Eucholoeops Ameghino, 1887 (Xenarthra, Tardigrada, Megalonychidae) from the Santa Cruz Formation, Argentine Patagonia: implications for the systematics of Santacrucian sloths

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ABSTRACT

New well-preserved remains of the megalonychid sloth *Eucholoeops* Ameghino, 1887 recovered under strict stratigraphic control from late Early Miocene Santa Cruz Formation (*c.* 19 to 14 Ma; Santacrucian Age), together with analysis of older collections, consideration of intraspecific variation in extinct and extant sloths, and assessment of the validity of the early literature on Santacrucian sloths, permit revision of the status of the numerous species erected for this genus. The current contribution deals with the systematics of *E. ingens* Ameghino, 1887, but its methodology provides a basis for revision of other *Eucholoeops* species, as well as other sloth genera recovered from the Santa Cruz Formation. The failure to make progress on the systematics of the Santacrucian taxa since their first description is shown to be due mainly to a combination of the poor quality of many of the specimens, which are often fragmented and incomplete and from older collections, as well as inadequate stratigraphic and geographic control of their recovery, an overly rigid reliance on the early literature that accompanied their descriptions, and lack of consideration for intraspecific variation. A neotype is designated for *E. ingens*, as the original specimen is no longer available. The species *E. latirostris* Ameghino, 1891, *E. externus* Ameghino, 1891, and *E. curtus* Ameghino, 1894 are considered as junior synonyms of *E. ingens*.

KEY WORDS
Xenarthra,
Sloths,
Eucholoeops,
late Early Miocene,
Santa Cruz,
neotype,
new synonyms.

RÉSUMÉ

Eucholoeops *Ameghino, 1887 (Xenarthra, Tardigrada, Megalonychidae) de la Formation Santa Cruz de Patagonie Argentine : implications pour la systématique des paresseux santacruziens.*

L'étude de nouveaux restes découverts sous un stricte contrôle stratigraphique et appartenant au paresseux mégalonychidé *Eucholoeops* Ameghino, 1887 provenant de la fin du Miocène inférieur de la Formation San Cruz (*c.* 19 à 14 Ma, âge Santacruzien) ainsi que l'observation d'anciennes collections, l'évaluation de la variation intra spécifique chez les paresseux actuels et fossiles et l'évaluation de l'exactitude de la littérature ancienne traitant des paresseux santacruziens, a permis de reconsidérer le statut de nombreuses espèces érigées pour ce genre. Les études menées actuellement sur le sujet traitent principalement de la systématique d'*E. ingens* Ameghino, 1887. L'étude de sa morphologie génère une nouvelle base pour la révision des autres espèces d'*Eucholoeops*, mais également pour les autres genres de paresseux qui proviennent de la Formation Santa Cruz. L'absence de progrès significatifs de notre connaissance de la systématique des taxons santacruziens depuis leur première description est principalement due à la mauvaise qualité de nombreux spécimens, souvent fragmentaires et incomplets et provenant de collections anciennes, mais également à l'insuffisance de contrôle stratigraphique et géographique lors de leur découverte, à la dépendance trop rigide à la littérature qui a accompagné leurs descriptions ainsi qu'à la non considération de la variation intraspécifique. Comme le spécimen originel d'*E. ingens* n'est plus disponible, un néotype a été désigné pour cette espèce. Les espèces *E. latirostris* Ameghino, 1891, *E. externus* Ameghino, 1891 et *E. curtus* Ameghino, 1894 sont considérés comme synonymes d'*E. ingens*.

MOTS CLÉS
Xenarthra,
Paresseux,
Eucholoeops,
fin du Miocène inférieur,
Santa Cruz,
néotype,
synonymes nouveaux.

INTRODUCTION

The late Early Miocene Santa Cruz Formation (*c.* 19 to 14 Ma), outcropping primarily in Argentine Patagonia along the Río Santa Cruz, the Atlantic coast between the Ríos Coyle and Gallegos, and Monte Observación (currently Cerro Observatorio; Marshall 1976; Vizcaíno *et al.* 2012), is among the most famous and fossiliferous vertebrate deposits in South America. This was Carlos Ameghino's impression over a century ago, as recorded in several letters sent between 1887 and 1902 to his paleontologist brother Florentino (Torcelli 1935, 1936; Vizcaíno 2011), a sentiment that was affirmed later by John Bell Hatcher (1903) and that remains true today (Vizcaíno *et al.* 2012). The abundant and well-preserved Santa Cruz fossils have been known for nearly 150 years, with the first recorded collections made from along the Río Gallegos by the British sea captain Bartholomew Sulivan, who sent the fossils to Charles Darwin (Marshall 1976; Brinkman 2003; Vizcaíno *et al.* 2012). Our knowledge of Santa Cruz fossils, however, stems primarily from the field expeditions of C. Ameghino (between 1887 and 1902) and J. B. Hatcher (during the late 1890s) (see Marshall 1976; Vizcaíno *et al.* 2012). The collections amassed by these researchers document an exceptionally rich faunal assemblage, taxonomically distinct from that of any living community (see Kay *et al.* 2012), that includes the remains of numerous extinct Xenarthra.

Xenarthrans comprise a main clade of placental mammals, although a consensus on patterns of relationships has not been achieved (e.g., see Asher & Helgen 2010; Meredith *et al.* 2011; O'Leary *et al.* 2013). O'Leary *et al.* (2013), based on a combined molecular and morphological study, found support for a sister group relationship of Xenarthra to all other placental mammals, a group identified by McKenna (1975) as Epitheria.

Xenarthra are among the more characteristic faunal elements of the South American Cenozoic. Although their current roster is depauperate (some 31 species, distributed primarily in South and Central America; Vizcaíno & Loughry 2008; Aguiar & Fonseca 2008), they have a rich fossil representation in South America, as well as the West Indies and North America (Gaudin & McDonald 2008; Fernicola *et al.* 2008; McDonald & De Iuliis 2008). Xenarthra includes Pilosa (sloths and anteaters) and Cingulata (armored xenarthrans, comprising extant and extinct armadillos and their extinct kin, the pampatheres and glyptodonts). The sloths or Tardigrada (= Phyllophaga = Folivora; see Delsuc *et al.* 2001; Fariña & Vizcaíno 2003; Vizcaíno & Loughry 2008) comprise a diverse group, with a wide range of body sizes, dietary habits, and locomotory abilities (e.g., Bargo & Vizcaíno 2008; McDonald & De Iuliis 2008; Vizcaíno *et al.* 2008; Bargo *et al.* 2012; Pujos *et al.* 2012; Amson *et al.* 2014).

The fossil history of sloths is extraordinarily rich and diverse. Indeed, tardigrades formed one of the largest and most distinctive elements of the Cenozoic fauna of South America and became geographically widespread in Central and North America. This report focuses on Megalonychidae, a clade that includes *Eucholoeops* Ameghino, 1887 as a basal member (Gaudin 2004; Pujos *et al.* 2007). It is one of the five main tardigrade clades usually recognized, the others being Bradypodidae, Mylodontidae, Nothrotheriidae, and Megatheriidae, and the only one that includes living and extinct members (see McDonald & De Iuliis 2008 for a review).

Megalonychidae includes one of the living tree sloth genera, the two-toed *Choloepus* Illiger, 1811, with the three-toed *Bradypus* Linnaeus, 1758, the other extant genus, being phylogenetically distantly removed from it (Gaudin 2004; Pujos *et al.* 2007). Megalonychids are generally considered a predominantly North American, Central American and West Indian group, since they were abundant and highly diverse in these areas during the Pleistocene (see e.g., McDonald & De Iuliis 2008). Additionally, the oldest certain member of the clade has been recovered from the West Indies (Late Oligocene; MacPhee & Iturralde-Vinent 1995). They are reasonably abundant during the Plio-Pleistocene in North America, though not diverse, with only two genera represented, *Megalonyx* Harlan, 1825 and *Pliometanastes* Hirschfeld & Webb, 1968 (Hirschfeld & Webb 1968). In South America, megalonychids are known from isolated remains in the Late Oligocene Deseadan of Patagonia (*Deseadognathus* Carlini & Scillato-Yané, 2004) and Bolivia (Pujos & De Iuliis 2007), but are more abundantly represented in the Santacrucian (late Early Miocene;

Eucholoeops and *Megalonychotherium* Scott, 1904) of Patagonia (Scott 1903, 1904; Bargo *et al.* 2012). They were also present in the Pleistocene of Peru and Chile (*Diabolotherium* Pujos, De Iuliis, Argot & Werdelin, 2007; Pujos *et al.* 2007, 2012; Shockey *et al.* 2009), Brazil (*Ahytherium* Cartelle, De Iuliis & Pujos, 2008 [Cartelle *et al.* 2008], and *Australonyx* De Iuliis, Pujos & Cartelle, 2009 [De Iuliis *et al.* 2009b]), and Venezuela (*Megistonyx* McDonald, Rincón & Gaudin, 2013).

Our current understanding of the systematics of the Santa Cruz sloths is based mainly on the work of Florentino Ameghino (e.g., Ameghino 1887, 1891, 1894), Scott (1903, 1904) and, to a lesser degree, Lydekker (1894). Despite the recovery of additional though largely unpublished remains, primarily collections recovered by H. T. Martin (in KUNHM; see below for abbreviations) and E. Riggs (in FMNH) (see Marshall 1975, 1976), our concept of these sloths has remained much as outlined by Scott (1903, 1904) over a century ago. Certainly, our views on species and phylogeny have changed considerably since then, but almost no further significant systematic work on these sloths has been undertaken by more recent researchers, with the exceptions of their inclusion in the cladistic analyses of Gaudin (2004) and Pujos *et al.* (2007), and De Iuliis' (1994) criticism of the traditional concept of *Hapalops* Ameghino, 1887, as a morphologically and phylogenetically central genus among later sloths.

It has long been appreciated that the systematics of the Santacrucian sloths is in dire need of revision. The generic names of these taxa have consistently appeared in the modern literature, but essentially only in faunal lists, with *Hapalops* and, more recently, *Eucholoeops* Ameghino, 1887, being the only notable exceptions. Our concept of these forms, what precisely they represent, how they are related to each other, and how they are distinguished from each other remains for the most part as ambiguous as when Scott last dealt with them. As noted by McDonald & De Iuliis (2008), and realized by Scott himself (though this did not prevent him from establishing his own new taxa), the plethora of genera and species erected by earlier workers (e.g., Ameghino 1887, 1891, 1894, 1897; Mercerat 1891; Lydekker 1894) were based in large part on fragmentary remains, and there are many more published taxa than can be justified on the available material (De Iuliis & Pujos 2006; De Iuliis *et al.* 2009a). Although this situation is particularly acute for *Hapalops*, it is also true for *Eucholoeops* (not *Eucholaeops* Ameghino, 1887; see below and Bargo *et al.* 2011), for which at least 15 species have been named in the literature (De Iuliis *et al.* 2009a).

Despite the realization of the problematic systematics, revision of the Santacrucian sloths has not been undertaken for two main reasons: the imposing nature of the material itself (abundant but generally fragmentary), and the fact that strict stratigraphic information was not available for the older collections. Fortunately, the recovery of new material under strict stratigraphic control over the past 15-20 years provides a basis on which the unraveling of the chaotic systematics of some of these sloths may begin. It is highly desirable that the systematics of these Santacrucian sloths be sorted out, because they represent one of the earliest well-known major radiations among sloths (including the earliest reasonably complete members of the clade) and thus have much to tell us about sloth evolution and diversity.

Among the more recent efforts at systematic collecting in this region are those of Bown & Fleagle (1993), who collected extensively from the Santa Cruz Formation, mainly at Monte Observación and Monte León in Santa Cruz Province (north of the Río Coyle), among other non-coastal localities. Systematic descriptions of the remains (housed in MACN; see Institutional Abbreviations) have not been published, except for the caenolestoid marsupials (Bown & Fleagle 1993). Somewhat later, Tauber (1997) recovered an important collection (housed in CORD-Pz) of some 60-70 species (*c.* 250 specimens) from the coastal localities between the Ríos Coyle and Gallegos.

Most recently and more relevant from the perspective of the current investigation, intensive fieldwork undertaken by a team led by the Museo de La Plata (Argentina) and Duke University (USA) between 2003 and 2012 at coastal localities between the Ríos Coyle and Gallegos (Fig. 1) has recovered some 1600 vertebrate specimens, mostly of mammals, and among them those of many xenarthrans and of sloths in particular (Vizcaíno *et al.* 2012). Of the latter, several well-preserved remains of *Eucholoeops* have been prepared and made available for analysis. The quality of their preservation, as already illustrated by their use

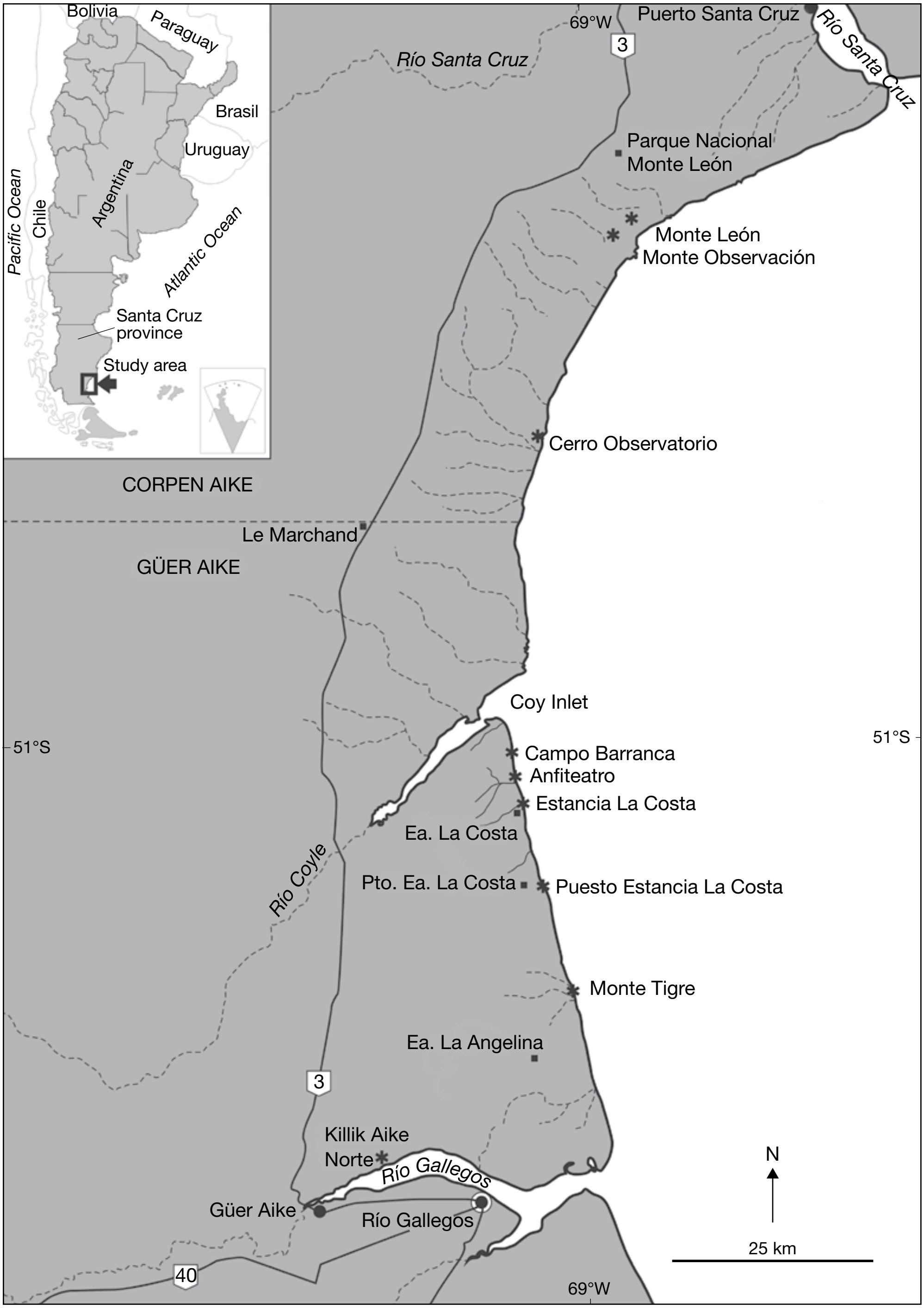

FIG. 1. — Geographic locations of fossil localities that have yielded *Eucholoeops* Ameghino, 1887 remains. Symbols: *, fossil localities; ■, notable places; ○, towns and cities. Abbreviations: **Ea.**, estancia; **Pto.**, puesto.

for the detailed analysis of the masticatory apparatus by Bargo *et al.* (2009) and Bargo *et al.* (2012), and their well-established stratigraphic provenance are such that they provide an irresistible opportunity to begin anew the task of resolving the systematics of this and other genera.

The purpose of the present contribution is to describe new remains of *Eucholoeops ingens* Ameghino, 1887, and compare them with previously known specimens to provide a basis for future systematic work on the numerous remains assigned to other species of this genus, which is in progress by the same authors. Until the latter work is completed, there is little to be gained and considerable potential for creating further confusion by attempting to compare the *E. ingens* material to that assigned either in the literature or museum records to other species of *Eucholoeops*. We have therefore refrained as much as possible from introducing these other remains here.

GEOLOGICAL CONTEXT

The Santa Cruz Formation (SCF), represented mostly by fluvial deposits that are mainly composed of volcaniclastic material, crops out in southern Argentine Patagonia, primarily as surface exposures along the Río Santa Cruz and the Atlantic coast between the Río Santa Cruz and the Río Gallegos, and westward into the Andean foothills (Bown & Fleagle 1993; Tauber 1997; see also Vizcaíno *et al.* 2006, 2010, 2012; Matheos & Raigemborn 2012). The stratigraphic sequence of the coastal SCF between the Ríos Coyle to the north and Gallegos to the south was subdivided by Tauber (1997) into the lower, highly fossiliferous Estancia La Costa Member, and the upper, poorly fossiliferous Estancia La Angelina Member. Among the 27 fossiliferous levels that have been identified, 23 occur in the Estancia La Costa Member and four in the Estancia Angelina Member (see Tauber 1997; Krapovickas *et al.* 2008; Vizcaíno *et al.* 2010). Several localities have been worked in this stretch of coast, such as Campo Barranca, Anfiteatro, Estancia La Costa, Puesto Estancia La Costa (Corriguen Aike of the older literature), Monte Tigre (Estancia La Angelina of the older literature), and Killik Aike Norte, among others (Tauber 1997, Kay *et al.* 2008; Vizcaíno *et al.* 2010, 2012; see Fig. 1).

Fleagle *et al.* (1995) dated with Ar/Ar several levels from the Monte Observación and Monte León localities, which yielded an age of 16.5 Ma for the SCF, and 19.33 Ma for the top of the underlying marine Monte León Formation. Recently, Perkins *et al.* (2012) provide new integrated results of the tephra correlations and radiometric ages indicating that the SCF spans the interval *c.* 18 to 16 Ma in the Atlantic coastal plain, and *c.* 19 to 14 Ma in the Andean foothills. These radiometric dates permit the assignment of the bulk of the coastal Santacrucian faunas to the late Early Miocene.

The new *Eucholoeops* remains utilized in this report derive from the intertidal Campo Barranca, Puesto Estancia La Costa, and Monte Tigre localities, all part of the Estancia La Costa Member. Although these localities are close in age, they are not contemporaneous. Puesto Estancia La Costa is about 17.5 to 17.4 Ma (Kay *et al.* 2012). Monte Tigre and Campo Barranca are, respectively, stratigraphically higher (thus younger) and lower (thus older) than Puesto Estancia La Costa, but within the time span noted above. The location, extent, stratigraphy, lithology and chronology of these localities were discussed by Kay *et al.* (2008, 2012), Vizcaíno *et al.* (2010, 2012), Matheos & Raigemborn (2012), Perkins *et al.* (2012), and Fleagle *et al.* (2012).

TAXONOMY

The genus and species *Eucholoeops ingens*, erected by Ameghino (1887), is based on a complete skull and mandible, largely covered by hard matrix (Ameghino 1889; Lydekker 1894) from the banks of the Río Santa Cruz (Ameghino 1889). According to Lydekker (1894), the specimen was never figured because of the enveloping matrix. Mones (1986) indicated that the specimen, housed in MLP, is lost. Lydekker (1894) noted its catalogue number as 9192 and 9193 in the collections of MLP. Although the specimen is no longer available (see Discussion) and was never figured, the diagnostic characteristics of *E. ingens* are generally consistent with the descriptions provided by Ameghino (1887, 1889). Further, the name has been used continuously from Ameghino's descriptions by subsequent authors (e.g., Mercerat 1891; Lydekker

1894; Scott 1904) that apparently had access to and observed the type material (but see Discussion), and no author has ever questioned the concept of this species, although intraspecific variation has been given little value in determination of possible synonyms (see below for more details).

