A Neotype for *Homunculus patagonicus* Ameghino, 1891, and a New Interpretation of the Taxon

MARCELO F. TEJEDOR

Facultad de Ciencias Naturales, Sede Esquel, Universidad Nacional de la Patagonia "San Juan Bosco," and CONICET. Sarmiento 849, (9200) Esquel, ARGENTINA; and, New York Consortium in Evolutionary Primatology (NYCEP), Department of Mammalogy, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; mtejedor@infovia.com.ar

ALFRED L. ROSENBERGER

Department of Anthropology and Archaeology, Brooklyn College, CUNY, 2900 Bedford Ave., Brooklyn, NY 11210, USA; and, City University of New York, Graduate Center, New York Consortium in Evolutionary Primatology (NYCEP), Department of Mammalogy, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; alfredr@brooklyn.cuny.edu

ABSTRACT

Homunculus patagonicus was first described by Ameghino in 1891. A few studies have since added to the literature but our understanding of the affinities of this late early Miocene species or its role in the evolutionary history of Patagonian primates and the platyrrhines as a whole has remained quite limited. This is partly due to the loss of the type specimen. Here we designate a neotype, MACN-A 5757, the best preserved mandible from the original Ameghino collection of primates of Santacrucian Land Mammal Age that was likely discovered in the same general area as Ameghino's type. Our reanalysis of the available craniodental material of *Homunculus patagonicus*, mostly from this series, indicates that its morphology strongly resembles that of modern pitheciines and their fossil relatives but tends to be more primitive. Like these other forms, *Homunculus* presents a derived incisor-canine complex, with a compact incisor battery, at least moderately high crowned but narrow incisors, and possibly a large, robust canine. The incisors are probably semi-procumbent, arrayed in front of the canines, and the mandible is probably relatively narrow anteriorly, a combination of features that parallels some of the advanced callitrichines, *Callithrix* and *Cebuella*. The mandibular profile is remarkably similar to *Aotus*, including the extinct *A. dindensis* from younger deposits of La Venta, Colombia. The partial cranium from the original series is notable for its flat frontal trigon, wide interorbital region, unenlarged orbits, deep maxilla and large maxillary sinus, and proclivous premaxilla. Long bones preserve limb proportions similar to modern quadrupedal platyrrhines, such as *Aotus* and *Callicebus*, which lack advanced leaping adaptations. Other Patagonian fossil pitheciines are discussed and compared, along with the additional records of this subfamily outside Argentina. Overall, *Homunculus* appears to have been a primitive pitheciine, with versatile adaptations resembling the quadrupedal, diurnal titi monkeys, including an emphasis on feeding on tough fruits.

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INTRODUCTION

The type specimen of *Homunculus patagonicus* Ameghino 1891, a mandibular fragment, is lost, and research-quality casts of it were never produced. Moreover, the dental remains which over the years have become informal replacements of the type in studies of Patagonian platyrrhines have not been adequately described or figured. Given the elevated interest in the evolution of New World monkeys (NWM), and the heightened pace of recovery and description of new forms, it is important to establish the anatomical and paleontological basis of the species. In this report we designate a new "type specimen," a neotype, in accordance with the recommendations of Article 75 of the International Code of Zoological Nomenclature (1999) in case of loss or destruction of a holotype, following the previous suggestion of Tejedor (2000). We also briefly review the systematics and paleobiology of the genus and discuss its place in the adaptive radiation of NWM. Table 1 summarizes all the previous records of the specimens here discussed and assigned to *Homunculus patagonicus*. Figure 1 locates all the Patagonian localities mentioned in the text.

A BRIEF HISTORY: THE FIRST REPORTS AND THE 20TH CENTURY

Homunculus patagonicus was the second fossil platyrrhine discovered in South America (Ameghino 1891) and the first evidence of Tertiary NWM. It followed Lund's (1840) report on the occurence of *Protopithecus brasiliensis* from the Pleistocene of Minas Gerais, Brazil. During his trips to Patagonia between 1891 and 1894, Carlos Ameghino found mandibular fragments, a partial cranium, and postcranial elements of primates in Santa Cruz Province, Argentine Patagonia. As a consequence, *Homunculus* became a 'popular' fossil of the Santa Cruz Formation and the Santacrucian South American Land Mammal Age (SALMA), one of the richest Middle Miocene vertebrate bearing deposits in South America.

The first specimens of *Homunculus* were described by Carlos' brother, Florentino Ameghino (Ameghino 1891, 1894, 1906). The most comprehensive assessment since then was provided by Bluntschli (1931), who may have figured all the original Ameghino specimens at his disposal; his study remains an important reference work. Other authors, in papers that have tended to focus on one system only (the dentition, cranium, or postcranium), have also discussed the meaning of the various specimens (e.g., Rusconi 1935; Kraglievich 1951; Hershkovitz 1981, 1984; Rosenberger and Fleagle 1981; Fleagle and Rosenberger 1983; Ford 1990; Tejedor 1996, 2000), but no new material was added to the collection until recently. There have been several misallocations. Although Florentino Ameghino first reported four genera in his first two publications on Santacrucian primates (Ameghino 1891, 1906), all but one have been allocated to other mammal groups, such as the marsupials and rodents. Later, Rusconi (1935) attributed a primate cranium from the Colhuehuapian SALMA of Chubut Province to his new species *Homunculus harringtoni*, subsequently recognized as the new genus *Tremacebus* by Hershkovitz (1974). Also, Stirton (1951) named the species *Homunculus tatacoensis* for a primate mandible from the Laventan SALMA in the Magdalena Valley, Huila Province, Colombia, but this was also transferred to a new genus, *Stirtonia*, by Hershkovitz (1970).

The original holotype of *Homunculus patagonicus*, MACN-A 634 (MACN: Museo Argentino de Ciencias Naturales, Buenos Aires; A: Ameghino collection), which has been missing for decades, came from the area of Río Gallegos. More precise details of the locality were never given by the Ameghinos, either in publications or in entries of the museum catalog. Many Santa Crucian fossils, including primates, continue to be discovered from extensive exposures of sediment that run for kilometers along the northern bank of Río Gallegos. According to the original description by Ameghino (1891), the type specimen was an adult, probably female, with the teeth fully erupted. It preserved the right corpus with the symphysis and i2-m1, plus roots of the incisors and m2.

In the same year, Mercerat (1891) briefly described an incomplete molar in a broken mandibular fragment that he named *Ecphantodon ceboides*. For convenience, we also regard this as part of the original Ameghino series. With no adequate explanation, Ameghino (1891, 1894) considered *Ecphantodon* indistinguishable from *Homunculus*, but this specimen is now also missing and it has not been mentioned since.

MACN-A 635 was named *Anthropops perfectus* by Ameghino (1891). Said to come from the coast of Santa Cruz province, the specimen is a symphysis with roots of all lower incisors, alveoli of right and left canines, roots of right p2-3, crown of right p4 and partial alveoli of left p2 and right m1. Ameghino (1891) distinguished *Anthropops* from *Homunculus* on the basis of the former's supposed V-shaped mandible, broader symphysis, and larger lower canine, in contrast to the U-shaped mandible and more procumbent and compressed symphysis of the type of *Homunculus*.

