Earliest Record of *Platychoerops* (Primates, Plesiadapidae), A New Species From Mouras Quarry, Mont de Berru, France

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ABSTRACT Plesiadapids are extinct relatives of extant euarchontans (primates, dermopterans, and scandentians), which lived in North America and Europe during the Paleocene and Early Eocene. The only genus of plesiadapid whose species are absent from Paleocene strata is *Platychoerops*. Further, *Platychoerops* is the only group found in sediments post-dating the Paleocene-Eocene boundary (PEB) by a substantial period of time based on large samples. It is also substantially different from other plesiadapids in dental features thought to reflect ecology. Its evolution has been linked to the rapid global climate change and faunal turnover marking the PEB. *Platychoerops* and *Plesiadapis tricuspidens* have been reconstructed as members of a single lineage by some authors. We describe a specimen (right p3m3) that we attribute to a new species, *Platychoerops antiquus*, from the unequivocally Paleocene (MP6) Mouras

Plesiadapid biochronology

The Plesiadapidae are members of the "plesiadapiforms" a demonstrably paraphyletic (Bloch et al., 2007), but potentially polyphyletic assemblage of primate-like Paleogene mammals that belong to the Euarchonta. At least some, if not all "plesiadapiform" taxa are likely to represent stem-primates (Bloch et al., 2007). Whether or not plesiadapids are phyletically primates, their cheek teeth are strikingly similar to those of early euprimates (Rose, 1994). Thus, they likely used a dietary niche very similar to that of the earliest euprimates (Szalay, 1968, 1972; Kay and Cartmill, 1977; Maas et al., 1988). The potential existence of strong ecological overlap has led various researchers to compare the temporal and geographic distributions of the plesiadapiform and euprimate radiations (Gingerich, 1976; Maas et al., 1988; Hooker, 1994). Of particular relevance then is the fact that plesiadapiforms in the families Plesiadapidae and Carpolestidae go extinct very near the PEB in North America, whereas two major groups of euprimates, adapiforms and omomyiforms, appear at the PEB (Gingerich, 1989; Rose et al., 2011). Judging from cheek tooth shape and size one may surmise that the earliest adaptform *Cantius* is a plausible ecological replacement for typical plesiadapids, while the earliest omomyiform, Teilhardina may repopulate niche space left open by the loss of carpolestids (Rose, 1975; Gingerich, 1976; Biknevicius, 1986; McKenna and Bell, 1997; Quarry of Mont de Berru, France. It has strong morphological affinities to *Platychoerops daubrei* yet co-occurs with many specimens of *Plesiadapis tricuspidens*, as well as the plesiadapid *Chiromyoides campanicus*. The existence of a species of *Platychoerops* prior to the PEB decouples the evolution of *Platychoerops* from the climate change and faunal turnover event associated with the PEB. Furthermore, the co-occurrence of *Platychoerops* with *P. tricuspidens* refutes the idea of a single lineage for these taxa. Instead, *Platychoerops* may be more closely related to North American *Plesiadapis cookei* (a previous alternate hypothesis). We suggest character displacement in a Paleocene immigrant population of *P. cookei* resulting from competition with sympatric *P. tricuspidens*, as a likely scenario for the evolution of *Platychoerops*. Am J Phys Anthropol 149:329–346, 2012. ©2012 Wiley Periodicals, Inc.

Strait, 2001). Furthermore, judging from postcrania carpolestids could have occupied a terminal branch/shrublayer niche similar to that inferred for small early eupri-

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mates (Bloch and Boyer, 2002). So, what lead to the demise of plesiadapids and carpolestids, and why did their niche re-open to Euprimates? It is argued that competition with rodents possibly along with changing climate (warming) eventually wiped out plesiadapids near the PE boundary (Van Valen and Sloan, 1966; Gingerich, 1976; Maas et al., 1988; Hooker, 1994; Boyer et al., 2010). Euprimates, being tropical animals (even today) and with specializations for more acrobatic arboreal locomotion (Rose, 1994; Silcox et al., 2009) may have been able to rely on similar dietary resources, and yet still successfully compete with diversifying rodents. Admittedly, much of this is speculation and must be more rigorously addressed by future research.

In Europe, the story is different: First, late Paleocene plesiadapids most likely did not contend with rodents, which do not appear until the PEB, but see Smith et al. (2010). Second, carpolestids were not present in Paleocene European faunas; instead, a convergently similar group of plesiadapoids, the saxonellids, likely filled a carpolestid-like niche (e.g., Russell, 1964). Finally, species in at least two genera of plesiadapid existed after the PEB for roughly another 3 Megannum (Ma) (Gingerich, 1976; Hooker, 1994; Boyer et al., 2010). The most abundant and longest surviving species are in the genus Platychoerops, which is generally recognized to be substantially different from other plesiadapids in the form of its cheek teeth and incisors (Gingerich, 1976; Boyer et al., 2010). The exclusively Eocene range of Platychoerops and its adaptively different dentition present a compelling contrast to the rest of Plesiadapidae. Presumably, its existence can be explained by the same factors that lead to the demise of its relatives near the PEB. But how? Gingerich (1976) posited that Platychoerops was the end member of a single evolving lineage starting with Plesiadapis tricuspidens, and with Plesiadapis russelli (known from the earliest Eocene Meudon site) as an intermediate. The material known for *P. russelli* is actually so similar to that of *Platychoer*ops that its appropriate generic assignment can be questioned (Hooker, 1994). The earliest Eocene occurrence of P. russelli therefore suggests that the morphological leap from more typical Plesiadapis-like dentitions to more folivorous-adapted *Platychoerops*-like dentitions had happened by the earliest Eocene. In Europe, a scenario can be constructed where the major environmental change at the PEB, and the appearance of euprimates and rodents with omnivorous-frugivorous tendencies, leads to a dramatic adaptive shift in *Plesiadapis* that result in Platychoerops (Hooker, 1994).

Boyer et al. (2012) suggested that *P. tricuspidens* is not the most plausible ancestor of *Platychoerops*, implicating the late Paleocene North American taxon *Plesiadapis cookei* instead. The scenario in which the evolution of *Platychoerops* results from a shift in selection due to environmental changes, also applies here; however, the changes at the PEB could not have been fully responsible for the adaptive shift in this case, because *P. cookei* has a number of distinctively *Platychoerops*-like traits (Boyer et al., 2010) suggesting the transition to folivory had already begun well before the PEB during the second biochron of the Clarkforkian (CF-2) North American Land Mammal age (NALMA), the last NALMA before the Eocene. The evolution of folivorous tendencies initially in *P. cookei* may instead be a response to the appearance of omnivore-frugivore rodent competitors at the beginning of the Clarkforkian (Maas et al., 1988; Boyer et al., 2010). Under this alternate scenario, *P. cookei* or its descendants must also have immigrated to Europe no later than the PEB. The immigration event would not be surprising, as there is evidence for other mammal immigrations at this time (e.g., Chester et al., 2010; Rose et al., 2011). However, *P. cookei* is missing from the last biochron (CF-3) of the Paleocene in North America, requiring the ad hoc supposition that it shifted its range to some unsampled location (rather than going extinct) before showing up in Europe, transformed into *P. russelli* and/or *Platychoerops*.

Finally, it has also been suggested that European and North American lineages were never distinct, with the implication that there was gene flow between North American and European lineages (Gingerich, 1976; Rose, 1981). In this scenario, Plesiadapis gingerichi from CF-1 in North America is 1) considered a probable subspecies of P. tricuspidens (Rose, 1981), and 2) portrayed as having evolved anagenetically into P. cookei [but see Bloch and Gingerich (1998) for an example of potential anachronistic co-occurrence]. Thus, in this scenario, P. cookei is simply another intermediate in the single lineage suggested by Gingerich (1976) from P. tricuspidens/P. gingerichi to P. russelli and later Platychoerops, not an alternative ancestor for Eocene plesiadapids. Results of a cladistic analysis by Boyer et al. (2012) are, however, at odds with this scenario as they posit a sister taxon relationship between the P. cookei-Platychoerops lineage and Plesiadapis fodinatus/Plesiadapis dubius. Under this scenario, at least two separate clades descended from a Plesiadapis churchillilike ancestor: one including P. tricuspidens (and possibly P. gingerichi and Plesiadapis simonsi); and another including P. fodinatus through Platychoerops. This scenario is in some ways surprising because it suggests multiple evolutions of large-bodied plesiadapids in the late Paleocene, instead of a single body size increase event: in the analysis of Boyer et al. (2012), P. fodinatus and P. dubius are linked to P. cookei by reduced premolar-type paraconules on P4, occasional presence of p4 paraconids (but see below), and crestiform cheek teeth.

Complicating these different scenarios is the description of *Platychoerops* georgi from several localities in England and mainland Europe (Hooker, 1994). Hooker (1994) proposed this taxon as a potential intermediate between P. tricuspidens and P. russelli, or at least as a sister taxon to a *P. russelli-Platychoerops* clade. This taxon was described based on isolated incisors premolars and molars. It exhibits an odd mix of features with Chiromyoides-like incisors, P. tricuspidens-like premolars, and Platychoerops-like molars. Hooker's hypothesis is mutually exclusive with the hypothesis that *P. cookei* is a member of the P. russelli-Platychoerops clade because it implies that major adaptive changes in the incisors and premolars occurred in the earliest Eocene (in a hypothetical taxon more derived and later occurring than georgi), whereas hypotheses including P. cookei Р. require that these changes begin in late Paleocene and precede the most major changes to the molar teeth.

