to the lower right of each box are sample sizes. Note that dentary sizes of *P. tricuspidens* and *P. cookei* are roughly the same, but *P. cookei* has significantly larger M_2 area. *P. daubrei* may have had a smaller dentary than *P. tricuspidens*, but it also has a larger M_2 area. Thus both *P. cookei* and *P. daubrei* appear to have larger M_2 areas for their dentary depth than *P. tricuspidens*. See Table 2 for measurement summaries and Table 3 for statistical tests. Taxon abbreviations: *Pc*, *Plesiadapis cookei*; *Pd*, *Platychoerops daubrei*; *Pt*, *Plesiadapis tricuspidens*.

different species analyzed here have significantly differently sized lower molar teeth (Table 3; Fig. 3). Furthermore, *P. cookei* has absolutely larger teeth than both *P. tricuspidens* and *P. daubrei* according to post-hoc, pairwise Mann–Whitney *U* and Tukey's HSD comparisons (Table 3; Fig. 3). However, *P. daubrei* has significantly larger teeth than the *P. tricuspidens* sample. The ratio of square root M_2 two-dimensional area (*2da*) to dentary depth (calculated from Table 2 means) is lower for *P. tricuspidens* at 0.26 and higher for *P. cookei* at 0.33. Gingerich (1976) measured more *P. daubrei* mandibles than were available for this study. Using his average value for dentary depth (15.00 mm) yields a ratio of 0.29. This indicates that *P. tricuspidens* has teeth that are proportionally smallest among the different species studied here, whereas *P. cookei* has the largest, and *P. daubrei* is intermediate.

The molars may also be compared with the premolars using the ratio of *2da* for P_4 to M_2 (as computed from means in Table 2). In *P. tricuspidens* the ratio is 0.68, whereas in *P. cookei* it is only 0.56 and in *P. daubrei* it is 0.91. However, because premolar size is not known to be correlated with body size, such a comparison does not reveal whether the molars are large relative to body size. It may, however, indicate the degree to which the premolars are important for processing food (see below).

Occlusal relief

The Kruskal–Wallis test and ANOVA comparing RFIs of a sample of M_2s of *P. cookei*, *P. tricuspidens*, and *P. daubrei* show significant among-taxon variance (Tables 2 and 3; Fig. 4). Furthermore, Mann–Whitney *U* test and Tukey's HSD pairwise comparisons show *P. cookei* to have significantly greater relief than *P. tricuspidens*, but significantly lower relief than *P. daubrei* (Table 3; Fig. 4). A detailed qualitative comparison of morphology in M_2s among the taxa reveals that the greater relief is likely accomplished by four features typically associated with greater reliance on leaves (Figs. 4 and 5). *P. cookei* has a more distolingually expanded entoconid, a more buccolingually expanded (or a more "open") trigonid, a higher trigonid relative to the talonid, and a more distolingually positioned metaconid (when compared with the protoconid). All of these differences should increase the shearing area present on *P. cookei* molars compared with those of *P. tricuspidens*. *P. daubrei* is more similar to *P. cookei*, differing even more drastically from *P. tricuspidens* in some of these same respects.

OPC (complexity)

As for RFI, Kruskal–Wallis test and ANOVA of OPC of M_2 reveal a significant added variance component among species groups (Tables 2 and 3; Fig. 4). Mann–Whitney *U* test and Tukey's HSD pairwise comparisons show *P. cookei* to have a significantly higher OPC than *P. tricuspidens*, but a significantly lower OPC than *P. daubrei* (Table 3; Fig. 4)

A similar pattern of results were obtained for OPC of P_4. One difference between the patterns is that, although still of intermediate complexity, the P_4 of *P. cookei* is much more similar to that of *P. tricuspidens* than to *P. daubrei*. A further difference is that pairwise comparisons of species groups with Mann–Whitney *U* tests using a Bonferroni-corrected critical value (following Kruskal–Wallis) fail to reveal significant differences (Table 3; Fig. 4B). The fact that *P. cookei* and *P. tricuspidens* differ at all is a surprising result given previous descriptions (e.g., Rose, 1981b). The explicit morphological explanation for these differences is given below.

Lower premolar molarization

Examination of *P. cookei* specimens housed at UM, YPM, and AMNH reveals that they have a more molarized P_4 than previously described, which is substantially more molariform than the condition seen in *P. tricuspidens* (Figs. 4 and 5). This explains the finding that *P. cookei* has a higher OPC than *P. tricuspidens*. Table A7 presents a qualitative scoring of P_4 morphology. Eleven out of 18 specimens examined have some development of

TABLE 3. Statistical tests

Metric	*N* (*Pt*, *Pc*, *Pd*)	Kruskal–Wallis and Bonferroni-corrected Mann–Whitney *U* *H*	Hc	*P*	*P* (*Pt* vs. *Pc*)	*P* (*Pt* vs. *Pd*)	*P* (*Pc* vs. *Pd*)
M_2 2da	(15, 20, 9)	33.32	33.36	$\ll 0.0001$	$\ll 0.0001$	0.120	$\ll 0.0001$
M_2 RFI	(15, 20, 9)	21.90	21.90	$\ll 0.0001$	0.020	0.0002	0.003
M_2 OPC	(15, 20, 9)	24.70	24.80	$\ll 0.0001$	0.010	0.0002	0.0004
P_4 2da	(5, 5, 4)	9.41	9.41	<0.01	0.04	0.06	1.00
P_4 OPC	(5, 5, 4)	10.52	10.52	<0.01	0.11	0.06	0.06
I^1 Index 1	(6, 6, 5)	13.35	13.36	0.001	0.04	0.02	0.02
I^1 Index 2	(6, 7, 5)	10.00	10.04	0.006	0.02	0.04	0.9
I^1 Index 3	(4, 4, 5)	8.50	8.50	0.01	0.09	0.06	0.8

Metric	*N* (*Pt*, *Pc*, *Pd*)	ANOVA and Tukey's HSD df	*F*	*P*	*Q*, *P* (*Pt* vs. *Pc*)	*Q*, *P* (*Pt* vs. *Pd*)	*Q*, *P* (*Pc* vs. *Pd*)
M_2 2da	(15, 20, 9)	2	102.50	$\ll 0.0001$	16.9, 0.0001	3.6, 0.041	13.3, 0.0001
M_2 RFI	(15, 20, 9)	2	21.30	$\ll 0.0001$	4.0, 0.020	10.0, 0.0001	6.0, 0.0005
M_2 OPC	(15, 20, 9)	2	23.70	$\ll 0.0001$	4.4, 0.009	10.5, 0.0001	6.1, 0.0004
P_4 2da	(5, 5, 4)	2	24.03	$\ll 0.0001$	7.4, 0.0008	9.1, 0.0003	1.7, 0.46
P_4 OPC	(5, 5, 4)	2	63.13	$\ll 0.0001$	4.2, 0.034	15.8, 0.0002	11.7, 0.0002

Pc, *Plesiadapis cookei*; *Pd*, *Platychoerops daubrei*; *Pt*, *Plesiadapis tricuspidens*; *H* and Hc, Kruskal–Wallis test chi-square statistics; *F*, ANOVA test statistic; *P*, probability of identity; *Q*, Tukey's HSD statistic. See Methods section and Table 1 for further description of measurements and statistical tests.

a trigonid basin on the mesial aspect of the protoconid. Six out of 18 have development of a paraconid. Most of the specimens with substantial development of a trigonid were not available to previous studies of *P. cookei* (Gingerich, 1976; Rose, 1981b).

