



# Tooth Root Size, Chewing Muscle Leverage, and the Biology of *Homunculus patagonicus* (Primates) from the late early Miocene of Patagonia

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**Abstract.** Inferences about the diet of Miocene platyrrhine monkeys have relied upon the morphology of the molar teeth, specifically the crests on the molars. Using a library of Micro-CT images of a broad comparative sample of living platyrrhines (callitrichines, cebines, pitheciids and atelids), late early Miocene *Homunculus*, and the early Miocene *Tremacebus* and *Dolichocebus*, we extend these inferences by examining the surface areas of the tooth roots, anchor points for the periodontal ligaments. From muscle scars on the skull, we estimate the mechanical leverage of the chewing muscles at bite points from the canine to the last molar. Extant platyrrhines that gouge bark to obtain exudates do not have especially large canine roots or anterior premolar roots compared with their less specialized close relatives. Extant platyrrhines that have more folivorous diets have much larger molar roots than do similar-sized more frugivorous species. *Homunculus patagonicus* has large postcanine roots relative to body size and poor masticatory leverage compared to the extant platyrrhines in our sample. The large postcanine roots, heavy tooth wear, and moderately-long shearing crests suggests a diet of abrasive, resistant foods. However, relatively poor jaw adductor leverage would have put the masticatory apparatus of *Homunculus* at a mechanical disadvantage for producing high bite forces compared to the condition in extant platyrrhines. *Tremacebus* and *Dolichocebus*, like *Homunculus*, have larger tooth root surfaces than comparable-sized living platyrrhines. They also resemble *Homunculus* in being more prognathic and having posteriorly-located temporalis origins - all features of a relatively poor leverage system.

**Resumen.** TAMAÑO DE LAS RAÍCES DENTARIAS, BRAZOS DE PALANCA DE LA MUSCULATURA MASTICATORIA Y BIOLOGÍA DE *HOMUNCULUS PATAGONICUS* (PRIMATES) DEL MIOCENO TEMPRANO DE PATAGONIA. Las inferencias sobre dieta de monos platirrininos miocenos se han basado en la morfología de los molares, específicamente las crestas. Aquí se estudia la superficie de las raíces de los dientes, área de anclaje del ligamento periodontal. Se utilizó una base de datos de imágenes Micro-CT de platirrininos actuales (calitriquininos, cebinos, pitécidos y atélidos), *Tremacebus* y *Dolichocebus* (Mioceno temprano) y *Homunculus patagonicus* (Mioceno temprano tardío). Basándose en las cicatrices musculares preservadas en los cráneos, se estimó el brazo de palanca de los músculos masticatorios en puntos de mordida desde el canino hasta el último molar. En los platirrininos actuales que se alimentan de exudados, las raíces de los caninos o premolares anteriores no son especialmente grandes; en los folívoros, las raíces de los molares son mucho más grandes que en los frugívoros de tamaño similar. Las raíces de los postcaninos de *H. patagonicus* son más grandes en relación a su tamaño corporal que en cualquier otro platirrinino viviente analizado; las raíces postcaninas grandes, el excesivo desgaste de los dientes y las crestas cortantes moderadamente largas sugieren un consumo de alimentos abrasivos y resistentes. Sin embargo, la palanca aductora relativamente pobre de la mandíbula indica una desventaja mecánica para producir fuerzas de mordida elevadas en comparación con platirrininos actuales. *Tremacebus* y *Dolichocebus* también poseen superficies de las raíces más grandes que los platirrininos vivientes de tamaño equivalente y se asemejan a *Homunculus* por ser más prognatos y por el origen del músculo temporal ubicado posteriormente, rasgos que indican un sistema de palancas relativamente pobre.

**Key words.** Primates. Platyrrhini. *Homunculus*. Miocene. Teeth. Diet.

**Palabras clave.** Primates. Platyrrhini. *Homunculus*. Mioceno. Dientes. Dieta.

## Introduction

Platyrrhines, or New World monkeys, are a diverse radiation of primates that includes a wide

range of body size and dietary preferences (Ford and Davis, 1992). Today, more than 70 platyrrhine species are recognized, belonging to three families (Schneider, 2000). In contrast, fossil platyrrhines are rare and fragmentary (MacFadden, 1990; Fleagle and Kay, 1997) and inferences about their paleobiology are largely limited to dental remains (Kay *et al.*, 2002), although a modest record of postcrania has allowed for locomotor inference in some species (Ford, 1990; Meldrum, 1993).

Primates first appear in the fossil record of South America in the late Oligocene (Deseadan), represented by teeth and jaws of the species *Branisella boliviana*

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Hoffstetter, 1969 from a single stratigraphic level at Salla, Bolivia (Hoffstetter, 1969; Wolff, 1984; Rosenberger *et al.*, 1991; Takai and Anaya, 1996; Kay *et al.*, 2002). All the other Tertiary records of platyrrhines are from the Miocene. These are from sites in Argentina, Colombia, Chile, and Brazil, with fossil primates from five Land Mammal Ages-Colhuehuapian, Santacrucian, Colloncuran, Laventan, and Huayquerian (Rusconi, 1935; Hershkovitz, 1970; Fleagle and Kay, 1989; Kay and Frailey, 1993; Flynn *et al.*, 1995; Fleagle *et al.*, 1997; Fleagle and Tejedor, 2002; Tejedor, 2005a, 2005b; Kay and Cozzuol, 2006; Tejedor *et al.*, 2006; Kay *et al.*, 2008a; Tejedor, 2008).

*Homunculus patagonicus* Ameghino, 1891 is the best-known and best-preserved fossil primate from the Tertiary of South America. It comes from the late early Miocene Santa Cruz Formation of Patagonia. *Homunculus* fossils come from a series of localities along the Atlantic coast of Santa Cruz Province and along the estuary of the Río Gallegos, Argentina (Tauber, 1991; Kay *et al.*, 2008b). The extraordinary completeness of the cranial specimens allows us an exceptional opportunity to reconstruct aspects of cranial functional morphology that are unavailable for other Tertiary platyrrhines.

Florentino Ameghino described several specimens now considered to belong to *Homunculus patagonicus*, including relatively complete mandibles, fragments of long bones, and a partial cranium (Ameghino, 1891; Bluntschli, 1931; Rusconi, 1935). Several decades later, another partial cranium (CORD-PZ 1130) was discovered and described by Tauber (1991). Since 2003, a yearly joint U.S.-Argentina field expedition has recovered four additional partial crania - including two that are nearly complete, a partial mandible, and additional long bone fragments from localities along the coast (Estancia La Costa, Puesto Estancia La Costa = Corrigüen Aike; Marshall, 1976) and at Killik Aike Norte on the north shore of the estuary of the Río Gallegos. An additional monkey cranium preserving the face and orbits from Killik Aike Norte was described in 2006 as a new genus and species, *Killikaike blakei* Tejedor *et al.*, 2006. This specimen is insufficiently complete for inclusion in our biomechanical analysis.

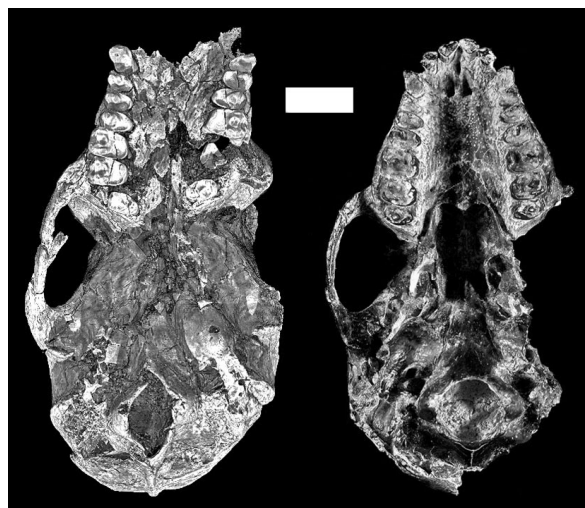
To date, most of the work on *Homunculus* has focused on its phylogeny and taxonomy (Bluntschli, 1931; Stirton, 1951; Hershkovitz, 1970, 1974; Rosenberger, 1978; Hershkovitz, 1981, 1984; Rosenberger *et al.*, 1990; Zhang *et al.*, 2000; Kay *et al.*, 2005; Tejedor and Rosenberger, 2008). Studies of cranial functional morphology are limited to an analysis of the molar structure (Fleagle *et al.*, 1997) and remarks on masticatory function in two papers by Tauber (1991, 1999) and one by Tejedor and Rosenberger (2008).