These different hypotheses for evolution of *Platychoer*ops have predictions that can be tested by new fossil evidence. If Hooker (1994) is correct in positing that *P. georgi* shows that the transition between more typical plesiadapids and *Platychoerops*-like ones occurred at the PEB (beginning with changes in molar form only), then no evidence of taxa with *Platychoerops*-like premolars or incisors should be found in the Paleocene of Europe. If Gingerich (1976) is correct in his hypothesis that *P. tricuspidens* is part of the same lineage as *P. russelli* and P. daubrei then neither P. russelli nor more derived *Platychoerops* species should ever be found to co-occur with P. tricuspidens. Here, we describe a five tooth mandibular dentition (NMB Bru4) consistent only with the diagnosis for *Platychoerops* among existing plesiadapid genera, from the Paleocene Mouras Quarry at Monte de Berru, co-occurring with dentitions of P. tricuspidens. We present a comprehensive quantitative documentation that this new specimen is dramatically differentiated from P. tricuspidens and is profoundly similar to P. daubrei. Nonetheless, we note several distinctive differences between the new specimen and known P. daubrei. Furthermore, the available evidence suggests this specimen is also different from *P. russelli* from the earliest Eocene Meudon, France site. Thus, we are compelled to name a new species. If it turns out that with greater sampling in the future, the new specimen is a variant of P. daubrei or P. russelli, it would not affect the major conclusions of this study. These conclusions regard the pattern of plesiadapid evolution and phylogeny as well as the paleoecological interactions and environmental changes that can explain those patterns as discussed above.

Provenance of the new specimen

The specimen we describe (NMB Bru4) comes from a collection acquired by the Natural History Museum of Basel in the early 1980's. The collection was excavated by a private collector in the 1970's from two lenses of pebble conglomerate (stratigraphically separated by roughly two meters) within the argillaceous white and vellow sands that unconformably overlay the fine white sands of the Sables de Rilly Formation (Guérin et al., 1970; Laurain and Meyer, 1986). These sites occur on the eastern end of Mouras Quarry, which in turn is on the Northeastern side of the Mont de Berru, near the village of Berru. Fossils from Mouras Quarry [also called "Berru" by Russell (1964), Gingerich (1976), and others] are interpreted to be sampled from sediments genetically and temporally equivalent to the Conglomérat de Cernay geological formation (Russell, 1964; Russell et al., 1966; Guérin et al., 1970; Laurain and Meyer, 1986), which apparently is in large part the source of Lemoine's Cernay fauna (Teilhard de Chardin, 1922), an important reference for biostratigraphic inference (MP 6). More specifically, NMB Bru4 comes from the stratigraphically lower of the two lenses excavated by the private collector (M. Duchamplecheval) from whom the sample was acquired. This lower lens was apparently directly stratigraphically superjacent to the local exposure of the upper boundary of the Sables de Rilly formation. The collector specifically remembers finding the NMB Bru4 partly because of the drama associated with losing the disintegrating bone of the mandible surrounding perfectly preserved teeth with roots (pers. com. M. Duchamplecheval). The Mouras Quarry collection at NMB includes other typical Paleocene mammals (Arctocyon primaevus, Pleuraspidotherium aumonieri, Orthaspidotherium edwardsi, P. tricuspidens, and Chiromyoides *campanicus*), but no Eocene ones.

Because the focal specimen is the first example of *Platychoerops* known from a Paleocene site, one may question whether it is a contaminant from an Eocene locality. Three types of information make this suggestion highly unlikely. First, good provenance data link the specimen to Mouras Quarry when it was initially discovered (above). Second, the mode of preservation (color and

fossil quality) is identical to the other above-mentioned typical Paleocene fossils from Mouras Quarry (Fig. 1). Finally, being a residual hill, the Mont de Berru is the only place where Cenozoic continental sediments are preserved in a radius of more than 10 km (Fig. 2). While there are other fossil localities rimming Mont de Berru, including the rich Lemoine Quarry, all have yielded only Paleocene fossils (Teilhard de Chardin, 1922; Russell, 1964). To the best of our knowledge, no continental fossil vertebrate has ever been found in the Eocene sediments that constitute the top of the Mont de Berru. The nearest fossil localities known to definitely yield Platychoerops, and thought to be Eocene (Sparnacian) in age are located ~ 30 km to the Southwest (Gingerich, 1976) of Mont de Berru (including those in villages of Mutigny, Avenay, and probably those in Pourcy: Aubry et al., 2005) in the Argiles à Lignites member of the Epernay formation. The Conglomérat de Meudon member of the Vaugirard formation, which yielded *P. russelli*, is ~ 160 km away, near Paris (Russell, 1968; Aubry et al., 2005). Appendix A provides a detailed summary of the history of fossil collecting around the Mont de Berru.

Institutional and locality abbreviations

Av, Avenay; Bru, Berru; Cy, Cernay Les Reims; NMB, Natural History Museum Basel, Switzerland. MNHN, Muséum National d'Histoire Naturelle, Paris.

MATERIALS AND METHODS Materials

The focal specimen in this study (NMB Bru4) was compared with other plesiadapid jaws present in the NMB Mouras Quarry collection (NMB Bru2, NMB Bru3, and NMB Cy1133). Furthermore, DMB obtained a sample of *Platychoerops daubrei* and *Plesiadapis tricuspidens* from the MNHN as molds taken directly from specimens [see Tables 3 and 4, as well as Boyer et al., (2010) for specimen numbers, and locality information]. Data on Relief Index (RFI) and Orientation Patch Count (OPC) from these specimens were published in Boyer et al. (2010).

Methods

Several different methods that rely on different types of representations of morphological form were used to assess the phenetic affinities of NMB Bru4 to other plesiadapids. Some of these methods emphasize features that have straightforward functional significance, while others emphasize overall morphology with less explicit connection to functional features.

All measurements were done on digital surface files of teeth. Surface files were created by scanning specimens or epoxy casts (EPOTEK 301[®] with gray pigment) of specimens at between 18 and 22 μ m resolution using either a Scanco μ CT40, a Scanco μ CT75 machine (Stony Brook University Center for Biotechnology), or a GE VTOMEX CT scanner (AMNH). CT data were exported as TIFF or DICOM formatted image stacks. Image stacks were opened in Avizo (v.6-7). The "label field" tool was used to segment teeth that were then saved initially as Avizo "surf" files.

Tooth size and proportions. Plesiadapis tricuspidens and Platychoerops daubrei have been previously shown to have statistically similar occlusal molar areas, but different premolar areas, and correspondingly different D.M. BOYER ET AL.



Fig. 1. NMB Bru4 from Mouras Quarry, Mont de Berru. Right p3–m3. *Platychoerops antiquus* sp. nov. (see Results and Discussion). All scale bars = 5 mm. A: Occlusal views of each tooth with m3 on the left, lingual toward the top **B**, Buccal (left) and lingual (right) views. Note the preservation of tooth roots as a result of their protection by the mandible during preservation. The mandible did not survive the collection process intact. The amber and burgundy hues and translucent quality of the enamel is characteristic of other Mouras Quarry specimens, yet different from the blacker, opaque nature of other known specimens of *Platychoerops* from Eocene localities. **C**: Stereopairs of each tooth. **D**: Stereopair of buccal view. **E**: Stereopair of lingual view.



• Other sites with fossil mammals (after Teilhard de Chardin, 1922)

Fig. 2. Geological sketch of the Mont de Berru with location on the French map. Country rocks surrounding the Mont de Berru are Campanian (Late Cretaceous) marine limestones. Black solid lines are main roads; circles are villages and black dots represent other sites sampled by Teilhard de Chardin in the 1920s, which yielded mammal remains (Teilhard de Chardin, 1922).

proportions of premolar to molar area (Boyer et al., 2010; see also Fig. 3).

Occlusal area was measured by orienting a 3D digital surface file of each tooth so that the occlusal plane coincided with the "plane" of the computer monitor. A screenshot that included a scale bar was taken. The image was then opened in Sigma Scan Pro 5.0, the pixel values were calibrated with the scale bar and the internal 2D area encompassed by the tooth was calculated. This metric is tooth area (Table 1).

Dental topography. Plesiadapis tricuspidens and Platychoerops daubrei have been previously shown to have statistically significantly different values of molar and premolar cusp relief and tooth crown complexity (Boyer et al., 2010). Cusp relief was calculated using the RFI following Boyer (2008) and Bunn et al. (2011). Briefly, to calculate RFI, tooth surface files were processed by first cropping away material below the cervical margin (i.e., the enamel-dentine junction) and then applying 100 iterations of smoothing to an initial surface file generated from the CT scan segmentation using the software Avizo (v.6-7). The surface area of the resulting image was then calculated, again using Avizo. RFI is the natural log ratio of the square root of the resulting area to the square root of the occlusal plane area, the calculation of which is described in the previous subsection.

The measure of crown complexity is OPC, rotated (OPCR). Calculation of OPCR begins by reducing the initial surface to a "2.5D" surface as described in Boyer et al. (2010). The rest of the process is done in Surfermanipulator software. All aspects of OPCR calculation follow those outlined in Boyer et al. (2010) and are not repeated here. See Table 2 for values of tooth surface area, RFI and OPCR.