A left partial cranium (MACN-A 5968, Figure 2) preserving the left orbit, part of the frontal and the maxilla was found at the locality of Corrigüen Aike, now known as Puesto Estancia La Costa (see Tauber 1991), between the rivers Coyle and Gallegos (Ameghino 1898, 1906; see also Rosenberger and Fleagle 1981). It was assigned to *Homunculus patagonicus* by F. Ameghino (1894) and has, for better or worse, become the iconic example of the species in lieu of a holotype.

MACN-A 5757, also from Corrigüen Aike, is the most complete mandible of *Homunculus patagonicus* (Figures 3 and 4), although the dentition is badly worn and broken (Ameghino 1898, 1906). It preserves all the teeth except the left lower canine and crowns of the incisors. We select this specimen as the neotype. A right femur (MACN-A 5758), partial ulna (MACN-A 5759), left radius (MACN-A 5960, and right distal humerus (MACN-A 5961), were said to be found associated with this mandible (Ameghino, personal MACN catalog).

TABLE 1. DESCRIPTION AND GEOGRAPHIC PROVENIENCE OF THE *HOMUNCULUS* MATERIAL DISCUSSED IN THE TEXT.

	Original name	**Description**	**Locality**
MACN-A 634- Holotype, now lost	*Homunculus patagonicus*	Right mandible and symphysis with i2-m1, roots of incisors and m2	Unknown but near the city of Río Gallegos, Santa Cruz Province
MACN-A 635	*Anthropops perfectus*	Symphysis, roots of lower incisors, alveoli of both canines, roots of right p$_{2-3}$, complete right p4, partial alveoli of left p2 and right m1	Unknown but near the city of Río Gallegos, Santa Cruz Province
MACN- A 5757*- Neotype	*Homunculus patagonicus*	Mandible with all teeth except the left c and crowns of incisors	Corrigüen Aike (=Puesto Estancia La Costa)
MACN- A 5758*	*Homunculus patagonicus*	Right femur	Corrigüen Aike (=Puesto Estancia La Costa)
MACN-A 5759*	*Homunculus patagonicus*	Partial ulna	Corrigüen Aike (=Puesto Estancia La Costa)
MACN-A 5760*	*Homunculus patagonicus*	Left radius	Corrigüen Aike (=Puesto Estancia La Costa)
MACN-A 5761*	*Homunculus patagonicus*	Right distal humerus	Corrigüen Aike (=Puesto Estancia La Costa)
MACN-A 5966	*Pitheculus australis*	Left mandibular fragment with m2	Monte Observación
MACN-A 5968	*Homunculus patagonicus*	Partial cranium	Corrigüen Aike (=Puesto Estancia La Costa)
MACN-A 5969	*Homunculus patagonicus*	Left part of a mandible preserving the ascending ramus and m2	Monte Observación
MACN-A 8648	*Stilotherium grande*	Right dp4	Monte Observación
MACN-A 10403	*Homunculus patagonicus*	Left mandibular fragment with m1-2	Monte Observación
MLP-55-XII-13-156	*Homunculus patagonicus*	Right m2	Monte León (?)
MLP 11-121	*Homunculus* sp.	Mandibular fragment with dp4-m1	?

* indicates probably associated material

Figure 1. Satellite image of Patagonia showing the localities mentioned in the text. From public domain sources.

The remaining primate specimens of the Ameghino collection have received scant attention since their original description (Ameghino 1894, 1906). MACN-A 5966 is a left mandibular fragment with an m2. MACN-A 5969 (Figure 5a) is part of a left mandible preserving the ramus and a rather well preserved m2. MACN-10403 (Figure 5b) is a left mandibular fragment with m1-2 fairly worn. All three come from Monte Observación, on the Atlantic coast, more than 100km north of Corrigüen Aike. Ameghino originally described MACN-A 5966 as *Pitheculus australis* (Ameghino 1891) and 5969 and 10403 as *Homunculus patagonicus* (Ameghino 1894, 1898). We refer all three to *H. patagonicus* (although Rosenberger has reservations about the assignment of 5969).

A lower second molar, MLP-55-XII-13-156, was collected by Carlos Ameghino, probably at Monte León, Santa Cruz Province, less than 200km north of Corrigüen Aike, but it remained undescribed. Catalog records at the museum in La Plata raise doubts about the exact provenance of this molar, and it would be the only primate found at this locality, which is close to Monte Observación. It is also indistinguishable in size and morphology from primate molars found much later at Monte Observación and allocated to *Homunculus patagonicus* (Tejedor 2000). Its provenience remains a question.

An isolated right cheek tooth from Monte Observación, MACN-A 8648, was described by Ameghino (1894) as a marsupial, *Stilotherium grande*. Reig (1955) did not think it was a species of *Stilotherium* or even a caenolestid marsupial. Herhskovitz (1981) identified the tooth as primate (following a personal communication from Larry Marshall), a probable dpm4, and allocated it to a new species of *Homunculus*, *H. grandis*. In 1984, Hershkovitz described MLP 11-12-1, a mandibular fragment with dp4 and m1, as *Homunculus* sp., because its deciduous premolar appeared almost identical to that of MACN-A 8648. This specimen came from an unprovenenced locality of the Santa Cruz Formation.

Almost 100 years after Carlos Ameghino first discovered primates in Patagonia, in February 1988, a paleonto-