The characteristics of the genus were clearly derived from its type species, with Ameghino (1887, 1889, 1891) distinguishing the additional *Eucholoeops* species that he named mainly on slight variations (e.g., in the form and size of teeth) from *E. ingens*. Several genera and species have been synonymized with *E. ingens*. Lydekker's (1894) review of the Santa Cruz sloths produced the most dramatic rearrangement, and recognized only *Eucholoeops* and *Pseudhapalops* Ameghino, 1891 (because he considered *Hapalops* a synonym of *Eucholoeops*) as valid genera for nearly all of the approximately twenty Santacrucian sloth genera that Ameghino had erected. Clearly, this view was as extreme in lumping as Ameghino's was in splitting. Lydekker (1894: 96) gave no objective reasons for most of his taxonomic decisions, besides stating that he was convinced that many of the characters utilized by Ameghino "are of no importance whatever" and due to individual, sexual, age variation, or imperfect preservation of the specimens. While merely stating an opinion does not make it correct, there is evidence that Lydekker was not entirely wrong, as is explained in further detail below. On the other hand, Lydekker's arrangement is almost certainly extreme and several more than just two of Ameghino's genera (of those that resemble the general *Hapalops* morphology) are valid. It is clear, for example, that *Hapalops* and *Eucholoeops* are both valid, as demonstrated by later, more attentive authors (e.g., Scott 1903, 1904).

Scott's (1903, 1904) reviews of the Santacrucian sloths have remained the most influential work on genera such as *Eucholoeops* and *Hapalops* and established the main differences between these sloths and their respective species. Scott (1904) considered *E. latirostris* Ameghino, 1891 as a synonym of *E. ingens*, and recognized only three other of the several *Eucholoeops* species as valid: *E. externus* Ameghino, 1891, *E. fronto* Ameghino, 1891, and *E. curtus* Ameghino, 1894. Lydekker (1894: 99) recognized only *E. ingens* of Ameghino's species, including several *Hapalops* species, but he was not particularly thorough in indicating his intentions, and he presumably meant to include all other species (referred to only as "Etc., etc." in his synonymy list of *E. ingens*) not explicitly listed under the synonymy of other taxa. However, he erected his own species, *E. titans* Lydekker, 1894. This report will deal only with the systematics of *E. ingens*. The remaining species will be considered in a subsequent study.

ABBREVIATIONS

Institutional abbreviations

AMNH	American Museum of Natural History, New York;
CORD-Pz	Museo de Paleontología, Universidad Nacional de Córdoba, Córdoba;
FLPU	Manuscripts Division, Firestone Library, Princeton University, Princeton;
FMNH	Field Museum of Natural History, Chicago;
MACN-A	Museo Argentino de Ciencias Naturales "B. Rivadavia", Colección Nacional Ameghino, Buenos Aires;
MCL	Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte;
MMLPU	Seeley G. Mudd Manuscript Library, Princeton University, Princeton;
MPM-PV	Museo Regional Provincial Padre M. J. Molina, Río Gallegos;
ROM	Royal Ontario Museum, Toronto;
KUNHM	University of Kansas Natural History Museum, Lawrence;
YPM-VPPU	Yale Peabody Museum of Natural History, Vertebrate Paleontology, Princeton University Collection, New Haven;
YUL	Manuscripts and Archives, Yale University Library, New Haven.

Other abbreviations

A	adult;
C-/c-	upper/lower caniniform tooth;
ch.	character;
F	female;
FL	fossiliferous level;
L	left;
M	male;
M-/m-	upper/lower molariform tooth;
Mc	metacarpal;
Mt	metatarsal;
R	right;
SA	subadult.

FOSSIL SPECIMENS

Eucholoeops ingens Ameghino, 1887

The material listed below forms the core group of specimens upon which the analyses carried out in this report are based. Although MPM-PV 3401 and FMNH P13125 and P13139 have appeared in the literature, they have not been subjected to detailed analyses for taxonomic purposes. The remains of these specimens are therefore listed in detail.

MPM-PV 3401 (Figs 2; 6A, B; 8A-C; 9A, B)

Skull (Fig. 2). Nearly complete, including isolated premaxillae, L zygomatic, and R C1; teeth present and well preserved. Ectotympanics, R zygomatic, and R pterygoid blade missing; skull relatively undeformed, particularly anteriorly, but with dorsoventral compression of cranial region and rostral roof, lateral deflection of L pterygoid blade, and slight damage to L orbitofrontal region.

Mandible (Fig. 6A, B). Nearly complete, preserving all teeth; R angular and tip of R coronoid processes missing; L dentary nearly undeformed, but R dentary pushed medially.

Postcranial (Figs 8A-C; 9A, B). Nearly complete R humerus (Fig. 8A-C), with minimal damage to greater tuberosity and distal articular surface; several L manus elements (Fig. 9A, B), including Mc I, Mc II, Mc III, proximal, middle, and ungual phalanges of digit 3, proximal and ungual phalanges of digit 1, and middle phalanx of digit 2.

Locality and stratigraphy. Puesto Estancia La Costa, Santa Cruz Province, Argentina; FL 7.2, Estancia La Costa Member, Santa Cruz Formation.

MPM-PV 3451 (Figs 3; 8D-F)

Skull (Fig. 3). Nearly complete and undistorted, missing ectotympanics, premaxillae, and zygomatics; pterygoid blades incomplete, but L blade is sufficiently preserved to indicate its outline.

Postcranial (Fig. 8D-F). L radius, nearly complete, missing small portions of bicipital tuberosity and distal articular surfaces.

Locality and stratigraphy. Puesto Estancia La Costa, Santa Cruz Province, Argentina; FL 5.3, Estancia La Costa Member, Santa Cruz Formation.

MPM-PV 3452 (Fig. 4A, C, E)

Skull. Missing calvarium, dorsal part of occiput, premaxillae, all teeth but L M4, R zygomatic, ectotympanics, and pterygoid blades; L zygomatic incomplete; maxillae, palate, including alveoli, and basicranium well preserved.

Locality and stratigraphy. Campo Barranca, Santa Cruz Province, Argentina; Estancia La Costa Member, Santa Cruz Formation.

MPM-PV 15046 (Fig. 4B, D, F)

Skull. Nearly complete, with some damage to L side and central portion of skull roof compressed ventrally; missing premaxillae, pterygoid blades, zygomatics, and ectotympanics. Palatal region, including all teeth except R C1, nearly complete and relatively undistorted; L C1 distorted. Postcranial: fragmentary pelvis preserving acetabular and sacral regions.

Locality and stratigraphy. Monte Tigre, Santa Cruz Province, Argentina; Estancia La Costa Member, Santa Cruz Formation.

FMNH P13125
(Figs 5A, C, E; 6C-F; 8G-I; 9C, D; 10; 11)

Skull (Fig. 5A, C, E). Incomplete, missing approximately posterior third, premaxillae, zygomatics, L C1; rostrum, palate, and remaining teeth largely well preserved and undistorted.

Mandible (Fig. 6C-F). Partially preserved dentaries, both missing portion anterior to about level of c1s; L c1 and L m1-m3 preserved; R m1-m3 broken within alveoli.

Postcranial (Figs 8G-I; 9C, D; 10; 11). R humerus, nearly complete, but deltopectoral shelf and ectepicondylar region damaged (Fig. 8G, H, I); R scaphoid, trapezium, trapezoid, magnum and unciform; L lunar, magnum, unciform, proximal portion of Mc II, and Mcs III-V (Fig. 9C, D); R femur, mainly in

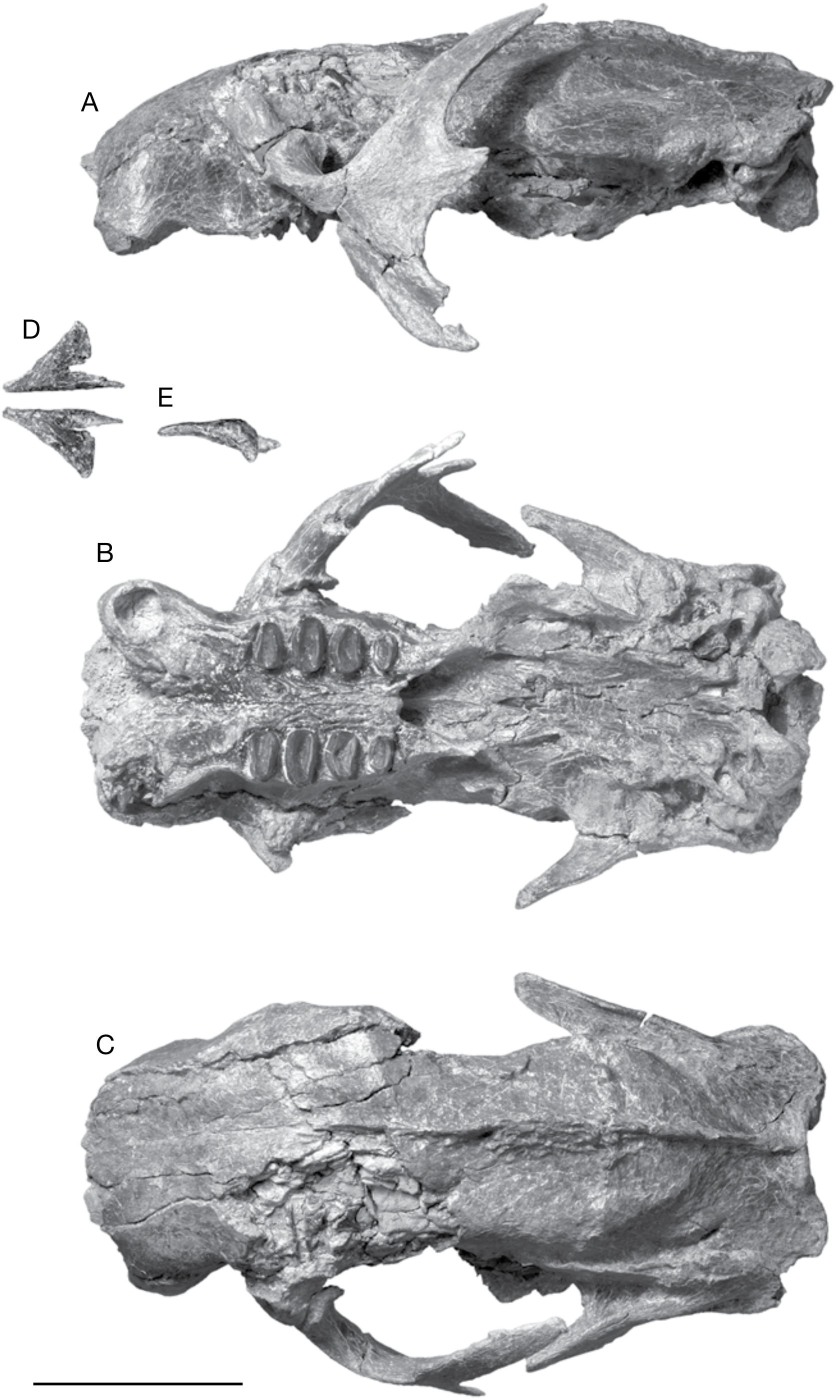

Fig. 2. — *Eucholoeops ingens* Ameghino, 1887, specimen MPM-PV 3401 (neotype): **A**-**C**, skull in left lateral (**A**), ventral (**B**), and dorsal (**C**) views; **D**, **E**, premaxillae in ventral (**D**) and lateral (**E**) (anterior towards left) views. Scale bar: 5 cm.

several large pieces, but reconstructed so shape and features largely reliable; tip of greater trochanter, most of lateral distal condyle, and portions of diaphysis missing (Fig. 10A-C); R tibia, mainly preserving diaphysis, medial half of proximal articular surface, and small portion of anterior part of distal articular surface (Fig. 10D, E); R fibula, nearly complete but plastered onto R tibia (Fig. 10D, E); R navicular, ectocuneiform, and Mts II-V, and L cuboid, partial ectocuneiform, and Mt III (Fig. 11).

Locality and stratigraphy. Estancia La Angelina (= Monte Tigre of Tauber [1997]), Santa Cruz Province, Argentina; Santa Cruz Formation.

FMNH P13139 (Fig. 5B, D, F)
Skull. Missing zygomatics, pterygoid flanges, ectotympanics (although the specimen preserves its stapes; see Patterson *et al.* 1992), L C1, and R posterolateral portion of basicranium, R cranial wall slightly compressed medially; preserves R and L molariforms; R C1 broken, L C1 and L lacrimal regions reconstructed.

Locality and stratigraphy. 12 miles north of Cape Fairweather (*c.* Estancia La Angelina), Santa Cruz Province, Argentina; Santa Cruz Formation.

REMARK

The following specimens considered in this report have been previously dealt with in the literature, primarily by Ameghino (1887, 1889, 1891, 1894) and Scott (1904). The remains are described as necessary in the Description and Comparison and Discussion sections. MACN-A 6413 (type of *E. curtus*, Fig. 7D-F; also MACN-A 6414, a L humerus associated with MACN-A 6413), MACN-A 4639 (type of *E. latirostris*, Fig. 7A-C), MACN-A 4640, 4641 (type of *E. externus*, Fig. 7G-J), MACN-A 4642.

EUCHOLOEOPS CF. *INGENS*

AMNH 9307 (assigned by Scott 1904 to *E. ingens*), MACN-A 11614 (assigned by MACN catalogue to *E. ingens*).

OTHER SPECIMENS USED FOR WORK

Ahytherium aureum *Cartelle, De Iuliis & Pujos, 2008*
MCL 21834 (Cartelle *et al.* 2008).

Eucholoeops
MPM-PV 3403 *E.* cf. *fronto* (preliminary assignment by Bargo *et al.* 2012); YPM-VPPU 15314 *E. fronto* (according to Scott 1904).

Hapalops
Assignment of specimens according to Scott (1903, 1904) unless indicated.
AMNH 9176, *H. brachycephalus* Ameghino, 1894; AMNH 9222, *H. rectangularis* Ameghino, 1887; AMNH 9250, *H. ruetimeyeri* Ameghino, 1894; AMNH 15155, 15531, *H. elongatus* Ameghino, 1887; FMNH P13141, *H. ruetimeyeri* (according to FMNH catalogue records); MPM-PV 3458, *Hapalops* sp. (preliminary assignment by current authors); YPM-VPPU 15523, *H. longiceps* Scott, 1903; YPM-VPPU 15595, *H. vulpiceps* Scott, 1904; YPM-VPPU 15597, *H. elongatus*.

Hyperleptus *sp. Ameghino, 1891*
MPM-PV 4251 (Bargo *et al.* 2012).

Megalonyx wheatleyi *Cope, 1871*
ROM 55503a, b.

EXTANT SPECIMENS

CHOLOEPUS DIDACTYLUS LINNAEUS, 1758

Skull and mandible
AMNH M133405 (A, M), M133410 (A, F), M133212 (J, F), 133416 (A, M), M133417 (J, M) M133429 (J, F), M133439 (A, M), M133444 (A, F), M133447 (J, M), M133449 (J, M), M133453 (J, M), and M133453 (SA, F).

Locality
Ilha de Marajó, Pará, Brazil; collected during March, 1936.

C. HOFFMANNI PETERS, 1859

Skull and mandible
AMNH M18891 (J, F), M18892 (J, M), M18893 (J, F), M18894 (J, F), M18895 (A, M), M18896 (A, M), M26900 (J, F), M26901 (J, F), M26905 (J, F), M26907 (A, F), M26908 (A, F), M26909 (A, F), M26911 (J, M), M26912 (J, M), M26913

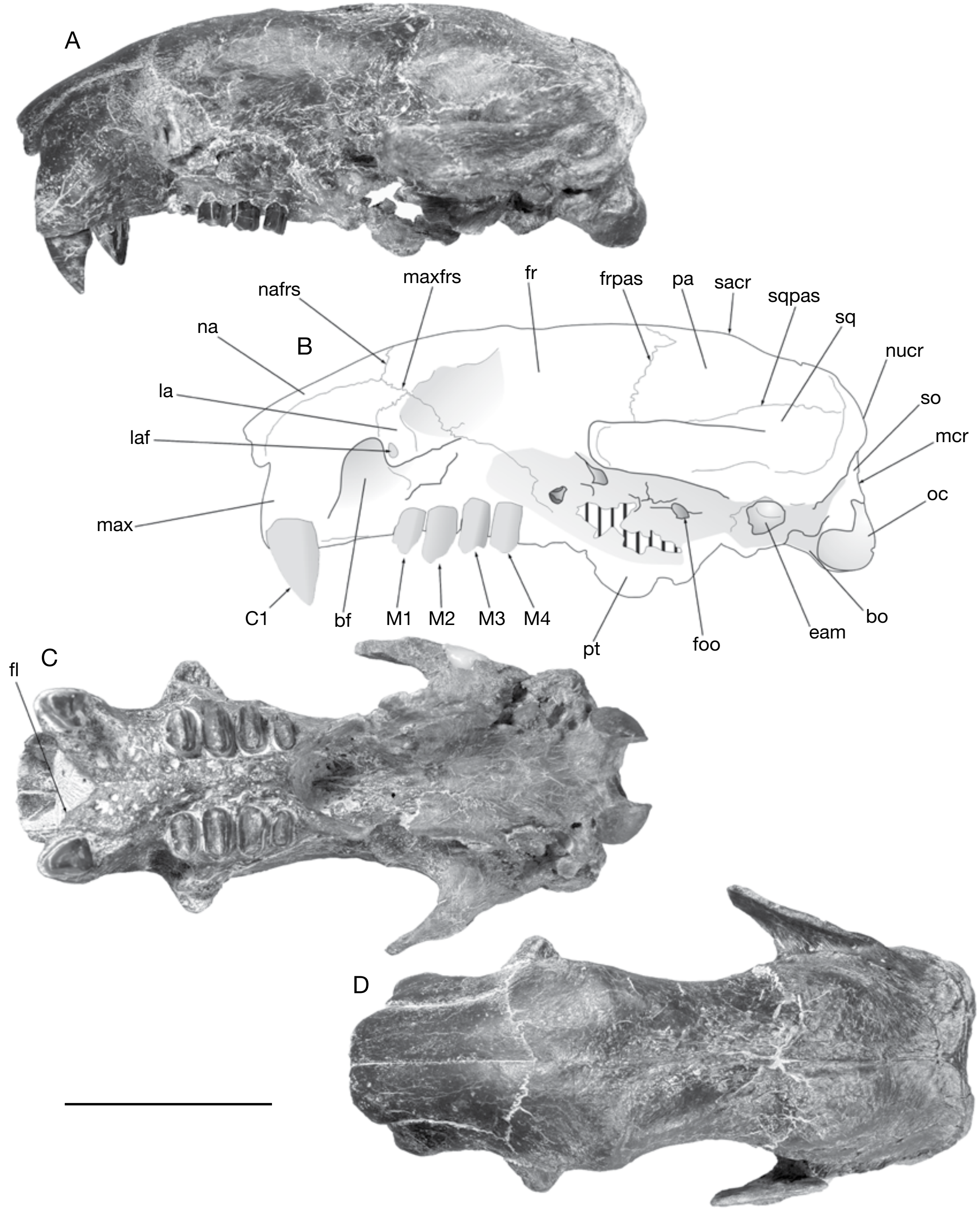

Fig. 3. — Skull of *Eucholoeops ingens* Ameghino, 1887 MPM-PV 3451 in left lateral (**A**, **B**), ventral (**C**), and dorsal (**D**) views (anterior towards left). Abbreviations: **bf**, buccinator fossa; **bo**, basioccipital; **C1**, caniniform tooth; **eam**, external auditory meatus; **foo**, foramen ovale; **fl**, flange of the premaxillar margin of the maxilla; **fr**, frontal; **frpas**, frontoparietal suture; **la**, lacrimal; **laf**, lacrimal foramen; **M1**-**M4**, upper molariform teeth; **max**, maxilla; **maxfrs**, maxillofrontal suture; **mcr**, median crest; **na**, nasal; **nafrs**, nasofrontal suture; **nucr**, nuchal crest; **oc**, occipital condyle; **pa**, parietal; **pt**, pterygoid; **sacr**, sagittal crest; **so**, supraoccipital; **sq**, squamosal; **sqpas**, squamosoparietal suture. Scale bar: 5 cm.

(J, F), M26914 (J, M), M26915 (A, F), M26916 (A, M), M26917 (J, F), M26918 (A, M), M26919 (A, F), M26920 (J, F), M26922 (J, F), M26924 (J, M), and M26925 (J, F).

Locality
Boquerón, Chiriquí, Panama; collected between October and December, 1901.

Remark
Additional fossil sloth remains are considered in this report based on literature descriptions and figures. These works are referenced in the text.

SYSTEMATICS

Order XENARTHRA Cope, 1889

Infra-order TARDIGRADA
Latham & Davies *in* Forster, 1795

Phyllophaga Owen, 1842: 167.

Folivora Delsuc, Catzeflis, Stanhope & Douzery, 2001: 1605-1615.

Family Megalonychidae Gervais, 1855

Genus *Eucholoeops* Ameghino, 1887

Type species. — *Eucholoeops ingens* Ameghino, 1887.

Diagnosis. — Much smaller than the Plio-Pleistocene grounds sloths but larger than Holocene and extant tree sloths; shares with other megalonychids large C1 and c1, prominent diastema, anteriorly divergent tooth rows, with caniniforms displaced laterally to remaining teeth, and oval to rectangular molariforms; muzzle prominent, short and broad, but less so than in *Ahytherium* and *Megistonyx*; differing from *Megalonyx* in possessing caniniforms that are triangular in section and a longer mandibular spout; differing from other megalonychids with triangular caniniforms (e.g., *Choloepus*, *Acratocnus* Anthony, 1916, *Neocnus* Arredondo, 1961) in having dorsoventrally deep, rather than anteriorly tapered, rostrum; differing from other megalonychids in possessing transversely expanded M2 and M3; width across buccinator fossae much less than width at preorbital rostrum; preorbital rostrum width greater than that of postorbital constriction; posterior surface of lacrimal markedly concave.