Automated correspondence determination and analysis (ACDA). Recent developments in computational geometry allow automated, algorithmic determination of the best geometric fit between different instances of the same anatomical structure (e.g., teeth; Boyer et al., 2011). The algorithm developed and tested by Boyer et al. (2011) finds geometric correspondences among anatomical objects that match accurately presumed "biological correspondences." In other words, the algorithm finds a global function that maps every point on the surface of one object to a unique point on the surface of another object. For teeth, points corresponding to cusp tips, crest lines, or junctions between crests and planes (e.g., where the cristid obliqua meets the postvallid) on one tooth are typically mapped precisely to equivalent points on other teeth. After application of this



Fig. 3. Surface renderings of tooth rows in occlusal and lateral views for comparison. NMB Bru4 cf. *P. daubrei* from Mouras Quarry reversed for comparison to other specimens. MNHN Mu 12301 *P. daubrei* is from Mutigny. NMB Cy1133, NMB Bru3, and NMB Bru2 *P. tricuspidens* are from Mouras Quarry. Note that despite variation in p4 morphology between NMB Cy1133 and NMB Bru3, they are much more similar to one another than either is to the p4 of NMB Bru4. Note also the large paraconids of NMB Bru4. Abbreviations: ac, accessory cusp between paraconid and protoconid; en, entoconid; hcl, hypoconulid; mc, metaconid; pc, paraconid. Scale bar = 5 mm.

algorithm to a sample of teeth, one achieves 1) a complete correspondence map between each pair of teeth and 2) a dissimilarity value (affinities and distances) for each pair of teeth, indicating how close they are in detailed aspects of shape. These dissimilarity relations are encoded in a matrix, similarly to geometric morphometric (GM) landmark analysis. This dissimilarity matrix can be used to calculate a low dimensional (i.e., two or three) representation that explains more or less of the variance in the dataset.

TABLE 1. Area measures in selected plesiadapid specimens

Specimen	Taxon	Locality	p4 A	m2 A	p4/m2
NMB Bru4 NMB Bru2 NMB Cy1133 MNHN Mu 12302	Platychoerops Plesiadapis Plesiadapis Platychoerops	Mouras Mouras Mouras Mutigny	$15.86 \\ 10.46 \\ 12.53 \\ 17.72$	$19.07 \\ 20.03 \\ 21.43 \\ 20.88$	$0.83 \\ 0.52 \\ 0.58 \\ 0.85$
MNHN Mu 12301	Platychoerops	Mutigny	15.22	18.70	0.81

Abbreviations: A, area of tooth surface projected into occlusal plane in square millimeters.

One benefit of this method is that it is faster and has been shown to be more accurate than manually collecting measurements and landmarks for some data sets (Boyer et al., 2011). Another benefit is that the shape quantification is more thorough and more objective than what is possible using a manually collected GM dataset. The phenetic affinities that result from this analysis cannot be questioned in terms of researcher competency or bias in data collection. This is not to say, however, that the algorithm is fail-safe. It can potentially perform poorly due to submitting samples with extreme morphological diversity or due to use of suboptimal parameter values (see Appendix B). Therefore, it is necessary to spot check for errors at least several of the correspondence maps it determines before trusting the distances it produces as reflections of overall dissimilarity between pairs of objects in the sample of interest. We use the ACDA of Boyer et al. (2011) to determine morphological distances between specimens in two different tooth samples. One is a m2 sample of nine *Platychoerops* teeth, 26 Plesiadapis teeth, and NMB Bru4. The other is a p4 sample of four *Platychoerops* teeth, three *Plesiadapis tricuspi*dens teeth, four Plesiadapis cookei teeth, and NMB Bru4. Each tooth surface was smoothed and subsampled to 20,000 faces using the software Geomagic Studio 11.0, before being submitted to analysis using the ACDA. See Appendix B for more details on algorithm parameters.

In Figure 4 we project a grid with unique combinations of numbers and colors in the grid cells on to .vtk formatted versions of the tooth surface, using the free software Paraview. The purpose of this is to allow inspection of the correspondence maps implemented by the algorithm.

We use the distance matrices generated by the ACDA for the following analyses: 1) we run nearest neighbor classification analysis, determining the five nearest neighbors to each tooth. This analysis is used to determine the geometric distinctiveness of the different known taxa and to evaluate with which taxon NMB Bru4 shares the closest phenetic affinity (Tables 3 and 4). 2) We run a Multidimensional Scaling (MDS) analysis to represent the variance in the dataset with a more limited set of variables (www.mathworks.com/help/toolbox/ stats/mdscale.html). In the context of this program, we set "P" equal to "2" and use the Continuous Procrustes distances as "D." Running this same analysis using the software SPSS v. 17 produces nearly identical results. We plot the two variables derived from MDS analysis of the distance matrix from each sample, to better illustrate phenetic affinities (Fig. 5).

Phylogenetic analysis. In this study, we identified a novel combination of character states in NMB Bru4, justifying its attribution to a new species. The combination of character states and the occurrence of this specimen in the Paleocene have implications for phylogenetic

TABLE 2. Relief index (RFI) an orientation patch count (OPC)

in Mouras Quarry piesiadapia specimens												
Specimen	Taxon	m2 RFI	p4 OPC	m2 OPC								
NMB Bru4 NMB Bru2 NMB Cy1133 NMB Bru3	Platychoerops Plesiadapis Plesiadapis Plesiadapis	0.527 0.450 0.459 na	58.25 37.25 41.88 32.88	71.38 59.38 63.38 na								

hypotheses that are best tested through cladistic analysis (with the understanding that additional fossil finds also help test these ideas). We also identified novel character state polymorphism in an already known species, which may also change results of cladistic analyses. We performed a cladistic analysis in Winclada (Nixon, 1999-2002) using NONA (Goloboff, 1999), based on a craniodental matrix modified from Boyer et al. (2012), which includes data on all plesiadapids except Plesiadapis georgi. We added three characters revealed to have a potentially informative phylogenetic signal by NMB Bru4, bringing the total number of characters to 69. The total number of ingroup taxa is 29 and there are 3 outgroups (see Boyer et al., 2012). Winclada was run using a heuristic search of 2000 replicates. To check the results of Winclada, we also ran the final analysis in PAUP 4.01B (Swofford, 1998).

RESULTS

Description and comparison of NMB Bru4

The preserved teeth are within the variation of *Platy-choerops* (Figs. 1 and 3–5; and supplementary material, a 3D pdf of NMB Bru4). However, species of this genus exhibit a substantial degree of variability.

p3. This tooth measures 4.25 mm (mesiodistal length) by 3.62 mm (buccolingual width). The tooth is thus above the reported range for p3 of Plesiadapis tricuspidens, but overlaps with that of *Platychoerops daubrei*. It is below the range reported for Plesiadapis cookei (Gingerich, 1976). The value reported for the single p3 attributed to *Plesiadapis russelli* is slightly smaller in length than that of NMB Bru4, such that it is between the P. tricuspidens and P. daubrei ranges; the width of the p3 attributed to P. russelli is nearly identical to that of the current specimen (Gingerich, 1976). The p3 of NMB Bru4 lacks a paraconid and entoconid, but exhibits a distinct metaconid. The protoconid is the main cusp on the p3: it projects well above the metaconid. It has a postmetacristid and very small cristid obliqua. There is a strong phase-1 wear facet that lies obliquely across the postvallid surface of the tooth and has worn through the enamel of the metaconid. This facet does not quite reach the cristid obliqua. The tooth lacks a buccal cingulid. There are vertical crenulations on the buccal surface. The tooth is a double-rooted tooth. This tooth conforms to the description of P. daubrei p3's (Gingerich, 1976). However, there is variation with the type of *P. daubrei* (MNHN Al-5156) having a well-developed paraconid, and the specimen MNHN Mu-12301 having only a single alveolus available for this tooth. The p3 attributed to P. russelli is said to present only a protoconid, to have only an "incipient" cristid obliqua and to have little expression/separation of entoconid and hypoconid cusps, making it more like P. tricuspidens or P. cookei in form (Gingerich, 1976), and quite different from the p3 of NMB Bru4.

D.M. BOYER ET AL.



Fig. 4. The grid-like texture reveals corresponding regions among these teeth as determined by the ACDA of Boyer et al. (2011). These correspondences serve as the basis for calculating Continuous Procrustes distances that were used to determine whether teeth belonged to *P. daubrei* or *P. tricuspidens*. **A:** m2's of NMB Bru4 *Platychoerops antiquus* sp. nov. (middle), *P. daubrei* MNHN MU 5560 (right), and *P. tricuspidens* MNHN BR NN2g (left). **B:** p4's of NMB Bru4 *P. antiquus* (right middle), *P. daubrei* MNHN MU 12302 (right), *P. cookei* UM 87990 (left middle), and *P. tricuspidens* NMB Cy1133 (left).

p4. This tooth measures 4.88 mm (mesiodistal length) by 3.89 mm (buccolingual width). It's length is thus larger than any length values reported for p4 of *Plesiadapis tricuspidens*, but overlaps with those reported for *Platychoerops daubrei* and *Plesiadapis cookei* (Gingerich, 1976). In width, it is smaller only than *P. cookei*, and overlaps with the other two taxa. Major cusps seen in p4 of NMB Bru4 are a paraconid, metaconid, protoconid, and hypoconid. The talonid is

well delimited lingually by a crest, which sports two small cusps that can be identified as hypoconulid and entoconid. In the major cusps represented, the p4 of NMB Bru4 is typical of p4's described for *Platychoerops*. The paraconid is a large cusp that is well separated from the metaconid (Figs. 1, 3, and 4b). This constitutes a distinctive difference from other *Platychoerops* in which the paraconid and metaconid are more closely appressed due to the more distal and apical position of the paraconid.