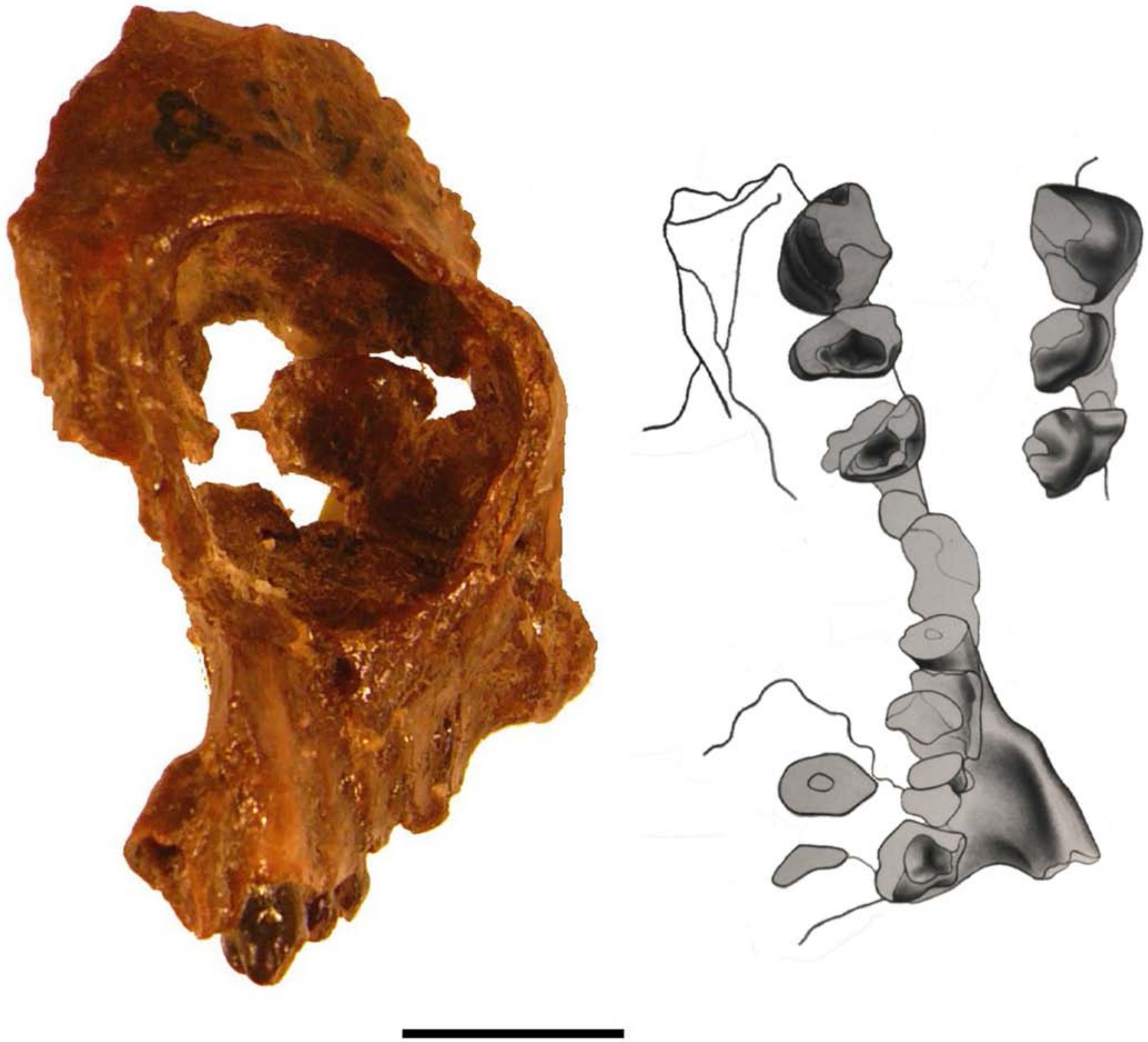

Figure 2. Left: Frontal view of MACN-A 5968, partial cranium of Homunculus patagonicus *from Corrigüen Aike (=Puesto Estancia La Costa). Right: occlusal view of the broken left dentition of the same specimen, with inset showing lateral view of C-P2.*

logical expedition from the State University of New York at Stony Brook together with MACN recovered isolated teeth and two mandibular fragments, each with two molars, at Monte Observación (Fleagle et al. 1988) on the Estancia Cañadón de las Vacas. Fleagle et al. (1988) and Tejedor (2000) listed the specimens as *Homunculus patagonicus*. A detailed comparative study of the material is in order, especially in the light of the discovery of new taxa from the coastal localities, such as *Killikaike blakei* (Tejedor et al. 2006). With the availability of radiometric dating, this discovery has become important because, following Bown and Fleagle (1993), this late early Miocene area is one of the most stratigraphically continuous and extensive sections of Santacrucian exposures. Based on $^{40}Ar/^{39}Ar$ dates from three levels of the lowest part of the section, the fossils date to about 16.4 Ma (Fleagle et al. 1995), the same age reported by Tejedor et al. (2006) for the locality of Killik Aike Norte, near the city of Río Gallegos. Fleagle et al. (1987) also reported *Homunculus* sp. from the Pinturas Formation in northwestern Santa Cruz Province, but subsequently (Fleagle 1990) referred this material to *Carlocebus intermedius*. Another important specimen of *Homunculus* was added by Tauber (1991), who described a partial cranium (CORD-PZ 1130) from Corrigüen Aike. Finally, Kay et al. (2005) reported—in a preliminary abstract—crania as well as a mandible and distal humerus, which they referred to *Homunculus*. These specimens came from Corrigüen Aike and Killik Aike Norte.

In addition to the above mentioned primates, Ameghino (1902, 1904, 1906) described other fossils as primates, but they later were reallocated to different mammalian groups.

Figure 3. MACN-A 5757, neotype mandible of Homunculus patagonicus *in lateral (top) and occlusal (bottom) views. Scale bar= 1 cm.*

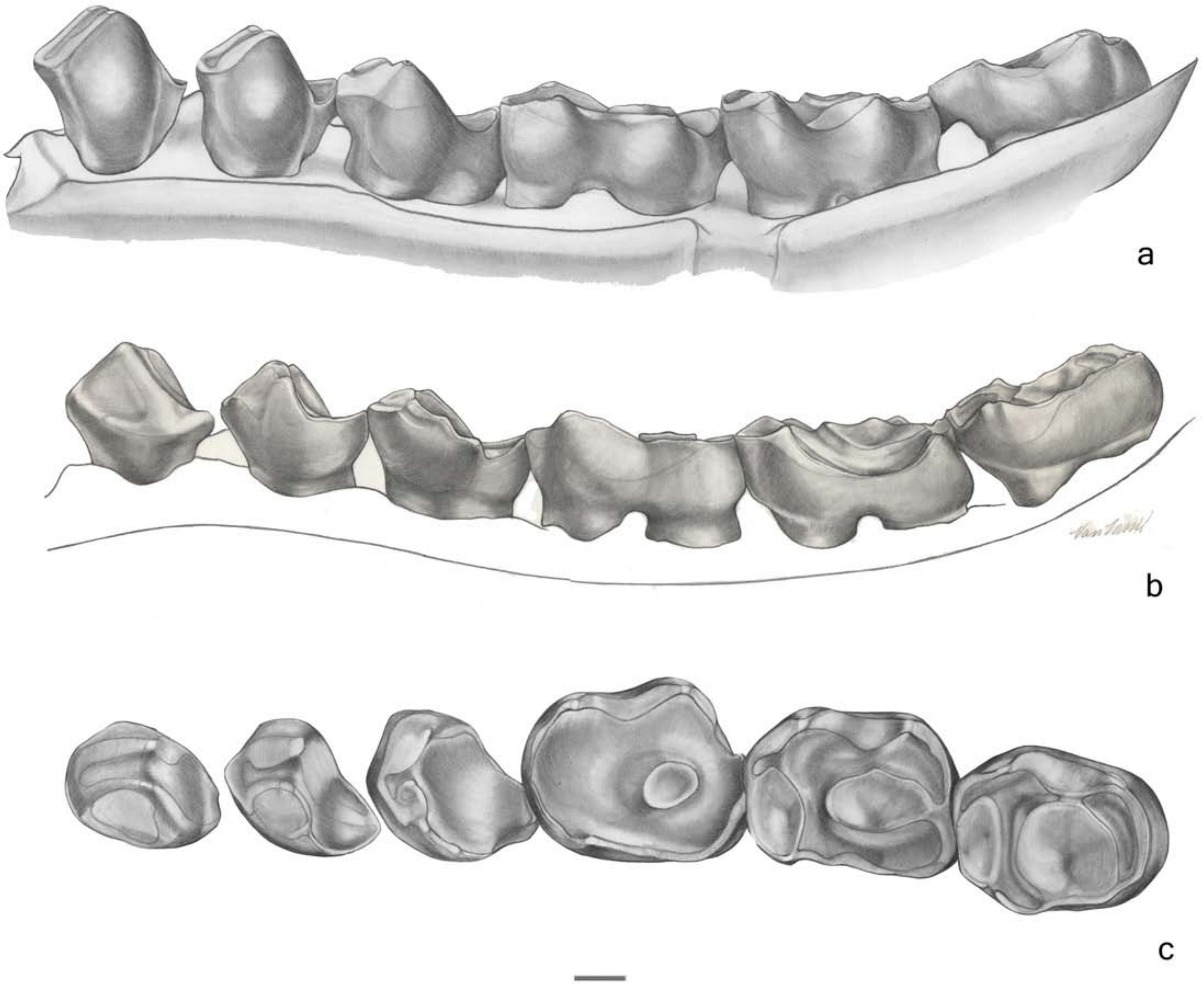

Figure 4. Renderings of the right postcanine toothrow of MACN-A 5757 neotype of Homunculus patagonicus, *in (a) buccal (reversed left to right for ease of comparison), (b) lingual, and (c) occlusal views. Scale bar= 1 mm.*