Distribution. — Santacrucian SALMA (late Early Miocene), Santa Cruz Province, Argentine Patagonia.

Eucholoeops ingens Ameghino, 1887

Eucholoeops ingens Ameghino, 1887: 21.

Eucholoeops latirostris Ameghino, 1891: 322.

Eucholoeops externus Ameghino, 1891: 322.

Eucholoeops curtus Ameghino, 1894: 410 (not p. 154 as incorrectly indicated in Scott 1904: 276).

Neotype. — MPM-PV 3401, designated here (Figs 2; 6A, B; 8A-C; 9A, B).

Locality and horizon. — Puesto Estancia La Costa, Santa Cruz Province, Argentina; Estancia La Costa Member, Santa Cruz Formation (late Early Miocene, Santacrucian SALMA). The specimen is also figured in Bargo *et al.* (2009: fig. 2; 2012: fig. 13.3).

Diagnosis. — Caniniform teeth very large; maxilla does not extend beyond alveolar wall of C1 laterally or ventrally and forms a pillar-like sheath surrounding C1; premaxillar margins of maxillae form wide V-shaped notch, with small anterior flange; preorbital width of rostrum considerably greater than width at postorbital constriction; differing from other *Eucholoeops* species, in which caniniforms are smaller, maxillae extend slightly anterior to caniniform alveolus, premaxillar margins of maxillae forming narrower V-shaped notch, with more pronounced anterior flange, and preorbital rostrum width slightly greater than that of postorbital constriction; dentary with marked concavity anterior to c1 alveolus; Mcs II-V subequal in length.

Referred material. — FMNH P13125, FMNH P13139, MACN-A 6413 (type of *E. curtus*), MACN-A 6414, MACN-A 4639 (type of *E. latirostris*), MACN-A 4640, 4641 (type of *E. externus*), MACN-A 4642, MPM-PV 3451, MPM-PV 3452, and MPM-PV 15046.

Description and comparison
Skull, mandible, and teeth
See Figures 2-7 and Tables 1, 2.

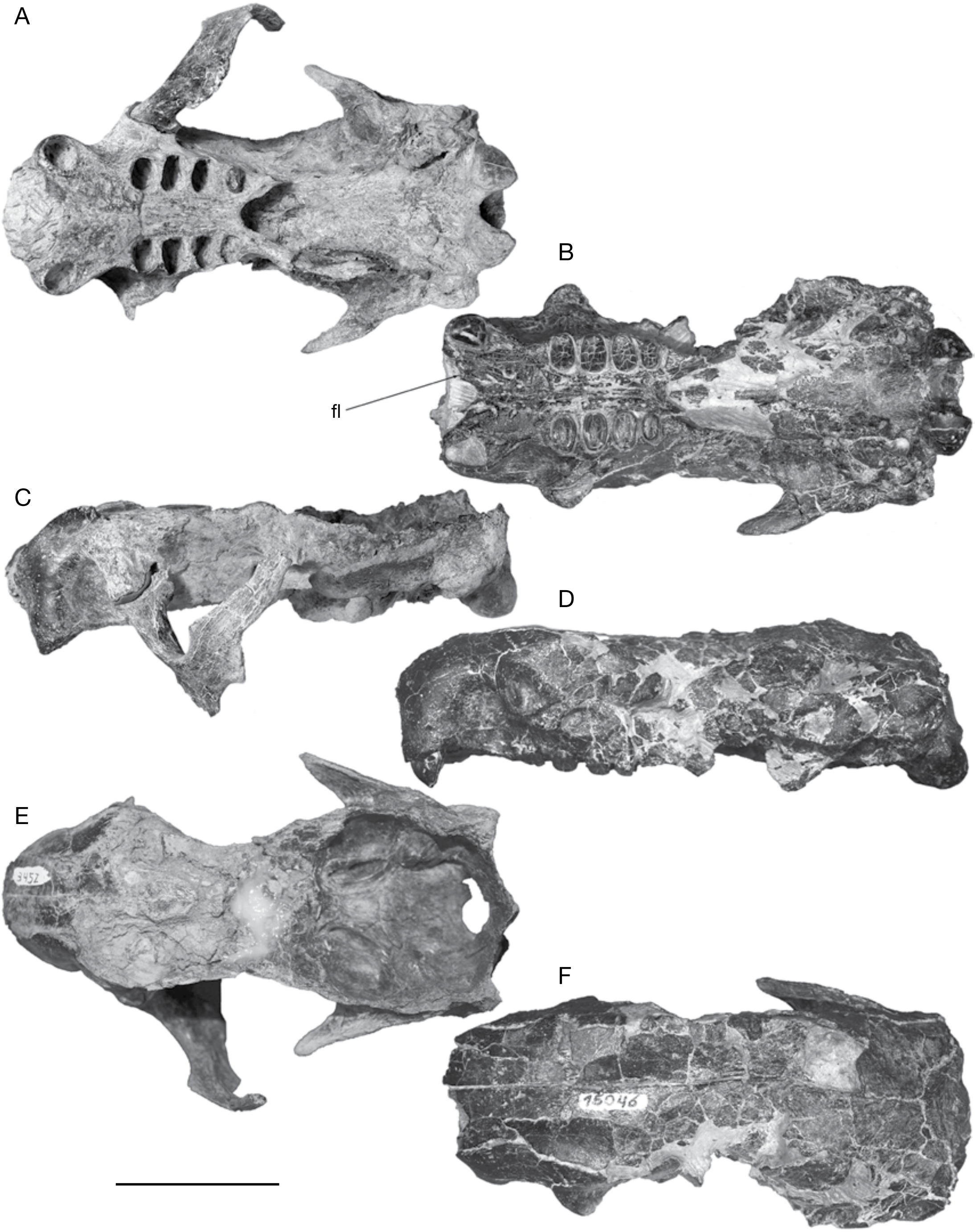

FIG. 4. — Skulls of *Eucholoeops ingens* Ameghino, 1887, specimens: **A**, **C**, **E**, MPM-PV 3452; **B**, **D**, **F**, MPM-PV 15046. **A**, **B**, ventral views; **C**, **D**, left lateral views; **E**, **F**, dorsal views (anterior towards left). Abbreviation: **fl**, flange of the premaxillar margin of the maxilla. Scale bar: 5 cm.

Skull (Figs 2-5; 7A-H)

The dorsal profile of the skull of *Eucholoeops ingens* is gently and regularly convex, with a very slight depression at its middle and another posteriorly, as opposed to the generally declining profile anterior to the middle of the cranium in *Hapalops*. The general form of the skull in *Eucholoeops* has long been conceptualized as having an enormously robust muzzle with a prominent depression between the facial and cranial parts of the skull, based on the illustration of *E. externus* by Scott (1904: pl. 56, fig. 1). This specimen is assigned here to *E. ingens*, and Scott's figure is considered inaccurate (see Discussion). The skull is usually regularly convex in some megalonychids (e.g., *Choloepus*, *Acratocnus*, and *Neocnus*: see Taboada *et al.* 2007) though more strongly so. The difference is due mainly to the more robust rostrum of *E. ingens* compared with these taxa. In other megalonychids such as *Neocnus*, *Parocnus* Miller, 1929 and, to a lesser degree, *Megalocnus* Leidy, 1868 and *Acratocnus* the rostrum is slender and elongated so that the profile over the orbital and facial regions (see Matthew & Paula Couto 1959; Paula Couto 1967; Taboada *et al.* 2007) is nearly rectilinear. In still others such as *Megalonyx*, the rostrum is very deep and the profile is doubly convex, over the cranium and the rostrum. In *Ahytherium* the rostrum is considerably shortened and the profile is shallowly concave at the nasofrontal contact.

The maxillae end abruptly anterior to C1, mainly following the curvature of this tooth, so that the nasal overhangs the maxilla. A similar condition exists in *Acratocnus*, *Choloepus*, and *Megalonyx*, but these are easily distinguished from *Eucholoeops* in that the rostrum tapers notably anteriorly in lateral view in *Acratocnus* and *Choloepus* and the teeth are not triangular in section in *Megalonyx*. The lacrimal foramen appears relatively lower owing to the deeper height of the muzzle in *E. ingens* compared to *Hapalops*. In *E. ingens* a pronounced and triangular depression lies on the ventral surface of the palate posterior to C1 and narrows into a trough extending along length of the diastema to M1. The presence of the depression and trough seem unrelated to accommodating c1. The depression and trough are ridged laterally and medially and do not extend onto the lateral surface of the maxilla. In *Hapalops* there is only a much shallower trough in this position and it is not consistently present (for example, it is not evident on the left side of FMNH P13141). Naples (1982) and Gaudin (2004) noted the presence of a postcanine fossa in the maxilla of *Choloepus* that receives the tip of c1. This differs from that of *E. ingens* in being deeper and restricted to the region immediately posterior to C1, rather than continuing as a trough to M1. Also, the fossa in *Choloepus* extends onto the lateral surface of the maxilla and is thus observable in lateral view, in contrast to *Eucholoeops*, in which it is restricted to the palatal surface. Gaudin (2004) signaled a postcanine fossa as characteristic of Megalonychidae, but the fossa is not present in a *Megalonyx wheatleyi* specimen (ROM 55503a, b, cast of skull and mandible) we examined and is apparently absent in the *Megalonyx* specimen figured by Leidy (1855), in which the caniniforms occlude differently; this is also true of the *Acratocnus* specimen illustrated by Anthony (1926), in which the teeth occlude similarly.

The premaxillae of *Eucholoeops ingens*, loosely connected to the maxilla and each other (as is usual in sloths), are approximately triangular, although their anterior tip is missing in MPM-PV 3401 (Fig. 2D, E). It is likely that the overall form of the premaxillae would have resembled the Y-shaped structure noted for *Eucholoeops fronto* and *Hapalops* by Scott (1903, 1904). Gaudin (2004) also scored *Eucholoeops* as having a Y-shaped premaxilla, and the preserved portions of MPM-PV 3401 do not necessarily contradict this author's assessment. The premaxilla of *Hapalops*, known from several species (e.g., *H. longiceps*, YPM-VPPU 15523, and *H. ruetimeyeri*, AMNH 9250), differs mainly in being more gracile, bearing a longer anterior process, and a wider opening between the lateral and medial rami. The lateral ramus of the premaxilla of *E. ingens* is considerably more robust though notably shorter than the medial ramus. The slender medial ramus tapers posteriorly, whereas the lateral ramus widens posteriorly into a blunt process that contacts the anteromedial margin of the maxilla, as occurs also in the Miocene nothrotheriid *Mionothropus*

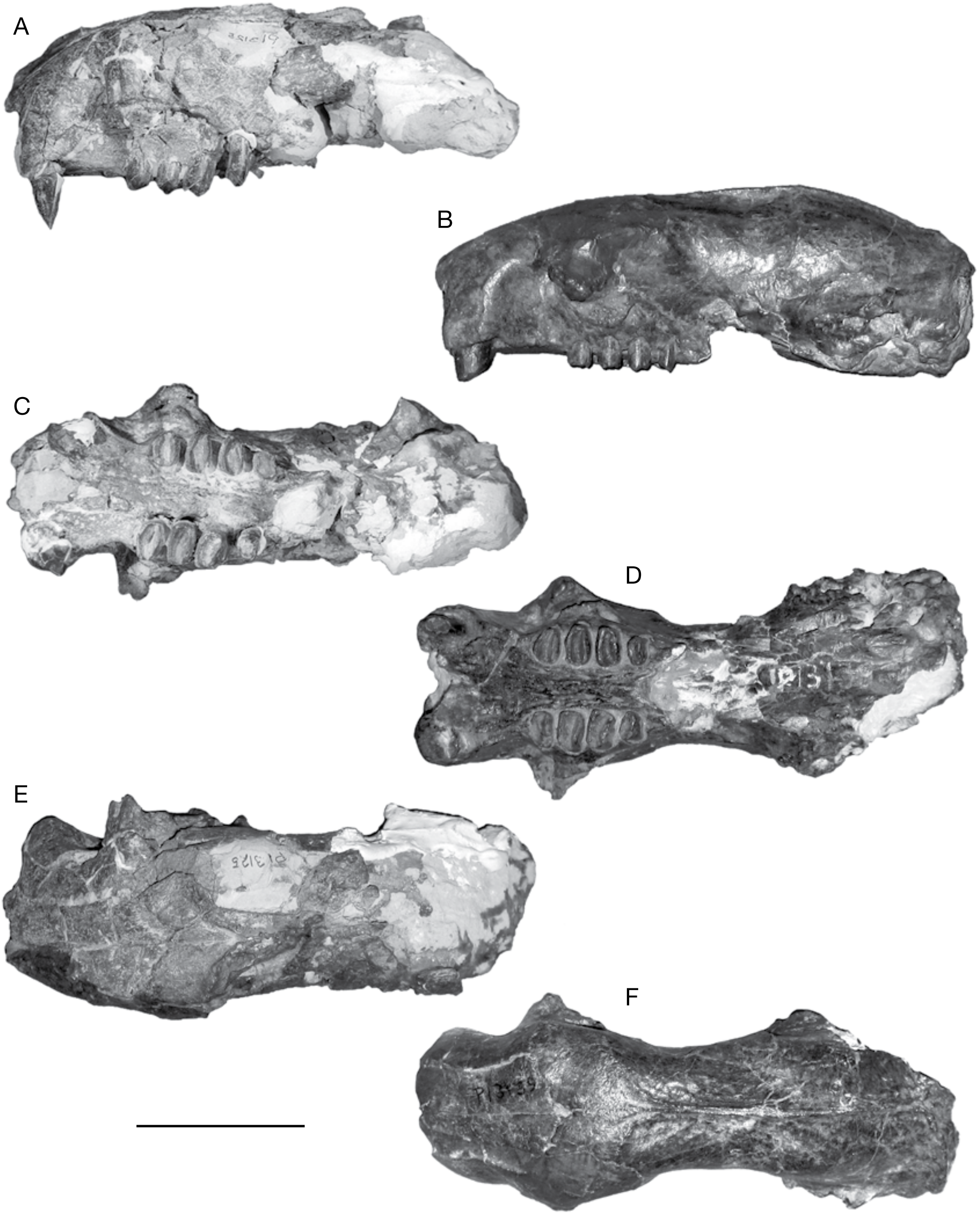

FIG. 5. — Skulls of *Eucholoeops ingens* Ameghino, 1887, specimens: **A**, **C**, **E**, FMNH P13125; **B**, **D**, **F**, FMNH P13139. **A**, **B**, left lateral views; **C**, **D**, ventral views; **E**, **F**, dorsal views (anterior towards left). Scale bar: 5 cm.

TABLE 1. — Skull and upper tooth measurements of *Eucholoeops ingens* Ameghino, 1887 (measurements in mm). Abbreviations: dentition: **C1**, transverse/mesiodistal diameters of caniniform (or its alveolus); **M1**-**M4**, transverse/mesiodistal diameters of molariform teeth or their alveoli; **L C1-OC**, length from the mesial margin of C1 (or anterior margin of its alveolus) to the posterior margin of the occipital condyles; **L C1-M4**, length from the mesial margin C1 to the distal margin M4 (or the anterior and posterior margins, respectively, of their alveoli); **L Dias**, diastema length; **L M1-M4**, length from the mesial margin of M1 to the distal margin of M4 (or anterior and posterior margins, respectively, of their alveoli); **W Pal C1**, palatal width between C1s (or their alveoli); **W Dias**, maximum width across maxillae at level of diastemata; **W Mast**, skull width across mastoid processes; **W C1**, maximum width across maxillae at level of C1s; **W M3**, maximum width between lateral borders of M3 alveoli; **W Pal**, minimum palatal width at M- (see Table); **W Preorbit**, dorsal width at preorbital constriction; **W Postorbit**, width at postorbital constriction; **W Temp**, width between temporal lines on frontals; ***c.***, estimated measurement; *****, measurements from Ameghino (1887); specimen not formally assigned to *E. ingens*, see text.

Catalogue number	**MPM-PV 3401 (neotype)**	**MPM 3451**	**MPM-PV 3452**	**MPM-PV 15046**	**FMNH P13125**
Dentition					
C1	–	10.2/ 11.7	–	–	–
M1	11.9/6.7	11.1/7.2	–	–	11.6/8.2
M2	13.2/7.4	13.3/7.3	–	–	13.1/8.3
M3	11.4/7.5	12.3/6.8	–	–	11.5/7.9
M4	8.6/5.7	9.2/4.2	8.4/4.8	–	8.5/6.6
L C1-OC	165.3	159.9	145.5	147.5	–
L C1-M4	65.2	63.7	60.9	59.3	64.9
L Dias	21.2	20.9	17.3	18.6	19.0
L M1-M4	34.4	32.8	33.4	30.9	37.5
W C1	*c.* 52 (26 × 2)	51.0	48.4	45.7	–
W Dias	35.5	30.6	31.9	28.3	29.6
W Mast	–	62.8	66.3	–	–
W M3	39.8	40.4	37.0	32.3	–
W Pal	13.4 at M4	13.9 at M3	13.2 at M4	10.9 at M2	–
W Pal C1	29.0	27.9	29	22.4	–
W Postorbit	*c.* 46 (23 × 2)	41.6	41.2	–	–
W Preorbit	–	46.2	43.2	50.0	–
W Temp	–	52.8	–	–	–

Catalogue number	**FMNH P13139**	**MACN A-6413 (type of *E. curtus*)**	**MACN A-4639 (type of *E. latirostris*)**	**MACN A-4640 (type of *E. externus*)**	**Without catalogue number (type of *E. ingens*)***
Dentition					
C1	–	*c.* 7.8/9.4	–	–	10/11
M1	10.2/6.8	9.1/6.1	–	10.2/7.2	11/7.5
M2	11.7/7.2	9.7/6.4	–	10.6/7.2	12/7.5
M3	11.3/6.8	9.1/5.7	–	10.2/6.9	12.5/7.5
M4	8.3/4.5	7.4/4.9	–	–	8.5/6.0
L C1-OC	–	115.2	–	–	172
L C1-M4	65.4	54.8	68.1	–	71
L Dias	20.3	16.5	22.9	21	23
L M1-M4	32.3	25.9	33.8	–	38
W C1	47.5	46.9	–	–	–
W Dias	30.2	28.2	29.0	–	–
W Mast	–	59.5	–	–	–
W M3	–	32.7	–	–	–
W Pal	–	11.4 at M4	–	–	–
W Pal C1	–	25.1	–	–	–
W Postorbit	–	35.4	43.6	–	–
W Preorbit	43.4	41.2	46.1	–	–
W Temp	–	42.3	–	–	–

Table 2. — Mandible and lower tooth measurements of *Eucholoeops ingens* Ameghino, 1887 (measurements in mm). Abbreviations: dentition: **c1**, transverse/mesiodistal diameters of caniniform (or its alveolus); **m1-m3**, transverse/mesiodistal diameters of molariform teeth (or their alveoli); **H Ramus**, maximal height of horizontal ramus at m3; **L c1-m3**, length from the mesial margin of c1 to the distal margin of m3 (or anterior and posterior margins, respectively, of their alveoli); **L Dias Mand**, length of mandibular diastema; **L Mand**, maximal mandibular length from anterior margin of spout to posterior margin of mandibular condyle; **L m1-m3**, length from the mesial margin of m1 to distal margin of m3 (or anterior and posterior margins, respectively, of their alveoli); **L Spout**, length of the spout from anterior to posterior margins of mandibular symphysis; **L**, left; **R**, right; *, measurements from Ameghino (1887); specimen not formally assigned to *E. ingens*, see text.

Catalogue number	**MPM-PV 3401 (neotype)**	**FMNH P13125**	**MACN A-4641 (type of *E. externus*)**	**Without catalogue number (type of *E. ingens*)***
Dentition				
c1	9.2/9.6	7.2/8.2	8.2/8.8	–/11
m1	12.0/7.8	11.9/8.4	10.1/7.7	–
m2	11.8/7.6	12.3/8.4	10.6/7.1	–
m3	R 10.4/10.0 L 10.4/10.5	10.2/9.7	9.6/8.8	–
H Ramus	36.2	–	31.4	35
L c1-m3	46.1		47.3	55
L Dias Mand	9.8	7.9	–	13
L Mand	140.4	–	–	–
L m1-m3	28.4	29.4	27.8	31
L Spout	33.7	–	–	35

De Iuliis, Gaudin & Vicars, 2011 from Peru and *Hapalops* (De Iuliis *et al.* 2011). In these last two genera, however, the medial ramus is about as long as the lateral ramus, although in *Hapalops* the posterior end of the medial ramus appears to have been at least partially reconstructed for *H. longiceps* (YPM-VPPU 15523), so that illustrations in Scott (1903: pl. 31) are somewhat misleading in this regard.

The anterior margins of the maxillae of ***Eucholoeops ingens***, with which the premaxillae articulate, describe a widely open V, with nearly rectilinear edges. A small and delicate triangular flange, barely detectable in some specimens and variable in size between left and right sides, is present in some specimens. A similar morphology occurs in a specimen of *Neocnus* illustrated by Gaudin (2011: fig. 21C). Typically in sloths, the anterior margin of the maxilla bears lateral and medial palatal processes that extend anteriorly in contacting the premaxillae. The medial process is triangular and fits between the lateral and medial rami of the premaxilla. In considering the extent of the lateral and medial palatal processes of the maxilla, Gaudin (2004: ch. 111) scored *Eucholoeops* as having a shorter medial than lateral margin. While technically and probably phylogenetically accurate, this does not capture the form in *E. ingens*: a lateral process is nonexistent (the maxilla ends with the wall of the alveolus of C1, as noted above), and the medial is barely, if at all, present. Nonetheless, the latter does fit between the lateral and medial premaxillary rami and so is homologous with the medial palatal flange of the maxilla.