Fig. 5. Plots of first two factors resulting from MDS of Procrustes distance matrixes. Minimum spanning trees were generated based on PCoA of the Procrustes distance matrix. **A**: Plot for m2 data set. **B**: Plot for p4 data set. These plots, like other data in this study, indicate that NMB Bru4 is referable to *Platychoerops* and that it co-occurred with *P. tricuspidens*. Also, note that the scales of plots in A and B are equivalent. Therefore, these plots show that p4 exhibits a proportionally larger amount of morphological disparity than m2.

There is a strong crest that runs down the mesial aspect of the paraconid (Fig. 1), distinct from the paracristid. There is no lingual expression of the anterior cingulid (Fig. 1) as in many specimens of *Platychoerops*. There is a strong phase-I wear facet on the paracristid. The protoconid and metaconid are closely spaced and linked by a strong metacristid. The tooth has a modest cristid obliqua, which terminates toward the base of the postvallid

D.M. BOYER ET AL.

TABLE 3.	Nearest	neighbors	(Nb)	generated	by	Automated	Correspondence	e Algorithm	for	m2 data set.
		<u> </u>		0	•		*	0		

Specimen	Taxon	Site	Quarry	Nb 1	Nb 2	Nb 3	Nb 4	Nb 5	Nb 6
NMB Bru4	(#)	Berru	Mouras	0	0	1	1	1	0
NMB Bru3	(+)	Berru	Mouras	1	1	1	1	1	1
NMB Cy1133	(+)	Berru	Mouras	1	1	1	1	1	1
MNHN-BR NN1a	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN1b	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR 14355	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR 12493	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN4a	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN4c	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR-L-51	P. tricuspidens	Berru	?	1	1	1	1	1	+
MNHN-CR 14363	P. tricuspidens	Berru	?	1	1	1	+	1	1
MNHN-R 424	P. tricuspidens	Berru	?	+	1	1	1	+	1
MNHN-CR 14355	P. tricuspidens	Berru	?	1	1	1	+	1	1
MNHN-R 129	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2a	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2b	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2d	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2f	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2g	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2h	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2i	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2k	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2m	P. tricuspidens	Berru	?	1	+	1	1	1	1
MNHN-BR NN2n	P. tricuspidens	Berru	?	+	1	1	1	1	1
MNHN-BR NN20	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2p	P. tricuspidens	Berru	?	1	1	1	1	1	1
MNHN-BR NN2q	P. tricuspidens	Berru	?	1	1	1	+	1	1
MNHN-MU 5939	P. daubrei	Mutigny	?	0	0	0	0	0	0
MNHN-MU 5560	P. daubrei	Mutigny	?	0	0	1	0	0	0
MNHN-MU 6184	P. daubrei	Mutigny	?	0	0	0	1	1	0
MNHN-MU 5578	P. daubrei	Mutigny	?	0	0	0	0	0	1
MNHN-MU 6189	P. daubrei	Mutigny	?	0	0	0	#	0	1
MNHN-MU 12302	P. daubrei	Mutigny	?	0	0	0	0	1	0
MNHN-AV 5762	P. daubrei	Avenay	?	0	0	0	0	1	1
MNHN-MU 12301	P. daubrei	Mutigny	?	0	0	0	0	0	1
MNHN-AL-J	P. daubrei	Reims	?	0	1	1	0	1	1

Cells with a "1" stand for *Plesiadapis tricuspidens*, cells with a "0" for *P. daubrei*. "#" stands for NMB Bru4, "+" stands for *Plesiadapis* from the Mouras Quarry collection at NMB. No incorrect classifications by nearest neighbors.

instead of reaching the metacristid as in certain *Platy-choerops* specimens. The occlusal and buccal surface of the tooth exhibit modest crenulation of enamel.

m1. This tooth measures 5.15 mm (mesiodistal length) by 3.88 mm (buccolingual width). The length of this tooth is thus larger than any length values reported for m1 of Plesiadapis tricuspidens, but overlaps with those reported for Platychoerops daubrei and Plesiadapis cookei (Gingerich, 1976). In width, it is smaller only than P. cookei, and overlaps with the other two taxa. It is strongly crestiform, as typical for this tooth in other Platychoerops. As for p4, this tooth is distinctive compared to those of *Platychoerops* in its very strong paraconid (Figs. 1 and 3). A strong crest runs vertically on the mesial aspect of the paraconid to meet the anterior cingulum (Fig. 1). This crest seems equivalent to a similar crest that connects the paracristid and anterior cingulum in *Platychoerops*. There is weak development of an accessory cusp between the protoconid and paraconid. Strong development of this accessory cusp is characteristic of typical Platychoerops (Fig. 3). There is breakage of apices of protoconid, metaconid, and hypoconid. The cristid obliqua ascends the postvallid to meet the metaconid, as in other plesiadapids (Figs. 1 and 3).

m2. This tooth measures 5.42 mm (mesiodistal length) by 4.26 mm (buccolingual width). The length of this

tooth is thus larger than any length values reported for m1 of Plesiadapis tricuspidens, but overlaps with those reported for *Platychoerops daubrei* and *Plesiadapis* cookei (Gingerich, 1976). In width, it is smaller only than P. cookei, and overlaps with the other two taxa. Again, there is a very strong paraconid with a strong crest running down it and connecting to the anterior cingulum (Figs. 1, and 3). While the development of the paraconid is atypical, it is not outside the *Platychoerops* range: it is developed to the same degree in MNHN Mu-5560 (Fig. 4a) and MNHN Mu-5578. As for the m1, an accessory cusp between the paraconid and protoconid is minimally expressed compared with known Platychoerops (Figs. 1, 3, and 4a). The cristid obliqua intersects the postvallid in this tooth. The cristid obliqua is strongly vertically curved as in *Platychoerops* (Fig. 3). The accessory crest that intersects and buttresses the cristid obliqua from within the talonid basin in typical Platychoerops is only weakly developed in NMB Bru4 (Figs. 1, 3, and 4a). The entoconid of NMB Bru4 is strongly projecting as in specimens of Platychoerops. The hypoconulid is expressed as a distinct cusp along the postcristid, but it is much smaller than and well-separated from the entoconid. In known *Platychoerops* the entoconid and hypoconulid tend to be twinned (Figs. 3 and 4a).

m3. This tooth measures 8.33 mm (mesiodistal length) by 4.63 mm (buccolingual width). This is within the reported range for both *Plesiadapis tricuspidens* and

IADLE	TABLE 4. Treatest neignoors (100) generated by Automated Correspondence Algorithm for p4 data set.												
Specimen	Taxon	Site	Quarry	Nb 1	Nb 2	Nb 3	Nb 4	Nb 5					
NMB Bru4	(#)	Berru	Mouras	0	2	2	2	1					
NMB Bru3	P. tricuspidens	Berru	Mouras	1	1	(#)	2	2					
NMB Cy1133	P. tricuspidens	Berru	Mouras	1	2	2	2	1					
R129	P. tricuspidens	Berru	?	1	2	1	2	2					
UM 82364	P. cookei	SC-19	na	1*	1	2	2	2					
UM 87990	P. cookei	SC-117	na	1^{*}	2	2	1	0					
YPM-PU 13293	P. cookei	\mathbf{SC}	na	2	1	2	1	(#)					
YPM-PU 17940	P. cookei	SC-143	na	1*	2	0	0	(#)					
MNHN AL-5164	P. daubrei	Reims	?	0	0	(#)	1	1					
MNHN MUT 17147	P. daubrei	Mutigny	?	0	0	1	(#)	1					
MNHN MU 12302	P daubrei	Mutiony	?	0	2	2	0	1					

TABLE 4. Nearest neighbors (Nb) generated by Automated Correspondence Algorithm for p4 data set

Cells with a "1" stand for *Plesiadapis tricuspidens*, cells with a "0" for *P. daubrei*; "#" for NMB Bru4. Asterisks show incorrect classification by nearest neighbor.

Platychoerops daubrei but smaller than that for *Plesia-dapis russelli* and *Plesiadapis cookei* (Gingerich, 1976). Unlike the paraconids of p4-m2 of NMB Bru4, the paraconid of m3 is relatively small in size and positioned close to the metaconid. The paraconid expression is thus comparable to that in the m3 of other plesiadapids. There is a strong entoconid unlike m3's of *P. tricuspi-dens*, but similar to those of *Platychoerops* (Figs. 1 and 3). The m3 is absolutely and proportionally large for an m3 of *Platychoerops*. The tooth lacks any expression of a posterior cingulid rimming the hypoconulid lobe exhibited by *P. daubrei*, *P. russelli*, and some individuals of *P. tricuspidens*.