Clenialites minusculus was described as a left mandible of a very small "prosimian." *Homunculites pristinus*, a left mandible and an upper molar, and *Pitheculites minimus*, upper and lower teeth, were described as the smallest known primate. These three taxa are caenolestoid marsupials. *Eudiastatus lingulatus* is a symphysis identified by Ameghino as another "prosimian," but it is currently interpreted as a notoungulate. *Homocentrus argentinus*, another alleged primate, is now interpreted as a worn rodent tooth. Finally, *Homunculus imago* (Ameghino 1894), based on a partial femur and ulna, is certainly not a primate.

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Infraorder Platyrrhini E. Geoffroy, 1812
Family Atelidae Gray, 1825
Subfamily Pitheciinae Mivart, 1865
Tribe Homunculini Ameghino, 1894
Homunculus patagonicus Ameghino, 1891

SYNONYMOUS SPECIES

Ecphantodon ceboides Mercerat, 1891
Anthropops perfectus Ameghino, 1891
Homunculus ameghinoi Bluntschli, 1931
Pitheculus australis Ameghino, 1894
Stilotherium grande Ameghino, 1894
Homunculus grandis (Hershkovitz 1981)

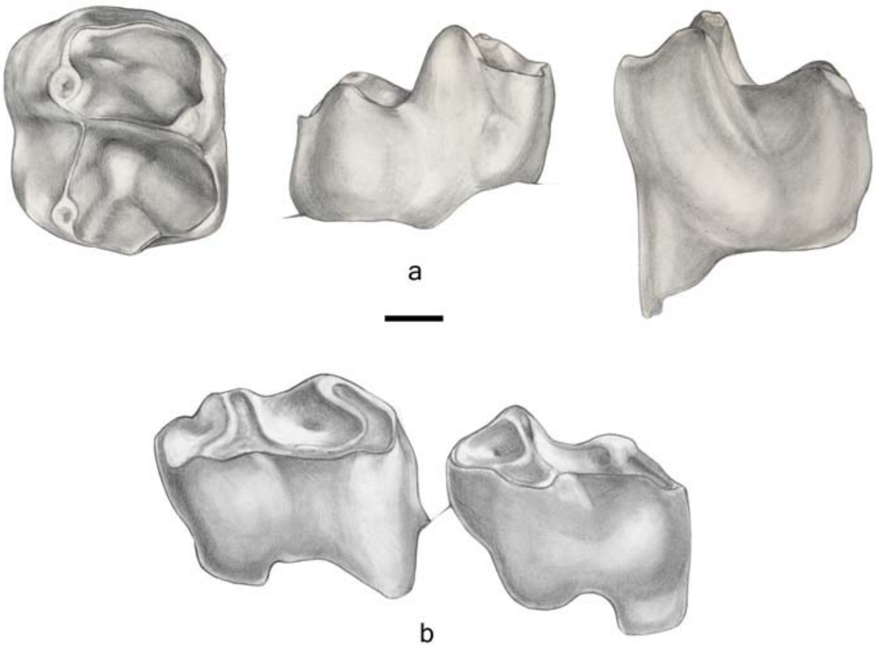

Figure 5. a) MACN-A 5969, left m2 of the mandibular fragment provisionally assigned to Homunculus patagonicus *in (from left to right) occlusal, lingual, and labial views; b) MACN-A 10403, left m1-2 of* Homunculus patagonicus *in ¾ buccal view. Scale bar= 1 mm.*

Neotype: MACN-A 5757; partial mandible preserving a complete but worn and damaged dentition lacking only crowns of the the left canine and the incisors. This is a replacement for the lost holotype specimen, MACN-A 634. Dental measurements of the neotype (in mm, right tooth row, mesiodistal followed by buccolingual diameters): i1 root= 1.7,1.9; i2 root= 1.7, 2.1; canine alveolus= ~3.6; p2=3.1,2.7; p3= 3.3,3.2; p4=3.5,3.2; m1=4.6,3.9; m2=4.6, ~3.4 ,m3=4.2, 3.4.

Hypodigm: the type and MACN-A 5968 (partial cranium); MACN-A 5969a (left mandibular fragment with ramus and m2); MACN-A 5966 (left mandibular fragment with m2); MACN-A 635 (symphysis with right p4), MACN-A 10403 (left mandibular fragment with m1-2); MLP 55-XII-13-156 (lower molar); MLP 11-121 (left mandibular fragment with dpm4 and m1); MACN-A 8648 (right dpm4); CORD-PZ 1130 (partial cranium).

Locality (for the neotype): Corrigüen Aike (=Puesto Estancia La Costa), on the Atlantic coast of Santa Cruz Province between the rivers Coyle and Gallegos, Argentina.

Horizon and age: Santa Cruz Formation, late Early Miocene, Santacrucian SALMA, approximately 16.1-16.5 Ma (Tejedor et al. 2006).

Emended Diagnosis: medium-sized pitheciine characterized by the following combination of features: anteriorly convergent toothrows; posteriorly deepening mandibular corpus (particularly resembling *Aotus* rather than the highly inflated *Soriacebus*, *Callicebus*, and *Xenothrix*, for example) and anteroposteriorly abbreviated ramus; incisors narrow and at least moderately high crowned, closely spaced and anteriorly emplaced ahead of the canines; p2 transversely compressed and wedge-shaped with a large preprotocristid C^1 honing facet; p3,4 with small talonids; m1-3 with moderately long talonids; relatively short trigonid with transversally oblique distal wall, especially in m1; orbits of moderate size, not enlarged as in *Aotus*, interorbital region relatively wide as in *Callicebus*, not narrow as in *Killikaike*, *Cebus*, and *Saimiri*; frontal bone not vaulted, as in *Aotus* or *Callicebus*, and differing from the vaulted frontal of *Killikaike* and living cebines; postorbital constriction narrower than in *Killikaike*; maxillary sinus relatively large; nasal bones relatively wide rostrally and premaxilla somewhat procumbent.