The lateral rostral wall between C1 and M1 is strongly concave ventrally, forming a deep antorbital or buccinator fossa in *Eucholoeops ingens*. Dorsally, however, the rostral wall bulges laterally, forming a "roof" over the fossa, so that the preorbital constriction (measured dorsally) is wider than the postorbital constriction. This resembles the condition in *Acratocnus*, but not *Hapalops*, in which the bulge is much less prominent, so that the preorbital constriction is narrower than the postorbital. In other megalonychids the preorbital constriction is narrower in *Neocnus* and *Parocnus*, about equal to the postorbital constriction in *Megalocnus* (Taboada *et al.* 2007), and wider in *Megalonyx* (Leidy 1855) and *Ahytherium*, in which the rostrum is also extremely shortened (Cartelle *et al.* 2008).

The lacrimal of *Eucholoeops ingens* lies dorsal to the more anterior molariforms and extends anterior to the mesial margin of M1 in *E. ingens*, *Mionothropus*, and *Choloepus* but not *Hapalops*; in *Acratocnus* the lacrimal lies almost entirely anterior to M1. The position of the lacrimal foramen, naturally, reflects this position, lying above the mesial margin of M1 in *E. ingens*, *Choloepus*, *Neocnus*, *Parocnus*, and *Mionothropus*, well anterior to M1 in *Acratocnus*, *Megalonyx*, and *Ahytherium*, and approximately between M1 and M2 in *Hapalops*. The relative size of the foramen is similar in all taxa except *Choloepus*, in which it is smaller. The posterior surface of the lacrimal is deeply concave in *E. ingens*.

The postorbital process of the frontal lies dorsal to M3 in *Eucholoeops ingens*, approximately as in *Mionothropus* and *Choloepus*. A small foramen for the frontal diploic vein lies just anterior to the process (see De Iuliis *et al.* 2011). The process lies farther posteriorly in *Hapalops*, approximately dorsal to M4, whereas in *Acratocnus* it lies above M1 and M2. The process of *E. ingens* is slightly better developed than in *Hapalops*, but much less prominent than in *Choloepus* and *Acratocnus*. The region between the postorbital process and the lacrimal is more elongated in *Hapalops*.

The temporal lines of *Eucholoeops ingens* (MPM-PV 3401, Fig. 2C) curve posteromedially, meeting just anterior to the frontoparietal suture to form a small sagittal crest that extends posteriorly to the occiput. The crest is similar in MPM-PV 3403 (*E.* cf. *fronto*), but not as raised in MPM-PV 3451 (Fig. 3C). There is variation in the form of the temporal lines and sagittal crest in *Hapalops*. Some species, such as *H. longiceps* (Scott 1903: fig. 17a) and *H. vulpiceps* (Scott 1904: pl. 44:1), follow the pattern just described for *E. ingens*. However, in other species, such as *H. brachycephalus* (Scott 1904: pl. 36:2) and *H. ruetimeyeri* (Scott 1903: fig. 17b; 1904: pl. 38:4), the temporal lines similarly converge, but do not meet to form a sagittal crest; they pass instead on either side of the midsagittal plane over the frontals, diverge as they extend onto the parietals and then converge again over the posterior part of the parietals. *Hapalops elongatus* (Scott 1904: pl. 38: 1, 2, 5) exhibits both patterns. Cartelle & Bohórquez (1982; see also De Iuliis 1996) observed similar intraspecific variation in the megatheriid *Eremotherium laurillardi* (Lund, 1842) and suggested that the states reflected sexual dimorphism. In *Acratocnus* the temporal lines converge more markedly, meeting well in advance of the frontoparietal suture to form a prominent sagittal crest. In *Mionothropus* the lines are not prominent and do not approach each other closely. In contrast, those of *Choloepus* are prominent and converge gradually; they may remain relatively far apart, though some specimens possess a short, distinct sagittal crest on the parietals.

The nasals of *Eucholoeops ingens* are broad posteriorly, narrow approximately at midlength and then widened again. This pattern seems typical for the other megalonychid sloths considered here (though not *Megalocnus*, in which the nasals are narrowed posteriorly) and *Hapalops* and *Mionothropus* (but not *Nothrotheriops* Hoffstetter, 1954, in which they are nearly of the same width throughout their length, and *Nothrotherium* Lydekker, 1889, in which they are slightly wider posteriorly) (see Cartelle & Fonseca 1983; De Iuliis *et al.* 2011; Scott 1903, 1904; Stock 1925; Taboada *et al.* 2007). Although the nasals are generally broken anteriorly, in specimens with reasonably well-preserved nasals, these bones extend about as far forward as or slightly beyond the maxillae (e.g., *Neocnus*, *Parocnus*, *Megalocnus*; see Taboada *et al.* 2007: 40, 41) and their anterior margins may be nearly straight and transversely oriented (*Neocnus*, *Megalocnus*), slightly convex anteriorly (*Parocnus*), or concave anteriorly (*Acratocnus*) (see Taboada *et al.* 2007: 40, 41; Anthony 1926: pl. 40). In *Hapalops*, *Mionothropus*, *Nothrotheriops*, and *Nothrotherium* the anterior margin bears a V-shaped notch between lateral and medial laminae (see Cartelle & Fonseca 1983, De Iuliis *et al.* 2011, Scott 1904, Stock 1925). This condition differs from that of *E. ingens*, in which the nasals are well preserved in MPM-PV 3451 (Fig. 3): the nasals extend well beyond and overhang the maxillae (Fig. 3A, B) and the medial half of the anterior margin is nearly straight and transversely oriented and the lateral half extends posterolaterally, so that overall the margin is, in dorsal view, convex (Fig. 3D).

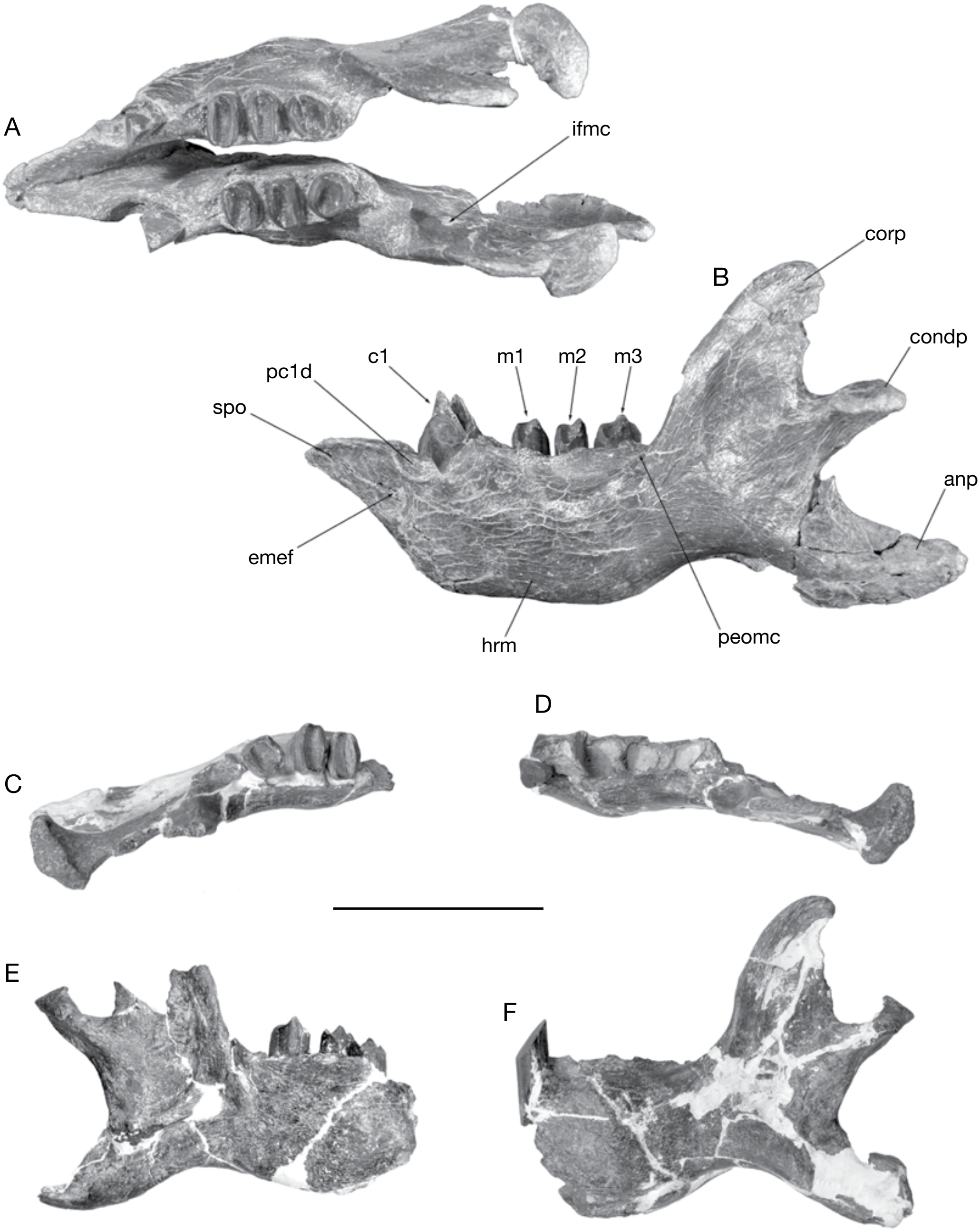

FIG. 6. — Dentaries of *Eucholoeops ingens* Ameghino, 1887, MPM-PV 3401: **A**, **B**, neotype; **C**-**F**, FMNH P13125; **A**, **C**, **D**, occlusal views; **B**, **E**, **F**, lateral views. Abbreviations: **anp**, angular process; **c1**, lower caniniform tooth; **condp**, condyloid process; **corp**, coronoid process; **emef**, external mental foramen; **hrm**, horizontal ramus; **ifmc**, internal foramen of the mandibular canal; **m1-m3**, lower molariform teeth; **pc1d**, pre-c1 depression; **peomc**, posterior external opening of the mandibular canal; **spo**, spout. Scale bar: 5 cm.

The strongly developed nuchal crests of *Eucholoeops ingens* overhang the occiput, resembling *Acratocnus*, although the crests are not as well developed in the latter. In contrast, the occiput of *Hapalops*, *Mionothropus*, and *Choloepus* is widely exposed in dorsal view. The supraoccipital of *Hapalops* bears a well-developed median crest, more so than that of *E. ingens*. The occipital condyles of the latter are relatively larger and project more prominently than in *Hapalops*, *Mionothropus*, *Acratocnus*, and *Choloepus*. The basioccipital, and thus the condyles, lie at approximately the same level as the alveolar margins (i.e. the palate) in *E. ingens*, as in *Hapalops* and *Choloepus*, but lie more dorsally in *Mionothropus* and *Acratocnus*. The occipital condyles extend considerably ventral to the external auditory meatus in *E. ingens*, but slightly less so in *Hapalops* and *Mionothropus* and are directly posterior to the meatus in *Choloepus* and *Acratocnus*. A more detailed analysis of the basicranium and auditory region is in progress.

The jugal of *Eucholoeops ingens* is loosely attached to the lacrimal and maxilla and does not contact the zygomatic process of the squamosal (i.e. the zygomatic arch is incomplete), as occurs in most sloths (see Gaudin 2004), but not all (e.g., the Pleistocene megatheriid *Eremotherium* Spillmann, 1948*,* the mylodontid *Mylodon* Owen, 1839*,* and the megalonychids *Megalonyx* and *Ahytherium*; Gaudin 2004; Cartelle *et al.* 2008). The base of the jugal of *Eucholoeops ingens* has an orbital wing that prevents a maxillolacrimal contact in the orbital region, in contrast to the condition noted in Gaudin (2004: ch. 109; the jugal is missing in the *Eucholoeops* specimens examined by this author, although its facet is preserved). *Eucholoeops ingens* thus resembles the condition that De Iuliis *et al.* (2011) described for most nothrotheriids. The contact, however, is present in most megalonychids (Gaudin 2004). The jugal forms the ventral rim of the orbit, which lies in about the same position typical for other mammals. This position occurs in sloths such as *Acratocnus* and *Choloepus*, as opposed to being displaced ventrally near the level of the alveolar margin, as occurs in some megalonychids such as *Megalonyx* (Gaudin 2004), *Ahytherium* (Cartelle *et al.* 2008), and other sloths, such as *Hapalops* (Scott 1904), the nothrotheriids *Nothrotherium*, *Nothrotheriops*, and the megatheriid *Eremotherium* (see Gaudin 2004).

The posterior part of the jugal bears three processes, as occurs in most sloths (Gaudin 2004). The ascending process of *Eucholoeops ingens*, resembling that of *Hapalops* and *Mionothropus*, is elongated and slender and extends posterodorsally above the zygomatic process of the squamosal, but is longer and tapers more gradually than in these taxa. A weak postorbital process is present along the anterior surface of its base. The middle process projects posteriorly toward the zygomatic process of the squamosal. It is prominent and approximately triangular, resembling that of *Hapalops* and *Nothrotheriops*, but more robust and pointed at its posterior extremity, rather than blunt. The robust descending process is shorter than the ascending process, but less so than in *Hapalops*. It is wide at its base and narrows ventrally, but not as strongly as occurs in *Hapalops*. Although the ventral extremity is incomplete, it is sufficiently preserved to indicate that the posterior margin is concave, thus imparting a hook-like appearance to the end of the process; it is not as curved as in *Nothrotheriops*, resembling more that of *Mionothropus*.

The auditory region of *Eucholoeops* is complex and will be described in a subsequent study.

Mandible (Figs 6; 7I, J)
The mandible of *Eucholoeops ingens* generally resembles that of *Hapalops* (and many other sloths, see below) in having a prominent spout, a deep horizontal ramus, and prominent processes. A main difference between *E. ingens* and *Hapalops* is that the dentary is more robust in the former. In *Hapalops* the horizontal ramus appears relatively gracile and elongated, with the spout extending farther anteriorly and the body being less deep. In both, as in many but not all sloths (see below), the ventral margin of the horizontal ramus is convex and nearly reaches or projects below the level of the ventral margin of the angular process. This ventral bulge lies ventral to the molariform tooth row. More anteriorly the margin of the dentary has a small ventral protuber-

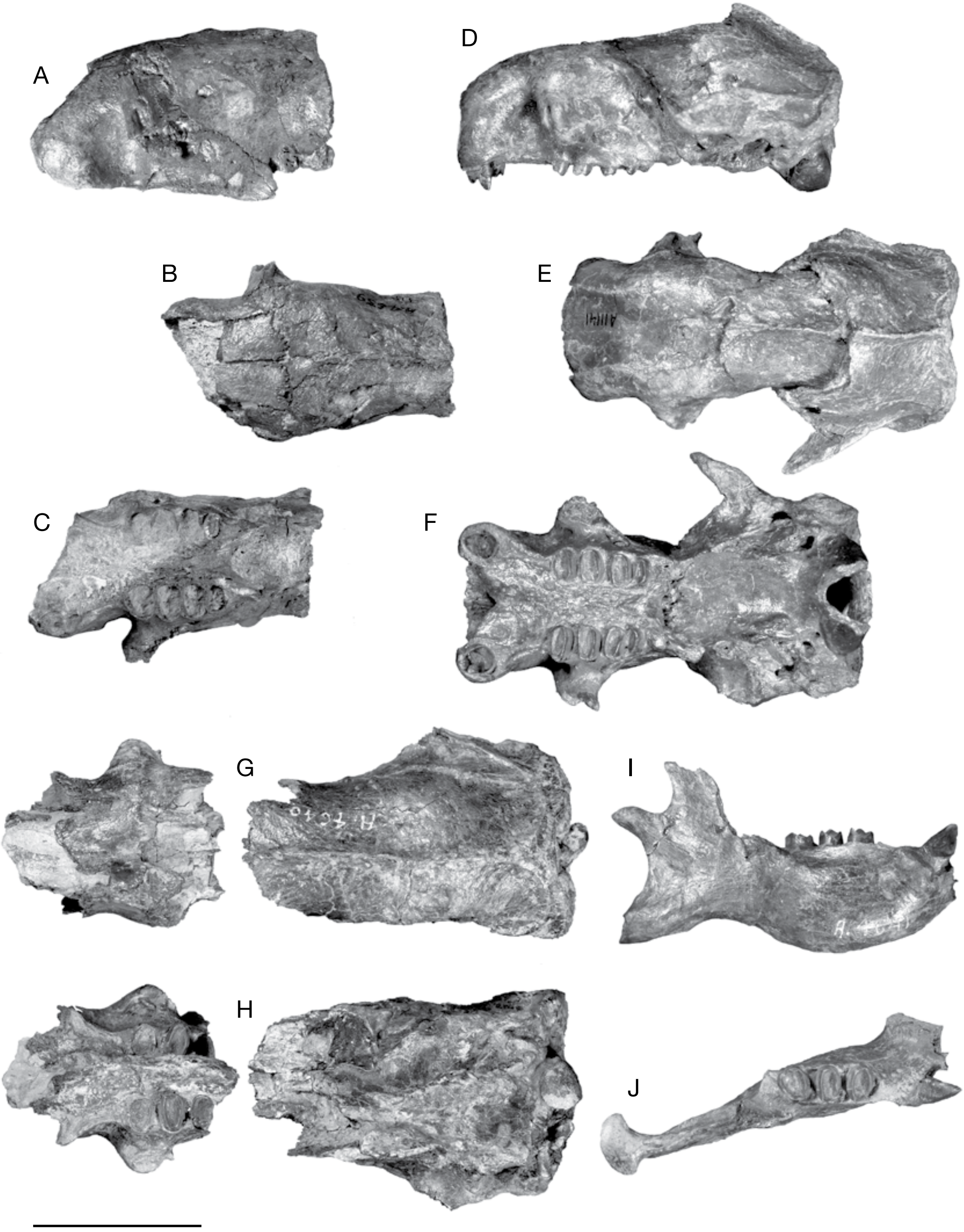

FIG. 7. — Type specimens referred to *Eucholoeops ingens* Ameghino, 1887: **A**-**C**, MACN-A 4639, type of *E. latirostris*, anterior part of skull in lateral (**A**), dorsal (**B**) and ventral (**C**) views (**A** reversed from original; anterior towards left); **D**-**F**, MACN-A 6413, type of *E. curtus*, in lateral (**D**), dorsal (**E**) and ventral (**F**) views (anterior towards left); **G**-**J**, MACN-A 4640, type of *E. externus*, skull remains: **G**-**H**, anterior towards left; **I**, **J**, R dentary (anterior towards right) in dorsal (**G**), ventral (**H**), lateral (**I**) and occlusal (**J**) views. Scale bar: 5 cm.

ance approximately coincident with the posterior end of the mandibular symphysis. This feature may be related to the presence of a caniniform tooth (although the base of this tooth is posterior to the protuberance), as the protuberance is not present in sloths such as in the nothrotheriid *Nothrotheriops*, and the megatheriids *Megatherium* Cuvier, 1796 and *Eremotherium*, in which the caniniform is either lost or molariform and part of the molariform tooth row (i.e. a pronounced diastema is absent). It is present in the nothrotheriid *Mionothropus*, in which small caniniforms are retained.

The ventral profile of the horizontal ramus of *Eucholoeops ingens* strongly resembles that of *Acratocnus*, although the spout is somewhat shorter and the angular process is positioned notably more dorsally in the latter. The profile varies among the remaining megalonychids, but is usually convex, as in *Neocnus*, *Parocnus*, *Megalocnus*, *Megalonyx*, and *Ahytherium*. A slight ventral protuberance is also present (though very slight in *Ahytherium*), except in *Megalocnus*; the caniniform, however, is strongly procumbent in the latter. In *Choloepus*, on the other hand, the ventral profile is nearly rectilinear and the angular process projects slightly below it. This condition resembles the typical condition described for mylodontid sloths, such as the mylodontine *Paramylodon* Brown, 1903 and the scelidotheriine *Scelidotherium* Owen, 1840 (see Stock 1925; McDonald 1987).

The spout of *Eucholoeops ingens* is shorter than in *Hapalops*, thus conforming to the condition in most megalonychids when the spout is present (it is strongly reduced in *Megalonyx* and *Megalocnus*). The spout extends slightly anterodorsally. Its ventral margin is gently concave in lateral view. A prominent trough-like depression lies on the dorsolateral margin of the dentary just anterior to c1. The depression faces dorsolaterally and receives C1. The depression is not present in *Hapalops*, although in lateral view the dorsal margin of the spout is gently concave just anterior to c1. Gaudin (2004) noted the presence of a depression on the lateral surface of the dentary just posterior to c1 in *Hapalops* and *E. ingens*. This depression is prominent and easily noted in some *Hapalops* specimens, such as *H. longiceps* (YPM-VPPU 15523) but appears absent in others, such as *H. elongatus* (YPM-VPPU 15597). In *E. ingens* MPM-PV 3401 (Fig. 6A, B) the depression is present but shallower than in *H. longiceps* YPM-VPPU 15523, whereas it is not notable in *E. ingens* FMNH P13125 (Fig. 6E, F), although this region is not well preserved in this specimen.