Quantitative comparisons

Tooth size and proportions. See Table 1 and Figure 3. Second molars of *Platychoerops* and *Plesiadapis tricuspidens* overlap in size (Boyer et al., 2010) and the NMB Mouras Quarry *Platychoerops* and *P. tricuspidens* dentitions are all within this range of overlap in their occlusal area. However, the p4 of *Platychoerops* is significantly larger than that of *P. tricuspidens* (Boyer et al., 2010). The p4 of NMB Bru4 is well outside the range for those of *P. tricuspidens* and well within the range for Eocene *Platychoerops*. The more simplified *P. tricuspi dens*-like p4's from NMB Mouras Quarry are smaller, such that they are well outside the range of values exhibited by Eocene *Platychoerops* and near/within that for *P. tricuspidens*.

Platychoerops specimens retaining both p4 and m2 show that the premolar is also proportionally enlarged compared with the condition in *P. tricuspidens* dentitions. The ratio of p4 area to m2 area in the new *Platychoerops* specimen is 0.83. This is in the range of Mutigny *Platychoerops daubrei* (MNHN Mu-12302 = 0.85, MNHN Mu-12301 = 0.81). However, the values exhibited by *P. tricuspidens*-like mandibles from the NMB Mouras Quarry collection have much lower ratios (NMB Bru2 = 0.52, NMB Cy1133 = 0.58) reflecting what appears to be typical for *P. tricuspidens* (Boyer et al., 2010).

Dental topography. See Table 2. RFI of m2 for NMB Bru4 is 0.53, which is just above the mean (0.52) and in the middle of the range (0.50–0.56) reported for *Platychoerops daubrei* by Boyer et al. (2010). It is well outside the range reported for *Plesiadapis tricuspidens* (0.40–0.50). The other two plesiadapid specimens are within the range reported by Boyer et al. for *P. tricuspidens* ratios (NMB Bru2 = 0.45, NMB Cy1133 = 0.46).

The complexity measure (OPC) for p4 in the NMB Bru4 is 58.25, which is slightly below the mean (62.25) but within the range (57.85–67.50) reported for *P. daubrei* by Boyer et al. (2010). However, the values exhibited by p4's of *P. tricuspidens*-like mandibles from the NMB Mouras Quarry collection have much lower complexity (NMB Bru2 = 37.25, NMB Cy1133 = 41.88). Even so, both of these specimens exhibit greater complexity than previously reported for *P. tricuspidens* (23.13–34.75). This is probably due to the presence of paraconids in these two specimens, which were absent from those included in Boyer et al. (2010).

Automated correspondence determination and analysis. See Tables 3 and 4 and Figures 4 and 5. The analysis was able to classify m2 specimens to their correct species with 100% success based on assigning each tooth to the taxonomic group of its nearest neighbor (Table 3), providing the necessary context for evaluating the affinities of the new specimen. For m2, the first, second, and sixth nearest neighbors of the NMB Bru4 are Eocene Platychoerops daubrei specimens. Likewise, the Mouras Quarry Platychoerops m2 constitutes the fourth nearest neighbor of MNHN Mu-6189 P. daubrei. However, it is not among the first six nearest neighbors of any 26 specimens of Plesiadapis tricuspidens. The m2's of two P. tricuspidens-like specimens (from the NMB Mouras Quarry sample) had *P. tricuspidens* specimens for all six nearest neighbors (Table 3).

For p4, specimens belonging to Platychoerops were always correctly classified as such, and no non-Platychoerops specimen was misclassified as Platychoerops. The first nearest neighbor of NMB Bru4 is a P. daubrei specimen, while the second is a *P. cookei* specimen. Out of four p4's belonging to Plesiadapis cookei, three of them were incorrectly classified as P. tricuspidens (Table 4), even though they actually seem to differ in some distinctive respects. Inspecting correspondence maps chosen by the algorithm, one finds m2's generally perfectly matched, cusp for cusp (Fig. 4a). However, the quality of the correspondence maps generated for the p4 data set was much more variable as judged against what is known to be lingual and buccal sides of these teeth and what has been argued about ontology of cusps by previous authors (Gingerich, 1976; Boyer et al., 2010). There are three different kinds of apparent mistakes made by the algorithm. 1) Some maps matched left sides of one tooth, to right sides of another. This was most frequent between premolariform type teeth of P. tricuspidens and

P. cookei to each other or of these teeth to more molariform ones of P. daubrei and NMB Bru4 (Fig. 4b: P. tri*cuspidens* is inverted compared to others). Additionally, 2) the trigonid cusps were not well matched even between premolars with a full complement of trigonid cusps (Fig. 4b: the paraconid of NMB Bru4 is matched to the paracristid of a *Platychoerops* specimen). Finally, 3) in P. cookei specimens with distinct paracristids (which develop phase I wear facets) and trigonid basins, these features were reconstructed as nonhomologous to those in Platychoerops specimens, in that the region within the trigonid basin on *Platychoerops* specimens was mapped to a region outside of and basal to this in P. cookei (Fig. 4b: note position of yellow patch 5 in P. cookei, NMB Bru4 and Plat. daubrei). While it is possible that evolutionarily some of these apparent "mistakes" represent true homologies (2-3 above) other cases are inarguable "mistakes." One must bear this in mind when interpreting the significance of the distance matrix and phenetic affinities determined by the algorithm for the p4 sample. It is possible that more careful choices of algorithm parameters could improve the p4 correspondence mappings; however, the number of values and combinations of values of parameters is too great to search manually and at present, we have no way to automate the search of parameter space for optimal mappings.

A MDS analysis on the Continuous Procrustes distance matrices recovered two components of variation that allowed complete separation between P. tricuspidens and P. daubrei in the case of both the m2 sample and the p4 sample (Fig. 5). The stress value for the m2 analysis was 0.343, while that for the p4 was 0.221. The relative error of embedding for the m2 analysis is 0.195, while that for p4 is 0.183. Note that the stress and error values for MDS are completely unrelated to accuracy of correspondence maps generated by the algorithm, and only reflect how well the interobject distances fit those of the original distance matrix. Stress and average error are positively correlated with sample size and the larger number of m2 specimens, relative to p4 specimens most likely explains the higher values here. Furthermore applying the minimum spanning tree based on Principle Coordinate Analysis (PCoA) of the Continuous Procrustes distance matrix also shows these groups to be distinct. Plotting m2 of NMB Bru4 in coordinate space with the rest of the sample after MDS analysis shows it to plot with the P. daubrei cluster, completely separated from P. tricuspidens. NMB Cy1133 and NMB Bru3 plotted within the MDS coordinate space occupied by P. tricuspidens specimens. However, plotting the p4 of NMB Bru4 with rest of sample shows an intermediate position between P. tricuspidens and P. daubrei. Applying the minimum spanning tree based on PCoA of the Procrustes distance matrix also shows NMB Bru4 to connect to both P. daubrei and P. cookei specimens. The p4 groups depicted by two variables resulting from MDS are not distinct when considering the connectivity of the minimum spanning tree based on PCoA. One P. cookei p4 connects to the *P. daubrei* group, while others connect to P. tricuspidens. However, as noted above, the correspondence maps used to generate the distance data for the p4 are suspect.

Phylogenetic analysis. The modifications and results for two different analyses are as follows: In the course of this study, we noticed that at least three plesiadapid



Fig. 6. Strict consensus cladogram of at least 2,137,590 trees. The tree length is 99. The consistency index is 64 and the retention index is 81.

specimens from the Mont de Berru collection at the NMB have dentitions that are largely consistent with identification as Plesiadapis tricuspidens (as documented above), yet exhibit small and distinct paraconids and metaconids on p4. Gingerich (1976) noted the presence of occasional metaconids, but did not mention paraconids for this species. Boyer et al. (2012) followed this description in their coding of *P. tricuspidens* in a 66 character matrix. Whereas P. tricuspidens was coded as lacking a paraconid, Plesiadapis dubius, Plesiadapis fodinatus, and Plesiadapis cookei were coded as polymorphic. The result of the cladistic analysis in Boyer et al. (2012) indicated that a clade containing the aforementioned taxa, but excluding P. tricuspidens was supported by (among other features) presence of a paraconid on p4. Thus, our new observation regarding the new sample of P. tricuspidens requires revision to the character matrix and presents the possibility of a new topology resulting. We made this change to the matrix of Boyer et al. (2012), reran their analysis, and found that this new information did not affect the number of trees, tree length, or resulting strict consensus topology.

Our second analysis aimed to evaluate the phylogenetic significance of the morphology of NMB Bru4 more formally. We added this specimen as a separate OTU and added codings for it to the matrix of Boyer et al. (2012). Because we observed additional characters of potential taxonomic relevance in this study we added those to the character matrix as well. Character 67 in this matrix is presence/absence of a posterior cingulid on m3. Character 68 in this matrix is presence/absence of a metaconid on p3. Character 69 in this matrix is absence/ presence of an m3 that is as large as that in *P. cookei*, *P. russelli*, and *Platychoerops richardsoni* (which have the largest molars of any known plesiadapid). See Appendix Table 1 and 2. Analyzing the matrix in Winclada and PAUP yielded identical strict consensus topologies, both with a tree length of 99, that were largely consistent with Boyer et al. (2012). The main difference was that the mosaic of states shared and differing between *P. cookei*, *P. russelli*, *P. richardsoni*, and NMB Bru4 eroded support for excluding *P. cookei* from the *Platychoerops* clade (Fig. 6).