DISCUSSION

MACN-A 5757 is the best mandible referrable to *Homunculus patagonicus*, making it the most fitting replacement type, although the postcanine dentition is heavily worn. Nevertheless, the specimen preserves nearly all the cheek teeth on both sides and either roots or crown remnants of the anterior teeth. The specimen has suffered damage over the years, as can be determined from published descriptions and drawings. For example, the right canine is now broken. Also, the coronoid process was once intact, and the posteroinferior part of the mandible was rather more complete than it is now, as clearly discerned from the literature (Ameghino 1906; Scott 1928; Rusconi 1935; Hershkovitz 1981), especially from the detailed report of Bluntschli (1931). Bluntschli pointedly explained that his published photograph of the mandible, hastily taken, lacked two pieces that had broken off the specimen, but these were apparently integrated into his graphic reconstruction (Figure 6a). That image closely resembles the depiction previously given by Scott (1928). Since the 1930s, the corpus and symphyseal region has suffered additional damage. Our assessement is that the symphysis has been restored incorrectly. Comparing Bluntschli's figures with the specimen in its current state (Figure 3) suggests that the symphysis and the incisor roots were originally more procumbent. This is consistent with the procumbency evident in the undistorted premaxilla. Overall, the lateral profile of the mandible most closely resembles the living *Aotus* (compare Figure 6a, b), in comparison to other selected living platyrrhines of its approximate size (Figure 6 c-f).

Ameghino's original catalog of fossils stored in the MACN indicates that MACN-A 5757 was found together with a right femur, partial ulna, left radius, and right distal humerus (the latter now missing), all at Corrigüen Aike in 1892. Figure 7 is taken from Bluntschli (1931) and represents the intact femur and radius; both specimens are today broken and restored. Figure 8 shows that the femur, MACN-A 5758, relative to m2 area, is of the appropriate size to belong to the same species, based on a comparison of selected living platyrrhines in the same general size range. This makes it likely that the femur does indeed belong to the same species as the mandible (see also Bluntschli 1931; Rusconi 1935). The radius, MACN-A 5760, is even more confidently linked with the mandible since the correlation (or Coefficient of Determination) between molar size and radius length is higher than between molar area and femur length (Figure 9). Thus, in general, the limb proportions of *Homunculus*, as suggested by the plot, are not remarkable, being comparable to the ratio found among other platyrrhines in this size range, with the exception of *Pithecia*, a genus that has especially long femora.

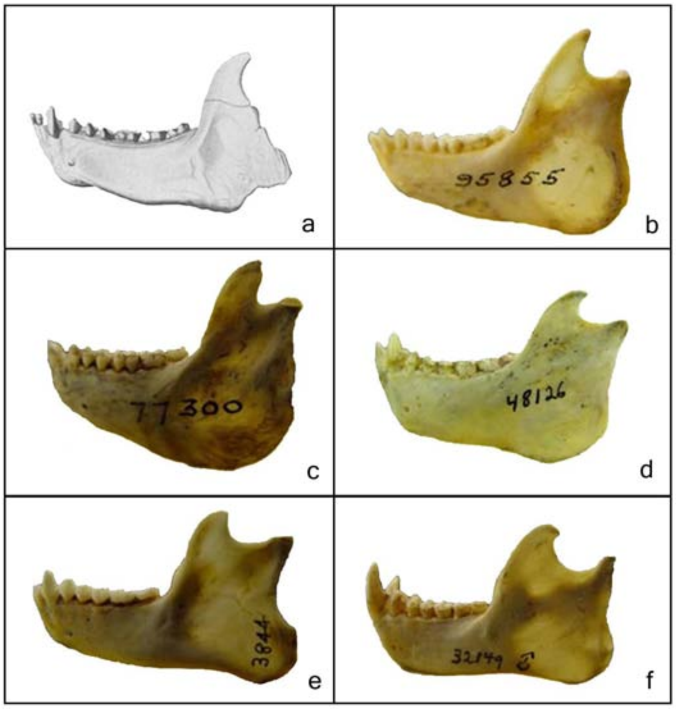

Figure 6. Bluntschli's reconstruction of MACN-A 5757 in lateral view (a) compared with the mandibles of Aotus *(b),* Callicebus *(c),* Pithecia *(d),* Leontopithecus *(e), and* Cebus *(f). All specimens are scaled to approximately the same mandibular size.*

A second specimen of crucial importance is the partial cranium MACN-A 5968 (Figure 2). It was found at Corrigüen Aike during Carlos Ameghino's trip to southern Patagonia in 1891-92. This specimen has been discussed by various authors (e.g., Ameghino 1898, 1906; Bluntschli 1931; Rusconi 1935; Rosenberger and Fleagle 1981; Fleagle and Rosenberger 1983; Tejedor 2000). As noted above, it preserves the left half of the face, orbit, part of the frontal plane, as well as the maxilla, part of the premaxilla including incisor alveoli, and the anterior part of the zygomatic bone. The teeth of this specimen are essentially destroyed (Figure 2b). Apart from the broken left canine root, the only other bits of dental information it provides are small pieces of the buccal margins of P3 and M3.

One of the frequent questions among scholars is whether this partial cranium belongs to the same individual/species as MACN-A 5757, and also the associated long bones; both were found at the same locality, which is not particularly extensive. In this regard, Bluntschli (1931) mentioned that during his research visit to the museum in La Plata, Florentino Ameghino told him the cranium was found in a different place, about 100m away from the mandible and postcranials. In addition, Bluntschli himself doubted that both specimens belonged to the same individual, noting that the color of the tooth enamel was different in the two; brown in the mandible, nearly black in the cranium. Soon after Bluntschli's publication, however, Rusconi (1935) mentioned that Carlos Ameghino informed him in a personal communication that the cranium, mandible, and long bones were found together, and he supported this idea.

Our assessment agrees with Bluntschli's suspicion (1935), based on an extention of his argument. The molars of MACN-A 5757 are very heavily and distinctively worn through to the dentine on all the postcanines, so excessively that all the molar talonids are nothing more than islands of enamel surrounded by the crown sidewalls. However, the pieces of P3 and M3 crowns preserved in the cranium show no signs that the marginal crests have been worn as in the lowers, or that enamel has been breached. On the other hand, the cranium does compare favorably with the lower jaw in size. The fit between MACN-A 5757 and MACN-A 5968 was examined by Zhang et al. (2000), who produced a 3D digital model of a composite reconstructed mandible and cranium based on high-resolution laser surface scanning. This confirms that they are a good match. We take this

Figure 7. a) MACN-A 5758, right femur of Homunculus patagonicus *in (left to right) anterior, posterior, medial, and lateral views; Homunculus femur; b) MACN-A 5760, right radius of* Homunculus patagonicus *in (left to right) anterior, posterior, medial, and lateral views. From Bluntschli (1931).*