Incisor form

Gingerich (1976) noted similarities between the upper incisors of *P. cookei*, *P. russelli*, and *P. daubrei*, to the exclusion of *P. tricuspidens*. His points are reiterated here: the posterocone is generally reduced in *P. cookei*, and the apical morphology is simplified compared with that of *P. tricuspidens*. *P. tricuspidens* has a large anterocone and laterocone and retains a distinctive mediocone and centroconule, whereas *P. cookei* typically has a reduced laterocone and lacks the mediocone and centroconule. The differences in prominence and/or presence of cusps on central upper incisors between *P. cookei* and *P. tricuspidens* are markedly evident in a qualitative side-by-side comparison of the two taxa (see Fig. 6). In the figure, the central incisors of these two taxa and *P. daubrei* are shown at the same scale. Despite the fact that the crown of I^1 is much larger in *P. cookei*, the anterocone, laterocone, and posterocone of this specimen are the same size or smaller than those in the otherwise much smaller specimen of a *P. tricuspidens* central incisor from Berru, France. The comparison can be followed to the incisor of *P. daubrei* which actually lacks the laterocone and has only a crest-like posterocone.

Shape indices of the incisors (Table 2; Fig. 7) exhibit significant variance among species (Table 3). Specifically, there is significant variance in posterocone projection, with *P. tricuspidens* having a proportionally larger posterocone than *P. cookei* and *P. daubrei* (Tables 2 and 3, index 1; Fig. 7). There is significant variance in the girth of the crown, with *P. tricuspidens* having a proportionally narrower crown than *P. cookei* and *P. daubrei* (Tables 2 and 3, index 2; Fig. 7). There is significant variance in the proportional length, or occlusal projection, of the crown, with *P. tricuspidens* having a proportionally shorter crown than *P. cookei* and *P. daubrei* (Tables 2 and 3, index 3; Fig. 7). However, small sample sizes render Bonferroni-corrected pairwise Mann–Whitney *U* comparisons nonsignificant for index 3. Finally, the proportional distance between the anterocone and laterocone (index 4) is significantly greater in *P. tricuspidens* than *P. cookei* (*t*-test: $t = -3.55$, $P = 0.01$; Mann–Whitney $U = 0$, $P = 0.02$). *P. daubrei* completely lacks an laterocone (e.g., Gingerich, 1976).

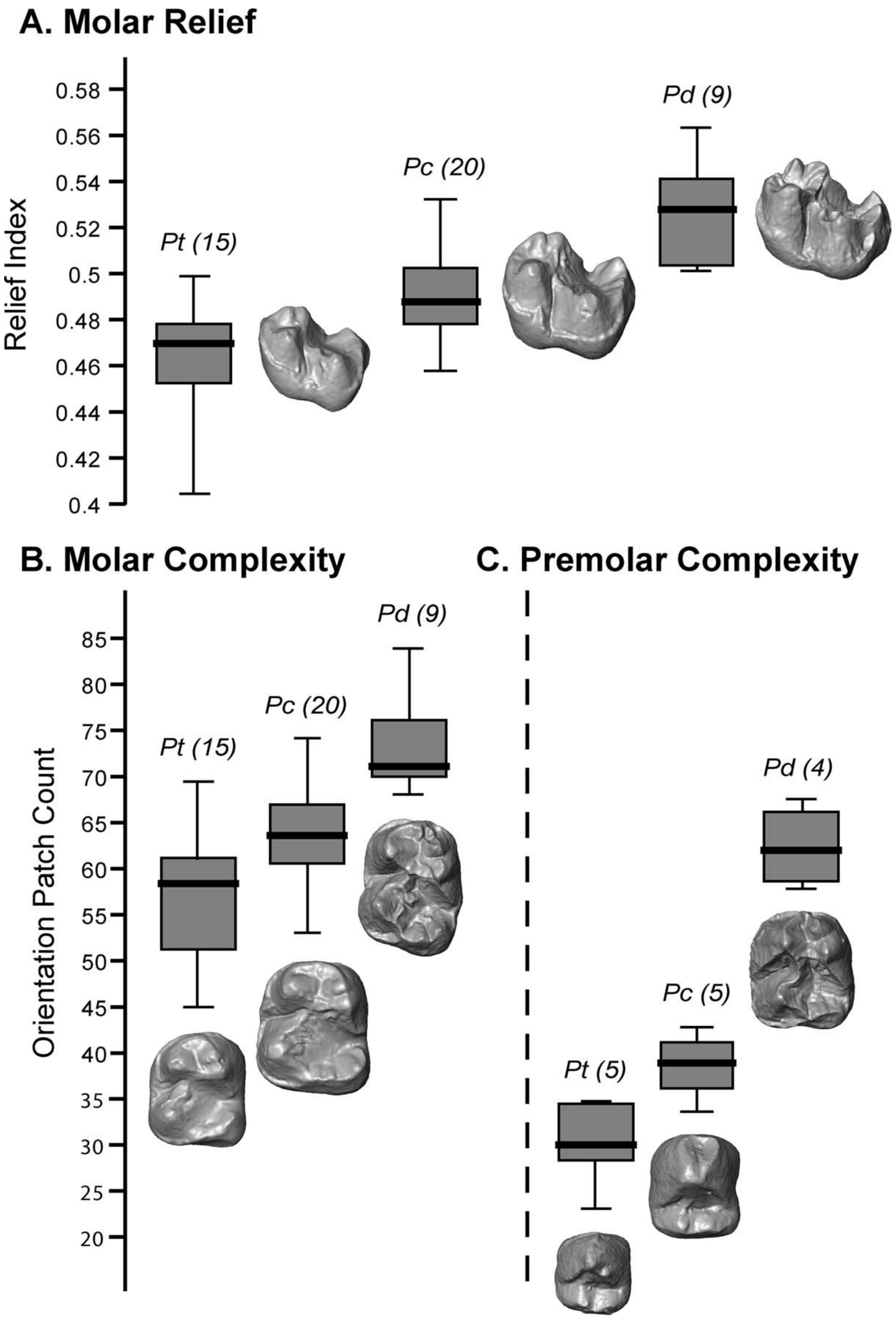
DISCUSSION

Ecological significance of molar size

The fact that the skull and dentaries of *P. tricuspidens* and *P. cookei* are not significantly different in absolute dimensions has implications for the observation that the M_2 and other molars of *P. cookei* are significantly larger than those of *P. tricuspidens*. It means that the dentition of *P. cookei* is probably larger relative to body size. Because proportionally larger teeth distinguish extant primate folivores from more omnivorous and frugivorous primates (Kay, 1975), the demonstration of larger teeth in *P. cookei* (and probably *P. daubrei* as well) supports Gingerich's (1976) hypothesis that it had a more specialized folivorous diet than *P. tricuspidens*.