TAXONOMIC ANALYSIS

Above, we have compared comprehensively and quantitatively NMB Bru4 to other late Paleocene and early Eocene species of plesiadapids showing overwhelming similarity to *Platychoerops daubrei* in most respects. However, some differences were also noted. Gingerich (1976) provides differential diagnoses for *Plesiadapis tricuspidens*, *Plesiadapis russelli*, *P. daubrei*, and the genus *Platychoerops* which must be referenced in order to formally justify a taxonomic attribution of NMB Bru4.

The diagnostic differences separating Platychoerops from Plesiadapis according to Gingerich (1976) are "having more molarized premolars, more complicated molars with highly crenulated enamel and in lacking the laterocone" (Gingerich, 1976:44). P. russelli is diagnosed as being "intermediate between P. tricuspidens and P. daubrei" (Gingerich, 1976:39). Technically P. russelli does not fit the current diagnosis of *Platychoerops* because it retains a laterocone on its central incisor, has a less fully molariform P4 and may have a more simple p3, therefore Gingerich (1976) included P. russelli in the genus Plesiadapis. Hooker (1994) moved P. russelli to Platychoerops without amending the generic diagnosis, which is why we continue to follow Gingerich's generic assignment here (as do Boyer et al., 2010, 2012). Because Gingerich (1976) included P. russelli in Plesiadapis, he also supplied diagnostic differences separating it from certain other species in the genus. Of particular relevance to this study are differences between P. tricuspidens and Plesiadapis cookei. P. russelli is said to differ from P. tricuspidens in "being larger, in lacking *Plesiadapis*-type paraconules on P3-4, and in lacking the centroconule crest and having a much smaller laterocone on I1" (Gingerich, 1976:39). P. russelli is said to differ from P. cookei in "having a more reduced laterocone on I1, in having an incipient paraconule on P4, and in consistently having a posterocinglid on m3" (Gingerich, 1976:39). Given these diagnoses and our observations, we amend the diagnosis of the genus Platychoerops and name a new species based on NMB Bru4.

SYSTEMATIC PALEONTOLOGY

Class: MAMMALIA Linnaeus, 1758. Order: PRIMATES Linnaeus, 1758. Family: PLESIADAPIDAE Trouessart, 1897. *PLATYCHOEROPS* Charlesworth, 1855.

Included species

Platychoerops richardsoni (type species) (Charlesworth, 1855) from the London Clay (division B?) of Herne Bay, Kent, England; *Platychoerops daubrei* (Lemoine, 1880) from Sparnacian lignites near Reims, France and *Plesia*-

dapis russelli (Gingerich, 1976) from the Conglomerat de Meudon, Meudon, France.

Emended diagnosis

Differs from other plesiadapid genera in having more molarized premolars (specifically in having at least an incipient molar-type paraconule on P4; in having p4 with a distinct molar-type paraconid, a metaconid that is similar in size to the protoconid, and a distinct trigonid basin; and in having a p4 that is at least 80% the size of m2 in occlusal area), in having more complex molars with greater crown relief and crenulated enamel; and in having a greatly reduced/absent laterocone and posterocone on I1.

PLATYCHOEROPS ANTIQUUS SP. NOV. (Figs. 1, 3, and 4).

Holotype

Right lower p3-m3 (NMB Bru4) with roots intact and m1 having been broken and glued back together.

Type locality

Late Paleocene (Thanetian) Mouras Quarry at Mont de Berru, near Reims, France.

Etymology

"Antiquus" (Latin) meaning ancient, for being the oldest recognized species of *Platychoerops*.

Diagnosis

Differs from *Platychoerops russelli* in having a welldeveloped metaconid on p3, lacking a posterior cingulid on m3, and having a substantially smaller m3. Differs from *Platychoerops daubrei* in having larger paraconids on p4 and m1 that are not closely appressed to the metaconids; and in lacking a posterior cingulid on m3. Differs from *Platychoerops richardsoni* in being smaller.

Discussion

Features differentiating NMB Bru4 from other plesiadapids. One of the major differences between NMB Bru4 and other *Platychoerops* and *Plesiadapis* is the strong paraconids that are situated more mesially, buccally, and basally than in other known specimens. In other *Platychoerops* and *Plesiadapis*, the paraconid is also twinned with the metaconid on m1-3, with the appression of these cusps usually strongest on the m2. Even on p4, other *Platychoerops* usually exhibit a twinning of the paraconid and metaconid. Nonetheless, rare isolated m2 specimens of *Platychoerops* from at least Mutigny, have nearly identical expression of the paraconid as compared with NMB Bru4.

The lack of a strong cingulid on m3 is another interesting difference between NMB Bru4 and both *P. tricuspidens* and other *Platychoerops*. Lack of a cingulid makes it more similar to *Plesiadapis cookei* among large plesiadapids. This could suggest that it is more basal than *Platychoerops russelli*. However, if *Plesiadapis cookei* is the ancestral stock for *Platychoerops*, *Platychoerops russelli* appears more primitive (anachronistically) in lacking a metaconid on p3 and having a very large m3 (in the range of that of *P. cookei*). Regardless of which features are basal, derived, or convergent, the mosaic expression of morphology in *P. russelli* and *Platychoerops antiquus* indicate that they are not anagenetically related.

Turning back to the distinctiveness of the paraconids in NMB Bru4, this trait does not constitute increased similarity with *P. cookei* and does not increase support for the hypothesis that *P. cookei* is phylogenetically closely linked to Platychoerops daubrei. However, this would also be problematic in the case for relating P. tricuspidens to P. daubrei. P. cookei, P. tricuspidens, and Eocene Platychoerops all typically exhibit similar degrees of twinning between paraconid and metaconid. Thus if NMB Bru4 represents a typical individual for Platychoerops antiquus, it would suggest that the twinning of paraconid and metaconid in later forms is a convergence with other plesiadapids. However, as some specimens of later *Platychoerops* still appear to exhibit low degrees of twinning on at least m2 (i.e., they have a large, distinct paraconid), it is possible that the evolutionary transition to *Platychoerops* simply involved an increase in variability regarding paraconid size and position. This hypothesis predicts that the paraconid distinctness in NMB Bru4 is not typical of all P. antiquus individuals and could be tested with further collecting. The mosaic pattern of similarities between P. cookei, P. antiquus, P. russelli, and P. daubrei therefore explains why cladistic analysis (Fig. 4) was unable to resolve the relationships among them, despite seemingly straightforward suggestions from overall morphology and chronological occurrence data.

Implications for previously identified transitional plesiadapid species. There are two plesiadapid taxa that have been described from very small composite samples of isolated teeth, which may alternatively represent previously unrecognized co-occurrences of *Plesiadapis* and *Platychoerops*.

Platychoerops russelli (referred to *Platychoerops* here) is one of these taxa. Gingerich's (1976) assignment of isolated teeth from Meudon to the single taxon P. russelli seems reasonable in that all preserved material appears essentially "intermediate" between *Platychoerops* mor-phology and that found in *Plesiadapis cookei* (Boyer et al., 2010, 2012) and/or P. tricuspidens (An I1 with a reduced laterocone and posterocone, a large p3, the lack of premolar-type paraconules on P3-4, and a very large m3 make it more Plesiadapis cookei-like, while the consistent presence of a posterior cingulid on m3 make it more Plesiadapis tricuspidens-like). However, Teilhard de Chardin (1922) had previously suggested that plesiadapid incisors from Meudon belong to Plesiadapis while the cheek teeth belong to Platychoerops. Our findings present the first definitive precedent for this possibility. Even so, we find little reason to suspect that *P. russelli* is chimeric. Another possibility is that the six fragmentary teeth comprising the total sample of P. russelli simply represent variation within Platychoerops daubrei, although Platychoerops incisor samples from Mutigny and Avenay suggest against this possibility as they do not include variants with vestigial posterocones and laterocones as seen in the incisors attributed to P. russelli.

Whereas *P. russelli* seems likely to be a single taxon despite its unassociated dentition, the composite of isolated teeth assigned to *Platychoerops georgi* (Hooker, 1994) seems more likely to represent multiple taxa or a

side branch of plesiadapid evolution. For this reason, we have not mentioned it among the included species of *Platychoerops*.

The combination of characters present in *P. georgi* are not consistent with its intermediate positioning between P. tricuspidens and P. daubrei under any scenario. It has *Chiromyoides*-like incisors with a crest formed between the mediocone, centrocone, and laterocone; a very large posterocone; and a short, robust crown. Hooker (1994) decides against a Chiromyoides attribution for these because the laterocone appears more *Plesiadapis*-like to him and because molars from Try (Marne) France, which he reidentifies as Chiromyoides (previously identified as Plesiadapis aff. remensis), are too large to match with the incisors. These incisors, if correctly associated with other material assigned to P. georgi, represent a shift in the opposite direction from that represented by P. russelli relative to P. tricuspidens. When Hooker (1994) described P. georgi, Platychoerops and Plesiadapis were not known to co-occur in latest Paleocene/earliest Eocene deposits, so it was natural to assume that the more *Plesiadapis*-like incisors and premolars he studied belonged with the same species as the more *Platychoerops*-like molars. However, the find described here provides definitive evidence of cooccurrence of Plesiadapis and Platychoerops. This suggests to us that Hooker's (1994) P. georgi also represents at least two plesiadapid species. The incisors and premolars probably represent P. tricuspidens, and Plesiadapis aff. remensis or Chiromyoides sp. while the molars probably represent P. daubrei or P. russelli.