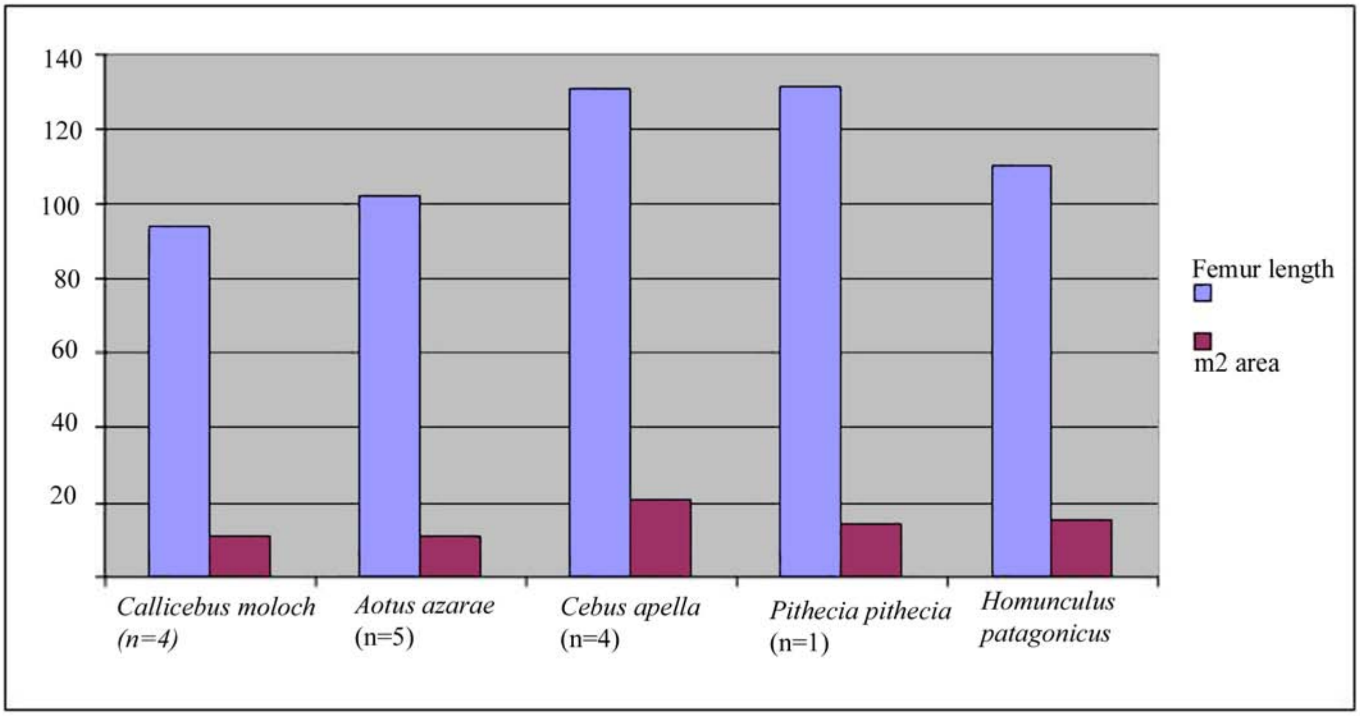

Figure 8. Histogram of femur length and m2 area comparing proportions of Homunculus patagonicus *and selected living platyrrhines.*

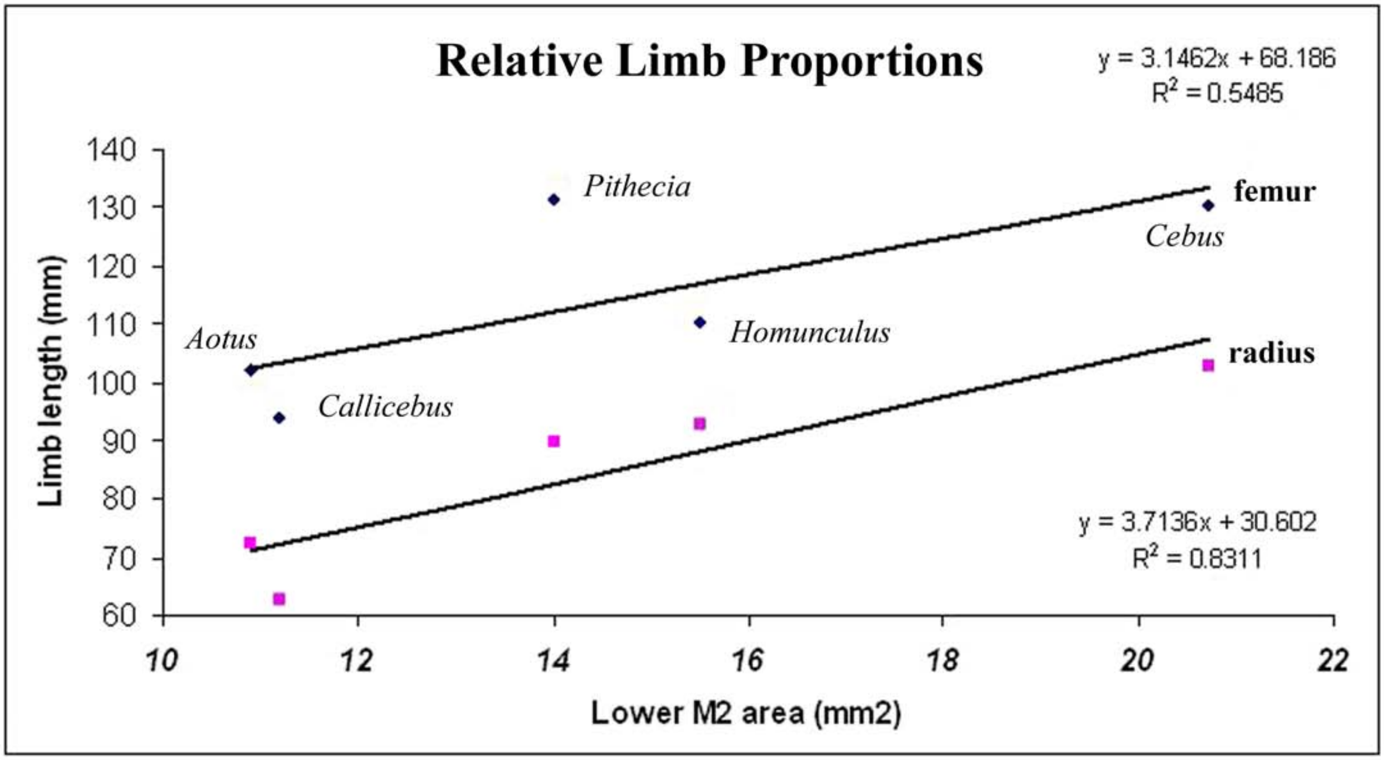

Figure 9. Regressions of radius and femur length on m2 area in Homunculus patagonicus *and selected living platyrrhines (samples as in Fig. 8).*

to mean that 5757 and 5968 probably belong to the same species, although perhaps not to the same individual.

In mandibular morphology, *Homunculus* and *Aotus* share a striking resemblance in lateral profile, especially the contour of the inferior aspect of the corpus. The same pattern is seen in the middle Miocene *Aotus dindensis*, from La Venta (Setoguchi and Rosenberger 1987). Although there is variation in the inferior contour of the corpus of *Aotus* mandibles, which occasionally resembles the dramatically expanded posteroinferior profile of *Callicebus*, the similarity of *Homunculus* and *Aotus* is impressive (Figure 6). Taking Bluntschli's (1931) reconstruction into account emphasizes the point. The ramus of *Callicebus* and *Aotus* are similar and quite different from those of cebines, for example, being characterized by a high, sometimes hooked coronoid, a ramus that is anteroposteriorly short and a gonial region that is enlarged—all resembances shared with *Homunculus* as well (Figure 6). There is little doubt that the enormously inflated gonial region of *Callicebus* is derived, which means that *Aotus* and *Homunculus* share the pattern thought to be primitive for pitheciines. Pitheciins are still more derived, as their mandibles have deepened anteriorly (thus reducing the emphasis upon gonial enlargement) in connection with their highly modified incisor-canine complex, a synapomorphous pattern that is not present in *Callicebus* and *Aotus*.