Molar crown morphology is correlated with diet AMEGHINIANA 47 (3), 2010

in primates (Butler, 1973; Kay, 1975, 1977; Corruccini and Beecher, 1982; Gordon, 1982; Janis, 1984; Teaford and Walker, 1984; Covert, 1986; Kinzey, 1992; Rosenberger, 1992; Strait, 1993; Kay *et al.*, 2004; Lucas, 2004). Dental morphology, especially the small incisors and moderately developed shearing crests on the cheek teeth suggest that *Homunculus* was a mixed frugivore-folivore (Fleagle and Kay, 1997; Fleagle *et al.*, 1997). An abrasive diet is inferred because most specimens of *Homunculus* have very high degrees of molar wear (figure 1) (Tauber, 1999). Extant frugivorous platyrrhines seldom show such a high degree of molar wear (Kay *et al.*, 2002).

Tauber (1991) suggested, based on the surface rugosity and sharp delineation of attachments for the temporalis and buccinator muscles, that this extinct platyrrhine had a very powerful masticatory system - more so than in extant pitheciines and more so than in early Miocene *Dolichocebus gaimanensis* (Kraglievich, 1951) and *Tremacebus harringtoni* (Rusconi, 1933).

Tejedor and Rosenberger (2008) compared *Homunculus* with pitheciines. They suggested that the morphology of the anterior dentition and the shape of the mandibular corpus in the former could be a precursor to the derived condition seen in modern pitheciines. These authors did not venture ecological inferences for *Homunculus* beyond the comparison to pitheciines. Rosenberger *et al.* (2009) summarized a view of the dietary adaptations of *Ho-*



**Figure 1.** Ventral views of *Homunculus patagonicus* specimens MPM-PV 3501 (left) and MPM-PV 3502 (right) / vistas ventrales de los especímenes de *Homunculus patagonicus* MPM-PV 3501 (izquierda) y MPM-PV 3502 (derecha). The picture at left is a volume reconstructed from CT scans / la imagen de la izquierda está reconstruida a partir de tomografías computadas. The picture at right is a photograph of the original specimen / la imagen de la derecha es una foto del espécimen original. Notice the heavy tooth wear on both specimens / nótese el excesivo desgaste dentario de ambos especímenes. Scale bar = 1 cm / escala = 1 cm.

*munculus* based on the teeth. They suggested that the prognathic incisors and premolar morphology indicate hard-fruit husking. They further note that *Homunculus* has large cheek teeth with heavy wear and well-developed molar shearing crests, suggesting some folivory, at least seasonally.

New cranial material for *Homunculus* permits us to refine the observations of Tauber (1991, 1999) and those of Tejedor and Rosenberger (2008) and Rosenberger *et al.* (2009). While it is impossible to evaluate the forcefulness of the chewing muscles directly in a fossil, it is possible to evaluate whether or not its skull geometry was especially well-suited to bite-force generation and absorption. Because several crania and mandibles of *Homunculus* are preserved, we can analyze muscle leverage in a composite specimen. Unfortunately, it is not possible to perform a detailed analysis on *Tremacebus* or *Dolichocebus* because known material is insufficient: an intact lower jaw has not been recovered for either species. However, we can offer some observations, based on the available cranial morphology.

Tooth root size may be a useful indicator of chewing forces (Wood *et al.*, 1988; Spencer, 2003; Kupczik and Dean, 2007). Therefore, it may be a valuable adjunct in reconstructing the diets of extinct species, particularly when tooth crowns are heavily worn or broken away. Bite force is transmitted through the tooth roots. The periodontal ligament is composed of Sharpie's fibers that anchor the root to the surrounding alveolar bone and act to resist root displacement (Beertsen *et al.*, 1997). A root that has a greater surface area can potentially accommodate more Sharpie's fibers, is likely to be more stable within its alveolus, and is better equipped to resist heavy or repetitive incisive or masticatory loads.

The goal of this study is to evaluate the hypothesis that the masticatory system of *Homunculus* was adapted for producing considerable bite force (Tauber, 1991, 1999) and to offer inferences about the properties of the foods in the diet of *Homunculus* based on masticatory biomechanics and tooth root size. We measured tooth root areas in *Homunculus* to test the hypothesis that this Miocene primate was eating extremely resistant foods that may have contributed to its high degree of molar wear. We also offer observations on *Tremacebus* and *Dolichocebus* where pertinent. These analyses are comparative, using a sample of extant platyrrhines with known diets.

Based on the anatomy of living platyrrhines we can evaluate several functional possibilities relating diet and tooth root areas. We assume that repeated loading cycles should favor large tooth root areas where the load occurs. There should also be systematic variation in the distribution of root area in relation to where chewing forces are generated. Canine

roots are expected to be larger in taxa that process primarily fruits and nuts as these species often perform a lot of forceful food processing with the canines. The hypothesized relationship between canine size and fruit consumption is potentially confounded by several factors: 1) Many species of platyrrhines exhibit canine sexual dimorphism but there is little evidence that diet or food acquisition behavior differs between males and females. 2) Some platyrrhines (e.g., Chiropotes) use their canines to pry open the husks of hard-shelled fruits to gain access to seeds; others (e.g., *Saguinus*) ingest soft ripe fruits taking few or no bites, thereby swallowing the seeds whole (Kinzey and Norconk, 1990). The former would be expected to have large canines whilst the latter may not. Folivores, by contrast, are expected to have larger roots on more posteriorly-positioned cheek teeth than on anterior teeth because most leaf-processing occurs posteriorly and should involve repeated chewing cycles.

Within our sample of extant platyrrhines, two comparisons of root area are particularly interesting: that between two atelids, *Alouatta guariba* and *Ateles geoffroyi*, and that between two callitrichine cebids *Callithrix jacchus* and *Saguinus fuscicollis*. In each of these pairs, there are differences in diet and/or food procurement. *Alouatta guariba* consumes a diet rich in leaves, immature leaves are preferred but mature ones are consumed in times of need, and only a small percentage of fruit is consumed (Chiarello, 1994). By contrast, *Ateles geoffroyi* consumes primarily ripe fruit and does not split open the seeds contained within the fruits (Cant, 1990; Chapman and Chapman, 1991; Strier, 1992). We would expect that postcanine tooth roots have larger areas in *Alouatta* than in *Ateles* due to the need for masticating tough leaves in *Alouatta*. We predict that canine root area (and incisor root area, for which we have no data) might be greater in *Ateles* due to the need for considerable anterior tooth use in processing fruits, but with the caveat that such differences may be masked by sexual selection and also depend on the manner in which the fruit is consumed (see footnote).

*Callithrix jacchus* uses its lower incisors and inciform lower canines to scrape and gouge tree bark in search of plant exudates, whereas *Saguinus fuscicollis* does not use its anterior teeth in this way (Sussman and Kinzey, 1984; Ferrari, 1993). We predict that anterior tooth roots (*i.e.*, the canine root) will have a larger surface area in *Callithrix* to accommodate forceful gouging. Vinyard and colleagues found that gouging in these callitrichids is not associated with large forces (Vinyard *et al.*, 2001) or with especially strong jaw adductor muscles (Taylor and Vinyard, 2004). Therefore, if our prediction is not met, it may be because gouging does not require large forces and this may be reflected in tooth root area.



A final prediction stems from ecological studies that suggest that *Pithecia* masticates extremely resistant seeds (Kinzey and Norconk, 1990; Kinzey, 1992). We predict that tooth root area in *Pithecia* will be great relative to the other extant species in our sample.

**Material. Acronyms:** CORD, Universidad Nacional de Córdoba, Córdoba, Argentina; NMNH, National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MPM, Museo Regional Provincial "Padre M.J.Molina", Río Gallegos, Argentina.

All measurements were taken from CT scans of skulls of extant platyrrhines and crania of extinct platyrrhines. A single specimen was scanned for each species; all are museum specimens.

We collected data on nine extant platyrrhine species: *Alouatta guariba*, *Ateles geoffroyi*, *Callithrix jacchus*, *Cebus nigrovittatus*, *Cebuella pygmaea*, *Callicebus torquatus*, *Mico argentatus*, *Pithecia* sp., and *Saguinus fuscicollis* (appendix 1).

We collected data on three extinct platyrrhine species: *Homunculus patagonicus*, *Dolichocebus gaimanensis*, and *Tremacebus harringtoni* (appendix 1). Root



**Figure 2.** Composite skull of *Homunculus patagonicus* / cráneo compuesto de *Homunculus patagonicus*. The cranium is a CT image of MPM-PV 3502 / el cráneo es una imagen de tomografía computada del MPM-PV 3502. The anterior part of the lower jaw is MPM-PV 3504 and the posterior part is a cast of MACN A 5969 / la parte anterior de la mandíbula pertenece a MPM-PV 3504 y la parte posterior es un calco del MACN A 5969. Photographs of these specimens were scaled so that the maxillary teeth would occlude with the mandibular ones / Las fotografías de estos especímenes fueron llevadas a la misma escala de modo que los dientes maxilares ocluyan con los mandibulares. MACN A 5969 has been flipped horizontally (the specimen is a fragment of a left mandible) / MACN A 5969 ha sido reflejada horizontalmente (el espécimen es un fragmento de mandíbula izquierda). It was necessary to reconstruct the posterior part of the mandibular angle to estimate the insertion areas for the masseter and medial pterygoid, and the coronoid process to estimate the insertion area for the temporalis / fue necesario reconstruir la parte posterior del ángulo mandibular para estimar el área de inserción del masetero y del pterigoides medio y el proceso coronoides para estimar el área de inserción del temporal. Scale bar = 1 cm / escala = 1 cm.