Ecological significance of molar surface shape

Occlusal relief (RFI) and complexity (OPC) of the M_2 distinguish the three species analyzed here, with *P. tricuspidens* being lower than *P. cookei*, which in turn is lower than *P. daubrei*. Previous studies have shown these metrics to differentiate (even distantly related) taxa by dietary preference (M'Kirera and Ungar, 2003; Evans et al., 2007a; Boyer, 2008) and that high values of both RFI and OPC strongly correlate with a fibrous and structural carbohydrate-dominated diet. These results therefore support the hypothesis that *P. cookei* is more folivorous than *P. tricuspidens*.


A. Molar Relief

B. Molar Complexity

C. Premolar Complexity

Fig. 4. Relief index in plesiadapid M$_2$s (**A**), orientation patch count in plesiadapid M$_2$s (**B**), and in P$_4$s (**C**). These values were calculated from the digital surface models of teeth. See Figure 3 for description of box plots and taxon abbreviations. Numbers in parentheses following taxon abbreviations are sample sizes. All taxa are significantly different for each set of comparisons (Table 3). In (A), an example of a digital model for each taxon is given in oblique buccal view to give a sense of differences in cusp and crest relief. In (B) and (C), a digital model is shown in occlusal view to give a sense of differences in complexity of this surface among taxa. Lower values of *P. tricuspidens* are consistent with the hypothesis of Gingerich (1974, 1976) that it is an omnivore. The high values of *P. daubrei* are consistent with the hypothesis that it is a committed folivore. The intermediate values of *P. cookei* are consistent with the hypothesis that it is more specialized toward folivory than *P. tricuspidens*, but more generalized than *P. daubrei* (Russell et al., 1967; Gingerich, 1976).

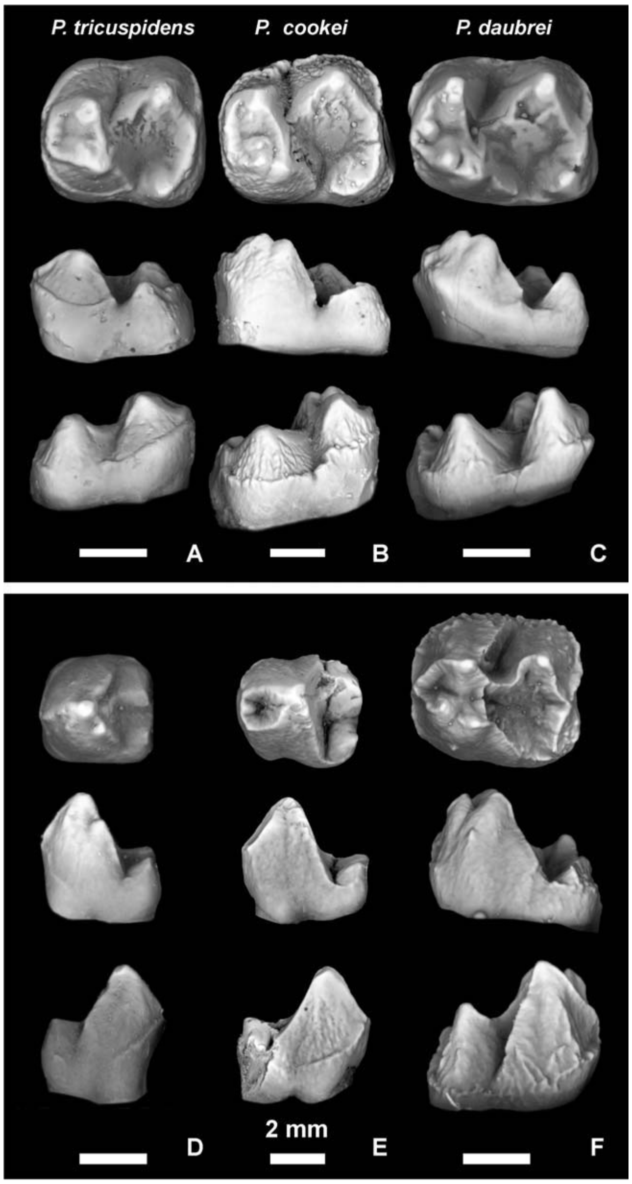


Fig. 5. Mandibular teeth of selected Plesiadapidae. M_2s (top) and P_4s (bottom) of (**A**, **D**) *P. tricuspidens* (unnumbered specimen from MNHN Berru collection, MNHN R 129), (**B**, **E**) *P. cookei* (UM 66719, UM 69265), and (**C**, **F**) *P. daubrei* [MNHN AL-5164, MNHN AL-J in occlusal, lingual and buccal views (top to bottom within each frame). Molars are scaled to the buccolingual width of talonid. Premolars are scaled to the molar of the same taxon. Note that the M_2s of *P. cookei* and *P. daubrei* are relatively longer than those of *P. tricuspidens*, have more buccolingually expanded trigonids, and are larger, better-developed entoconids. Note that P_4s of all three taxa are virtually unworn, but only that of *P. tricuspidens* lacks a trigonid basin, even though it has metaconid. Furthermore, the P_4 of *P. cookei* has the beginnings of a paraconid, visible in occlusal view. All scales represent 2 mm.