The coronoid process of *Eucholoeops ingens* and *Hapalops* are about equally high, but that of *Hapalops* appears relatively shorter because the condyle is more dorsally positioned in the latter. In *E. ingens* the condyle lies just dorsal to the level of the molariforms, and so resembles the condition of *Choloepus* among megalonychids (and mylodontids such as *Paramylodon* and *Scelidotherium*). In other megalonychids, such as *Acratocnus*, *Ahytherium*, *Megalocnus*, *Megalonyx*, *Neocnus*, and *Parocnus*, the condyle is more dorsal (especially *Megalocnus*), and the height of the coronoid varies. For example, it is well above the condyle in *Choloepus*, *Ahytherium*, and *Megalonyx*, at about the same level as the condyle in *Acratocnus*, *Neocnus*, and *Parocnus* (in these the condyle is somewhat shorter than in *E. ingens* and *Hapalops*), and lower than the condyle in *Megalocnus* (in which the coronoid is nonetheless tall). Except for a slightly more dorsal position of the condyle in *Hapalops*, the form and relative positions of the condyle and coronoid process in *E. ingens* resemble more those in *Hapalops* than in other megalonychid sloths.

The angular process in *Eucholoeops ingens* is prominent, as in *Hapalops*. Its ventral margin, in both taxa, reaches to about the same level as the ventral bulge of the dentary, as is also true in *Neocnus*. It lies slightly dorsal to the ventral margin in *Acratocnus*, and much more so in *Parocnus* and *Megalocnus* (see Scott 1904; Anthony 1926; Matthew & Paula Couto 1959; Taboada *et al.* 2007). The margin between the condyle and angular process outlines a fairly deep and smooth semicircular notch, as also occurs usually in *Hapalops*, as well as *Megalonyx* and *Ahytherium* among megalonychids; it is much shallower in *Choloepus* and in the remaining megalonychids and more angular in the latter group, except *Megalocnus* (see Taboada *et al.* 2007). It is also somewhat angular in *H. elongatus* (YPM-VPPU 15597). In overall relative positions, form, and sizes of the angular, condyloid, and angular processes, *E. ingens* most resembles *Hapalops*. A single mental foramen is present on either side in MPM-PV 3401 (Fig. 6B). The foramen lies in a depression of the dentary and opens anterior to the deep notch before the c1 alveolus.

Position of the posterolateral opening. Descriptions of the position of the posterolateral opening of the mandibular canal are somewhat ambiguous. In sloths it is always near or on the base of the anterior margin of the ascending ramus. It has been described, except for megatheriines (see below), as either opening anterolaterally or laterally from the base of the ascending ramus or from the lateral surface of the horizontal ramus. However, the opening is always associated with the base of the anterior margin of the ascending ramus, but depending on the opening's dorsoventral position and relation to the molariform teeth, it may appear as opening from the ascending ramus or the horizontal ramus. For such reasons, it is useful to also consider the position of the opening with respect to these other features. In *Eucholoeops ingens* the opening lies entirely ventral to the alveolar margin and below the distal half of m3, and thus appears on the lateral surface of the horizontal ramus. This is the typical condition in other megalonychids, although there is variation relative to the molariform teeth and dorsoventral position. For example, it is, exceptionally, more ventral in *Neocnus* and lies below m2. In some megalonychids, such as *Megalonyx* and *Parocnus*, its position is approximately as in *E. ingens*. In *Choloepus* the opening is below m3 but its posterior portion may intersect the alveolar border. In *Acratocnus* and *Megalocnus* it lies below m2. In *Ahytherium* the position of the opening varies, and may lie just medial or lateral to the base of the anterior margin of the coronoid process, and from the distal margin of m3 to the mesial half of m3. In MCL 21834, the holotype of *Ahytherium aureum*, the more posterior position occurs in the R dentary and the more anterior position in the L dentary. The condition in *Mionothropus* and *Nothrotheriops* is similar, with the opening lying ventral to the alveolar margin below m3, and as well in *Scelidotherium* and *Paramylodon*, with the difference being that it lies below m4 (which is equivalent to m3 in the above discussed taxa, as all four lower teeth are molariform). In contrast, it lies more dorsally in *Hapalops* (e.g., YPM-VPPU 15523, 15597; AMNH 9222), lying about level with the alveolar margin and posterior to m3, and thus appears on the anterior margin of the base of the ascending ramus. Scott (1903) indicated that its position varies intraspecifically, at least for *H. elongatus*, as is apparent in two specimens that Scott (1904: pl. 40: figs 2a, 4; respectively AMNH 15155 and 15531) assigned to this species: in AMNH 15531 it is entirely ventral to the alveolar margin; in AMNH 15155 it intersects the margin. In megatheriines it lies medial to the base of the ascending ramus. Taxonomic importance has also been given to the presence of two openings in this region. However, this is individual variation, as is indicated by the presence of one and two openings in the same individual (e.g., MPM-PV 4251, *Hyperleptus* sp., and MPM-PV 3458, *Hapalops* sp.). Scott (1903) reported such variation in a specimen of *H. longiceps*, and considered it an abnormality.

It might be expected that, to some degree at least, the position of the opening would be correlated to the position of the anterior margin of the ascending ramus, but a survey of sloths suggests that any possible correlation is not straightforward. In *E. ingens*, as in *Choloepus*, *Hapalops*, *Mionothropus*, and *Nothrotheriops*, the anterior margin of the coronoid process is posterior to m3 and leaves this tooth entirely exposed in lateral view. *Megalonyx* and *Ahytherium* are similar except that m3 is partially covered. In other megalonychids (e.g., *Acratocnus*, *Megalocnus*, *Neocnus*, and *Parocnus*), however, the anterior margin of the coronoid lies farther anteriorly, with m3 being usually entirely (and in some taxa m2 partially) covered in lateral view.

Dentition

Bargo *et al.* (2009) noted the main features of the dentition of *Eucholoeops ingens* and provided detailed descriptions of the occlusal surfaces for their analysis of mastication in this sloth. Here, comparative descriptions among taxa are provided, as well as an assessment of intraspecific variation in *E. ingens*. The dentition includes an upper and lower caniniform and four upper and three lower molariforms. The caniniform is considerably enlarged, projecting beyond the level of the molariforms. C1 and c1 are approximately triangular in section and with a nearly vertical wear facet, that of C1 on the distal and of c1 on the mesial surface of the tooth. The apex of each tooth is sharply pointed. C1 projects more strongly past the upper molariforms than does c1 past the lower molariforms. The diastema is pronounced, particularly in the upper tooth row. The form and size of the caniniform teeth are sufficient to distinguish *E. ingens* from any other Santacrucian sloth. Enlarged caniniforms are characteristic of megalonychids, though they are not always sharply pointed. *Eucholoeops ingens* strongly resembles *Choloepus* and *Acratocnus* and some species of *Neocnus* (see MacPhee *et al.* 2000) in this respect. Those of *Ahytherium* are also sharply pointed, but they are not as large as in *E. ingens*, *Choloepus*, and *Acratocnus*. The c1 of *E. ingens* projects about as strongly as in *Acratocnus* (as illustrated by Gaudin 2004: fig. 10). In contrast to the condition of *Choloepus*, c1 does not project far enough to require accommodation by a fossa posterior to C1. The caniniforms in megalonychids such as *Megalonyx*, *Megalocnus*, and *Parocnus* are clearly distinguished from those of *E. ingens* in being incisiform (see Leidy 1855; Matthew & Paula Couto 1959; Taboada *et al.* 2007).

The upper molariforms are generally oval to rectangular in shape, with long axis oriented vestibulolingually. This is a common pattern in megalonychids (but see below), nothrotheriids, and planopsines, and occurs in some less derived megatheriines (e.g., *Megathericulus* Ameghino, 1904 and *Anisodontherium* Brandoni & De Iuliis, 2007, Middle and Late Miocene, respectively; Pujos *et al.* 2013).

Eucholoeops ingens is notable in that its molariforms, particularly M2 and M3, tend to be transversely expanded, and in some specimens these teeth appear mesiodistally compressed. M2 and M3 are the largest molariforms, although there is variation, including individual, as to which is largest (Fig. 4B). M4 is the smallest upper tooth. It may be transversely oval (MPM-PV 3451; Fig. 3C) or nearly trapezoidal (MPM-PV 3401; Fig. 2B), but its section varies, even within individuals. For example, its distal surface may be convex or slightly indented, producing either an oval or somewhat reniform section. Despite the overall general resemblance of the molariforms among megalonychids, there are some notable differences, as is evident from figures and descriptions in, for example, Anthony (1926), Cartelle *et al.* (2008), Matthew & Paula Couto (1959), and Taboada *et al.* (2007). Among these differences, we may note that some molariforms tend to be somewhat triangular to trapezoidal rather than oval in *Ahytherium*, *Megalonyx*, *Neocnus* and, to a lesser extent, *Parocnus*. In some megalonychids, the long axis of some molariforms tends to be oriented obliquely to the long axis of the tooth row, as occurs in M1 to M3 in *Acratocnus*, M3 in *Ahytherium*, M1-M2 in *Parocnus*, and M1 in *Megalocnus*. Lastly, several molariforms may be reniform, with a distal apicobasal sulcus, in *Acratocnus*, *Megalocnus*, and *Parocnus*.

The sample of mandibles securely associated with skull material is considerably smaller than skull remains, so that the lower teeth are less well represented than the uppers. Indeed, only two individuals, MPM-PV 3401 (Fig. 6A, B) and FMNH P13125 (Fig. 6C-F), possess reasonably well-preserved skulls and associated mandibular remains (and that for FMNH P13125 is not particularly complete). The m1 and m2 are of similar size and shape, resembling the upper molariforms in being transversely oval in section. The section of m3, though still oval, is nearly circular (MPM-PV 3401, Fig. 6A) or squared (FMNH P13125, Fig. 6C, D), and its long axis is oriented linguodistally to vestibulomesially rather than nearly transverse. As for the upper molariforms, differences may be noted in the lower molariforms of other megalonychids. For example, m1 is more nearly trapezoidal to oval in *Neocnus* and *Ahytherium* (based on alveolar morphology), reniform (with mesial apicobasal sulcus) in *Parocnus*, and triangular in *Megalocnus*, as is m2 in the latter.

As noted already in this section, there is variation in size, shape, and section of any particular tooth. In addition to these general dental characteristic, there is also variation in the occlusal surface and features of the teeth. This is easily apparent in MPM-PV 3401, in which features such as size, shape, and height of cusps and crests differ between left and right side teeth (Fig. 6A, B; see also Bargo *et al.* 2009: fig. 2G). These differences do not appear to be related to preservation.

Postcranial Skeleton
See Figures 8-11.

Humerus (Fig. 8A-C, G-I)
The humerus of *Eucholoeops ingens* is known from MPM-PV 3401, FMNH P13125 (measurements for these are given at the end of this section), and MACN-A 6414 (see Discussion). The humerus has a proximal, subcylindrical proximal portion that widens markedly into a flattened distal portion, which, as noted by De Iuliis *et al.* (2011), occurs in nearly all sloths except mylodontids. The head is well exposed between the tubercles in anterior view as in *Acratocnus antillensis* Matthew, 1931 (Taboada *et al.* 2007), *Ahytherium*, *Neocnus*, *Hapalops elongatus*, *Mionothropus*, and *Nothrotherium*; it is less evident in anterior view in *Acratocnus odontrigonus* Anthony, 1916 (Anthony 1926), *Megalonyx*, *Parocnus*, and *Nothrotheriops*, whereas it is more exposed in *Megalocnus* (see Anthony 1926, Cartelle *et al.* 2008, Matthew & Paula Couto 1959, and Taboada *et al.* 2007). The tubercles are widely separated in *E. ingens*, as in the sloths mentioned above, with the lesser tubercle larger than the greater tubercle, as in *Hapalops* (Scott 1904: pl. 41). The tubercles are subequal in the megalonychids *Acratocnus*, *Ahytherium*, *Megalocnus*, *Neocnus*, and the nothrotheriids *Mionothropus*, *Nothrotheriops* (Stock 1925: pl. 8; McDonald 1985), and *Nothrotherium* (Reinhardt 1878; GDI pers. obs.). The greater tubercle projects farther proximally than the lesser tubercle in *E. ingens*, as occurs in *Ahytherium*, *Megalonyx*, *Parocnus*, and *Nothrotherium*, and as is usual in sloths neither tubercle projects more proxi-

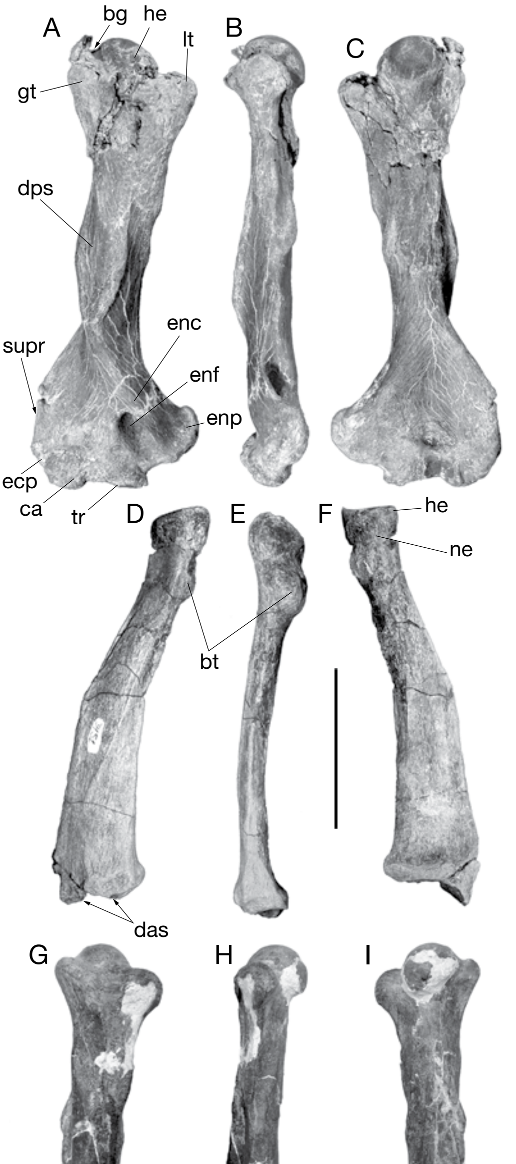

Fig. 8. — Forelimb long bone elements of *Eucholoeops ingens* Ameghino, 1887: **A**-**C**, right humerus (MPM-PV 3401, neotype) in anterior (**A**), medial (**B**) and posterior (**C**) views (proximal towards top); **D**-**F**, left radius (MPM-PV 3451) in anterior (**D**), lateral (**E**) and posterior (**F**) views (proximal towards top); **G**-**I**, right humerus (FMNH P13125) in anterior (**G**), medial (**H**), and posterior (**I**) views (proximal towards top). Abbreviations: **bg**, bicipital groove; **bt**, bicipital tuberosity; **ca**, capitulum; **das**, distal articular surface; **dps**, deltopectoral shelf; **enc**, entepicondylar crest; **enf**, entepicondylar foramen; **ecp**, ectepicondyle (lateral epicondyle); **enp**, entepicondyle (medial epicondyle); **gt**, greater tubercle; **he**, head; **lt**, lesser tubercle; **ne**, neck; **supr**, supinator ridge; **tr**, trochlea. Scale bar: 5 cm.

mally than the head (one exception being *Parocnus*). In *Acratocnus antillensis*, *Mionothropus* and *Hapalops*, the lesser tubercle projects slightly farther proximally than the greater tubercle, whereas in *A. odontrigonus*, *Megalocnus*, *Neocnus*, and *Nothrotheriops*, the tubercles project to approximately the same level. The bicipital groove is broad and shallow in all taxa.

The deltopectoral shelf, as noted by De Iuliis (2003) and De Iuliis *et al.* (2011), is a raised, flattened, and distally tapered structure on the central third of the anterior diaphyseal surface of many sloths. The shelf is defined laterally by the deltoid ridge and medially by the pectoral ridge. The latter begins just distal to the medial margin of the greater tubercle. The deltoid ridge begins laterally on the diaphyseal surface, just distal to the greater tubercle. The ridges become more pronounced distally, converging to form a strongly raised triangular eminence. The deltopectoral shelf of *Eucholoeops ingens* (MPM-PV 3401; Fig. 8A-C) is a well-developed and prominently raised structure, as described for *Hapalops* (De Iuliis *et al.* 2011), in which the ridges are strongly raised into crests and flared. The position of the shelf in *E. ingens* occupies just more than the lateral half of the diaphysis, approximately as in *Hapalops elongatus* (FMNH P13133 and YPM-VPPU 15160) and *H. ruetimeyeri* (AMNH 9250; Scott 1904: pls 41, figs 4 and 42, fig. 4, respectively, illustrated the YPM-VPPU and AMNH specimens) whereas in *H. longiceps* (YPM-VPPU 15523; Scott 1903: pl. 32, fig. 2) the shelf nearly covers the entire anterior diaphyseal surface. Among megalonychids, *E. ingens* resembles, in the form and extent of the shelf, *Neocnus* and *Megalocnus* (though in the latter the shelf is wider distally), whereas *Acratocnus* resembles more the condition in *H. longiceps*. *Parocnus* resembles *E. ingens*, but the shelf ends farther proximally. In *Ahytherium* the shelf is not as raised, owing to weaker ridges that do not project beyond the margins of the diaphysis, and in *Megalonyx* the shelf is less raised as well, owing to a weaker pectoral ridge.

The supinator ridge extends proximally almost vertically from the ectepicondyle, and forms a distinct angle to continue proximomedially. This resembles the condition in *Acratocnus*, *Ahytherium*, *Megalonyx*, and *Neocnus*, but the vertical portion is shorter in *E. ingens* and *Ahytherium*. It is notably elongated in *Acratocnus* and *Neocnus* and in *Acratocnus major* (which is a synonym of *A. odontrigonus* according to White & MacPhee 2001) it is especially prominent, forming a robust hook-like proximal extension (Anthony 1926: pl. 49, fig. 2a). The ridge is somewhat less prominent and more sloped proximomedially in *Megalocnus* and *Parocnus* and a distinct angle is not present. The entepicondyle of *E. ingens* is drawn proximomedially into a robust process, resembling that of *Megalonyx* and *Hapalops* in forming a small proximal protuberance, as illustrated by Scott (1903: pl. 32, fig. 2); but caution is necessary, as in many cases the humeri illustrated by Scott, and indeed other skeletal elements, have at least some reconstruction, whereas his illustrations disguise this fact and give the false impression of being based on complete specimens.

Measurements of the humerus

MPM-PV 3401. Greatest length: 201 mm; anteroposterior/transverse diameter of humeral head: 30/29 mm; maximal width of deltopectoral shelf: 27 mm; diaphyseal thickness at deltopectoral shelf: 27 mm; distal width: 76 mm.

FMNH P13125. Greatest length: 191 mm.

Radius (Fig. 6D-F)

The radius of *Eucholoeops ingens* is known from MPM-PV 3451 (Fig. 6D-F) and FMNH P13125 (measurements given at the end of this section). The head is strongly inclined distomedially, approximately as in *Acratocnus odontrigonus* (Anthony 1926: pl. 48, fig. 5), *Hapalops longiceps* (Scott 1903: pl. 32, fig. 3), and *H. ruetimeyeri* (Scott 1904: 42, fig. 6). The head is less steeply inclined in other megalonychids (e.g., *Ahytherium*, *Megalocnus*, *Megalonyx*, and *Parocnus*). The neck is short and slightly constricted. The bicipital tuberosity is prominent; its position is approximately as in *Neocnus* and *Acratocnus antillensis*, whereas it is farther distal in *A. odontrigonus* (see Anthony 1926; Taboada *et al.* 2007). The tuberosity projects mainly posteriorly. Distal to the tuberosity the diaphysis extends gently distomedially to just past its midlength, and then continues more nearly distally.

This produces a prominent bend in the diaphysis, so that the distal end is offset medially with respect to the proximal end (see De Iuliis *et al.* 2011), as occurs in many sloths (e.g., some megalonychids and megatheriines), although in other sloths the bend is very slight – e.g., in the megalonychids *Megalonyx* and *Parocnus* the proximal and distal ends are essentially aligned longitudinally. The position of the bend also varies. For example, it occurs in about the same position as in *E. ingens* in *Ahytherium*, *Megalonyx*, and *Hapalops*, but much farther proximally in *Acratocnus* and *Megalocnus*, and farther distally in *Neocnus*. The medial diaphyseal surface bears an angle at this position, which is associated with the prominent medial muscular scar, probably for the insertion of the *m. pronator teres*. In *Eucholoeops ingens*, as in *Ahytherium*, *Megalonyx*, and *Neocnus*, this angle is fairly gradual or rounded, but it is much more abrupt in *Megalocnus* and *Hapalops*. Apparently, this character varies in *Acratocnus odontrigonus* (compare Anthony 1926: fig. 72 and pl. 48, fig. 5a). Distally from this angle the lateral and medial margins extend nearly parallel to each other to the distal articular surface, as is typical among sloths. The distal articular surface is extensive and concave for articulation with the proximal carpals, and faces more distally whereas in other Santacrucian sloths, it faces more distolaterally. The diaphysis of *E. ingens* is also curved, bowing anteriorly. The two specimens differ in degree of curvature, with that in MPM-PV 3451 (Fig. 6D-F) being less prominent. However, it is not clear that this represents intraspecific variation, as the diaphysis of FMNH P13125 is more heavily damaged.

Measurements of the radius

MPM-PV 3401. Greatest length: 164 mm, anteroposterior/transverse diameter of radial head: 20/23 mm; minimal width at neck: 19 mm; width at pronator teres process: 25 mm; distal width: 37 mm.