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areas were measured on two specimens of *Homunculus* (MPM-PV 3501 and 3502), but data for MPM-PV 3501 were omitted from the analysis because many of the tooth roots in this specimen are damaged. To estimate masticatory leverage in *Homunculus*, it was necessary to use a scaled composite of three specimens: one cranium (MPM-PV 3502), and two fragmentary mandibles (MACN A 5969 and MPM-PV 3504) to perform this analysis on *Homunculus patagonicus* (figure 2). We discuss below our reasons for allocating MPM-PV 3502 to *H. patagonicus* (appendix 2).

MPM-PV 3502 is from Killik Aike Norte, Argentina, and is the only relatively complete and undistorted cranial specimen for the species. We took representative measurements on a second, somewhat distorted skull (MPM-PV 3501) from Puesto Estancia La Costa, to confirm that the patterns we saw in root size for MPM-PV 3502 (see below - Results) were also present in other specimens of *Homunculus*. Despite the presence of another primate species of similar size from Killik Aike Norte, *Killikaike blakei* (Tejedor *et al.*, 2006), we allocate MPM-PV 3502 to *H. patagonicus* because it strongly resembles specimens of the latter from other localities (see Discussion).

The mandibular specimens used in our reconstruction come from Estancia La Costa (MPM-PV 3504) and Monte Observación (now Cerro Observatorio, Marshall, 1976) (MACN A-5969). MPM-PV 3504 is very similar in all comparable respects to the neotype designated for *Homunculus patagonicus*, also from Corriguen Aike (Tejedor and Rosenberger, 2008). The analyses of *Tremacebus* and *Dolichocebus* are based on the type specimens of those taxa.

## Methods

Skulls were scanned in the high-resolution X-ray CT facility at the University of Texas (Austin). Slice thickness varied between 0.04 mm and 0.1 mm for specimens of different size. Stacks of 8-bit jpg files were assembled in VGStudio Max 1.2 (Volume Graphics, Heidelberg, Germany). Lateral views of three-dimensional renderings of skull surfaces were used for orientation. Tooth root area measurements were taken from volume renderings of the tooth roots and leverage measurements were taken as two-dimensional lateral projections using the skull surface rendering, employing the "non-perspective" setting. Measurements were calibrated using caliper measurements of the original skulls and using the associated CT scan data.

## Roots

We measured root area of all maxillary teeth

**Table 1.** Measurements used as a proxy for body size (mm) / *medidas utilizadas como indicadores para tamaño corporal (mm)*. **BB**, bicondylar breadth / *ancho bicondilar*; **PB**, palate breadth / *ancho palatal*; **TFL**, temporal foramen length / *largo del foramen temporal*; **TRL**, tooth row length / *largo de la serie dentaria*; **IH**, infratemporal height / *altura infratemporal*; **GM**, geometric mean of the five measurements above / *media geométrica de las cinco medidas mencionadas arriba*. See Spencer (1999) for explanations of measurements / *ver Spencer (1999) para una explicación sobre las medidas*. For all specimens, TRL was measured from the P2 to the posterior-most molar, whether the M2 or the M3 / *para todos los especímenes, TRL fue tomada desde P2 al molar más posterior*. See the appendix for abbreviations of species names and specimen numbers / *ver apéndice para las abreviaturas de las especies y números de especímenes*.

	A.f.	A.g.	C.j.	C.n.	C.p.	C.t.	M.a.	P.sp.	S.f.	D.g.	H.p.	T.h.
BB	59.2	64.6	24.2	47.3	18.9	48.0	24.6	49.2	24.9	24.7	32.4	23.7
PB	35.9	29.0	11.8	24.4	9.1	24.1	12.2	20.5	13.2	17.4	17.5	15.4
TFL	38.6	35.3	15.2	24.2	11.4	23.4	16.4	25.2	17.1	23.9	22.6	24.5
TRL	30.2	22.8	7.3	17.3	5.9	17.5	7.6	14.4	7.8	19.4	16.9	12.8
IH	46.9	47.0	15.9	43.8	11.7	38.1	15.9	36.6	16.5	23.7	21.2	22.3
GM	41.0	37.1	13.8	29.2	10.6	28.3	14.3	26.6	14.8	21.6	21.5	19.1

from the canine to the most posterior molar from CT scans. We used the segmentation function in VGStudio Max 1.2 to outline the roots in three dimensions. Outlines of roots were selected on each slice (slice thickness = 0.05-0.01 mm) and the entire root segment was compiled at the end to yield root area. The boundary between root and crown was estimated using the base of the enamel cap; the enamel of the tooth crown is distinguishable in CT scans based on its density.

Following Spencer (1999, 2003), tooth root areas were scaled to a geometric mean of five cranial measurements (see table 1). These measurements are all taken from the face; therefore, any possible differences in brain size between fossil and extant platyrrhines would not affect this geometric mean. Spencer also scaled root area to crown area; however, crown area itself varies with diet: folivores and insectivores, in general, have larger tooth crowns than do frugivores (Kay, 1975; Anthony and Kay, 1993). Therefore, we did not use crown area as a scaling variable.

All statistical analyses were performed in JMP 7.0 (JMP, Version 7. SAS Institute Inc., Cary, NC, 1989-2007).

#### *Chewing force: muscle dimensions and leverage*

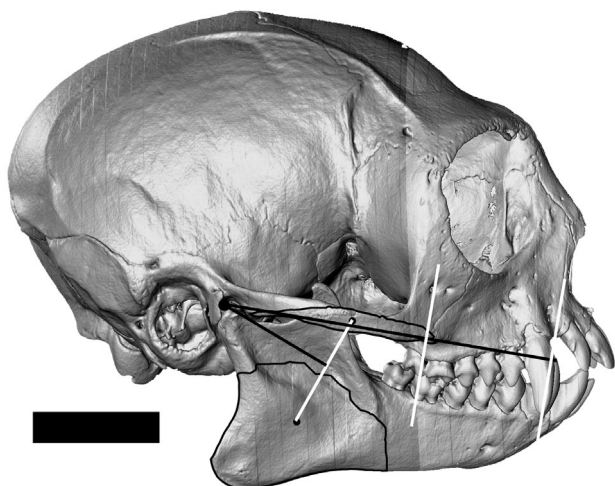
The physiological cross-sectional area (PCSA) of a muscle gives an estimate the amount of force it is capable of producing (Weijs and Hillen, 1985). PCSA is an estimate of the amount of muscle that contracts in parallel to generate a load, and can be calculated from preserved muscles (Perry and Wall, 2008). PCSA indicates the potential force of a muscle; the actual force depends on many other variables, including activity patterns (Hylander *et al.*, 2000). Despite the availability of data on chewing muscle PCSAs for a

few species of extant platyrrhines (Schumacher, 1961; Anapol *et al.*, 2008), we do not know enough about the anatomical correlates of PCSA in platyrrhines (*e.g.*, attachment scars on the skull) to reconstruct chewing muscle PCSA in fossil platyrrhines.

In the absence of directly measured chewing muscle cross-sectional areas (as is true for all fossil species), the best approximation of muscle force is estimated muscle leverage. Chewing muscle leverage can be estimated from the centroids of attachment areas of the muscles when they are visible on the bony specimens. By comparing the leverages of the chewing muscles across species, one can gauge the relative effectiveness of the jaw adductor muscles. To estimate jaw adductor leverage for the extant platyrrhines and for *Homunculus* we took the following steps:

1) Based on the muscle scars, we traced the estimated areas of origin and insertion of the temporalis, masseter, and medial pterygoid muscles onto two-dimensional lateral images of skulls that had been generated from CT volumes. Published descriptions of dissections of platyrrhine chewing muscles (Stark, 1933; Schumacher, 1961; Schön, 1968; Madeira and de Oliveira, 1979) and a dissection of the chewing muscles in *Cebuella pygmaea* (by JMGP) guided this procedure.

2) Using the software ImageJ (United States National Institutes of Health, public domain), we calculated centroids for all areas of attachment. We traced a line of action for each muscle by joining the centroid of the origin area to the centroid of the insertion area. The lever arm for each muscle is a perpendicular line drawn from the line of action to the center of the mandibular condyle. By convention, moments were taken about the mandibular condyle; no joint reaction force was calculated (Stern, 1974; Tattersall, 1974; Hylander, 1975; Demes and Creel, 1988; Vizcaíno *et al.*, 1998).