While the damaged condition of the anterior teeth makes it difficult to interpret MACN-A 5757 with full confidence, our previous discussions of this part of the dentition (e.g., Rosenberger 1992) are suported by our current reevaluation of the information provided by Bluntschli (1931). Overall, we are impressed by a pattern of resemblances that *Homunculus* shares with various pitheciines, living and fossil. As in *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*, and *Soriacebus*, the lower incisors are narrow, compact in their arrangement, spaced *en echelon*, and they appear to have been at least moderately high crowned (see Rosenberger 1992, for metrics). They also are somewhat inclined, which is a resemblance to *Soriacebus*. This pattern does not resemble *Callicebus*, in which genus the incisors have become autapomorphously retracted and verticalized in tandem with canine and premaxillary reduction. Species of *Aotus* also stand out among all these forms in having autapomorphously wide incisors, with a broad combined apical margin, reflecting the greatly enlarged central upper incisors.

Bluntschli's (1931) illustration of the canine complex is also revealing. The specimen currently shows that the p2 carries an impressively large, flat honing facet for the maxillary canine, which is broken and worn. This facet and the postcanine diastema separating p2 from the lower canine suggest that the upper canine was of substantial diameter. Bluntschli showed that the size and shape of the original lower canine is notable as well. He presents it as a pointed projecting tooth, with some graphic suggestions of having a rather triangular cross section and a telling flat distal wear surface for the maxillary canine. While we conservatively interpret this information, it is highly suggestive that this pattern is more pitheciin-like than *Callicebus*-like. It appears to correspond, in general, with the *Aotus* morphology. Furthermore, Bluntschli shows a pre-canine diastema and a butressed symphysis. We thus conclude that the canines are not reduced in *Homunculus*; rather, the canine-incisor complex was very well developed for a species of this size. The canine alveoli of MACN-A 635 ("*Anthropops perfectus*") also are rather large, corresponding to a non-reduced canine.

We propose that among fossil forms for which we have relevant evidence, *Homunculus* shows more resemblances to *Soriacebus* in the anterior dentition than has been previously realized, although we emphasize that the latter is more derived overall in this character complex and we also acknowledge that our assessment is difficult to validate since the specimen has been damaged since the time of Bluntschli (1931). Nevertheless, there appears to be an integrated set of similar features shared by *Homunculus*, *Soriacebus*, and pitheciins, with the two fossils sharing what are likely to be the more primitive character states. For example, like *Homunculus* the incisors of *Soriacebus* are narrow, at least moderately tall, inclined, staggered and emplaced anterior to the canines, although the canines seem to be rather robust, pointed and pyramidal in shape. *Nuciruptor* (Meldrum and Kay 1997) as well as *Cebupithecia* have essentially the same pattern in the incisors and canines, though the details differ.

Our conclusion regarding the incisor-canine complex is that *Homunculus* shares the derived pattern found uniquely among pitheciines but in the most primitive configuration yet discovered. In other words, we hypothesize that the more advanced morphologies seen in forms such as *Soriacebus*, *Nuciruptor*, *Proteropithecia*, *Cebupithecia*, and other pitheciins could have evolved out of a *Homunculus*-like morphology. By the same token, the autapomorphous morphologies of *Callicebus*, on the one hand, and *Aotus*, on the other, also can be derived from this pattern. Adaptive explanations for the origins of this complex have been discussed by Kinzey (1992) and Rosenberger (1992), who agreed that pitheciines were initially adapted to harvesting fruits with tough pericarp, possibly to gain advantage by acquiring fruits before they were fully ripe. This may have been a selective response to increased seasonality of fruiting cycles (Kinzey 1992; Rosenberger 1992) or to a set of more limited food resources in habitats that were more "marginal" and less productive than currently is the case in much of Amazonia (Rosenberger et al. in press). As the adaptive radiation of pitheciines unfolded, pitheciins may have transformed into seed-predators, with the incisor-canine complex evolving additional biomechanical adptations for breaching hard-shelled fruits in order to extract seeds.

The postcanine teeth of *Homunculus* have been favorably compared with *Callicebus* ever since Gregory (1922) as, for example, both seem to have relatively large molars, low but well developed cusps, moderate crests and short trigonids. Another view has been that *Homunculus* shares more important resemblances with *Alouatta* (Hershkovitz 1984). It should be emphasized that those ideas were presented before there were any dental remains of early Miocene pitheciines other than the Ameghino *Homunculus* series. While we find little justification for Hershkovitz's view, we do find the comparisons with *Callicebus* valuable. Based on the neotype and the rest of the hypodigm, what can be said about the cheek teeth of this genus is still limited. Additional information may be gleaned from the dentitions of the new skulls when they are described (Kay et al. 2005). The cranium described by Tauber (1991) also had worn and broken upper teeth.

The cranial material of *Homunculus* has received far more attention (e.g., Rosenberger and Fleagle 1981; Fleagle and Rosenberger 1983; Tauber 1991). Comparisons have been made with *Dolichocebus*, *Tremacebus*, and *Killikaike*, the three Patagonian genera for which there is cranial material (Rosenberger 1979; Rosenberger and Fleagle 1981; Fleagle and Rosenberger 1983; Kay et al. 2005; Tejedor et al. 2006) Based on the two *Homunculus* crania well known thus far (MACN-A 5969 and CORD-PZ 1130), but especially based on CORD-PZ 1130 which is more complete and better preserved, the pertinent points are these. The frontal is not domed but relatively flat. The interorbital region is relatively wide. The orbits, which probably were completely closed off behind, are similar in relative size to those of *Callicebus*, not enlarged as in *Tremacebus* or *Aotus*. The face is somewhat prognathic, with an everted premaxilla. The nasals were relatively wide at the nasal aperture. Together, these features compare well with *Callicebus* overall, but there are numerous difference between the two. The most distinctive one concerns the premaxilla, which is highly abbreviated, autapomorphically, in *Callicebus* and in *Aotus*.

An additional similarity shared with *Callicebus* is in the conformation of the maxillary sinus (Figure 10). As shown by comparing a cross section through the M3s of *Homunculus*, based on a laser surface scan of the face, and comparable sections of modern platyrrhine specimens, both *Callicebus* and *Homunculus* have large maxillary sinuses beneath the orbit, contrasting the condition in the much larger-bodied *Cebus* and also *Aotus*, where the maxillary sinus is reduced in order to accommodate the enlarged eyeballs (Setoguchi and Rosenberger 1987).

CONCLUSION

We select a well-preserved mandible with worn teeth described by Ameghino (1898) as the neotype of *Homunculus patagonicus*, to replace the now-lost holotype, a partial mandible with six teeth described earlier in 1891. As a result of fixing the type, it is possible to assign a number of other fragments to this long-known taxon and survey its morphology and adaptations.