Dental topography. Use of dental topographic metrics proved a powerful tool in this analysis in showing different plesiadapid specimens at Mouras Quarry to be strongly differentiated in dietarily significant topographic features (e.g., Boyer et al., 2010), suggesting niche partitioning among sympatric large-bodied plesiadapids during the late Paleocene in Europe. NMB Bru4 has high cusp/crest relief on its m2 and high complexity on both m2 and p4 indicating a strongly folivorous diet. NMB Bru3 and NMB Cy1133 have dramatically lower relief and complexity indicating a more generalized diet (Boyer et al., 2010).

Automated correspondence determination and analysis. Because topographic data do not quantify variation relative to homologous features (e.g., particular cusps), we ran the ACDA of Boyer et al. (2011) to assess whether NMB Bru4 was also more Platychoerops-like in the relative sizes and configurations of corresponding cusps and crests. We found that the m2 data set was an ideal case for the ACDA of Bover et al. (2011) because correspondence maps generated between virtually all pairs of teeth were extremely accurate regarding identifiable surface features. Furthermore, the analyses proved to sort reliably Plesiadapis from Platychoerops teeth. Unfortunately, the performance of this method on the p4 dataset was much less successful in a number of ways described in the results. We attribute the problematic performance with p4 data set to at least three factors: 1) the more extreme variability present in this dataset compared with the m2 dataset, 2) the more simple and sometimes bilaterally symmetrical structure of isolated p4's, and 3) the computational difficulty involved in searching the potential parameter space of the algorithm for values that might find correspondence maps more successfully (see Appendix B).

One benefit of this method is that because variation is standardized to the area of tooth surfaces, the diversity in shapes represented by different tooth samples can be compared directly. Comparing the m2 and p4 plots with axes of the same scale in Figure 5 demonstrates the much stronger diversity of p4 relative to m2 (i.e., the p4 data have a larger range of values on both axes).

SUMMARY AND CONCLUSIONS

Morphology of NMB Bru4 strongly suggests that it is a previously unrecognized species of plesiadapid. Its morphology is closest to and is consistent with previous (Gingerich, 1976) and amended (this article) diagnoses for the genus *Platychoerops*. Thus we assign it to the species *Platychoerops antiquus*. The co-occurrence of *P*. antiquus of Plesiadapis tricuspidens at the Paleoceneaged Mouras Quarry of Mont de Berru therefore demonstrates that P. tricuspidens and Platychoerops were not part of a single lineage as proposed by Gingerich (1976). Because there is no substantially earlier record of P. tricuspidens than those from the conglomeratic lenses overlying the Sables de Rilly Formation around the Mont de Berru, it is difficult to entertain an alternative possibility that an earlier occurring population of P. tricuspidens evolved into the Mouras Quarry Platychoerops. Cladistic analysis confirms these phylogenetic implications, showing that *P. antiquus* is in a clade with other *Platychoerops* species as well as *Plesiadapis* cookei, to the exclusion of Plesiadapis dubius and Plesiadapis fodinatus, followed by P. tricuspidens, Plesiadapis simonsi, and Plesiadapis gingerichi. Instead, this pattern of co-occurrences and cladistic topology are more consistent with derivation of Platychoerops from an immigrant North American taxon, most likely Plesiadapis cookei; however, cladistic topologies alone are not resolved enough yet to support specifically this scenario. In addition, the Paleocene occurrence of P. antiquus demonstrates that the evolution of the ecomorphologically unique plesiadapid genus *Platychoerops* (with large premolars relative to the molars, molariform premolars, high relief, and highly complex premolars and molars) was not a function of Paleocene-Eocene boundary environmental and faunal changes. Instead, it seems likely that character displacement from competition with P. tricuspidens in the late Paleocene could have caused the transition to Platychoerops in an ancestral population most closely related to P. cookei with more incipient adaptations to folivory. It still appears that the adaptations to folivory exhibited by Platychoerops allowed it to survive into the Eocene for several million years whereas other plesiadapids succumbed to extinction earlier.

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APPENDIX A: HISTORY OF STUDY AND TERMINOLOGY OF CERNAY FOSSILS

The Cernay fauna is the reference fauna of level MP6 of the Paleogene European biochronological time-scale. Our discovery shows the inclusion of a new taxon, *Platychoerops*, previously indicative of later faunas. We therefore review the context in which the Cernay fauna has been accumulated and identified.

Geology

The Paris Basin is a subsident basin that accumulated marine and continental sediments over more than a kilometer thickness since the Triassic. The Paleogene in the Basin is marked by a Paleocene marine transgression coming from the North and Northwest. However, the South and eastern parts of the Basin were emerged in the Late Paleocene and river systems together with estuaries or deltas developed on land and on the coasts.

The Mont de Berru, of interest here, is a geological feature situated between the villages of Cernay-lès-Reims to the West, Berru to the East and Nogent l'Abesse to the Southeast (Fig. 2). It is a residual hill

TABLE A1. Codes for Characters 67-69

Taxon	67	68	69
Purgatorius	0	0	0
Elphidotarsius wightoni	0	0	0
Carpolestes simpsoni	0	0	0
Plesiadapis tricuspidens	0&1	0	0
Plesiadapis cookei	0	0	1
Plesiadapis rex	0	0	0
Plesiadapis anceps	0	0	0
Nannodectes intermedius	0	0	0
Nannodectes gidleyi	0	0	0
Pronothodectes gaoi	0	0	0
Platychoerops daubrei	1	1	0
Plesiadapis churchilli	0	0	0
Plesiadapis insignis	0	0	0
Plesiadapis walbeckensis	0	0	0
Plesiadapis remensis	0	0	0
Plesiadapis praecursor	0	0	0
Pronothodectes matthewi	0	0	0
Pronothodectes jepi	0	0	0
Plesiadapis dubius	0	0	0
Plesiadapis simonsi	?	?	0
Plesiadapis gingerichi	0	0	0
Plesiadapis fodinatus	0	0	0
Nannodectes gazini	0	0	0
Nannodectes simpsoni	0	0	0
Chiromyoides minor	?	?	?
Chiromyoides potior	?	?	?
Chiromyoides caesor	?	?	?
Chiromyoidesmajor	?	?	?
Chiromyoides campanicus	0	0	0
Platychoerops russelli	1	0	1
Platychoerops richardsoni	1	?	1
NMB Bru4	0	1	0

TABLE A2. Character codes for NMB Bru4

								,											-
20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21
?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?	?	?
60	59	58	57	56	55	54	53	52	51	50	49	48	47	46	45	44	43	42	41
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
											69	68	67	66	65	64	63	62	61
											0	1	0	?	?	?	?	?	?
	? 59 ?	? 58 ?	? 57 ?	? 56 ?	? 55 ?	? 54 ?	? 53 ?	? 52 ?	? 51 ?	? 50 ?	1 49 ? 69 0	1 48 ? 68 1	1 47 ? 67 0	1 46 ? 66 ?	1 45 ? 65 ?	? 44 ? 64 ?	? 43 ? 63 ?	? 42 ? 62 ?	? 41 ? 61 ?

Character number in bold with code below. See Boyer et al. (2012) for character descriptions.

that preserves early Cenozoic continental sediments on top of Cretaceous marine limestones. There, Paleocene and Eocene sediments crop out and are differentiated in several geological formations: the Sables de Rilly Formation (a white and very fine well sorted sand) of Thanetian age lying uncomformably on top of the Upper Cretaceous Campanian marine limestones, the Conglomérat de Cernay formation of Thanetian age and Ypresian marls and sands partly covered by nondifferentiated Upper Eocene sediments on top of the hill (Aumonier and Eck, 1873; Teilhard de Chardin, 1922; Russell, 1964).

The Conglomérat de Cernay formation became well known for its rich content of Paleocene fossils as early as the late 1800's (Lemoine, 1880). It is a fluvial formation with lateral facies and thickness changes; it is variously composed of sands, muds, marls, lignitic fine layers or lenses, and calcareous pebbles or gravels (Teilhard de Chardin, 1922; Russell, 1964). Published sedimentological sections on two well-exposed sites on the Mont de Berru (Lemoine Quarry to the West, Teilhard de Chardin, 1922; and Mouras Quarry to the East, Russell, 1964) show its lateral facies variations.

Guérin et al. (1970) and later Laurain and Meyer (1986) described the stratigraphy and lithologies at the Mouras quarry and indicate where historical fossil discoveries were made. White and yellow sands, unconformably overlying the white Sables de Rilly and showing intercalations of coarser sands and gravels, yielded vertebrates. These remains were embedded in lenses of the same facies, and apparently same stratigraphic position as the Conglomérat de Cernay. Younger marls deposited in eroded parts of the latter sands also yielded a vertebrate fauna. The vegetation cover being dense at Berru, precise stratigraphic correlations between different outcrops prove very difficult. A visit to the eastern side of the Mont de Berru by DMB, LC and local villagers of Berru (see acknowledgements) on June 2, 2012 confirmed the stratigraphic sequence given in Guerin et al. (1970) at an outcrop [N 49° 16' 07.1"/E 004° 08' 26.5" (Datum: WGS 1984)] located about 50 m east of what we were told is Russell's excavation from the late 1950's [N 49° 16' 05.3''/E 004° 08' 22.1" (Datum: WGS 1984)]. At the time of our visit, much of Mouras Quarry had been back-filled. This activity has little bearing on the areas that yielding published fossils, as these sites are at the very top of the Quarry and on its eastern margin well separated from the back-filling work.