**Figure 3.** Reconstructed CT image of the skull of a female *Mico argentatus* (NMNH 238463) in lateral view / imagen reconstruida de tomografía computada del cráneo de una hembra de *Mico argentatus* (NMNH 238463) en vista lateral. Each small black dot is the centroid for an area of attachment of the masseter, and the white line connecting the small black dots is the hypothetical line of action of the muscle / cada punto negro pequeño es el centroide del área de inserción del masetero y la línea blanca que conecta los puntos negros es la línea hipotética de acción del músculo. The large black dot represents a center of rotation (at the condyle), and the black line joining the condyle to the line of action is the lever arm of the masseter / el punto negro grande representa el centro de rotación (en el cóndilo) y la línea negra que une el cóndilo con la línea de acción representa el brazo de momento del masetero. Two white lines are drawn perpendicular to the occlusal plane: one through the paracone of the M2, another through the apex of the canine / se dibujan dos líneas blancas perpendiculares al plano oclusal: una a través del paracono del M2, la otra a través del ápice del canino. A black line drawn from the condyle to each of these lines is the load arm for each bite point / la línea negra trazada desde el cóndilo a cada una de estas líneas es el brazo de carga para cada punto de mordida. The length of the lever arm divided by the length of the load arm at a particular point is the leverage of the masseter for that bite point in a vertical bite / el largo del brazo de palanca dividido por el largo del brazo de carga a un punto particular es el brazo de palanca del masetero para ese punto de mordida en una mordida vertical. Scale bar = 1 cm / escala = 1 cm.

3) Onto the same images, we drew load arms parallel to the occlusal plane (that is, normal to an assumed vertical bite force, see figure 3) (Vizcaíno and Bargo, 1998; Vizcaíno *et al.*, 1998; De Iuliis *et al.*, 2000; Bargo, 2003; Vizcaíno *et al.*, 2006). The distance from the condyle to bite points on the upper teeth, measured parallel to the occlusal plane, was used to estimate the length of the load arm for those bite points. The tip of the paracone was selected as the bite point for each postcanine tooth.

4) The leverage for a given muscle at a given bite point was determined by dividing the lever arm length of the muscle by the load arm length at the bite point.

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**Figure 4.** Comparison of tooth roots in *Homunculus* (above) and *Pithecia* (below) / comparación de las raíces dentarias de *Homunculus* (arriba) y *Pithecia* (abajo). Scale bar = 1 mm / escala = 1 mm.

## Results

### Roots

Root surfaces as reconstructed in *Homunculus* MPM-PV 3502 are illustrated in figure 4. Using the least squares model, log tooth root area of the canine and cheek teeth was regressed against log geometric mean of the five cranial measurements for all specimens in the sample (table 2, figures 5 and 6).

Root area scales isometrically to the geometric mean for all teeth; that is, the 95% confidence interval for the slope encompasses the slope that is expected by isometry (*i.e.*, a slope of 2.0).

In all cases among platyrrhines, canine root area is greater than that of any premolar (table 3). However, canine root area is often less than that of the M1 and M2. There is no consistent trend in root area across the premolars. In all but one case, M1 root area > M2 root area > M3 root area. The exception is *Alo-uatta* in which M2 > M1 > M3.

*Callithrix jacchus* and *Saguinus fuscicollis* are similar-sized callitrichines; in the former, tree exudates form a much larger part of the diet than in the latter (Coimbra-Filho and Mittermeier, 1976). *Callithrix jacchus* generally has larger tooth root areas at each tooth position (relative to the geometric mean) than



**Table 2.** Descriptive statistics for LS regressions against the cranial geometric mean / estadísticos descriptivos para las regresiones LS contra las medias geométricas del cráneo. RA, root area (mm<sup>2</sup>) / RA, área de la raíz (mm<sup>2</sup>); GM, cranial geometric mean (mm) / GM, media geométrica del cráneo (mm). All data were logged (base ten) prior to regression analyses / todos los datos fueron transformados a logaritmo en base 10 antes del análisis de regresión. Expected slope for regressions is 2 / pendiente esperada para la regresión es 2. For the M3, n = 7; in all other cases, n = 12 / para el M3, n = 7; en todos los otros casos, n = 12. The sum is composed of root areas C-M2 / la suma está compuesta por las áreas de las raíces C-M2.

y	r2	Slope	y-intercept	95% C.I. of Slope	
				Lower	Upper
C RA	0.8637	1.9518	-0.6085	1.4054	2.4983
P2 RA	0.8935	1.8260	-0.7700	1.3819	2.2702
P3 RA	0.8574	1.8584	-0.7868	1.3244	2.3924
P4 RA	0.8960	1.8361	-0.6996	1.3953	2.2770
M1 RA	0.8241	1.9788	-0.7849	1.3346	2.6230
M2 RA	0.8347	2.1919	-1.1584	1.5046	2.8792
M3 RA	0.4804	1.6190	-0.5697	-0.3167	3.5547
SUM	0.9155	1.9612	-0.0243	1.5412	2.3811

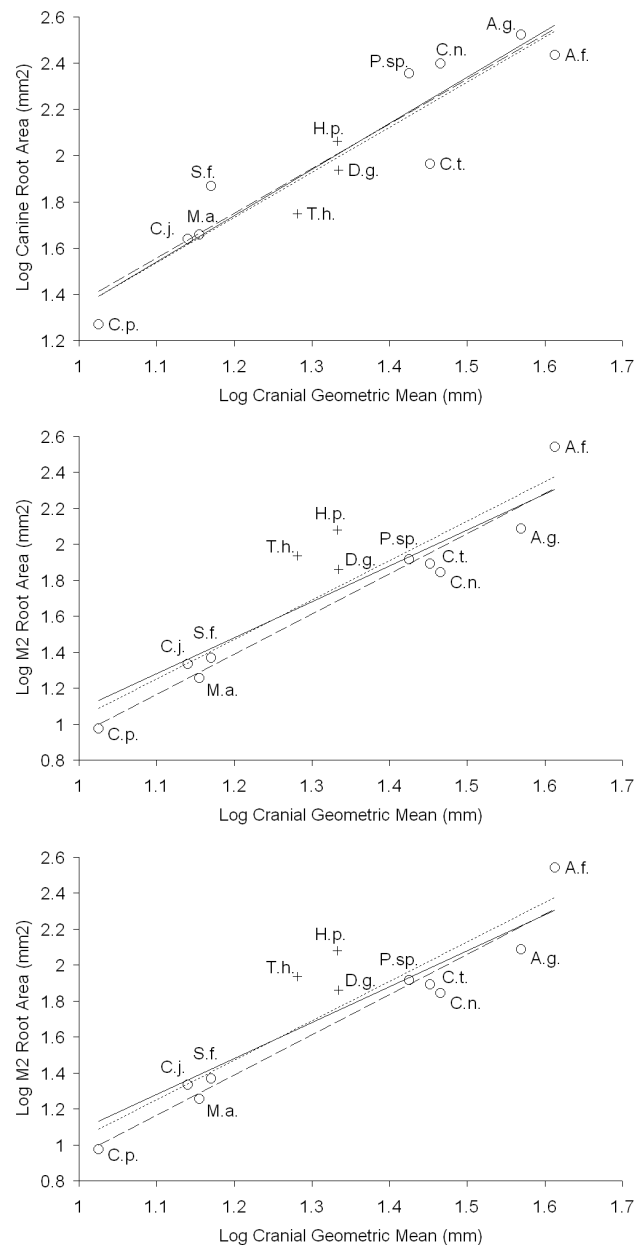
does *Saguinus fuscicollis*. This difference is most pronounced in the most posterior teeth, whereas canine root area is larger in *Saguinus*.

*Ateles geoffroyi* and *Alouatta guariba* are similarly-sized atelids; the former is mainly frugivorous, whereas the latter is mainly folivorous (Schoeninger *et al.*, 1997). Relative to the geometric mean, canine root area is greater in *Ateles* than in *Alouatta*; however, for all other tooth positions, root area is greater in *Alouatta* than in *Ateles*. We used female specimens for both species.