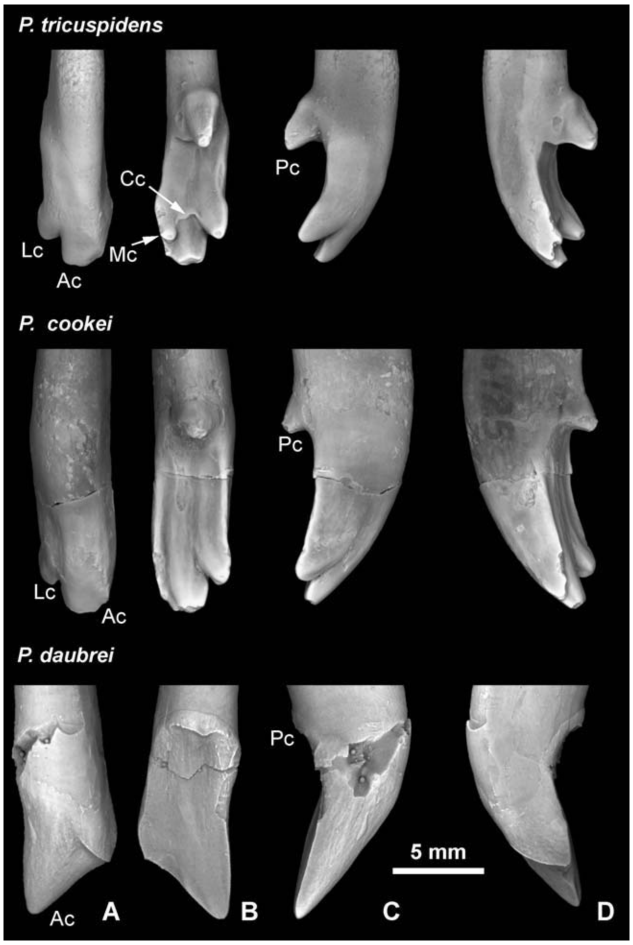


Fig. 6. I^1s of *P. tricuspidens* (unnumbered specimen from MNHN Berru collection, top row), *P. cookei* (UM 66725, middle row), and *P. daubrei* (MNHN MUT 17158) in (**A**) anterior, (**B**) posterior, (**C**) lateral, and (**D**) medial views. Note that despite being smaller overall, *P. tricuspidens* has a posterocone (Pc) that is larger, and an anterocone (Ac) and laterocone (Lc) that are the same sizes as those in *P. cookei*. Furthermore, *P. cookei* lacks the mediocone (Mc) and centroconule crest (Cc) of *P. tricuspidens*. The small cusps and simplified form of the *P. cookei* I^1 make it very similar to that of *Platychoerops* which is interpreted to have lost the Lc (Gingerich, 1976). See Figure 7 for quantification of these features.

Although RFI and OPC covary in this study, they are not metrically dependent because OPC does not take into account the steepness of each slope. For example, a blade-like tooth has high occlusal relief, but low complexity. On the other hand, a tooth with low relief could have many small scale crenulations and have a high OPC. A benefit of using such metrics over more traditional measures of tooth functionality such as shearing-crest lengths and relative crushing areas (e.g., Kay, 1975; Gunnell, 1989; Anthony and Kay, 1993) is that they require fewer inferences regarding homology of tooth surface features, and patterns of occlusion and jaw movement. Furthermore, because these metrics do not rely on landmark identification, natural wear of tooth surfaces does not substantially degrade measurement accuracy. These metrics change with wear, but such variance likely corresponds to real variance of functionality (King et al., 2005).

The full functional significance of the RFI and OPC measures is still being ascertained (M'Kirera and Ungar, 2003; Evans et al., 2007a; Veiberg et al., 2007; Boyer, 2008). We can see two possible reasons to increase RFI: 1) to improve the ability of tooth surfaces to fracture foods, such as by increasing cusp height or crest length

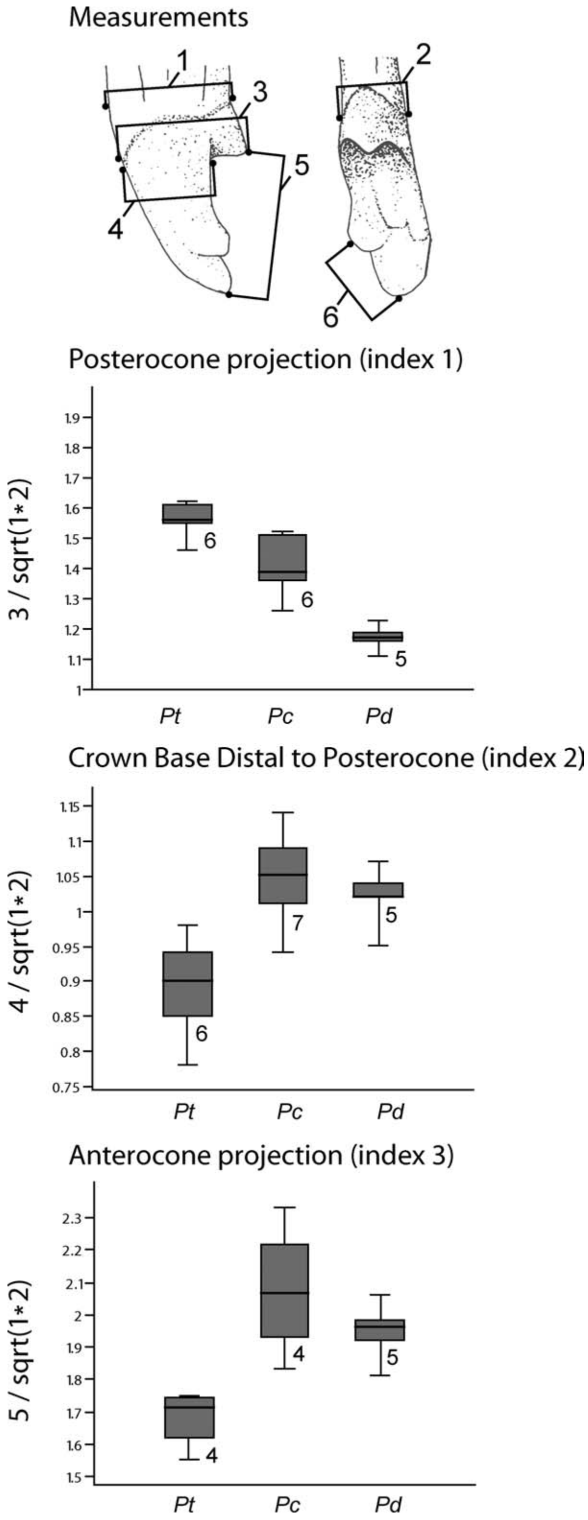


Fig. 7. Plots of shape indices of plesiadapid I^1s using illustrated measurements. See Figure 3 for description of box plots, and taxon abbreviations. Note that posterocone projection decreases from *P. tricuspidens* to *P. cookei* to *P. daubrei*, but girth (index 2) and length (index 1) of the crown distal to the posterocone are relatively larger in the latter two taxa compared with the former. These three indices are all standardized to the crown-base dimensions and so are not interdependent. They are independent with respect to crown base dimensions. See Table A1 for description of numbered measurements.

(Evans and Sanson, 1998), and 2) to increase resistance to wear by providing a greater amount of dental material to be worn, i.e. increasing tooth height or hypsodonty. M'Kirera and Ungar (2003) analogized occlusal relief with relative shearing area, traditionally captured using a shearing quotient (e.g., Anthony and Kay, 1993, Kirk and Simons, 2001). This falls into the first category, where it is presumed that a greater crest length will improve tooth function. M'Kirera and Ungar (2003) measured occlusal relief for only the occlusal surface above the bottom of the lowest basin; so they did not include a measure of total crown height, but only the height of features on the crown. RFI, as measured by Boyer (2008) and in this study, quantifies whole tooth relief using the surface area of the entire crown, and so it includes an indication of increased resistance to wear and crown height (hypsodonty) as well as crown feature height.