FMNH P13125. Greatest length: 164 mm.

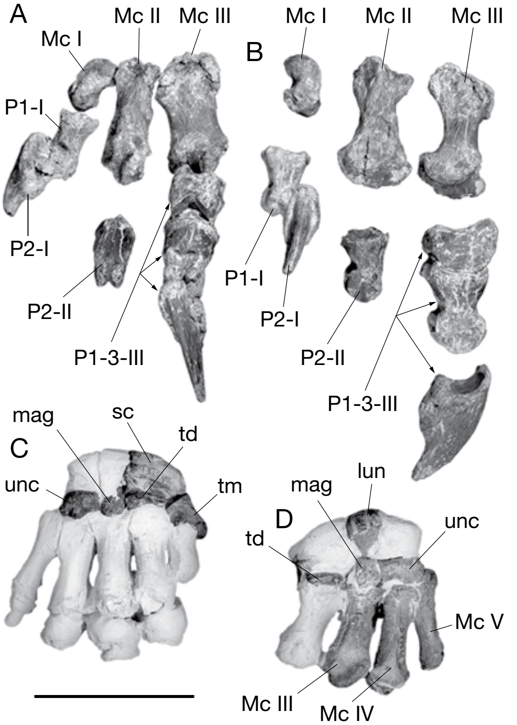

Fig. 9. — Manus elements of *Eucholoeops ingens* Ameghino, 1887: **A**, **B**, L manus elements of MPM-PV 3401 (neotype) in dorsal and medial views respectively (proximal towards top); **C**, **D**, partial R and L manus respectively of FMNH P13125 (proximal towards top). Abbreviations: **lun**, lunar; **mag**, magnum; **Mc I**-**Mc V**, metacarpals 1 to 5; **P1**-**P3**, first-second-third phalanx, followed by Roman numeral indicating digit number; **sc**, scaphoid; **tm**, trapezium; **td**, trapezoid; **unc**, unciform. Scale bar: 5 cm.

Manus (Fig. 9)

The manus of *Eucholoeops ingens* is incompletely known. The carpals are known mainly from FMNH P13125 (Fig. 9C, D), with only the R scaphoid, trapezium, trapezoid, magnum, and unciform, and L lunar (this specimen may not belong to the same individual; a hand-written noted accompanying the specimen in the FMNH collections has the last digit of the specimen number, following “P1312”, blotted out and illegible; the note suggests it may belong to P13133, assigned to *Hapalops elongatus*) being reasonably complete. These elements, however, have been incorporated into plaster reconstructions of the R and L manus and are unavailable for detailed study. All the metacarpals are known. MPM-PV 3401 preserves Mcs I-III, and FMNH P13125 preserves MC III-V. Phalanges are only preserved in MPM-PV 3401.

The lunar of *Eucholoeops ingens* resembles that typical for sloths, with a strongly convex proximal surface for articulation with the radius. Medially the lunar articulates with the scaphoid, which has a broad though similarly convex proximal articular surface. The scaphoid articulates distally with the trapezium and trapezoid and laterally with the magnum. The magnum articulates proximally with the lunar, medially with the scaphoid, as noted, and trapezoid, distally with Mc III, and laterally with the unciform. The magnum is wider distally than proximally, as occur in *Megalonyx* and nothrotheriids, whereas in *Hapalops* it is wider proximally (see De Iuliis *et al.* 2011). The unciform is deeper laterally than medially, articulating distolaterally with Mc V, distally with Mc IV, and medially with the magnum. It may also have articulated with MC III, as in *Hapalops* (Scott 1903: pl. 33, fig. 2) and *Mionothropus* (De Iuliis *et al.* 2011: fig. 11), but the proximal end of Mc III is apparently incomplete in FMNH P13125 (Fig. 9C, D) and not well preserved in MPM-PV 3401 (Fig. 9A, B).

Mc I (MPM-PV 3401) is the smallest metacarpal, being only about half the length of the others. It articulates with the trapezium proximally, via a saddle-shaped facet, and Mc II laterally. The remaining metacarpals of *Eucholoeops ingens* are approximately equal in length to each other, with Mc III (as usual among sloths) being the most robust, and more robust in MPM-PV 3401 than in FMNH P13125 (Fig. 9A, B, D). Mcs II and IV are about equally robust, followed by Mc V. The pattern of metacarpal lengths in *Eucholoeops* is atypical among sloths, in which Mcs II and III are usually about equal in length, but roughly half the length of Mcs IV and V, as in *Megalonyx*, *Hapalops*, *Mionothropus*, *Nothrotheriops*, and *Nothrotherium* (see De Iuliis *et al.* 2011). In this regard, *E. ingens* resembles more the condition in *Megalocnus*, in which Mcs II-IV are subequal in length, with Mc V being slightly longer. Mcs I-IV have a keeled distal articular surface, whereas Mc V is blunt distally. The proximal and distal phalanges of digit 1, the middle phalanx of digit 2, and all three phalanges of digit 3 are known for *E. ingens*. The distal phalanges of digits I and III are unguals, the latter being much the larger. The morphology of the phalangeal elements does not differ from that reported for other fossil sloths.

Femur (Fig. 10A-C)

The femur of *Eucholoeops ingens* is known only from FMNH P13125 (Fig. 10A-C; greatest length = 212 mm; width at third trochanter approximately 46 mm). It is damaged, missing part of the head and parts of the diaphysis, but is sufficiently well preserved to provide a general description and some measurements. The femur is wide and flattened anteroposteriorly, as occurs generally in ground sloths. It is relatively elongated and gracile, with its proximal half slightly wider than and at a distinct angle to the distal half (not considering trochanters). In these regards it closely resembles the form in *Acratocnus odontrigonus* AMNH 17363a (Matthew & Paula Couto 1959: pl. 41, fig. 2), although the femur assigned by Taboada *et al.* (2007: 51) to *A. antillensis* is nearly rectilinear, as is the femur, AMNH 17363b, assigned by Anthony (1926: pl. 51, fig. 3a, b) to *A. odontrigonus*. It would appear that either there is considerable variation in *Acratocnus* in the form of the femur or this genus is in need of revision. In any event, the femur of *E. ingens* is more strongly “bent” than in AMNH 17363a, and the form and relationships among the head and greater trochanter differ from those of that specimen. A bent femur also occurs in *Megalocnus* but the diaphysis is markedly wider and the greater and third trochanters are much more prominent in the latter. In other megalonychids, such as *Ahytherium*, *Megalonyx*, and *Neocnus* (and *Acratocnus* AMNH 17363b), the diaphysis is much more nearly rectilinear. That of *Megalonyx* differs from the others in being particularly wide and of nearly uniform width. That of *Ahytherium*, not as wide but also of nearly uniform width, is distinguishable by the great width across the epicondyles. The greater trochanter of *Eucholoeops ingens*, though missing its proximal tip, is approximately as in *Megalonyx* and *Parocnus* in relative size and degree of proximal projection, being well distal to the head. The trochanter extends farther proximally, nearly reaching the level of the head, in *Megalocnus*, in which it is particularly massive (note that the images of *Megalocnus* and *Parocnus* are apparently reversed in Taboada *et al.* 2007: 54). Variation is apparent in this character in *Acratocnus odontrigonus* (see Anthony 1926: pl. 51, figs 2, 3a) and *Neocnus gliriformis* (see Taboada *et al.* 2007: fig. 2.4), with the greater trochanter being distal to and nearly at the same level as the head. In *Ahytherium* the greater trochanter is distally displaced. The lesser trochanter is not preserved in *Eucholoeops ingens* (Fig. 10A, B). The third trochanter is prominent and is positioned at about midlength, approximately as in other megalonychids (except *Parocnus*, in which it appears to be absent). The prominent appearance of this trochanter in *E. ingens* compared to other megalonychids may be partly due to the marked bend of the diaphysis.

The distal articular surface of the femur bears three articular surfaces. The patellar trochlea, for articulation with the patella, is transversely broad, as in other megalonychids. Although the region between the patellar trochlea and the medial articular condyle has been partly reconstructed in FMNH P13125, the two surfaces appear to have been contiguous, connected by a smooth and narrow isthmus. The trochlea and lateral articular condyle are not contiguous, as is clear from Fig. 10C. The patellar trochlea is contiguous with the medial and lateral articular surfaces for the tibia in some megalonychids, such as *Acratocnus*, *Megalocnus*, and *Parocnus*. In *Megalonyx* the medial and lateral surfaces butt against the patellar trochlea, whereas in *Neocnus*, the lateral is separated from the medial surface, which butts against the trochlea. They are not contiguous in *Ahytherium*. The femur of *Hapalops* is relatively less elongated than that of *Eucholoeops ingens*, but like the latter is slightly wider proximally than distally. Its diaphysis differs in being nearly rectilinear and the greater trochanter projects more proximally, nearly reaching the level of the head, as described above for some megalonychids. The third trochanter appears more prominent in *Hapalops* and lies slightly more proximally than in *E. ingens*, and the distal articular facets are contiguous.

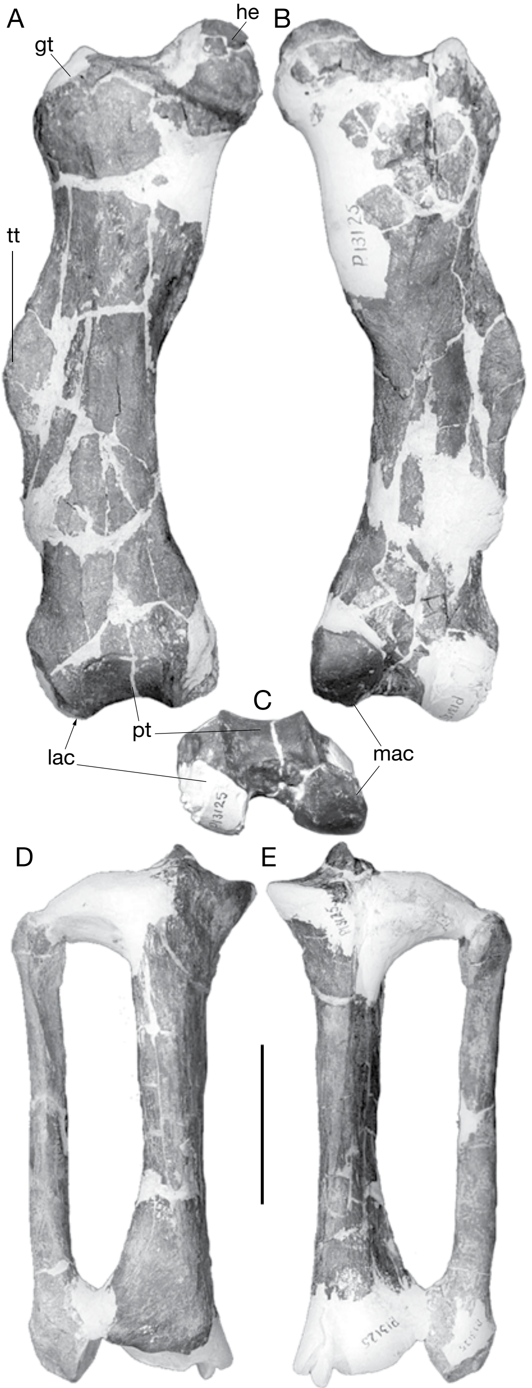

Fig. 10. — Hind limb long bones of *Eucholoeops ingens* Ameghino, 1887, FMNH P13125: **A**-**C**, R femur in anterior, posterior, and distal views respectively (proximal towards top in **A**, **B**; anterior towards top in **C**); **D**, **E**, R tibia and fibula in anterior and posterior views respectively (proximal towards top). Abbreviations: **gt**, greater trochanter; **he**, head; **lac**, lateral articular condyle; **mac**, medial articular condyle; **pt**, patellar trochlea; **tt**, third trochanter. Scale bar: 5 cm.

Tibia and fibula (Fig. 10D, E).

The R tibia (greatest length, measured along anterior surface = 156 mm; minimal diaphyseal width, measured just past midshaft = 18 mm) and fibula (greatest length = 146 mm; maximal diaphyseal width = 12 mm) are known only from FMNH P13125. The tibia is elongated and slender, resembling more that of *Acratocnus* and *Neocnus* rather than *Megalocnus*, *Megalonyx*, and *Parocnus*, whereas the fibula is relatively stout compared to those of other Santacrucian sloth such as *Hapalops* (e.g., Scott 1903: pl. 33, fig. 3; 1904: pl. 41, fig. 6; pl. 42, fig. 8), the mylodontid *Analcimorphus* Ameghino, 1891 (YPM-VPPU 15561; Scott 1904: pl. 49, fig. 4), and the megatheriid *Prepotherium* Ameghino, 1891 (YPM-VPPU 15568; Scott 1904: pl. 61, fig. 2; note that Scott labeled the figured specimen as YPM-VPPU 15368 but this is probably an error as the specimen is recorded as 15568 on the catalogue card and YPM-VPPU online database, whereas the database describes 15368 as consisting of proterotheriid litoptern remains). The fibular diaphysis is of nearly constant diameter in *Eucholoeops ingens*, whereas it tends to be wider proximally (*Hapalops*, *Analcimorphus*) or distally (*Prepotherium*). In this regard among megalonychids, it resembles more that of *Megalocnus* than *Acratocnus*, *Parocnus*, and *Neocnus* (see Anthony 1926; Matthew & Paula Couto 1959; Taboada *et al.* 2007).

Pes (Fig. 11)

Only a few elements of the pes of *Eucholoeops ingens* are known, all from FMNH P13125. These include Mt II-V (Fig. 11A-I), the cuboid (Fig. 11K-M), the ectocuneiform, and navicular (Fig. 11N-P). In addition, there are several other preserved bones that may be pes elements, but they cannot be articulated with the elements just listed or compared with elements of other ground sloths, given the dearth of published descriptions and illustrations of ground sloth pedal elements, and so we are unable to identify them unambiguously. The elements, being generally similar to those described and illustrated by Stock (1925) for *Hapalops* and *Nothrotheriops*, are described only briefly below.

The cuboid is a blocky element with three well-defined articular surfaces (Fig. 11K-M). The proximal surface bears two nearly flat facets that meet at an acute angle: a medial facet articulating with the astragalus and a lateral facet articulating with the calcaneum. Distally, the cuboid bears a transversely elongated, smooth and slightly saddle-shaped facet for Mts IV and V. The navicular is an ovate, bowl-like element (Fig. 11N-P). Its proximal surface bears a deep, concave facet, with a central prominence, for articulation with the astragalar head. Its distal surface bears articular facets for the ecto-, meso- and entocuneiform.

Mt II. Based on the preserved portions (the plantar projection is missing) of Mt II in *Eucholoeops ingens*, this element strongly resembles that of *Hapalops* in shape and proportions (Fig. 11A-C). In lateral view the proximal end of Mt II in *Hapalops* is dorsoplantarly expanded, compared to its shaft, with much of this expansion due to its plantarly projecting portion, whereas the dorsal portion projects little beyond the shaft. In *Nothrotheriops* the proximal end is also expanded but dorsal and plantar projections are about equal.

Mt III of *E. ingens* resembles that of *Hapalops*, but is relatively longer and with a slightly better developed shaft (Fig. 11D, E). This condition contrasts with that in *Megalonyx* (McDonald 1977) and, particularly, *Nothrotheriops* (Stock 1925), in which Mt III is strongly compressed proximodistally so that it effectively has no shaft. The proximal surface bears the dorsoplantarly elongated and concave facet for the ectocuneiform, resembling more that of *Nothrotheriops* than that of *Hapalops*.

Mt IV. The proximal surface of Mt IV is dorsoplantarly elongated, more like that of *Hapalops* though not as wide plantarly, in contrast to the more quadrate shape in *Nothrotheriops* (Fig. 11D, G, H). It also resembles that of *Hapalops* in lacking a facet dorsomedially. A similar facet was described in *Nothrotheriops* as articulating with the ectocuneiform (Stock 1925).

Mt V. Although Mt V is incomplete proximally, a flange was apparently present proximolaterally (Fig. 11D, I, J). The flange is particularly large in *Megalonyx* and *Nothrotheriops*, but less so in *Hapalops*. Based on the preserved portions in FMNH P13125, the flange in *E. ingens* may not have been as large as in *Hapalops*. As in *Hapalops* and *Nothrotheriops*, the shaft narrows considerably before widening again distally. The distal end resembles that of *Hapalops* but is more expanded. The distal articular surface bears a convex and dorsoplantarly elongated facet, similar to the elliptical convexity described by Scott (1903) for *Hapalops longiceps*, which contrasts with the keeled articular surfaces of Mts II-IV. The form of the surface in Mt V suggests the presence of at least one phalanx for digit 5, possibly nodular as described by Stock (1925) for *Nothrotheriops*. This author noted that Scott illustrated a complete digit 5 for *Hapalops longiceps*, but this occurs in the figure of the mounted reconstruction (Scott 1903: pl. 30). Scott (1903: 203; 1904) did not illustrate any digit 5 phalanges in the plates of individual skeletal elements and noted only that all "the phalanges of the fifth digit have been lost," implying that he lacked direct evidence for the reconstruction of a complete digit 5.

In terms of length, Mt IV is the longest of the series (Fig. 11C, D), exceeding slightly the length of Mt V, as occurs also in *Megalonyx* (McDonald 1977), *Nothrotheriops*, *Paramylodon* (Stock 1925), and *Hapalops* (Scott 1903, 1904). Mt V of *Megalocnus* is longer than Mt IV, which is slightly longer than Mt III (Matthew & Paula Couto 1959). In *Eucholoeops ingens* Mt III is slightly shorter than Mt V, and Mt II is slightly shorter than Mt III. In *H. longiceps* Mts II and III are subequal (length given as 3.8 cm by Scott 1903: 197 and as reflected in his pl. 33, fig. 4). The condition in *H. elongatus* is unclear: Scott's illustrations (1904: pl. 41, figs 1, 2) indicate that Mt III is decidedly shorter than Mt II, but his reported measurements (1904: 231) indicate only a marginal difference of between 1 and 2 mm. In *Megalonyx* Mts II and III are subequal in length (McDonald 1977). The condition in *Nothrotheriops* is distinctly different than in *E. ingens* and *H. longiceps*, as Mt III is notably shorter than Mt II (Stock 1925). In *Megalocnus* Mt II is longer than Mts III and IV, and nearly as long as Mt V (Matthew & Paula Couto [1959]). In *Paramylodon* Mt III is notably longer than Mt II (Stock 1925).

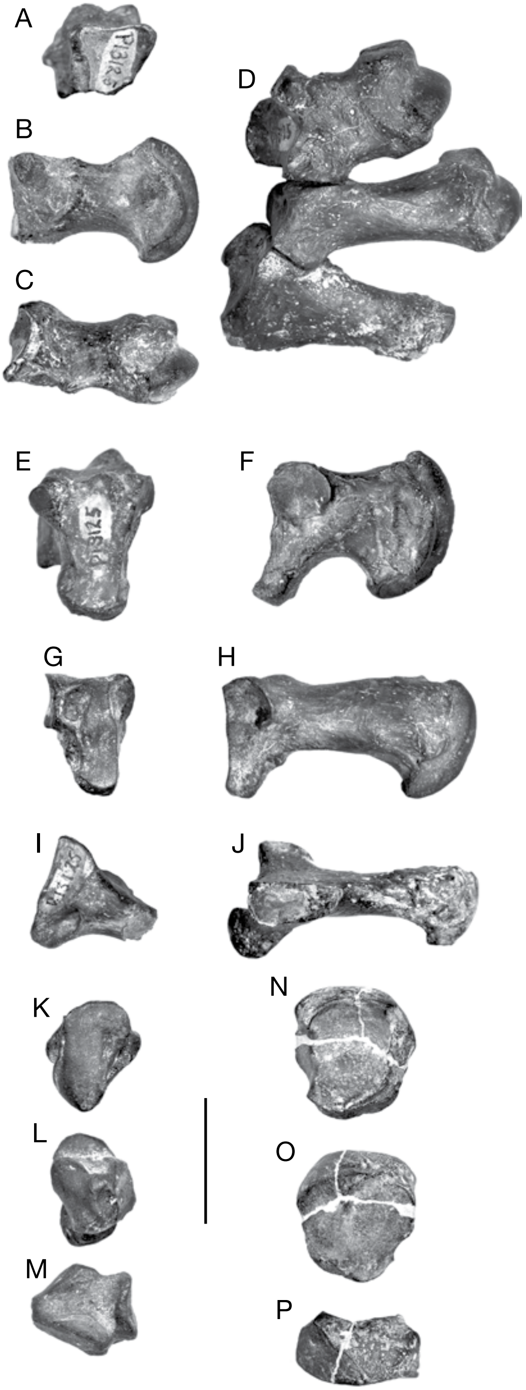

Fig. 11. — Pes elements of *Eucholoeops ingens* Ameghino, 1887, FMNH P13125: **A**-**C**, R Mt II in proximal, medial, and dorsal views respectively; **D**, R Mts III-V in dorsal view; **E**, **F**, R Mt III in proximal and lateral views respectively; **G**, **H**, R Mt IV in proximal and lateral views respectively; **I**, **J**, R Mt V in proximal and lateral views respectively; **K**-**M,** L cuboid in distal, proximal, and dorsal views respectively; **N**-**P**, R navicular in proximal, distal, and dorsal views respectively. Scale bar: 2 cm.