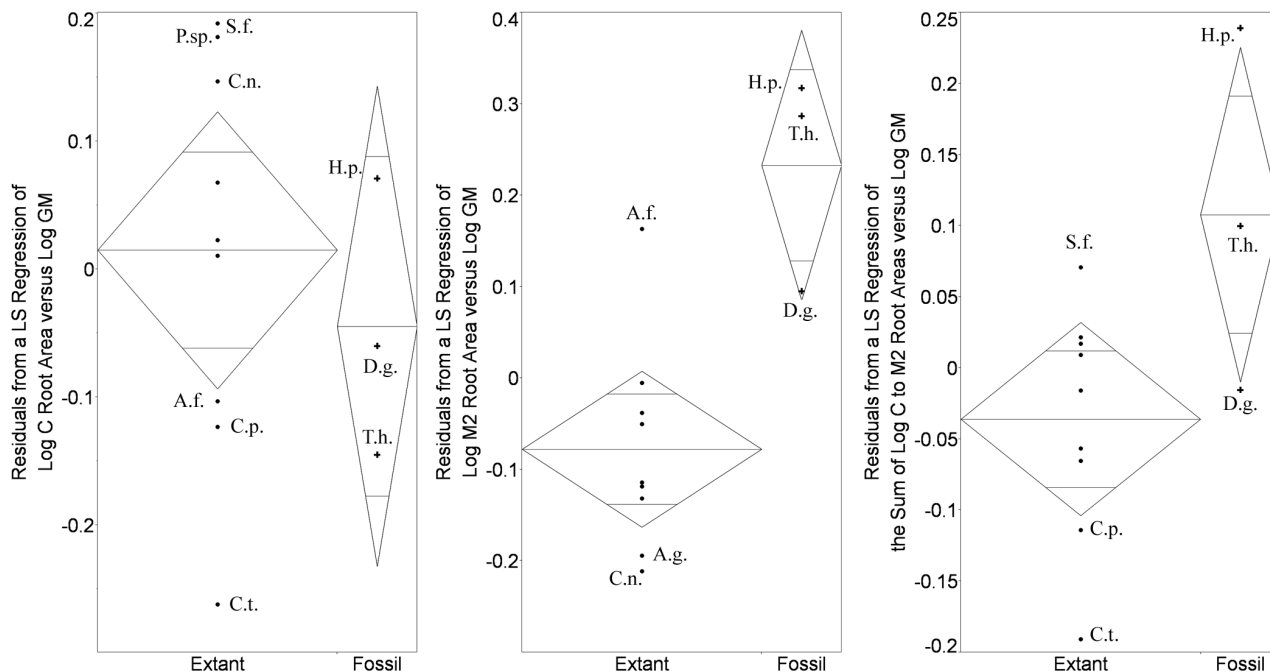
Total C-M2 root area relative to the geometric mean in *Homunculus patagonicus* is greater than in any other platyrrhine in this sample (figures 5.3, 6.3). The difference is especially pronounced for the molars (figures 5.2, 6.2). The only exception is the canine root, which is small compared to some extant platyrrhines (*e.g.*, *Saguinus*).

*Tremacebus* resembles *Homunculus* in having relatively larger M2 roots than any living platyrrhine in our sample (figures 5.2, 6.2). *Dolichocebus* also follows this pattern: its M2 roots are larger than those of any extant platyrrhine in our sample, with the exception of *Alouatta guariba*. Total C-M2 root size of *Tremacebus* and *Homunculus* likewise exceed those of extant platyrrhines (figures 5.1, 6.1) but that of *Dolichocebus* overlaps the extant platyrrhine range because its canine and premolars are more modest in size (figures 5.1, 6.1).

Tooth root surface area differs between the two *Homunculus* specimens measured (table 3). The canine, especially, has a much greater surface area in MPM-PV 3501 than in MPM-PV 3502. Canine root cross-sectional area and length are slightly greater in the former specimen, but these small differences amount to a large difference in surface area.



**Figure 5.** Tooth root size / tamaño de la raíz dentaria. Least squares (LS) regressions of root area versus the geometric mean (GM) of five cranial measurements, in log space / regresiones de cuadrados mínimos del área de la raíz dentaria versus la media geométrica de cinco medidas del cráneo, transformadas a logaritmo. Raw data for root area are in mm<sup>2</sup> and for the geometric mean are in mm / unidades del área de la raíz en mm<sup>2</sup> y de la media geométrica en mm. The theoretical slope of isometry is 2.0 as indicated by the solid line, while the regression line is shown by the dotted line / la pendiente esperada para isometría es 2.0 como lo indica la línea continua, mientras que la línea de regresión se indica en línea punteada. The dashed line is fitted to only extant taxa / la línea entrecortada es la recta de regresión utilizando sólo los taxones actuales. Abbreviations for species names as in table 1 / abreviaturas de las especies como en la tabla 1. Descriptive statistics are listed in table 2 / estadísticos descriptivos listados en la tabla 2. Extinct species are marked with crosses / las especies extintas están indicadas con cruces. 1, canine root area / área de la raíz del canino, 2, M2 root area / área de la raíz del M2, 3, sum of root areas C to M2 / suma de las áreas de las raíces del C al M2.



**Figure 6.** Comparison of tooth root area residuals for extant and extinct taxa / comparación de los residuos de las áreas de las raíces dentarias para los taxones vivientes y extintos. Plots showing residuals from least squares regressions of log root area versus log geometric mean / diagramas de los residuos de las regresiones de cuadrados mínimos de los log del área de la raíz versus el log de la media geométrica. Abbreviations for species as in table 1 / abreviaturas de las especies como en tabla 1. Extinct species are marked with crosses / las especies extintas están indicadas con cruces. The middle horizontal line depicts the group mean and the vertical tips of the diamonds represent the 95% confidence limits / la línea horizontal representa la media del grupo y los extremos verticales de los diamantes los límites de confianza de 95%. 1, canine / canino, 2, M2 / M2, 3, sum of C-M2 / suma de C-M2. Among these comparisons, the difference between fossil and extant forms is significant only for M2 ( $p=0.02$ , Wilcoxon 1-way test), but approaches significance for the sum of C-M2 ( $p=0.079$ ) / entre estas comparaciones, la diferencia entre las formas fósiles y vivientes es significativa sólo para el M2 ( $p=0.02$ , Wilcoxon 1-way test), pero la suma de C-M2 ( $p=0.079$ ) está próxima a un valor significativo. *Homunculus* lies beyond the confidence interval for extant primates for all tooth positions, except the canine / *Homunculus* cae fuera del intervalo de confianza de los primates vivientes para todas las piezas dentarias, excepto el canino.

*Leverage*

Most of the extant platyrrhines in our sample have similar patterns of muscle leverage. Lever arm lengths are given for the temporalis, masseter, and medial pterygoid muscles in table 4, as are load arm lengths at all measured bite points.

Figure 7 shows the variation in leverage at the canine and the M2. *Callithrix* has the greatest masseter and medial pterygoid leverage and also has considerable temporalis leverage. *Saguinus*, *Callicebus*, and *Alouatta* have strong masseter and medial pterygoid leverage, but weak temporalis leverage. Additionally, *Alouatta* has the greatest masseter leverage in our sample, at all tooth positions. *Cebuella* reverses this pattern with relatively high temporalis leverage and relatively low masseter and medial pterygoid leverage. Among extant platyrrhines, *Cebus* has the greatest temporalis leverage at all bite points; but has very poor medial pterygoid leverage and only moderate masseter leverage.

The most striking result is that *Homunculus* has the poorest muscle leverage in the sample for all muscles at all tooth positions.

**Discussion**

*Roots*

Our method for measuring tooth root area captures true root area, even for very complicated tooth root shapes. Spencer (2003) admitted that his method using two dimensional projections of roots failed to account for parts of the root that were concealed behind the roots in the foreground.

Using a geometric mean of cranial measurements as a scaling variable is superior to using crown area when the aim is to detect dietary effects on tooth root area. This is because crown area is known to vary with diet in primates (Kay, 1975; Anthony and Kay, 1993). Crown area may be useful for understanding how bite pressure is related to tooth root area (Demes and Creel, 1988). However, bite pressure is likely only loosely related to crown area; the area of interest is actually the contact area between teeth and food. The latter may be more or less than crown area, depending on such additional variables as tooth relief and the ductility of food.



**Table 3.** Root areas (mm<sup>2</sup>) for all teeth examined / areas de las raíces (mm<sup>2</sup>) de todos los dientes examinados. Abbreviations for species names as in table 1 / abreviaturas de las especies como en la tabla 1. The M3's are broken away in *Dolichocebus* / los M3 están rotos en *Dolichocebus*.

	C	P2	P3	P4	M1	M2	M3
A.f.	273	143	172	187	283	347	218
A.g.	333	105	126	127	160	122	82
C.j. (f)	44	19	22	24	27	22	-
C.j. (m)	54	-	26	-	31	20	-
C.n.	250	106	107	104	100	70	48
C.p.	19	10	12	12	13	9	-
C.t.	92	51	57	59	92	78	36
M.a.	45	20	20	23	27	18	-
P.sp.	226	65	81	78	87	82	53
S.f.	74	30	30	32	31	23	-
D.g.	86	52	25	64	78	73	-
H.p. (3502)	116	82	92	101	162	120	76
H.p. (3501)	206	88	77	102	143	141	100
T.h.	56	32	43	56	114	86	34

As predicted, there appears to be a signal for folivory versus frugivory in tooth root size. Folivorous *Alouatta* has larger postcanine tooth roots relative to its cranial geometric mean than does frugivorous *Ateles*. The former also has larger postcanine tooth crowns than the latter. Spencer (2003) suggested that large molar roots might be associated with leaf processing. The large size of the tooth roots - especially the molars - of *Alouatta* relative to *Ateles* supports this suggestion. It is not clear whether heavy loads or repeated loads are more likely to select for greater root area, or whether leaf-processing requires heavy loads or just repeated loads. Either way, both loading situations likely favor large roots.

Our prediction regarding canine root area in *Ateles* versus *Alouatta* also holds: canine root area is greater in *Ateles* than in *Alouatta*. This is consistent with the explanation that fruit-processing favors large canine roots.