Primates with a high shearing crest length and initially high RFI have been demonstrated to have diets consisting of large amounts of structural carbohydrate (Kirk and Simons, 2001; M'Kirera and Ungar, 2003; Boyer, 2008). However, it has been demonstrated that the lengths of shearing crests on a tooth are maintained and sometimes increase even as the crown wears away when it is expected that RFI would be decreasing (King et al., 2005). Like shearing crest length, OPC is also apparently maintained and may even increase as the crown wears down and relief decreases as in *Propithecus* (Evans et al., 2007a,b; King et al., 2008). Because crest length and OPC appear to be less affected by wear than relief values, they may be more direct measures of functionality of teeth in animals with fibrous diets, such as folivores.

The second advantage of increasing RFI is that it should increase the duration of tooth functionality: the greater the initial RFI of a tooth, the more chewing cycles it should sustain before the tooth's cusps and crests are worn down to the bottom of its enamel basins. When this happens, all of the enamel is quickly eroded from the occlusal surface of the tooth. As a consequence, shearing crest length and OPC are also reduced drastically (Lanyon and Sanson, 1986; King et al., 2005, 2008). This interpretation is consistent with the observation that lifespan and unworn molar crown heights covary among species of deer (Veiberg et al., 2007).

Ecological significance of premolar form

Molarization of premolars is a known correlate of specialization for a more folivorous diet (Osborn, 1907; Gingerich, 1976; Van Valen, 1982; Jernvall et al., 2008). In fact, a molariform P_4 is one of the features cited as reflecting a leafy diet for *P. daubrei* (Gingerich, 1976). Why this should be the case can be explained by the correlation between tooth row OPC and herbivory discussed earlier and demonstrated by Evans et al. (2007a): as demonstrated in Tables 2 and 3, a more molariform P_4 adds more to the complexity of the tooth row and is thus beneficial to an herbivore. Analyses of tooth-row OPC of the taxa examined in this study might be predicted to be even more distinct than the M_2 and P_4 alone. The incipient trigonid of *P. cookei* and the better-developed one of *P. daubrei* appear similar in form. The molarization of P_4 seems likely to have initiated and progressed in a similar way in the lineages leading to *P. cookei* and *P. daubrei*.

Given that more complex premolars have increased importance for chewing relative to simple ones, it is interesting to note that the extremely molarized premolars of *P. daubrei* are also proportionally much larger than those of *P. cookei* and *P. tricuspidens*.

Ecological significance of incisor form

Gingerich (1976) argued that the apical cusps of the central incisor formed a structure analogous to a "seed cup" of certain bird bills. Therefore, the demonstrated reduction in the laterocone of *P. cookei* relative to that of *P. tricuspidens* (index 4) and the previously discussed lack of mediocone and centroconule (Gingerich, 1976) of *P. cookei* may indicate that it did not use its incisors to harvest small seeds. The reduction of the postercone projection and increased crown girth (indices 1 and 2) demonstrated to distinguish both *P. cookei* and *P. daubrei* from *P. tricuspidens* appears functionally significant. Both differences reflect a reduction in the relative size of the notch formed between the apex of the I^1 and its posterocone. In *P. tricuspidens*, and other plesiadapids with a similar I^1, distinct transverse wear striations develop in the apex of this notch, but the tip of the posterocone remains intact throughout a large range of progressive wear. On the other hand, several *P. cookei* specimens do not have substantial wear focused in this notch even though the tip of the posterocone is worn away (e.g., YPM-PU 13293, UM 88183). Furthermore, no available specimens of *P. daubrei* exhibit wear in this area, including those with wear developed on more distal parts of the crown. Thus the reduction of the posterocone may reflect a change in occlusal pattern in which the posterocone was not important for providing a shearing (Gingerich, 1976) or guiding surface for the lower incisor. What this means explicitly in terms of dietary changes is not immediately straightforward, but it is consistent with other data presented here suggesting that *P. cookei* and *P. daubrei* were similarly specialized toward a diet unlike that utilized by *P. tricuspidens*.

Paleoenvironmental significance of evolution of folivorous plesiadapids

Gingerich (1976) hypothesized that evolutionary changes in the inferred plesiadapid diets may reflect a response to changing climate and available herbaceous resources. Maas et al. (1988) presented evidence consistent with the hypothesis that the eventual extinction of plesiadapids was a result of competition with rodents, but competitive pressures could also have selected for new dietary specializations among plesiadapids.

Plant macrofossils (Wilf, 2000) and stable isotope records from marine cores and the terrestrial realm (e.g., Zachos et al., 2001) indicate moderate warming and aridification from the middle of the late Paleocene to the end of the epoch. Corresponding environmental changes may have selected for more dietarily specialized plesiadapids like *P. cookei* in North America and *P. russelli* in Europe, as contrasted with earlier large forms like *P. tricuspidens*. The rapid climate change at the beginning of the Eocene epoch (e.g., Bowen et al., 2001; Zachos et al., 2001; Wing et al., 2005) resulted in commensurate changes in flora (Wing et al., 2005). Keeping pace with climate change, more rapid environmental changes may have increased selective pressures and the rate of evolution of dietary specialization in plesiadapids, yielding forms like *P. daubrei*. If such a scenario is true then ultimately a consistent and congruent pattern of associations between reconstructed climate, environment, and plesiadapid dietary specialization should be discernable in North America and Europe in the late Paleocene and early Eocene. If competitive interactions with rodents and other taxa substantially influenced patterns of plesiadapid evolution, such associations will be more difficult to elucidate.

SUMMARY AND CONCLUSION

In summary, *P. cookei* is found to be essentially intermediate between *P. tricuspidens* and *P. daubrei* in a number of dietarily significant features of the molar, premolar, and incisor dentition. Specifically, *P. cookei* is intermediate in M_2 relief (RFI), M_2 complexity (OPC), P_4 complexity (OPC), and I^1 posterocone relative size. These findings support the hypothesis of Gingerich (1976) that *P. cookei* was less omnivorous and more specialized to a folivorous diet than *P. tricuspidens*. On the other hand, *P. cookei* shows greater molar enlargement relative to its skull, dentary, and P_4 than other taxa studied here, and it is indistinguishable from *P. daubrei* in I^1 crown relative girth and length. These features suggest that *P. cookei* is not a perfect intermediate on an ecological or evolutionary spectrum leading from *P. tricuspidens* to *P. daubrei*. Furthermore, skull and dentary measurements demonstrate *P. cookei* and *P. tricuspidens* to have been the same absolute sizes (despite differences in molar tooth sizes), where as *P. daubrei* was probably slightly smaller (on the basis of tooth and dentary measurements). Changes in dietary adaptations focused around the end of the Paleocene and the Paleocene–Eocene boundary may reflect evolutionary responses to environmental changes beginning at these times.