We conclude from our reanalysis of the *Homunculus patagonicus* craniodental material that its morphology is of a pattern that strongly resembles modern pitheciines and their fossil relatives. Due to our limited knowledge of the cheek teeth, the crucial dental evidence for this position relates to

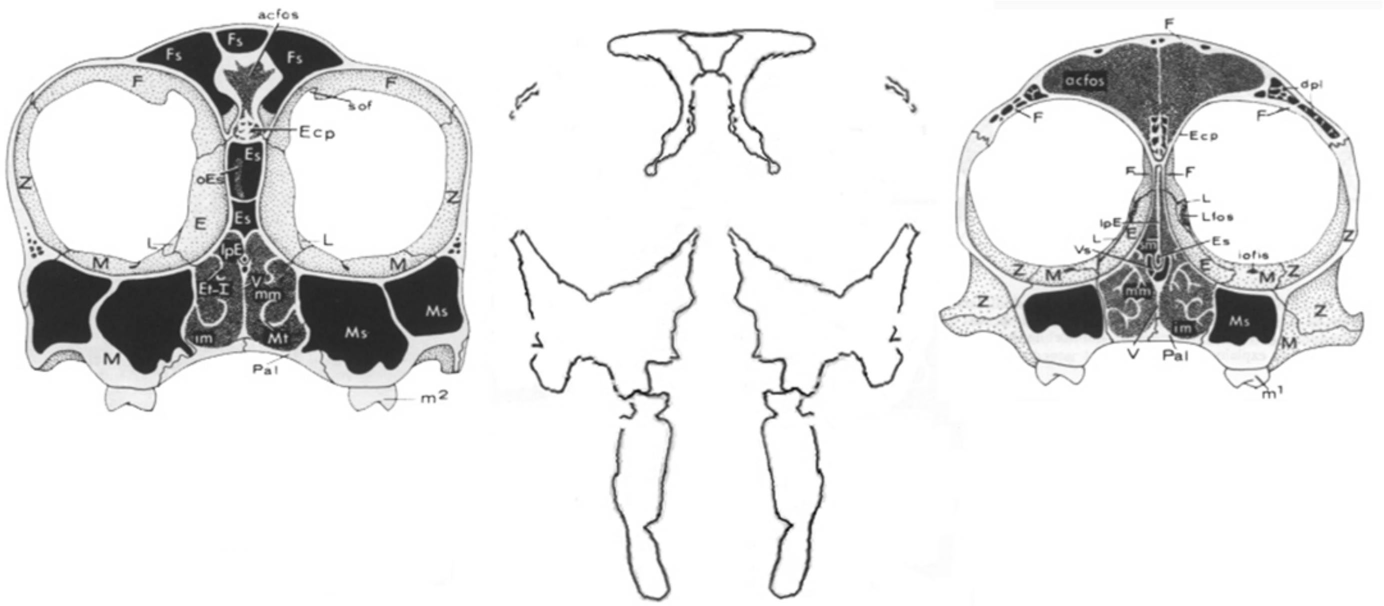

Figure 10. Comparable cross sections of the faces of Callicebus *and* Cebus, *left and right, respectively, and* Homunculus patagonicus, *middle, based on graphic reconstructions derived from laser surface scanning, with the MACN A-5757 mandible articulated at M3/m3. The image highlights similarities* Homunculus *shares with* Callicebus, *including: large, laterally extensive maxillary sinus (also visible on the broken original); broad interorbital region; flat frontal; relatively deep mandible; and, unusually downturned zygomatic process, the latter seen only in* Callicebus *and* Aotus. *Adapted from Hershkovitz (1977) and Zhang et al. (2000).*

the incisor-canine complex. With odd incisors and canines, pitheciines are a derived group of platyrrhines best known by the modern seed-eating and sclerocarpic sublineage of saki-uakaris, or pitheciins, comprised of *Pithecia*, *Chiroptes*, and *Cacajao*. This adaptive complex also is demonstrated in their extinct South American relatives, including *Soriacebus*, *Cebupithecia*, *Nuciruptor*, and *Proteropithecia*. A less derived, or alternate, version of the anterior tooth complex is found in the other lineage of pitheciines, the homunculins, which include *Aotus*, *Callicebus*, and *Tremacebus*.

Overall, *Homunculus* is less derived than most of the modern genera, and thus the more primitive features it shows are important aspects for comparison. For example, among homunculins, *Callicebus* has less extreme morphological adaptations than pitheciines for husking hard shells, is not reliant on seeds for protein (see Norconk 2007), and has an alternately modified canine complex founded on diminutive canines related to their monomorphism/monogamy mating complex. *Homunculus* compares favorably concerning the first two points, but earlier studies suggest strongly that its canines were not reduced. *Aotus* retains the fundamental baseline for a front-tooth dominated pitheciine by presenting an unusual battery of incisors, but with a different morphological emphasis. While still retaining the moderate to high crowns thought to be ancestral in the subfamily (Rosenberger 1992), *Aotus* incisors have evolved in a different direction by becoming autapomorphically broad. This is evident in the lower and in greatly broadened upper central incisors in some species, which may be proportionately the largest of any anthropoid. *Homunculus* does not compare well here, lacking any indications of exaggerated incisor breadth.

Thus, our assessment is that *Homunculus* is part of the pitheciine ecophylogenetic radiation, as an anatomically primitive member. A prominent gnathic feature signifying this is the mandibular morphology, which bears a striking overall resemblance to *Aotus*. A mandible that deepens posteriorly is an atelid trait, derived relative to other platyrrhines but primitive among pitheciines. But cranially, *Homunculus* is more *Callicebus*-like, lacking the large orbits and eyes of the nocturnal *Aotus* and *Tremacebus* (Fleagle and Rosenberger 1983; see also Kay et al. 2004). By way of summary, this means that *Homunculus* may be a primitive representative of the subfamily, while the other Miocene genera, including *Soriacebus*, *Cebupithecia*, *Proteropithecia*, and *Nuciruptor*, may be early representatives of the "more advanced steps" in the pitheciin direction. *Cebupithecia* and *Proteropithecia* are even more derived in the saki-uakari direction with more modern incisors, canines, and postcanines. The little we know of the postcranium is consistent with this picture. Based on the original Ameghino series, the limb proportions of *Homunculus* resembled the generalized quadrupeds *Aotus* and *Callicebus* (and *Cebus* among cebids) but differed from *Pithecia*, a derived, long-legged leaper.

Little is known about the environment in which *Homunculus* lived. Following Tauber (1997a), in his work concerning the paleoecology of the Santa Cruz Formation, *Homunculus patagonicus* was associated with the environmental changes reflected during the deposition of the Estancia La Costa member, which involved a climatic deterioration and a less humid environment with more seasonal and drier conditions. The partial cranium of *Homunculus patagonicus*, CORD-PZ 1130, was found by Tauber (1991) in Fossiliferous Level 6, along with several other faunal remains that are not typical of tropical habitats, such as large, predatory phorusrhacid birds and large ungulates (Tauber, 1997b). As discussed by Rosenberger et al. (in press), the habitats of the Miocene Patagonian primates could have been less biotically productive and less diverse taxonomically than today's "average" platyrrhine habitat, i.e., Amazonia or the Mata Atlantica, with more marginal conditions probably resembling the gallery forests along the rivers existing today in the northeastern Argentine Mesopotamia.

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