Canine root area is smaller in *Callithrix jacchus* than in *Saguinus fuscicollis*, contrary to our initial expectations based on the assumption that gouging behavior should impose heavy loads on the anterior dentition. Indeed, our findings accord with those of Taylor and Vinyard (2004) who report that physiological cross-sectional area of the masseter muscle is actually less in *Callithrix jacchus* than in *Saguinus oedipus*, contrary to the prediction that gouging involves high bite forces. Anterior tooth root *shape* might provide a better signal for gouging in callitrichids as the canine and incisor roots of *Callithrix* are more mesiodistally compressed than those of *Saguinus*.

This may be an adaptation to resisting bending in the anteroposterior plane.

The *Callithrix* specimen in our sample is a female. Although little sexual dimorphism is expected for callitrichids, we measured the tooth roots of a male *Callithrix jacchus* cranium (USNM 503885) to rule out the possibility that sexual dimorphism explains the difference in tooth root area between *C. jacchus* and *S. fuscicollis*. Canine root area of the male *Callithrix* is greater than that of the female *Callithrix*; however, it is still less than that of the male *Saguinus*. Therefore, the difference in root size between *Saguinus* and *Callithrix* cannot be explained by sexual dimorphism alone.

Another comparison of interest is that of *Pithecia* to the other extant platyrrhines. *Pithecia* is a hard-object feeder (Kinzey, 1992; Peres, 1993). This species is expected to have large anterior tooth roots compared to the other platyrrhines in our sample. We found that canine root area is great in *Pithecia* compared to its cranial geometric mean (see figure 5). However, among the extant platyrrhines, *Saguinus* has a relatively larger canine root than *Pithecia*. Furthermore, premolar root area is not particularly great in *Pithecia* compared to the other extant platyrrhines in our sample. Although the foods consumed by *Pithecia* are very resistant to fracture, the closely related genus *Chiropotes* breaks open fruits that are considerably more resistant than those consumed by *Pithecia* (Kinzey and Norconk, 1990; Kinzey, 1992). Spencer (2003) found that the canine roots of *Chiropotes* are considerably larger than those of *Pithecia* (relative to a cranial geometric mean).

The great tooth root surface area observed in the Miocene platyrrhines, especially *Homunculus*, suggests that these roots were able to resist considerable bite loads. Root surface areas for the posterior dentition are especially great in *Homunculus*, suggesting this taxon may have used powerful and/or repeated bites at the molars to break down its food. However, this dietary signal is not supported by the estimates of muscle leverage or by the sizes of the muscle scars (see below).

Differences between MPM-PV 3501 and MPM-PV 3502 in root surface area are small and variable for the posterior teeth; this variation is likely due in part to root damage and distortion in the former specimen. The difference in canine root surface area, however, is considerable. Because these two specimens are anatomically very similar in most other respects (see appendix 2), this difference in canine root size might be attributed to canine sexual dimorphism. Root dimensions in a third specimen (MPM-PV 3503 from PLC) are similar to those of MPM-PV 3502 (from Killik Aike); these specimens might represent females while MPM-PV 3501 from PLC would represent a male. More detailed comparisons are required to test this hypothesis.

**Table 4.** Lever arms for the three muscle groups and load arms for all tooth positions (mm) / *brazos de palanca de los tres grupos musculares y brazos de carga de todas las posiciones de los dientes (mm)*. **Temp.**, temporalis muscle / *músculo temporal*; **Mass.**, masseter muscle / *músculo masetero*; **M.P.**, medial pterygoid muscle / *músculo pterigoides medio*. The load arm is measured to the paracone / *el brazo de carga se midió al paracono*. All data are in mm / *todas las medidas en mm*. Abbreviations for species as in table 1 / *abreviaturas de las especies como en tabla 1*.

	A.f.	A.g.	C.j.	C.n.	C.p.	C.t.	H.p.	M.a.	P.sp.	S.f.
	Lever Arms									
Temp.	13.43	15.42	6.43	14.66	4.57	9.76	7.41	6.14	15.07	5.57
Mass.	27.93	24.76	8.90	16.58	6.02	18.38	11.30	7.98	23.03	9.41
M.P.	19.97	21.45	9.57	10.88	5.64	17.43	11.32	7.77	17.37	9.37
	Load Arms									
C	68.17	64.52	23.55	48.54	18.58	48.32	41.86	25.37	57.03	25.91
P2	62.76	59.54	21.43	42.87	16.80	44.57	38.00	22.49	51.27	23.11
P3	57.39	56.07	19.72	38.99	15.34	41.89	35.29	20.74	48.38	21.34
P4	52.46	51.92	18.11	35.58	14.15	39.67	32.36	19.31	45.11	19.75
M1	49.38	48.64	16.88	32.15	13.02	37.25	29.52	17.85	42.18	18.32
M2	42.23	43.44	14.75	26.95	11.17	32.21	24.46	15.58	37.62	15.96
M3	34.09	38.45		22.38		28.45	20.30		33.51	

*Leverage*

The pattern of chewing muscle leverage in platyrrhines is likely related to cranial morphology and diet. The lever arms for the masseter and medial pterygoid are generally long in primates that have the mandibular condyle positioned well above the occlusal plane; whereas, the temporalis lever arm is short (Greaves, 2000). *Callicebus* and *Alouatta* both have deep jaws with high condyles; their masseter and medial pterygoid muscles have considerably more leverage than the other platyrrhines in the sample, but their temporalis leverage is poor. *Alouatta*'s considerable masseter leverage might be an adaptation for generating great bite force at narrow gaps (e.g., during mastication of flat food items like leaves).

The temporalis muscle is likely important in producing force when the mouth is gaped widely (Perry, 2008), for example, when a large food item is bitten or during gouging. This may partly explain why *Callithrix* has considerable temporalis leverage; nevertheless, *Callithrix* also has considerable leverage for the medial pterygoid and masseter.

Species rankings for leverage are very different for the temporalis versus the masseter/medial pterygoid at all tooth positions. However, for a given muscle, species rankings vary little from one tooth position to another. This suggests that the teeth are similarly spaced along the tooth row in this sample of extant platyrrhines, but that the locations of the jaw adductor attachments vary. One notable exception is that at the canine *Ateles* has greater medial pterygoid leverage than *Alouatta*, but at the M3 *Ateles* has much less medial pterygoid leverage than *Alouatta*. The AMEGHINIANA 47 (3), 2010

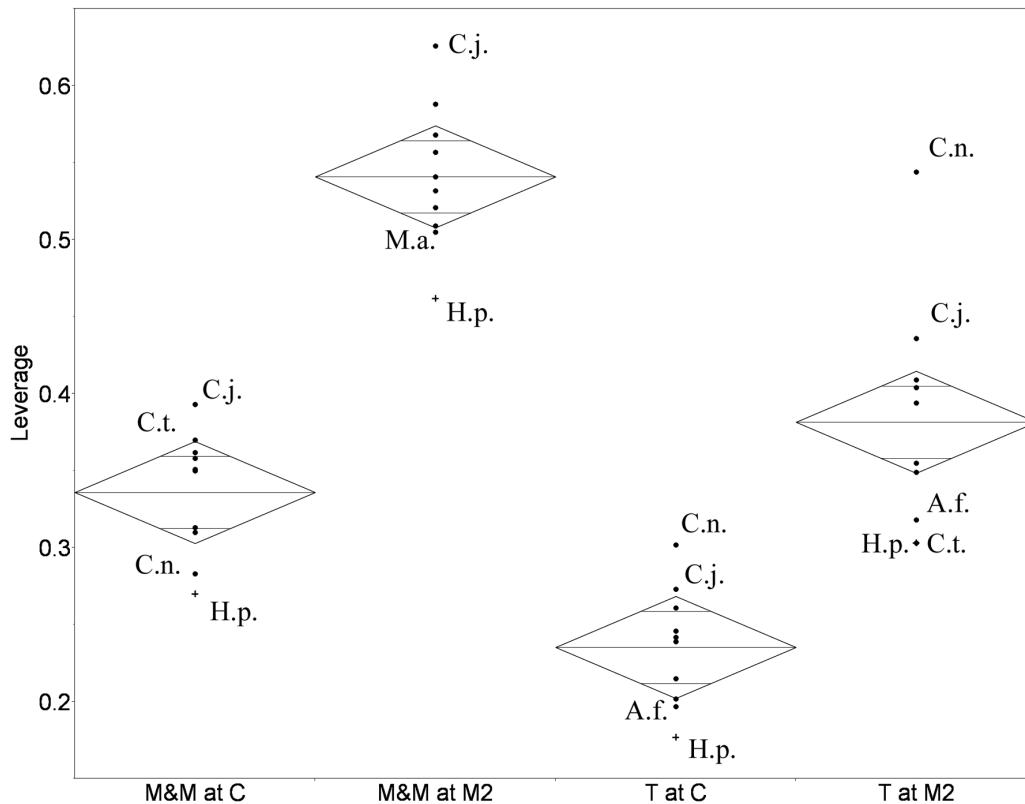
same is true to a lesser degree for masseter leverage in these two taxa. This result is consistent with the expectation that chewing muscle leverage is maximized at points along the tooth row where food is most heavily loaded. Thus these differences in leverage likely reflect *Alouatta*'s emphasis on leaves and *Ateles*'s emphasis on fruits.