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APPENDIX

TABLE A1. List of caliper measurements

Cranial measurements (Fig. 1)	
1	Nasal: Maximum mediolateral width of anterior end
2	Nasal: Maximum anteroposterior length
3	Nasal: Maximum mediolateral width of posterior end (along frontal suture)
4	Premaxilla: Unilateral maximum mediolateral width at anteroposterior level of juncture with maxilla $\sim$ level of I^2
5	Premaxilla: Distance to anterior margin of I^2, foramen measured from anterior margin of bone
6	Premaxilla: Distance between I^1 and I^2 alveoli
7	Premaxilla/frontal: length of suture on dorsum of skull
8	Maxilla: Anteroposterior length in palate with measurement starting at anterior margin of suture with palatine
9	Maxilla: Unilateral mediolateral width in palate at level of I^2 alveolus
10	Maxilla: Unilateral mediolateral width in palate at anterior margin of P^2 or P^3 alveolus
11	Maxilla: Length of tooth row from P^3 to M^3
12	Maxilla: Distance between I^2 and P^3
13	Maxilla/palatine: Unilateral mediolateral width of palate at level of M^3
14	Maxilla: Unilateral mediolateral width of maxilla at level of M^3, measurement starts at midline (not palatomaxillary suture) and ends at lateral edge of alveolar process
15	Maxilla: maximum unilateral mediolateral width due to projection of maxillary zygomatic process
16	Maxilla: on zygomatic process, anteroposterior distance of expansion of maxilla for attachment of masseter
17	Maxilla/zygomatic: Length of suture on anterior surface of maxilla
18	Maxilla/Frontal: Length of suture on dorsum of skull
19	Frontal: Maximum unilateral mediolateral width from metopic suture to most lateral point of contact with lacrimal and maxilla
20	Frontal: Maximum anteroposterior length along midline from nasal contact to parietal contact
21	Parietal: Unilateral mediolateral width at posterior contact with squamosal along nuchal crest
22	Parietal: Length of sagittal crest
23	Parietal: Maximum bilateral mediolateral width at postorbital constriction
24	Squamosal: Mediolateral width of glenoid
25	Squamosal: Anteroposterior length of glenoid, measured along medial margin, slightly obliquely going from postglenoid foramen to most anterior point on glenoid
26	Squamosal: Dorsoventral projection of postglenid process
27	Palatine: Anteroposterior length from anterior suture with maxilla to postpalatine torus
28	Palatine: Unilateral mediolateral distance to outer margin of postpalatine torus
29	Basioccipital: Bilateral mediolateral width at anteriormost point (spheno-occipital synchondrosis)
30	Basioccipital: Maximum anteroposterior length
31	Exoccipital: Bilateral mediolateral distance between hypoglossal foramina
32	Exoccipital: Bilateral mediolateral width at posterior margin of skull (between tips of jugular processes)
33	Exoccipital: Unilateral mediolateral distance from midline to outer margin of occipital condyle
34	Exoccipital: Maximum mediolateral width of occipital condyle, measured laterally from lateral edge of foramen magnum
35	Exoccipital: Dorsoventral height of occipital condyle, not including anteromedial projection of facet
36	Zygomatic: Dorsoventral depth at lateral margin of excavation for orbits
37	Zygomatic: Distance from anterior zygomatic/maxilla contact to lateral margin of excavation for orbits on zygomatic
38	Orbits: Unilateral mediolateral distance between midline and lateral edge of excavation for orbit on zygomatic
39	Basicranium: Distance from anterolateral margin of ectotympanic bone to stylomastoid foramen
40	Exoccipital: Mediolateral width of foramen magnum
41	External auditory meatus mediolateral length, measured from lateral tip to medial margin of annular component of ectotympanic bone
42	External auditory meatus anteroposterior length, measured posterior to postglenoid foramen.
GM	Geometric mean of all measurements except 7, 41–42 (number of measurements available for calculation)
Upper central incisor measurements (Fig. 7)	
1	Mesiodistal length of root at base of crown
2	Mediolateral width of root at base of crown
3	Mesiodistal length of crown at posterocone
4	Mesiodistal length of crown immediately distal to posterocone
5	Distance between anterocone tip and posterocone tip
6	Distance between anterocone tip and laterocone tip (not applicable to *Platychoerops*)
Index 1	Ratio of measurement 3 to square root of product of measurements 1 and 2
Index 2	Ratio of measurement 4 to square root of product of measurements 1 and 2
Index 3	Ratio of measurement 5 to square root of product of measurements 1 and 2
Index 4	Ratio of measurement 6 to 5

TABLE A2. Cranial measurements of plesiadapids[a]

Specimen	MNHN CR 125	Pellouin skull	UM 87990
Taxon	*P. tricuspidens*	*P. tricuspidens*	*P. cookei*
Locality	Berru, Paris Basin, France	Berru, Paris Basin, France	sc-117, Bighorn Basin, Wyoming
Measures			
1	4.30	–	4.84
2	30.69	–	31.35
3	1.51	2.0	4.57
4	7.68	–	8.61
5	16.25	–	15.93
6	5.50	–	3.87
7	9.60	–	–
8	35.78	30.36	29.37
9	4.44	5.75	5.53
10	6.89	8.02	7.71
11	21.16	20.8	22.16
12	15.14	12.37	14.04
13	6.66	6.84	6.8
14	13.89	13.26	15.12
15	27.99	24.76	26.1
16	3.79	3.47	2.33
17	15.01	17.70	18.44
18	8.38	–	8.84
19	14.15	–	15.11
20	20.68	19.69	21.02
21	10.09	8.63	10.82
22	41.88	38.52	41.00
23	11.31	10.85	11.66
24	13.54	14.02	10.12
25	13.98	13.52	11.52
26	4.01	4.54	3.69
27	13.83	11.16	12.57
28	4.26	3.74	4.45
29	6.37	6.94	6.00
30	14.82	14.4	14.42
31	10.94	10.54	10.59
32	24.97	25.00	26.00
33	8.30	8.50	8.60
34	4.39	4.05	4.38
35	6.48	5.06	5.36
36	8.97	9.78	7.86
37	16.69	–	16.55
38	27.21	–	24.00
39	11.95	12.45	10.8
40	8.95	6.88	8.71
41	11.60	11.50	4.80
42	6.80	6.60	12.00
GM	10.6 (39)	10.28 (30)	10.71 (39)

[a] See Table A1 for descriptions.

TABLE A3. Dentary data on P. cookei

Specimen	Dentary depth at M_2	Tooth wear (relative age)
YPM-PU 18097	18.12	–
YPM-PU 21589	19.48	–
YPM-PU 19551	19.36	–
YPM-PU 13292	15.94	Moderate wear
YPM-PU 18312	15.83	Slight wear
YPM-PU 17973	19.70	–
UM 67187	15.76	Moderate-heavy wear
UM 65720	17.00	Moderate wear
UM 82364	13.96	Slight wear
UM 69913	16.55	Slight wear
UM 73653	15.70	Slight wear
UM 73704	17.83	Heavy wear
UM 69265	13.25	Unworn
UM 66919	16.12	Light moderate wear
UM 66701	18.13	Light moderate wear
UM 65049	14.02	Moderate wear
UM 87990	14.04	Unworn
UM 71764	16.20	–
Mean	*16.50*	