DISCUSSION

Taxonomic assessment

Among the issues to be dealt with in revising the genus *Eucholoeops* are the lack of a type specimen and the utility of the older literature. With regard to the former, Ameghino described the specimen on which the taxon is based, but did not provide a catalogue number. We designate a neotype, MPM-PV 3401 (Figs 2; 6A, B; 8A-C; 9A, B), for *Eucholoeops ingens*, the type species of the genus, according to Article 75.1 of the International Code of Zoological Nomenclature (ICZN 1999) as the name-bearing type specimen is no longer available (see Taxonomy, above), and a type is required for clarifying the taxonomic status and type locality of the taxon. With regard to the original specimen on which Ameghino based *E. ingens*, exhaustive searches at the two likeliest institutions, MLP and MACN, that might have housed the specimen have failed to locate it (though Lydekker [1894], and Mones [1986] indicated it was housed at MLP). We may be fairly confident that W. B. Scott observed the original type (see below), but it is not clear that Mercerat (1891) and Lydekker (1894) did. The latter described it (but possibly based on Ameghino 1889; see below), identifying it as a skull and mandible, MLP 9192 and 9193, that was covered in matrix and not worthy of illustration. However, it is uncertain that these catalogue numbers represent the material described by Ameghino (1887). The catalogue records at MLP indicate an entry for these numbers, assigned to *Eucholoeops ingens*, in Mercerat's handwriting. This list may indeed be a catalogue of the Santacrucian specimens recovered by Carlos and described by Florentino, and thus MLP 9192 and 9193 may be the correct catalogue numbers assigned to the original type of *E. ingens*. However, specimens with these catalogue numbers cannot be located in that institution.

Part of the problem with types is that we cannot be sure which specimens were in the possession of MLP as opposed to being in Ameghino's private collection in the years immediately following the latter's resignation, in January 1888, from MLP over differences with its director F. P. Moreno. Ameghino (1891, 1895) makes repeated reference to the fact that authors such as Mercerat (1891) and Lydekker (1894) had not examined certain specimens in his private collection, but that such material was freely available for study (see below).

The reason for this state of affairs is the possibility that many of the fossil specimens recovered from the banks of the Rio Santa Cruz in 1887 by Carlos Ameghino under the aegis of MLP (where he was employed initially as an Assistant Preparator of Paleontology and then as Travelling Naturalist), a collection briefly and almost completely described by F. Ameghino (1887), were appropriated from MLP by the latter into his own (and Carlos') private collection, as suggested by B. Patterson (in Marshall 1980; see also Fernicola 2011). If this were the case, then Ameghino's (1889) illustrations and more detailed descriptions of many of the species described in 1887 (as well as of several new Santacrucian species) is rendered understandable; and it also explains why many of the relevant specimens are housed in the Ameghino Collection of MACN (Fernicola 2011). Both Florentino, in 1902, and Carlos, in 1903, became employees of the Museo Nacional de Buenos Aires, the precursor of the MACN, and their collection was eventually incorporated as the Ameghino Collection of the MACN in 1935 by order of the Minister of Justice and Public Instruction Manuel Iriondo, in compliance with law 11459 of the National Congress of Argentina passed in 1928.

In any event, Florentino Ameghino's personal possession of many of these fossil remains is also indicated by Scott (in Hatcher 1903: ix), who noted that Ameghino "permitted the freest possible use of his great private collection of Patagonian fossils, a collection which is especially valuable because it contains by far the largest number of the type-specimens of the genera and species named from Patagonian formations." Presumably, Scott was referring to many of the original types based on the 1887 collection, although there is the possibility that F. Ameghino switched types, choosing new types as Carlos, who continued to prospect the localities after 1887, recovered new and often better specimens, as suggested by R. Pascual (in Marshall 1980).

It is clear, then, that W. B. Scott had access to and examined the relevant material in MLP and Ameghino's collection during the former's research trip to La Plata and Buenos Aires in 1901 (Letter of Florentino to Carlos, dated 14 October 1901; Torcelli 1935; Vizcaíno 2011). It is the absence of an MLP catalogue number for the original type of *E. ingens* in Scott's thorough reports that casts doubt on Lydekker's (1894) identification of MLP 9192 and 9193 as the type material. Scott usually provided institutional numbers of material he described, though one might speculate that the specimens were removed from MLP before the numbers were written on them; whereas, he identified those in Florentino's possession as "in the Ameghino collection" (for example, Scott 1904: 269). As for types in the Ameghinos' private collection, Simpson (1984) noted that Scott had photographed them and had presented a duplicate set of prints to Florentino. The whereabouts of Florentino's set is unknown. Searches for Scott's prints at the most likely archival repositories (FLPU, MMLPU, YPM-VPPU, and YUL) have not yet been fruitful.

Our doubts on the types and the value of the initial taxonomic diagnoses also stem from the earlier literature (i.e. Ameghino 1887, 1891; Mercerat 1891; Lydekker 1894) on *Eucholoeops* (and other Santacrucian taxa). Indeed, relying on this literature for reaching objective taxonomic decisions is highly frustrating because it is replete with insults, inconsistencies, uncertainty over specimens, unsupported assertions, reciprocal accusations of incompetence, and allusions to duplicitous behavior. This situation was caused partly by then current curatorial practices: catalogue numbers were not always assigned to specimens or recorded in the literature, type-bearing specimens were not necessarily illustrated, and an institutional repository was not required for publication. It is also the result of the rancorous relationship between some (though not all; see Simpson 1984; Vizcaíno 2011) staff at the MLP (where Mercerat, a Swiss geologist was employed beginning in 1889; Bondesio 1977) and Ameghino, whose position there ended on decidedly poor terms in January, 1888 (Fernicola 2011). Such circumstances may seem trivial today and only of historical interest, but they helped produce the publications that must be dealt with in revisions of *Eucholoeops* and other Santacrucian sloths. It is worth presenting several passages from those papers and the correspondence among the researchers to illustrate what confronts us.

Mercerat (1891) set the tone for the exchanges at the beginning of his paper. Noting that the material on which Ameghino had established a taxon belonged to the MLP, Mercerat (1891: 5) stated that "Conviene hacer notar esto porque dicho autor parece que intencionalmente silencia quien le proporcionó el vasto material que describe en su obra *Mamíferos fósiles de la República Argentina* y que constituye, como en otra ocasión hemos dicho, las nueve décimas partes de ella" and "este autor traza un cuadro analítico de los géneros de la familia de los *Orthotheridae*, en el que indica caracteres que no le ha sido posible constatar en el material que da a conocer, y que resultan erróneos. Además, en la determinación del material de que se ha servido, ha incurrido en confusiones lamentables." Ameghino (1891) responded to Mercerat's criticisms, prefacing his taxonomic arguments with a reproduction of the correspondence between himself and F. P. Moreno (the Director of MLP who had denied Ameghino access to the collections; Simpson 1984) and Mercerat that revealed the denial of Ameghino's request to examine specimens in MLP, the collections of which included the many Pampean fossils that Florentino had, ironically, presented to the MLP as part of the agreement for his employment in this institution. In stinging rebukes to various of Mercerat's observations, Ameghino (1891: 346, 347) noted that the former "se toma la libertad de observar" but had in fact "nada que observar: he dicho que las cuatro muelas inferiores estaban en serie continua, y por consiguiente debía buscar una pieza que presentara esos caracteres; si no la ha encontrado, solo prueba la manera lastimosa de como han sido tratadas las colecciones del museo" and that the specimen "a que hace alusión… como tipo de mi *Schismotherium fractum* no es la que yo he descrito." Further on, Ameghino (1891: 348) stated that: "Si yo he comparado el cráneo de… es porque los conocía, y el autor ha hecho muy mal, malísimamente en decir el contrario; es un desmentido que como en el caso de… importa una falta de educación. Que el no conozca esos cráneos no quiere decir que yo no los conozca, sino simplemente que las colecciones del museo de La Plata son muchos mas incompletas que las mías. Puede venir a mi casa en donde encontrara a su disposición los cráneos intactos de las mencionadas especies" and "dice que el pretendido *E. Lafonei* Mercerat, 1891 es mas pequeño que *E. latifrons* Mercerat, 1891 y por las medidas resulta el contrario."

Lydekker's (1894) tone was similar to Mercerat's. The former identified the overarching reason for the chaotic state of Santacrucian mammalian taxonomy early in his report (though dealing specifically with glyptodonts), noting that many of Ameghino's taxa were "established on the evidence of such fragmentary and imperfect specimens that it is frequently almost or quite impossible to determine to what forms they really belong", but he also revealed his dissatisfaction with (and perhaps even contempt of) Ameghino's abilities in adding that "I have accordingly made no attempt to give the complete synonymy of a group whose study has been made unnecessarily complex by incompetent workers (Lydekker 1894: 3)." Despite his criticisms of Ameghino (and at least with respect to reliance on fragmentary remains, Ameghino was and remains far from unique), and possibly Mercerat, Lydekker's own analyses were rather superficial and his efforts were not particularly thorough. Almost without fail, his methodology consisted merely of stating his opinion, without attempting to provide supporting evidence. Typical examples of such practice, in this case dealing with *Eucholoeops* itself, are that he was "convinced that many of the characters on which Ameghino relies for generic distinction, such as the form and position of the first upper tooth, the shape and size of the premaxillae and maxillae, and the position of the superior aperture of the alveolar canal, are of no importance whatever, and are due either to individual or sexual variation, to difference of age, or to the imperfection of the specimens themselves" (Lydekker 1894: 96). Lydekker (1894: 99) believed that other species of the genus were based on smaller specimens that presented "no differences of specific value". As to effort, Lydekker did not bother to examine many of the specimens on which Ameghino had made his decisions and that were still in the latter's possession. Surprisingly, he made no attempt to contact Ameghino (Letter of Florentino to Carlos, dated 26 December 1893; Torcelli 1935; Vizcaíno 2011) during his stay in Argentina, other than, as noted by Simpson (1984: 81), to write "a note to Ameghino, not quite apologizing, saying that as he was the guest of Moreno he had been unable to visit" him.

As for Mercerat, it is clear that he was, even for those times, out of his element as a paleontologist (although Carlos Ameghino considered him a competent geologist; letter of Carlos to Florentino, dated 21 October 1892; Torcelli 1935; Vizcaíno 2011). Mercerat's (1891) observations, analyses, and evaluation of the Santa Cruz fossils consist of little more than the most cursory and elementary of descriptions, accompanied by a few measurements. We would agree with Bondesio's (1977: 76) assessment that "La incorporación de Mercerat al Museo de La Plata se hizo en uno de los momentos más preciosos de la investigación paleontológica argentina, y tuvo en sus manos la mejor oportunidad para haberse constituido en uno de los más felices aportadores al conocimiento de los vertebrados fósiles de nuestro territorio. Sin embargo, debemos convenir que sus trabajos carecieron de relevancia y poca aportación hicieron al conocimiento de la particular fauna de mamíferos y aves del continente sudamericano."

Given the factors outlined above, it becomes evident that the early literature so far discussed is of limited use, other than as a guide for establishing taxonomic priority. The work of Scott, with regard to *Eucholoeops* as well as other Santacrucian taxa, is altogether different in its scope, methodology, balance, and attitude towards Ameghino. As noted above, Scott did observe Ameghino's specimens and had considerable contact with him. Indeed, Scott spent many of his afternoons in Florentino's home (initially taken there and introduced by the MLP anthropologist R. Lehmann-Nietsche), and came to greatly admire Ameghino as a scientist (Simpson 1984). It is no wonder then that Scott (1903, 1904) produced a relatively unbiased revision of the Santacrucian sloths and his work may be considered as that of first reviser for taxonomic purposes.

Having stated this, we should address the lingering perception among paleontologists that Scott's volumes (at least those on the Santacrucian sloths) still "set the standard" for the field (as, e.g., by Croft & Engelman 2014: 237). This notion is misguided. Certainly, the works are classics, but, magnificent though they may be, careful comparison indicates that Scott's material, primarily of the YPM-VPPU collection, lacks precise stratigraphic information and is neither as complete nor well preserved as Scott presented it; often his artwork misleads as to completeness and quality of preservation (we provide examples below). While his work must be consulted, it must also be evaluated for usefulness in light of modern collections and methodologies, rather than trusted on its status as a classic; this is particularly true for systematic work.

MORPHOLOGY AND TAXONOMIC ASSIGNMENTS

Scott (1904) determined the more notable diagnostic features of *Eucholoeops*, but these are based almost entirely on specimens of *E. ingens*, the main features of which are unmistakable, based on Scott's (1904) descriptions. However, several of Scott's conclusions regarding the species of *Eucholoeops* are not as clearly supported. For example, he noted the existence of at least two well-characterized species, *E. ingens* and *E. fronto*. He considered two others, *E. externus* and *E. curtus*, as tentatively valid. For each of the first two, he suggested the existence of sexually dimorphic metric and morphological differences between larger, more robust, purportedly male individuals and smaller, more gracile, purportedly female individuals. For example, he suggested that a nearly complete mandible of *E. ingens* (AMNH 9307) probably belonged to a female as it appeared "considerably smaller than the robust animals with large caniniform teeth which I have regarded as the males" and c1 "is hardly larger than in *Hapalops* and projects comparatively little beyond the line of the other teeth" (Scott 1904: 267, 268). He provided measurements of this specimen and a "Male" of the Ameghino collection that suggest a slight difference in size. However, there are several concerns with Scott's logic.

One is that both mandibles were isolated, without associated skulls, so that the basis for comparison is suspect. As well, at least one of the features, a difference in the alignment of c1 with respect to the remaining teeth, has not been demonstrated. The more recently recovered collections do not support such distinctions or, at least, suggest that we cannot make facile taxonomic judgments based on isolated and incomplete mandibular remains, because there are so few examples for which the skull and mandible from a single individual are known. There is a general resemblance among most of the mandibular remains discussed by Scott (1904) and MPM-PV 3401 and they can probably all be assigned more broadly to the same genus (i.e., *Eucholoeops*, although such assertions must await the detailed analysis of the material assigned to other species of this genus). The c1 of MPM-PV 3401 (Fig. 6A, B) is notably larger than in AMNH 9307. Moreover, it is triangular, whereas that of AMNH 9307 is almost circular. The dentary of MPM-PV 3401bears a marked sulcus anterior to the c1 alveolus, a feature barely indicated in AMNH 9307. The male of the Ameghino collection resembles MPM-PV 3401 in all respects, as does YPM-VPPU 15314, which Scott (1904) assigned instead to *E. fronto*. There is a size difference between the c1s of AMNH 9307 and the male of the Ameghino collection, with YPM-VPPU 15314 approximately intermediate between them (these specimens are all illustrated by Scott 1904: pls 56, 57). Preliminary analyses of the recent collections suggest that there are indeed two main forms of *Eucholoeops*, one certainly corresponding to *E. ingens* as classically described by Scott; the other may correspond to Scott's descriptions of *E. fronto*. Assignment of the latter to *Eucholoeops* rests on features of the skull, including details of the auditory region and dentition that do not correspond precisely to the features identified by Scott, who mainly compared *E. fronto* to *Hapalops*, rather than *E. ingens*. However, as the systematics and diagnosis of the other *Eucholoeops* species is in progress by the current authors, this report deals with *E. ingens* and its synonyms to provide a basis on which further work on *Eucholoeops* may proceed.

Among the more easily recognizable features of *E. ingens* is the large size of the caniniforms, particularly the uppers, and the morphology of the maxilla in forming the C1 alveolus, where it assumes a pillar-like sheath around the caniniform and does not extend anteriorly either ventrally on the palate or laterally on the rostrum. Ameghino (1889, 1891, 1894) noted this as a generic characteristic. Scott (1904) noted this feature for *E. ingens* and *E. fronto*, but here we consider it characteristic only of the former. In addition, the C1s are set somewhat lateral to the plane passing through the molariform tooth row, so that the palate widens anteriorly. The combination of the large caniniforms and unextended maxilla gives the rostrum a truncated appearance compared to the condition typical of *Hapalops* and other Santacrucian sloths. The molariform tooth rows are parallel, as in *Hapalops,* several other Santacrucian taxa, and most sloths. In the extant *Choloepus* the molariform tooth rows diverge anteriorly. The molariform teeth are similar to those of *Hapalops* in being essentially transversely oval or nearly rectangular in section, as noted by Scott (1904), but at least M2 and M3 are easily distinguishable in being transversely expanded. Ameghino (1887, 1889, 1891, 1894) noted this feature but did not emphasize its significance, describing the teeth as transversely oval or rectangular, as he also did for *Hapalops*. Scott (1904) drew attention to the form of the middle molariforms, noting they were broad transversely and much compressed mesiodistally, although it is the breadth of the teeth that are distinct compared to those of other sloths such as *Hapalops*; in any event, Scott (1904), made these observations only for *E. fronto*.

Other easily recognized features characterize *Eucholoeops ingens*. Among the more notable is that the maxillary width at the diastema (or across the buccinator fossae) is considerably less than the preorbital width of the rostrum, widened to accommodate the large C1s. This creates a "roof" over the buccinator fossae. The preorbital width also exceeds the width of the postorbital constriction. The relationship among these three widths characterizes other species of *Eucholoeops*, but the differences are most notable in *E. ingens*. The combination of these features and the form of the maxilla related to the C1 alveolus clearly identifies this species. The form of the anteroventral, or premaxillary, margin of the maxilla is also distinct. Together the L and R maxillae form a broad V-shaped notch for articulation with the premaxillae. The maxillary margin bears only a small anteriorly directed flange in its middle portion (Figs 3C; 4B), which is delicate and often not preserved. Another potential important feature (though one requiring further comparative analysis) is that the posterior surface of the lacrimal is strongly concave. The dentary is robust and bears a marked concavity just anterior to the c1 alveolus. Although there seem to be few postcranial features unique to *Eucholoeops ingens*, the subequal lengths of Mcs II-V and the bent femoral shaft stand out, but these also require further comparative analysis.

In addition to skull remain such as MPM-PV 3401 and 3451 (Figs 2 and 3, respectively), and FMNH P13125 and 13139 (Fig. 5A, C, E, and Fig. 5B, D, F, respectively), which are of similar size and clearly exhibit the features characteristic of *Eucholoeops ingens*, several other specimens are assigned to this species. We provide our reasons for these taxonomic assignments below.

Scott (1904) considered *E. latirostris* Ameghino, 1891 a synonym of *E. ingens*. We agree with this assessment. *Eucholoeops latirostris* is based on MACN-A 4639 (Fig. 7A-C), which is reasonably undeformed and preserves slightly more than the anterior half of a skull, with the R anterior zygomatic root, and L M5. The remaining teeth are absent but represented by their alveoli (thus Ameghino's 1891 measurements for the other teeth are unreliable), except that for L C1, which is not preserved. The premaxillae and anterior parts of the nasals are also missing. Ameghino (1891) considered *E. latirostris* to be the size of *E. ingens* (an assertion borne out by comparison with MPM-PV 3401, which it barely exceeds in size), but considered it distinct based on its prominent and wide rostral region, very large teeth, and a narrowed palate between the tooth rows. However, comparison and measurements indicate that MACN-A 4639 cannot be distinguished on these features from other *E. ingens* specimens, and thus we follow Scott's (1904) synonymy. It is also worth noting that Ameghino's (1891) measurement for M1-M4, given as 53 mm, is erroneous (correct measurement is given here in Table 1).

Two of the other *Eucholoeops* species recognized by Scott (1904), *E. externus* and *E. curtus*, require attention. As is clear from the Systematic Palaeontology section, they do not seem to be distinguishable from *E. ingens*. The type of *E. externus* includes a partial skull, MACN-A 4640, and R dentary, MACN-A 4641 (Fig. 7G-J). The skull and dentary have different catalogue numbers, but belong to the same individual and were discussed together in Ameghino's (1891) original description. Although the skull material is the same as that depicted by Scott (1904: pl. 56, fig. 1), the latter's illustration is not an accurate representation of the material, at least not in its present state. Given the inaccuracies in several of Scott's published illustrations on the Santa Cruz sloths, it is not clear whether Scott's illustration of *E. externus* represents an earlier condition of the fossil or is due to artistic license.

The illustration presents the skull as a single structure with a complete right maxillary wall, including the C1 alveolus, and what appears to be the base of C1 in position. The illustration of the dentary is reasonable accurate, except for the condition of the c1 alveolus, the relevance of which will be made clear below. In its current state, however, the skull is preserved as anterior and posterior halves. The anterior part is broken immediately posterior to M3, and does not fit together with the posterior part, representing essentially the braincase region of the skull, even though fresh breaks are not evident. Additionally, the anterior part of the maxillary wall is broken, so that only the distal half of the C1 alveolus is preserved, and there is no indication of the base of a C1 as illustrated by Scott (although a partial C1 is present among the remains of this specimen; see below). Further, both anterior and posterior parts of the skull are distorted – it is nowhere near as well preserved as Scott's figure would lead one to believe – and the R and L sides are separated vertically, with the L tooth row lying about 1 cm dorsal to that of the right side.

Given these circumstances, there is little basis for the form of the skull as depicted by Scott, and thus our comment above in Descriptions and Comparisons on the inaccuracy of the dorsal skull profile. Ameghino's (1891) original description remarked that *E. externus* was notably smaller than *E. latirostris* (which he considered to be about the size of *E. ingens*) and was easily distinguished from other *Eucholoeops* species by a vestibularly (rather than mesially) facing wear facet of c1. Scott (1904) followed Ameghino in noting the form of c1, but further stated that C1 bore a lingually-facing wear facet, a characteristic that Ameghino, interestingly enough, did not mention. With regard to the validity of *E. externus*, Scott (1904: 269) stated that "if its peculiarities are not abnormal, the species is well distinguished. The principal characteristic is given by the shape of the caniniform teeth, which are very large and indicate that the animal was a male; the lower bites inside of the upper one, instead of behind it, and thus its abraded surface presents outward, not forward as it does in almost all other known Santa Cruz Gravigrada; similarly the worn surface of $\underline{1}$ is internal, not posterior".