Jaw adductor leverage in *Homunculus* is poor relative to all other platyrrhines examined. This is partly a consequence of the length of its rostrum. *Homunculus* is prognathic relative to the extant platyrrhines (figure 8). Therefore, its load arm at any given bite point is longer than that of the other monkeys. Nevertheless, in addition to having long load arms, *Homunculus* also has short lever arms.

The origin of the temporalis is more posteriorly located in *Homunculus* than in extant platyrrhines, but the temporalis insertion is no more anteriorly located. To a lesser degree, the insertions of masseter and medial pterygoid are also more posteriorly located, but the masseter and medial pterygoid origins are no more anteriorly located. This means that the line of action of each muscle passes closer to the condyle than in the extant species, and therefore, the lever arms in *Homunculus* are shorter.

Based solely on information about the origins of these muscles (but not on their insertions), it is likely that *Dolichocebus* and *Tremacebus* also had poor chewing muscle leverage because both crania are relatively prognathic, and the temporalis origin is situated posteriorly on the cranium.

*Homunculus patagonicus* has large maxillary tooth roots relative to the extant platyrrhines studied. Also, the cheek teeth are heavily worn in most specimens of this species. These signs point to a diet of very tough



**Figure 7.** Comparison of muscle leverage / comparación del esfuerzo de torsión de los músculos. Plots showing muscle leverage for temporalis and for masseter plus medial pterygoid at two different bite points / diagramas mostrando el esfuerzo de torsión de los músculos temporal y masetero, más el pterigoides medio en dos puntos de mordida diferentes. Leverage is lever arm length divided by load arm length / el esfuerzo de torsión es la longitud del brazo de palanca dividida por la longitud del brazo de la carga. Abbreviations for species as in table 1 / abreviaturas de las especies como en tabla 1. Extinct species are marked with crosses / las especies extintas están indicadas con cruces. Diamonds as in figure 6. / diamantes como en la figura 6. Data are in table 4 / datos en tabla 4. M&M, masseter and medial pterygoid; T, temporalis / M&M, músculos masetero y pterigoides medio; T, músculo temporal.

foods. However, there is no reason to believe that *Homunculus* had especially large chewing muscles. There is no sagittal crest and the temporal lines are not especially prominent. The muscle scars are not especially deep, and the zygomatic arches are only moderately flared, leaving only a modest amount of space for the chewing muscles in the temporal fossa.

Jaw adductor leverage in *Homunculus* is not as great as in the extant platyrrhines studied here. This finding complements the above inference about overall muscle size. Assuming modest chewing muscle cross-sectional area and activity, and in spite of its large tooth roots, this Miocene primate was probably not especially well-adapted to producing heavy bite loads during chewing.

#### *Inferences about masticatory function and diet*

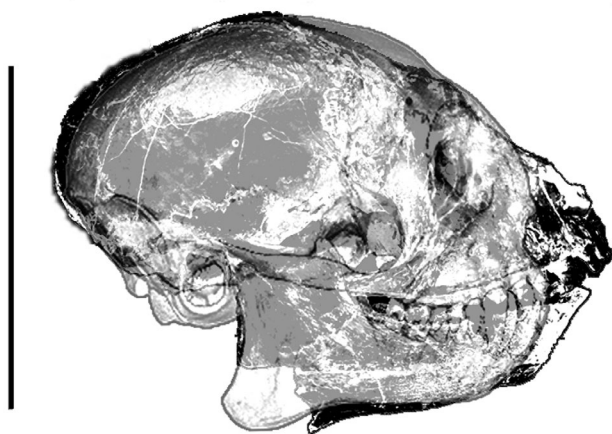
The following features characterize the masticatory system of *Homunculus*: moderate molar shearing (Fleagle *et al.*, 1997), heavy postcanine tooth wear

(Tauber, 1991), large postcanine tooth roots, and modestly developed musculature with poor leverage. One possible explanation for the co-occurrence of these traits is that *Homunculus* consumed both fruits and leaves, but that neither required very forceful mastication. Perhaps during mastication, bite forces were never high.

A diet of fruit and leaves may not be sufficient to explain the high degree of tooth wear seen in most specimens of *Homunculus*. Leaves and other plant matter ingested by *Homunculus* might have been heavily protected by silica inclusions and/or might have been covered with exogenous abrasives (Sanson *et al.*, 2007).

Other interpretations are possible: *Homunculus* may have eaten foods that required more masticatory cycles than typically seen in living platyrrhines. This would lead to the inference that its foods were more fibrous than those of most platyrrhines. Another interpretation relates to seasonality. *Homunculus* is found as far south as 55 degrees South latitude, almost 3000 kilometers south of the southern edge of





**Figure 8.** Skull of *Callithrix jacchus* (NMNH 503895f) superimposed on the composite skull of *Homunculus patagonicus* / Cráneo de *Callithrix jacchus* (NMNH 503895f) sobrepuesto en el cráneo compuesto de *Homunculus patagonicus*. This image shows the degree of prognathism of *Homunculus* in relation to *Callithrix* and the more posterior extent of the temporalis origin / esta imagen muestra el grado de prognatismo de *Homunculus* en relación a *Callithrix* y la ubicación más posterior del músculo temporal. The original images are scaled to equal skull height at the anterior edge of the postorbital bar (black vertical line at left) and were superimposed at the mandibular condyles / las imágenes originales fueron llevadas a la misma escala para igualar la altura del cráneo en el borde anterior de la barra postorbital (línea negra vertical de la izquierda) y fueron superpuestas a nivel del cóndilo mandibular.

the distribution of living platyrrhines, and just 1,200 kilometers north of the Antarctic Circle. The paleolatitude of this locality was several degrees even further south in the early Miocene. An abrasive diet may have been a feature of the long season of low plant productivity at this latitude.

Tauber (1991, 1999) described a new cranium of *Homunculus* and made dietary inferences based on cranial features. He suggested that *Homunculus* had a very powerful masticatory system, more powerful than that of pitheciines. This was based partly on rugosity for the attachment of the buccinator muscle and partly on dental morphology. Even if the size of the buccinator muscle can be judged from scars on bone, it is uncertain what, if anything, it has to do with food properties. The buccinator is located within the cheek and aids the tongue to maintain a food bolus on the teeth and likely plays an important role in suckling (Tomo *et al.*, 2002); its bony attachments are slight. Because the buccinator muscle does not generate force to fracture foods, the physical properties of foods have likely had no adaptive influence of the muscle.

Tauber also suggested that the origin of the temporalis from the cranial surface indicates that this was a powerful muscle. We have examined all known crania of *Homunculus patagonicus* and have found nothing to suggest that the temporalis mus-



**Figure 9.** Comparison of cranium of *Homunculus* MPM-PV 3501 (below) to cranium of *Pithecia* NP5 (above) / comparación de los cráneos de *Homunculus* MPM-PV 3501 (abajo) y de *Pithecia* NP5 (arriba). The bony surface associated with the masticatory muscles is not obviously more developed in *Homunculus* / la superficie del hueso asociada con los músculos masticatorios no está más desarrollada en *Homunculus*. The extent of the scar for the origin of temporalis is similar in both specimens / el área de la cicatriz del origen del músculo temporal es similar en ambos especímenes. Compare also with specimen MPM-PV 3502 in figure 2 / comparar también con el espécimen MPM-PV 3502 en figura 2. Scale bar = 1 cm / escala = 1 cm.

cles were especially large compared to those of extant platyrrhines. The temporal lines are slight, the lateral surface of the skull for the origin of the deep temporalis is only moderately rugose, and the temporal fossa (through which the temporalis passes toward its insertion) is small (figure 9). *Homunculus* probably did not have a powerful masticatory system compared to extant pitheciines. The former has poor masticatory leverage and its cranial anatomy suggests only modestly-sized chewing muscles. Although the diet of *Homunculus* probably included very abrasive, resistant foods, at least seasonally, it was probably not capable of generating masticatory forces like those used by extant pitheciines.

#### Acknowledgements

We thank the Patagonia field crews, seasons 2003 to present, for their efforts in collecting Miocene mammals, including primates, from the Santa Cruz Formation of coastal Argentina. We thank the Battini family for their hospitality during the fieldwork. We thank the staff of the Museo Regional Provincial "Padre Ma-

nel Jesús Molina" (Río Gallegos, Argentina), the staff of the National Museum of Natural History (particularly L. Gordon), and J. Fleagle (Stony Brook University), for allowing us to borrow specimens of platyrrhines for CT scanning and study. Special thanks to M. Colbert and the staff of the University of Texas (Austin) MicroCT Facility for making the scans used in this study. Ch. Wall and R. Madden provided insightful suggestions throughout the execution of this study. We thank two reviewers and the editorial staff for helping us to improve the quality of this paper. This project was funded by the National Science Foundation, the National Geographic Society, the Agencia Nacional de Promoción Científica y Tecnológica (PICT 26219), the Universidad Nacional de La Plata (N474), and Midwestern University.