TABLE A4. Dentary data on P. tricuspidens *and* P. daubrei

Specimen	Taxon	Dentary depth at M_2
MNHN R 420	*P. tricuspidens*	16.06
MNHN Br L S1	*P. tricuspidens*	14.82
MNHN R 129	*P. tricuspidens*	15.24
MNHN R 132	*P. tricuspidens*	14.61
MNHN Br 12505	*P. tricuspidens*	17.50
MNHN Br 12502	*P. tricuspidens*	19.52
MNHN Br 12500	*P. tricuspidens*	14.84
MNHN Br 12504	*P. tricuspidens*	12.82
MNHN Br 12506	*P. tricuspidens*	16.25
MNHN Br 12507	*P. tricuspidens*	15.91
MNHN Br 12498	*P. tricuspidens*	16.03
MNHN Br 12499	*P. tricuspidens*	16.62
MNHN Br 14062	*P. tricuspidens*	17.61
MNHN Br 14053	*P. tricuspidens*	15.84
MNHN R 422	*P. tricuspidens*	17.63
MNHN R 421	*P. tricuspidens*	18.44
MNHN Br 14616	*P. tricuspidens*	15.41
MNHN R 424	*P. tricuspidens*	20.32
MNHN Berru L-S2	*P. tricuspidens*	18.96
MNHN Berru L-S3	*P. tricuspidens*	17.17
MNHN R 432	*P. tricuspidens*	17.62
MNHN R 433	*P. tricuspidens*	12.69
MNHN Br 13881	*P. tricuspidens*	13.26
MNHN Br 10181	*P. tricuspidens*	14.51
MNHN Br 10198	*P. tricuspidens*	15.58
MNHN Br 10119	*P. tricuspidens*	17.90
MNHN R 423	*P. tricuspidens*	15.54
Berru Divers A	*P. tricuspidens*	12.82
Berru Divers C	*P. tricuspidens*	12.35
Berru Divers D	*P. tricuspidens*	14.03
Berru Divers E	*P. tricuspidens*	14.75
MNHN R 403	*P. tricuspidens*	14.60
MNHN R 431	*P. tricuspidens*	15.24
MNHN Br 14054	*P. tricuspidens*	15.01
MNHN Br 11832	*P. tricuspidens*	14.76
MNHN R 402	*P. tricuspidens*	18.46
MNHN R 401	*P. tricuspidens*	17.27
Mean	*P. tricuspidens*	*15.89*
MNHN AL-5156	*P. daubrei*	14.38
MNHN Mu 12301	*P. daubrei*	11.77
MNHN Mu 12302	*P. daubrei*	12.53
Mean	*P. daubrei*	*12.89*

TABLE A5. Tooth measurements of P. cookei

Specimen	Tooth	Taxon	Region	Basin	Locality	RA	Age	*2da*	*3da*	RFI	OPC
UM 80720	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-19	Cf-2	56.4	29.39	78.05	0.488	64
UM 82364	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-19	Cf-2	56.4	25.72	71.79	0.513	67
UM 65050	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-20	Cf-2	56.4	26.20	71.59	0.503	67
UM 69913	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-136	Cf-2	56.4	32.49	94.08	0.532	63
UM 65720	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-62	Cf-2	56.4	27.73	75.46	0.501	62
UM 71764	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-62	Cf-2	56.4	32.01	85.59	0.492	67
UM 79636	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-116	Cf-2	56.4	25.04	67.03	0.492	60
UM 69995	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-220	Cf-2	56.4	27.68	75.76	0.503	61
UM 87990 (L)	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-117	Cf-2	56.4	23.38	61.26	0.482	53
UM 8801	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-117	Cf-2	56.4	29.79	78.26	0.483	68
YPM-PU 18097	M_2	*P. cookei*	Wyoming	Clark's Fork	sc	Cf-2	56.4	30.89	81.97	0.488	68
YPM-PU 17937	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-143	Cf-2	56.4	34.10	85.2	0.458	59
YPM-PU 17939	M_2	*P. cookei*	Wyoming	Clark's Fork	sc-143	Cf-2	56.4	34.54	86.39	0.458	55
YPM-PU 13293 (L)	M_2	*P. cookei*	Wyoming	Clark's Fork	Sc	Cf-2	56.4	28.03	74.35	0.488	62
AMNH 16895	M_2	*P. cookei*	Wyoming	Clark's Fork	BH	Cf-2	56.4	33.92	86.52	0.468	74
AMNH 86795	M_2	*P. cookei*	Wyoming	TP	ML	Cf-2	56.4	31.83	81.97	0.473	65
AMNH 88126	M_2	*P. cookei*	Wyoming	TP	TL	Cf-2	56.4	27.82	78.37	0.518	67
AMNH 88158	M_2	*P. cookei*	Wyoming	TP	L7	Cf-2	56.4	30.16	76.78	0.467	70
YPM-PU 18312	M_2	*P. cookei*	Wyoming	Clark's Fork	sc	Cf-2	56.4	26.98	71.31	0.486	55
YPM-PU 13293 (R)	M_2	*P. cookei*	Wyoming	Clark's Fork	sc	Cf-2	56.4	28.66	76.86	0.493	61
UM 87990 (L)	P_4	*P. cookei*	Wyoming	Clark's Fork	sc-117	Cf-2	56.4	14.25	nm	nm	36
YPM-PU 13293	P_4	*P. cookei*	Wyoming	Clark's Fork	sc	Cf-2	56.4	17.95	nm	nm	33
YPM-PU 17490	P_4	*P. cookei*	Wyoming	Clark's Fork	sc-143	Cf-2	56.4	19.05	nm	nm	39
UM 82364	P_4	*P. cookei*	Wyoming	Clark's Fork	sc-19	Cf-2	56.4	14.40	nm	nm	42
UM 87990 (R)	P_4	*P. cookei*	Wyoming	Clark's Fork	sc-117	Cf-2	56.4	15.73	nm	nm	41

BH, Buckman hollow; Cf, Clarkforkian; E, Europe; ML, main locality; MP, mammalian palaeogene reference levels; NA, North America; nm, not measureable; PE, palaeogene European biozones; RA, relative age; sc, Sand Coulee; TL, Taeniodont locality; TP, Togwotee Pass area.