Probably, the easiest solution on the validity of *E. externus* is, as hinted at by Scott, to consider the form of its caniniforms anomalous – it is the only such known case – and consider the species a synonym of *E. ingens*. However, we suspect that the situation may be more straightforward than this, as it is more likely that the position of c1 is incorrect; that is, it was improperly repositioned during reconstruction of the dentary. This suggestion is based on the abundant amount of glue or mastic within the alveolus, surrounding c1, and forming the reconstructed and laterally bulging alveolar wall. There is evidence from the maxillar caniniform to support this contention. Although broken, the preserved remains of C1 cannot be positioned to fit within the remnants of the C1 alveolus so that the wear facet faces lingually, as the dimensions of the tooth so positioned exceed the width of the alveolus. On the other hand, C1 does fit into the alveolus if positioned normally, i.e., with the wear facet facing distally.

Ameghino's and Scott's claim that *E. externus* is smaller than *E. ingens* is not supported by evidence. Among the few measurements that should be considered reliable (Table 1) we may take as example the mandibular tooth row length, which was given as 55 mm by Scott (1904) for Ameghino's type of *E. ingens*. In MACN-A 4641 the length is 47.3 mm. This is approximately the same length as in MPM-PV 3401 (46.1 mm), which is the only well preserved mandible certainly associated with a skull. Scott (1904: 268), in any event, recognized almost identical lengths for AMNH 9307 and a "Male" of the Ameghino collection (46.5 and 47 mm, respectively) as belonging to *E. ingens*. For comparison using a skull measurement, the length of the diastema is nearly identical in MPM-PV 3401 (21.2 mm) and MACN-A 4640 (21 mm). We propose that the evidence outlined above sufficiently supports synonymizing *E. externus* with *E. ingens*, and have taken this decision. We suggest that preparation of MACN-A 4641 be undertaken to determine the position of c1. Regardless of the true position of the caniniforms, the overwhelming similarities in morphology and size between MACN-A 4640 and 4641 and other *Eucholoeops ingens* specimens argue for recognizing the condition in *E. externus* as an anomaly.

MACN-A 4642 is a partial R maxilla of a juvenile individual (separated at the palatal and maxillonasal sutures). Its posterior parts are missing. The M1, the anterior half of the M2 alveolus, and the basal portion of C1 are preserved. This specimen is assigned by MACN records to *E. externus*, although there is no basis for such assignment: the very base of the C1 wear surface is preserved and it faces distally, as usual in these sloths. This specimen may thus confidently be assigned to *E. ingens*.

Scott (1904: 276) also considered Ameghino's (1894) *Eucholoeops curtus*, based on MACN-A 6413 (Fig. 7D-F; the skull was recatalogued and has two numbers, the other being MACN 11141; the correct number is MACN-A 6413, Fernicola 2011) as a valid species, noting that the skull "is remarkable for its shortness and breadth." Although he allowed that to some degree this appearance was caused by longitudinal compression, he nonetheless considered this individual unusual; and so it is, as the form exhibited by MACN-A 6413 remains, as it was in Scott's day, the only known example. However, the specimen is more distorted than Scott allowed, and we consider that its chief (and probably only) distinguishing characteristic has been overemphasized. The skull was almost certainly recovered in two pieces; the region where these have been glued together is clearly evident. In addition, there has been longitudinal compression, particularly noticeable in the rostral region. Further, the skull was broken and telescoped during its preservation, with the parietals thrust forward over the frontals and the basicranium pushed through the choana. Scott (1904: 277, figs 33, 34) mentioned the telescoping, but his figures do not accurately reflect the degree of damage. MACN-A 6413 is certainly among the smaller of the *Eucholoeops* specimens resembling *E. ingens,* but it is not clear how much its length has been compromised; at least 13 mm of the frontals are observable beneath the parietals. The several measurements reported for MACN-A 6413 must be considered suspect. For example, Ameghino (1894) and Scott (1904) reported length (from maxilla to occipital condyles) as 117 mm, but its true length (adding the 13 mm of the frontals beneath the parietals) must have been at least 130 mm, which is very close to that of MPM-PV 3452 (Fig. 4A, C, E). This similarity is consistent with other reliable lengths for MACN-A 6413, such as tooth row lengths and widths. The pattern that emerges, in comparing the several measurements available for the skulls discussed in this report (Table 1), is that there is a gradual increase in size between the smallest and largest individuals. This topic is considered again below, but for the purposes of the status of *E. curtus*, it indicates that there is no objective basis for accepting its skull as either particularly short or broad, and it is much more reasonable to accept it as among the smaller individuals of *E. ingens*. The L humerus, MACN-A 6414 (missing its proximomedial portion and the proximal portion of its ectepicondyle), is indicated as associated with MACN-A 6413 by Ameghino's catalogue and MACN-A catalogue records, although it differs in preservation from MACN-A 6413. Even so, there is reason to accept this assignment as correct, as there are no detectable morphological differences from the humerus of MPM-PV 3401, and MACN-A 6414 is slightly shorter (167 mm) than MPM-PV 3401, which is consistent with the difference in proportions of their skulls.

MACN-A 11614 is catalogued as *Eucholoeops ingens*. The specimen is a skull missing the R half of the facial region and the R dentary. The rest of the skull is largely preserved, but is considerably damaged and distorted, although the dentary is reasonably well preserved. The individual is among the largest specimens, with C1-M4 length reaching nearly 67 mm. The dental characteristics are

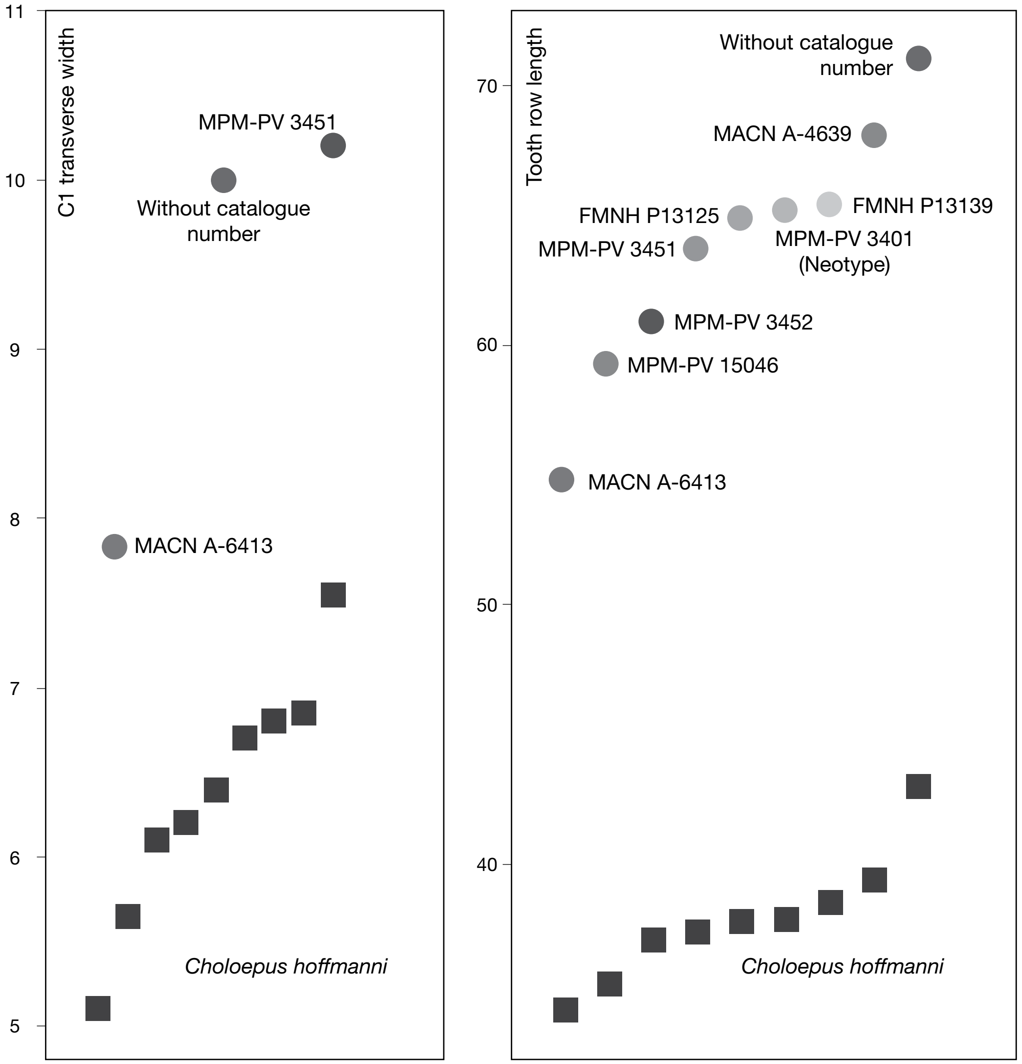

Fig. 12. — Scatterplots comparing C1 (left plot) and tooth row (L C1-M4; right plot) lengths (in mm) of: ●, *Eucholoeops ingens* Ameghino, 1887; ■, *Choloepus hoffmanni* Peters, 1859, based on measurements presented in Tables 1 and 3.

clearly of the *Eucholoeops* type. However, it is not clear that MACN-A 11614 belongs to *E. ingens*. Despite the condition of the skull, the L rostral region is sufficiently well preserved to suggest that the maxilla continued anteriorly beyond the C1 alveolus, unlike all other specimens assigned to *E. ingens*. Assignment to this species is therefore doubtful and we defer discussion of MACN-A 11614 to a subsequent report.

We noted above, in connection with the discussion of the type of *Eucholoeops curtus*, that we have admitted a degree of variation in assigning the specimens considered here to *Eucholoeops ingens*, unless otherwise indicated. That such variation might exist in a fossil species should, of course, come as no surprise. The older (e.g., Scott 1903, 1904; Stock 1925) as well as the more recent (e.g., Cartelle & De Iuliis 2006;

McDonald 2006) literature has attested to the existence of such variation among fossil sloth species and it has been noted above that the number of named taxa among the Santacrucian sloths is much higher than can be justified based on the available evidence. Although several of the older authors were fully aware of intraspecific variation, many remained hampered by typological thinking, which in all fairness was a then common paradigm, and often erected species on inadequate remains exhibiting seemingly minor metric and morphological differences. In a tributary lecture to Charles Darwin given in 1882 in the Instituto Geográfico Argentino, Buenos Aires, Ameghino clearly stated his point of view: "Se han criticado mis clasificaciones, diciendo que yo formo un número exagerado de especies, y que la mayor parte de las formas a las cuales considero como tales son simples variedades. Enhorabuena: acepto la crítica, porque me es indiferente que a esas formas se las llame especies, razas o variedades, o lo que se quiera, pues todo eso prueba lo que ya dijo Darwin: que las clasificaciones son artificiales y no naturales. Lo que yo necesito es distinguir esas formas con un nombre para no confundirlas con otras, poder jalonarlas y pasar así sucesivamente de unas a otras" (Ameghino in Torcelli 1915: 46). This practice, not least among sloth researchers, continued through much of the last century (see Cartelle & De Iuliis 1995, 2006) and into the recent past (De Iuliis 2010), and reveals a limited understanding of the modern biological population concept and its application to fossil species.

Among the issues involved in recognizing fossil species is just how much variation we are willing to admit, especially when we are presented with exceedingly small sample sizes. Several studies have indicated that some fossil sloth species display a wide degree of metric and morphological variation (e.g., Cartelle & De Iuliis 2006; McDonald 2006; see also Prothero & Raymond 2008). The remains assigned here, essentially comprising a sample of nine (measurements have been given for Ameghino's original type, but this specimen is not formally assigned to *E. ingens*) adult individuals, reflect this pattern. For example, C1-M4 length (see Table 1; considered as an indicator of size as it is among the few consistently preserved and relatively undistorted features) ranges between 54.8 in MACN-A 6413 (type of *E. curtus*) and 71 mm (as given by Ameghino 1887, 1889 and reproduced by Scott 1904 for the original type of *E. ingens*, a value that cannot be verified as this specimen is no longer available), so that the latter is approximately 29% larger than the former. This figure is reduced to about 24% if MACN-A 4639 (type of *E. latirostris*) is considered as the largest currently observable specimen, a figure that reflects the variation in at least one species of modern sloths (see below). The material also documents differences in proportions; for example, diastema length is longer in MPM-PV 3401 than in FMNH P13125, but the reverse is true of C1-M4 length. In addition, there are differences among the specimens in morphological characteristics, particularly in form of the dentition (as noted in the descriptions). The differences among the *E. ingens* remains noted here mirror to a large degree the size variations described for the megatheriids *Eremotherium laurillardi* by Cartelle & De Iuliis (1995, 2006), *E. eomigrans* De Iuliis & Cartelle, 1999 by De Iuliis & Cartelle (1999), and *Megatherium americanum* Cuvier, 1796 by De Iuliis (1996), but fall well short of the sexually dimorphic variations described for *E. laurillardi* (Cartelle & De Iuliis 1995, 2006) and for the mylodontid *Paramylodon harlani* (Owen, 1840) (McDonald 2006; see Pujos *et al.* 2012 for a general opinion). In this respect, it appears that the sexual dimorphism suggested by Scott (1904) based on the form of the caniniform teeth of *Eucholoeops ingens* seems doubtful, but remains a possibility that can be tested when we have accumulated sample sizes for *E. ingens* approaching those recovered for *Eremotherium laurillardi*, *Megatherium americanum*, and *Paramylodon harlani*. For now, the most that can be said for the *E. ingens* remains is that the smaller individuals, unsurprisingly, generally have smaller caniniforms and differences among specimens may readily be accepted as intraspecific variation.

We feel that it is important to assess the validity of the wide degree of variation mentioned in the preceding paragraph, because there remains

TABLE 3. — Skull and tooth measurements of extant two-toed sloths *Choloepus hoffmanni* Peters, 1859 and *C. didactylus* Linnaeus, 1758. Abbreviations: **C1**, transverse/mesiodistal diameters of caniniform; **L C1-M4**, length from the mesial margin of C1 to the distal margin M4; **L Dias**, diastema length; **L M1-M4**, length from mesial margin of M1 to the distal margin of M4; **W Pre**, dorsal width at preorbital constriction; **W Pst**, width at postorbital constriction.

Specimen	C1	L C1-M4	L Dias	L M1-M4	W Pre	W Pst
Choloepus hoffmanni						
AMNH M18895	4.9/5.3	35.4	11.1	19.8	27.4	32.8
AMNH M18896	5.9/6.3	38.6	10.5	22.8	29.9	36.4
AMNH M26907	5.7/7.1	37.6	9.5	22.5	29.7	33.1
AMNH M26908	6.0/7.4	37.2	8.7	21.9	27.9	31.6
AMNH M26909	6.5/7.2	34.4	8.4	20.1	28.3	32.5
AMNH M26915	6.3/7.3	39.4	10.6	23.2	29.4	34.5
AMNH M26916	5.4/5.9	37.9	11.7	21.1	30.7	35.9
AMNH M26918	7.0/8.1	43.0	11.4	23.9	37.3	38.2
AMNH M26919	5.7/6.7	37.4	10.6	21.1	32.4	35.2
Choloepus didactylus						
AMNH M133405	6.2/6.8	40.2	12.3	22.0	34.6	39.4
AMNH M133410	5.9/6.2	39.2	12.2	21.5	31.4	36.0
AMNH M133416	6.6/7.6	38.2	11.0	22.2	35.9	37.7
AMNH M133439	6.5/8.7	38.9	10.9	20.7	34.2	36.5
AMNH M133444	6.0/5.8	34.6	11.7	20.5	33.1	37.9

resistance to accepting it for *E. laurillardi* and *M. americanum* (e.g., Guérin & Faure 2000, 2007; Brandoni *et al.* 2008), and we feel the same may result for the current report on *Eucholoeops ingens*. It is worth noting that the *E. laurillardi* and *E. eomigrans* material considered by Cartelle & De Iuliis (1995, 2006) and De Iuliis & Cartelle (1999) included large samples from single localities. In contrast, the *Eucholoeops ingens* material considered here was recovered from three localities (Puesto Estancia La Costa, Campo Barranca, and Monte Tigre; see Geological Context, above) and is thus not contemporaneous. The remains, being fossils, have been subjected to (in some cases considerable) postmortem deformation. Some of the variation documented in *Eucholoeops ingens* may thus reflect phyletic change as well as postmortem deformation.

However, invocation of such factors may not be necessary: in assessing the degree of variation reported for some fossil sloth species, it is worth considering the degree of variation existing in modern sloth populations; at the very least, such comparators better inform our taxonomic decisions. To this end, the adult remains amenable to measurement of two species, *Choloepus hoffmanni* and *C. didactylus*, were recorded (Table 3). For each species, the remains are from a single, contemporaneous, natural population (Boquerón, Chiriquí, Panama and Ilha de Marajó, Pará, Brazil, respectively) and did not suffer postmortem distortion. For the nine individuals of *C. hoffmanni*, C1-M4 length ranges from 34.4 to 43.0 mm, representing a difference of 25%, a value that closely mirrors the difference reported above for *Eucholoeops ingens* (see also Fig. 12). Moreover, the modern population also reflects proportional differences with respect to C1-M4 and diastema length. For the smaller sample (n=5) of *C. didactylus*, the size difference between the smallest and largest individuals is 16%. As for sexually dimorphic differences, although the largest and smallest individuals belong respectively to a male and a female in both samples, there are females that are larger than males, and the second smallest individual is a male. Such results, particularly for *C. hoffmanni*, are in line with the metric variation reported for *E. ingens* and strengthen the taxonomic decisions taken here.

Modern sloth populations also document a wide degree of morphological variation, including anomalous conditions. For example, three sutural patterns among the frontal, lacrimal, nasal, and maxilla are present in the sample of eight juvenile or subadult individuals of *Choloepus didactylus*, one of which also has a supernumerary tooth in the R dentary between c1 and the normal m1; one of the adult individuals of *C. hoffmanni* has an elongated and oddly worn L M2 that extends over the alveolus of M3 and an elongated rather than nearly cylindrical R M3; both species exhibit intraspecific variation (as well as between L and R sides of the same individual) in the size and form of teeth.

We suggest that the application of the information on the variation in modern sloth species noted above is consistent with the variation suggested in the sample of *Eucholoeops ingens* presented in this report. A glance at Table 1 and Figure 12 reveals a gradual increase from the smallest to largest specimens, without notable gaps in the series. This is consistent with the differences observed for the similar sample of *Choloepus hoffmanni*. The morphological differences among the individuals are likewise of the nature documented in modern sloth species (not to mention those documented for several fossil species). There is thus no objective basis on which to justify the specific separation of the remains assigned here to *E. ingens*.

CONCLUSIONS

From the preceding account, there emerge three types of conclusions that influence our interpretations of the systematics of *Eucholoeops* and other Santacrucian sloths: on historical issues, on the taxonomic assignment of specimens, and on the value of metric and morphological intraspecific variation.

The lengthy argument presented in the Taxonomic History section of the Discussion provides evidence that, at least in the case of *Eucholoeops* and other Santacrucian sloths, the allegedly unprejudiced tradition of reviewing the early literature before reaching objective taxonomic decisions becomes largely counterproductive if it is not done through an understanding of the historical context in which that literature was produced. Indeed, reliance on that older literature is partly responsible for our lack of progress on the systematics of the Santacrucian sloths over the past century – the lack of identifying specimen numbers, the contradictory opinions, often spurred by personal vendettas, and duplicitous behaviour (among other factors) combine to produce a sort of frustrating paralysis, so that it has been much easier to ignore rather than attempt to unravel the obvious systematic problems. No doubt, this may be also true for many of Ameghino´s species, at least those named after he left the Museo de La Plata in January 1888.

Careful evaluation of all the historical evidence available and the usual metric and morphological analyses of specimens have allowed us to make taxonomic decisions on most of the specimens assigned to *Eucholoeops ingens* in the old Santacrucian collections (in AMNH, FNMH, MACN, MLP, and YPM-VPPU), as well as the new MPM-PV collection.

As noted above, we designate MPM-PV 3401 as the neotype of *Eucholoeops ingens*, the type species of the genus, following exhaustive searches for the original type specimen in the MLP and MACN, according to Article 75.1 of the International Code of Zoological Nomenclature (ICZN 1999). Our specific assignment of other specimens varies. The following species and specimens are synonymized with and/or assigned to *Eucholoeops ingens*: *Eucholoeops latirostris* (type, MACN-A 4639), *E. externus* (type, MACN-A 4640, 4541; MACN-A 4642) and *E. curtus* (type, MACN-A 6413), FMNH P13125, 13139, MPM-PV 3451, 3452, and 15046.

Finally, the fact that the morphological differences among the individuals assigned to *Eucholoeops ingens* are similar to those documented in modern sloth species indicates that the application of information on the variation in modern species can be a valuable tool in evaluating the existence of intraspecific variation in all Santacrucian sloths, and should be considered in undertaking systematic analyses and taxonomic decisions. In addition, the literature establishing the intraspecific variation and possible dimorphism in fossil sloth species, such as *Eremotherium laurillardi*, *E. eomigrans*, and *Paramylodon harlani*, should not be ignored.

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