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**Recibido:** 17 de abril de 2009.

**Aceptado:** 7 de enero de 2010.

## Appendix 1

Abbr.	Extant species	Catalog Number
A.f.	<i>Alouatta guariba</i>	NMNH 518255f
A.g.	<i>Ateles geoffroyi</i>	NMNH 291056f
C.j.	<i>Callithrix jacchus</i>	NMNH 503895f (female)
		NMNH 503885m (male)
C.n.	<i>Cebus nigrivittatus</i>	NMNH 338960f
C.p.	<i>Cebuella pygmaea</i>	NMNH 337324m
C.t.	<i>Callicebus torquatus</i>	NMNH 406411f
M.a.	<i>Mico argentatus</i>	NMNH 238463f
P.sp.	<i>Pithecia</i> sp.	NP5 Fleagle Collection
S.f.	<i>Saguinus fuscicollis</i>	NMNH 518577m

## Appendix 1. (Continuation / continuación).

Fossil species		Origin	
D.g.	<i>Dolichocebus gaimanensis</i>	MACN 14128 (Type, cranium)	Gaiman, Chubut, Argentina.
		MPM-PV 3501 (cranium)	Puesto Estancia La Costa, Santa Cruz, Argentina.
		MPM-PV 3502 (cranium)	Killik Aike Norte, Santa Cruz, Argentina.
H.p.	<i>Homunculus patagonicus</i>	MPM-PV 3504 (mandible)	Estancia La Costa, Santa Cruz, Argentina.
		MACN A-5969 (mandible)	Monte Observación, Santa Cruz, Argentina.
T.h.	<i>Tremacebus harringtoni</i>	Type, Rusconi Collection 661 - but catalogued as 619 (cranium)	Sacanana, Chubut, Argentina.

## Appendix 2

Allocation of MPM-PV 3502 to *Homunculus patagonicus*

A critical aspect of our reconstructions is to assure that the specimens used in the reconstructions all belong to the same taxon, *Homunculus patagonicus*. This particularly is an issue with the skull MPM-PV 3502, which has not yet been described. All relevant species and specimens have been examined by one of us (RFK) and a detailed description and assessment of their allocation to *Homunculus* is in progress (Kay *et al.*, 2005). Until 2006 the consensus was that all specimens of primates from coastal exposures of the Santa Cruz Formation belonged to a single species, *Homunculus patagonicus*. Two events have modified this picture. Tejedor *et al.* (2006) named a new genus *Killikaikae blakei* from Killik Aike Norte on the estuary of the Río Gallegos. The type, MPM-PV 5000, is the rostral part of a cranium with most of its upper cheek teeth. Because the type specimen of *Homunculus patagonicus* is now lost, Tejedor and Rosenberger (2008) proposed a neotype, MACN-A 5757, a mandible from Puesto Estancia La Costa. Unfortunately, the teeth of the neotype are too heavily worn to discern most of the details of the dental anatomy and the type specimen of *Killikaikae* preserves no mandibular dentition. Therefore, only specimens in the hypodigm of *Homunculus*, as proposed by Tejedor and Rosenberger (2008), can be compared to the type of *Killikaikae*. One member of the hypodigm of *Homunculus patagonicus* is a partial skull CORD-PZ 1130, described by Tauber (1991) from the same locality as the neotype. Another is a distorted and broken orbit and maxilla, MACN-A 5968, also from Corriguen Aike, preserving virtually the same anatomy as CORD-PZ 1130. Two other adult skulls come from this same locality: a virtually complete but distorted skull, MPM-PV 3501 (figured by Tafforeau *et al.*, 2006), and another less complete skull (MPM-PV 3503) preserving the same parts as CORD-PZ 1130. We have chosen to compare our material mostly with the published specimen CORD-PZ 1130. Examination of the anatomy of all these specimens together suggests that we are dealing with one species or at most two species of the same genus and that MPM-PV 3502 is most similar to CORD-PZ 1130 and less so to MPM-PV 5000.

In the original description, Tejedor *et al.* (2006) do not offer a differential diagnosis of *Killikaikae blakei* from *Homunculus patagonicus*, but in a later paper, Tejedor and Rosenberger (2008) list the following differences.

1) *Homunculus* is said to have larger canines than *Killikaikae*. This does not appear to be a diagnostic difference between the two species: the canine occlusal dimensions of CORD-PZ 1130 (*Homunculus patagonicus* from Puesto Estancia La Costa) (mesiodistal: 2.85 mm x buccolingual 3.10 mm) are nearly identi-

cal to those of the type of *K. blakei*, MPM-PV 5000 (2.8 mm x 3.4 mm). MPM-PV 3502 has slightly larger canines than *K. blakei*. Canine dimensions in MPM-PV 3501 and MPM-PV 3502 are similar, though somewhat greater in the former. Canine length in MPM-PV 3501 is 13.34 mm as compared to 12.63 mm in MPM-PV 3502. Canine cross-sectional area at the cemento-enamel junction is 8.33 mm<sup>2</sup> in MPM-PV 3501 and 7.99 mm<sup>2</sup> in MPM-PV 3502. This small difference represents a great difference in root surface area. Nevertheless, canine dimensions of all specimens from both named taxa fall within the range of variation of non-sexually dimorphic platyrrhines like *Aotus* (see Kay *et al.*, 1987).

2) They state that the interorbital region is relatively wider in *Homunculus* than it is in *Killikaikae*. The interorbital breadth of four specimens from PLC has a mean of 5.27 mm and a range of 5.06 to 5.52 (that of CORD-PZ 1130 is 5.2 mm). Interorbital breadth is 4.4 mm in MPM-PV 5000. The interorbital dimension in MPM-PV 3502 is 4.2 mm, closer to *K. blakei*. However, there is considerable variation in interorbital dimensions even in non-sexually dimorphic platyrrhine species. Hartwig (1993) gives a coefficient of variation of 7.0 for seventeen specimens of the extant platyrrhine *Callicebus hofmannsi*. In his sample of four specimens of *Callicebus personatus*, the measured interorbital breadths range from 4.24 mm to 5.46 mm, overlapping virtually the entire range of published breadths of *H. patagonicus* and *K. blakei*. Pending recovery of more specimens there does not appear to be sufficient variation in this dimension to warrant recognition of two taxa.

3) The profile of the frontal bone is said to be 'low' in *Homunculus* whereas it is more vaulted in *Killikaikae*. MPM-PV 3502 resembles *Homunculus* in this respect and, like CORD-PZ 1130 and the other frontal specimens from PLC, has a slightly depressed area posterior to the glabellar point, whereas the corresponding area in *Killikaikae* is slightly convex.

4) The postorbital constriction is said to be narrower in *Homunculus* than in *Killikaikae*. This is difficult to determine accurately in CORD-PZ 1130. Nevertheless, MPM-PV 3502 has a far narrower postorbital constriction than does MPM-PV 5000, and in that respect resembles *Homunculus*.

A detailed comparison of other cranial and dental proportions of MPM-PV 5000 and CORD-PZ 1130 reveal some other differences.

1) The anterior root of the zygomatic arch of CORD-PZ 1130 is deeper dorsoventrally than in MPM-PV 5000. MPM-PV 3502 agrees with CORD-PZ 1130 in that respect.

2) The M2 is more transverse in MPM-PV 3502 than in *Killikaikae* (MPM-PV 5000 and MPM-PV 1607, a referred specimen). The ratio of M2 buccolingual breadth to mesiodistal length is 1.57 in MPM-PV 3502 versus 1.33 and 1.38 in MPM-PV 5000 and MPM-PV 1607. Thus MPM-PV 3502 repeats in the M2 the *shape* difference shown between *Killikaikae* and *Homunculus* in the P3.

Overall, *Killikaikae* and *Homunculus* are strikingly similar in most

details of dental and cranial morphology. Most of the morphological differences mentioned above are subtle and have yet to be placed in the context of within-species variation in samples of living platyrrhines. Several other cranial and dental characters could be compared, but that is beyond the scope of this study. Furthermore, given that the holotype of *Killikaika blakei* is a subadult, many of the diagnostic characters of this species, such as the

shape of the frontal and the length of the rostrum are of limited comparative value as they are likely to change through ontogeny. Nevertheless, *Killikaika* and *Homunculus* (as represented by CORD-PZ 1130) do differ in a number of ways. And where they differ, MPM-PV 3502 more closely resembles *Homunculus*. Therefore, we are confident that MPM-PV 3502 should be allocated to *Homunculus patagonicus*.