TABLE A6. Tooth measurements of P. tricuspidens *and* P. daubrei

Specimen	Tooth	Taxon	Region	Basin	Locality	RA	Age	*2da*	*3da*	RFI	OPC
MNHN Av 5762	M_2	*P. daubrei*	France	Paris	Avenay	MP 9 (PE V)	54.8	22.68	62.10	0.504	84
MNHN AL-J	M_2	*P. daubrei*	France	Paris	Reims	Eocene	<55.8	20.67	60.43	0.536	70
MNHN Mu 5578	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	15.57	42.56	0.503	68
MNHN Mu 5939	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	19.58	56.28	0.528	76
MNHN Mu 5560	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	22.74	70.12	0.563	76
MNHN Mu 6184	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	18.72	50.95	0.501	72
MNHN Mu 6275	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	18.22	49.61	0.501	70
MNHN Mu 12302	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	20.99	62.82	0.548	70
MNHN Mu 12301	M_2	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	18.70	55.22	0.541	71
MNHN AL-5164	P_4	*P. daubrei*	France	Paris	Reims	Eocene	<55.8	19.91	nm	nm	65
MNHN MUT-17147	P_4	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	18.48	nm	nm	58
MNHN Mu 12302	P_4	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	17.72	nm	nm	68
MNHN Mu 12301	P_4	*P. daubrei*	France	Paris	Mutigny	MP 8 (PE III)	54.8	15.22	nm	nm	59
MNHN Br 12493	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	16.80	42.95	0.469	60
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	17.42	43.79	0.461	55
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	18.82	48.28	0.471	59
MNHN Berru L-51	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	22.97	59.73	0.478	62
MNHN Cr 14363	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	16.23	40.68	0.459	61
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	18.72	47.65	0.467	51
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	16.81	40.93	0.445	61
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	17.22	38.66	0.404	47
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	15.81	40.77	0.474	65
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	20.95	51.55	0.450	45
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	17.86	45.99	0.473	67
MNHN R 424	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	17.37	46.13	0.488	50
MNHN R 129	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	17.43	47.34	0.499	55
MNHN Cr 14355	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	15.84	39.15	0.452	52
MNHN Berru "nn"	M_2	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	16.06	43.31	0.496	59
MNHN Br 14062	P_4	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	10.14	nm	nm	23
MNHN R 132	P_4	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	11.48	nm	nm	35
MNHN R 129	P_4	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	10.09	nm	nm	35
MNHN Berru L-S1	P_4	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	11.70	nm	nm	30
MNHN R 424	P_4	*P. tricuspidens*	France	Paris	Berru	MP 6-7 (PE I)	57.2	12.08	nm	nm	28

nm, not measureable; nn, no catalogue number.

TABLE A7. P_4 morphology in P. cookei

Specimen	P_4 trigonid Basin	P_4 paraconid
YPM-PU 17940	Slit-like trigonid basin	No
YPM-PU 17939	No trigonid basin	No
YPM-PU 21009	No trigonid basin	Yes
YPM-PU 17937	No trigonid basin	? – Worn
YPM-PU 13292	No trigonid basin	Yes
UM 67187	Dimple-like trigonid basin	Yes
UM 65720	Slit-like trigonid basin	No
UM 82364	Slit-like trigonid basin	No
UM 73653	No trigonid basin	No
UM 73704	Slit-like trigonid basin	? – Worn
UM 69265	Expansive trigonid basin	No
UM 87990	Expansive, trigonid basin	No
UM 69995	Slit-like trigonid basin	Yes
UM 65031	No trigonid basin	No
UM 88001	No trigonid basin	No
UM 80270	Expansive, trigonid basin	No
UM 71764	No trigonid basin	Yes

TABLE A8. Incisor measurements and shape variables for plesiadapids

Specimen	Taxon	Locality	M 1	M 2	M 3	M 4	M 5	M 6	CA*	Ind-1	Ind-2	Ind-3	Ind-4
YPM-PU 17977	*P. cookei*	CF, sc	7.46	4.36	8.69	5.78	11.58	2.73	5.70	1.52	1.01	2.03	0.24
YPM-PU 18118	*P. cookei*	CF, sc	6.76	3.92	–	5.44	10.80	2.67	5.15	–	1.06	2.10	0.25
YPM-PU 13293	*P. cookei*	CF, sc	6.85	4.48	6.97	5.79	12.90	3.10	5.54	1.26	1.05	2.33	0.24
UM 66725	*P. cookei*	sc-117	6.72	4.28	7.30	5.45	9.83	2.69	5.36	1.36	1.02	1.83	0.27
UM 88183	*P. cookei*	sc-117	6.66	3.93	7.04	5.57	–	–	5.12	1.38	1.09	–	–
UM 65049	*P. cookei*	sc-20	7.13	3.68	7.76	4.83	–	2.14	5.12	1.51	0.94	–	–
UM 69265	*P. cookei*	sc-201	7.12	4.60	8.00	6.52	–	2.19	5.72	1.40	1.14	–	–
UM 69995 (L)	*P. cookei*	sc-220	–	–	–	–	–	3.07	–	–	–	–	–
UM 69995 (R)	*P. cookei*	sc-220	–	–	–	–	–	3.22	–	–	–	–	–
MNHN Cr 14359	*P. tricuspidens*	Berru	4.38	2.67	5.53	3.34	5.93	2.06	3.42	1.62	0.98	1.73	0.35
MNHN Cr 14369	*P. tricuspidens*	Berru	–	–	5.44	3.37	7.30	2.04	–	–	–	–	0.28
MNHN Br "nn"	*P. tricuspidens*	Berru	4.83	3.22	5.74	3.70	–	–	3.94	1.46	0.94	–	–
MNHN Br "nn"	*P. tricuspidens*	Berru	5.13	3.14	6.21	3.14	6.23	2.21	4.01	1.55	0.78	1.55	0.35
MNHN Br "nn"	*P. tricuspidens*	Berru	4.70	2.96	6.02	3.38	6.52	2.12	3.73	1.61	0.91	1.75	0.33
MNHN Br "nn"	*P. tricuspidens*	Berru	5.40	3.16	6.47	3.68	6.99	1.96	4.13	1.57	0.89	1.69	0.28
MNHN Br "nn"	*P. tricuspidens*	Berru	6.06	3.56	7.18	3.95	–	–	4.64	1.55	0.85	–	na
MNHN MUT 17158	*P. daubrei*	Mutigny	6.29	4.51	6.36	5.70	10.56	na	5.33	1.19	1.07	1.98	na
MNHN Mu 17076	*P. daubrei*	Mutigny	–	–	5.90	4.89	9.56	na	–	–	–	–	na
MNHN AL-5173A	*P. daubrei*	Reims	6.09	4.05	6.13	5.05	8.98	na	4.97	1.23	1.02	1.81	na
MNHN AL-5173B	*P. daubrei*	Reims	–	–	5.59	4.49	–	na	–	–	–	–	na
MNHN Mu 5555	*P. daubrei*	Mutigny	5.91	4.36	5.64	5.18	9.76	na	5.08	1.11	1.02	1.92	na
MNHN Mu 6502	*P. daubrei*	Mutigny	5.41	–	5.29	4.36	7.96	na	–	–	–	–	na
MNHN Mu 6447	*P. daubrei*	Mutigny	5.04	3.77	5.05	4.15	8.54	na	4.36	1.16	0.95	1.96	na
MNHN AL-5172	*P. daubrei*	Reims	6.67	4.52	6.40	5.70	11.30	na	5.49	1.17	1.04	2.06	na

CA, square root of cross-sectional area of incisor root = (M 1) × (M 2); CF, Clark's Fork Basin; Ind, index; M, measurement; na, not available or not applicable; nn, no catalogue number; TP, Togwotee Pass. See Table A1 and Figure 7 for descriptions and illustrations of measurements and indices.

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