History of discoveries

The beginning of field investigations around the town of Reims and more specifically the village of Cernay-lès-Reims dates back to second half of the 19th century

when Aumonier and Eck (1873) described the geology of the "Montagne de Berru," now known as Mont de Berru to the east of Cernay-lès-Reims. Thereafter a naturalist from Reims, Dr. Victor Lemoine, excavated the Mont de Berru until the end of the 19th century. He published his results from 1878 to 1896 in more than 15 articles and communications to the Académie des Sciences, Association Française pour l'Avancement des Sciences and French Geological Society (see list in Teilhard de Chardin, 1922). Lemoine gathered an impressive collection of fossil mammals from the Mont de Berru and from other sites located in the vicinity where the Conglomérat de Cernay formation crops out. Lemoine himself indicated that most of the fossils he could find came from the Mont de Berru and especially from one single site; he called Cernay (see below for nomenclature of sites; Lemoine 1880, 1896). His work led him to establish a typical mammal fauna for all the prospected sites of the area and that he called the "Cernaysian fauna" ("faune cernavsiene"). This fauna, thus a composite of various sites, was quickly found to be homogeneous in composition between the different sites Lemoine excavated, most of his information actually coming from a single locality ("Cernay"). He further stated that although this fauna was mostly derived from the Conglomérat de Cernay geological formation, it also appeared to occur in other closely related geological formations. His collections are deposited at the Museum National d'Histoire Naturelle in Paris (MNHN). Depéret (1907) briefly synthesized the stratigraphic framework of the Paleogene around Reims paying tribute to the work of Lemoine and others. He mentioned other discoveries made by local people, not while excavating for fossils but rather while digging a well.

The prospection on the Mont de Berru continued after the death of Lemoine in 1897 and Teilhard de Chardin in 1919 and 1920 investigated the hill at different sites and outcrops including Lemoine's "Cernay" site. He published his sedimentological and paleontological results in 1922. Later Russell from the MNHN returned and excavated from 1957 up until 1960 in two different quarries, the Lemoine Quarry and a newer (discovered in 1955) fossiliferous locality close to the village of Berru, the Mouras Quarry. His discoveries, together with the Lemoine collection, form the basis of his seminal dissertation on the European Paleocene mammals (Russell, 1964). Russell et al. (1966) describe another fossiliferous level in this quarry, a lense ("Lentille"), which is different from the first investigated deposit excavated in the late 1950's, but still inside the Conglomérat de Cernay formation. The plesiadapids found in this Lentille were later reinvestigated by Gingerich (1976). After Russell's work, no other excavation organized by scholars was ever re-opened but several amateur paleontologists continued to investigate the area. One of them, Marc Duchamplecheval, found other fossiliferous levels in the Mouras Quarry in the 1970's and the Naturhistorisches Museum Basel (NMB), among others, acquired parts of his collections. The fossil described in this article comes from his collections.

Nomenclature

Some confusion has arisen with time on the use of terms referring to the localities that yielded fossil mammals in the Paleocene of the area around Cernay-lès-Reims. This confusion has much to do with a certain inconsistency from Dr. Lemoine, who never precisely located his discoveries. This was also common practice at that time. Lemoine gathered fossils from many localities but stated, as recalled above, that the most productive one was a single site on the Mont de Berru: he named it "Cernay" because it was located on the territory of the village of Cernay-lès-Reims. This led to some confusion when he named the whole Paleocene fauna of the Reims region the "Cernay fauna" or "Cernaysian fauna." In his writing, it is therefore often difficult to tell whether a discussed fossil can be attributed to the "Cernay (=Lemoine) Quarry" in particular, or whether it could have come from any of the sites Lemoine excavated in the Conglomérat de Cernay formation, and attributed to the "Cernay fauna." The second option often seems more likely from contextual cues. Later on, Teilhard de Chardin (1922) renamed Lemoine's "Cernay" site "Gîte Lemoine" to refer to the main place where Lemoine found fossils. This name remained valid up until today and Russell (1964) used the name Lemoine Quarry ("carrière Lemoine") to refer to it (see also Fig. 2). However, Russell also used the name "Cernay" to refer to this quarry while comparing to the new site he excavated in the late 1950s: "Mouras Quarry," named after a company that opened this quarry. Since Mouras Quarry is located on the territory of the village of Berru east to Cernay-lès-Reims and to the Mont de Berru, Russell would also call it simply "Berru." Russell et al. (1966) mentioned this important synonymy when describing a new fossiliferous layer inside Mouras Quarry, different from the first deposit he worked on in the late 1950s. This new layer being, geologically speaking, a lense (lentille in French), they named it "Lentille de Berru" or simply "Lentille" and this term was then later used by Gingerich (1976). The latter also exclusively used the name Cernay to refer to fossils believed to be derived from the Lemoine Quarry due to their being labeled "Cernay" in the MNHN collections and due to Russell's confirmation of their provenance (pers. comm. Gingerich, May 2012).

Later, other fossiliferous levels (at least one) were found inside this quarry by amateur paleontologists (constituting the collection of the NMB, pers. comm. Duchamplecheval, February 2012), but no real stratigraphical data exist to position the discoveries relative to one another (such as already mentioned by Russell et al., 1966 for "Lentille" and his other deposit of Mouras Quarry). A communication with M. Duchamplecheval (June 2012) gave us better stratigraphic control on the finds. It appears that most of the fossils he collected, including NMB Bru4, come from the base of the sandy formation unconformably overlying the white Sables de Rilly. Another level he excavated, slightly higher in the same formation (about 2 m higher), also yielded other specimens, mostly skulls (including one of *P. tricuspi*- *dens*), but we do not mention these discoveries in this article.

The same names, Cernay and Berru, are thus used for villages (Cernay-lès-Reims and Berru), geographic or geological features (the Mont de Berru), fossiliferous sites (Lemoine and Mouras Quarries, respectively), and faunas (the Cernaysian or Cernay fauna of Lemoine and all other subsequent authors). However, it is clear that when Cernay is used as a fossiliferous locality name, it refers to Lemoine Quarry. In addition, when Berru is used as a fossiliferous locality name, it refers to Mouras Quarry with the exclusion of Russell et al. "Lentille." The Cernay fauna (or Cernaysian fauna) is a composite fauna, which faunal list is composed of species found in the Conglomérat de Cernay formation whatever the precise location of the contributing sites. The two most important sites in terms of number and quality of fossils found are the Lemoine and Mouras Quarry. The Cernay fauna, although a composite and because of its richness and the very slight, if any, age difference between the contributing sites, is now the reference level MP6 of the Paleogene European biochronological time-scale.

APPENDIX B: DETAILS ON ACDA METHODS

Several parameters are adjustable and can improve or degrade the correspondence maps identified by the algorithm. That is, if parameters are chosen correctly the algorithm will not make mistakes such as matching the buccal side of one tooth to the lingual side of another, etc. Further details on standard implementation of the ACDA can be obtained from Boyer et al. (2011).

- 1. The algorithm can be run with or without a feature called "Moser's projection." We run the analysis without for both data sets. Moser's projection forces the deformation involved in mapping one tooth to another to be area preserving.
- 2. The morphological distance between two surfaces is computed by optimizing the discretized Continuous Procrustes Distance (CPD) over a collection of candidate maps generated by examining pairs of feature points (like cusp tips). There are few parameters controlling the discretization of the CPD and the choice of feature points, as follows:
 - a. We used 50 (m2) or 150 (p4) points to approximate the Continuous Procrustes functional: we choose the points by taking local feature points (local maxima of gauss curvature is used here) and adding evenly distributed points using farthest point sampling until we get to 50 points or 150 points.
 - b. The feature points pairs used to identify potential correspondence maps are chosen as local maxima of some curvature function over the surface. In the case of m2 dataset, we used the "conformal factors" (which measures the local scaling of the surface, and tends to reveal extremities). For the p4 dataset, we used the "mean curvature" that tends to pick areas for which the sum of the two principle curvatures is high. The reason we used curvature for p4 is that it tends to pick more points than the conformal factors, and on the p4 dataset there are not many extremities (i.e., not as many distinct cusps).

- c. The local maxima of the curvature function are defined by two parameters: the size of neighborhood in which we ask a value to be maximal, and smoothing level of the function. We have used local neighborhoods of size 8 and 12 smoothing iterations for m2; and local neighborhood size of 15 and 15 smoothing iterations for p4. The smoothing, as well as local neighborhood size, is used to remove "noise" in the surface model that could incorrectly be identified as biological feature points otherwise.
- d. Finally, because the edge of the tooth surface can be "noisy" we typically specify a standard margin to be ignored by the analysis. We specify 3% of the surface around the edge be ignored by the algorithm's calculations for both data sets.

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