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SYSTEMATICS OF THE EARLY MIOCENE *EUCHOLOEOPS* (XENARTHRA, FOLIVORA, MEGALONYCHIDAE). THE STATUS OF *EUCHOLOEOPS LATIFRONS*

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SYSTEMATICS OF THE EARLY MIOCENE *EUCHOLOEOPS* (XENARTHRA, FOLIVORA, MEGALONYCHIDAE). THE STATUS OF *EUCHOLOEOPS LATIFRONS*

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Abstract. Previous efforts have recently clarified the systematics of the megalonychid sloth *Eucholoeops ingens* from the Early–Middle Miocene Santa Cruz Formation (~18 to 15.6 Ma, Santacrucian Age) of Argentine Patagonia. This report continues the revision of *Eucholoeops* through the analysis of specimens previously assigned in the literature and museum records to this genus, but excluded from these earlier works. The comparative analyses conducted here, incorporating specimens of the closely similar *Hapalops*, suggest that two species of *Eucholoeops*, *Eucholoeops ingens* and *Eucholoeops latifrons*, also from the Santacrucian of Argentine Patagonia, are valid. Cranial and postcranial characters exhibit consistent though subtle differences between them as well as similarities, suggesting that they are specifically distinct though congeneric. Similarities include: a relatively short, wide rostrum; preorbital width nearly equivalent to or greater than the postorbital constriction; little or no maxillary extension beyond the upper caniniform alveolus; large, triangular caniniforms; mesiodistally compressed molariforms; less prominent humeral deltopectoral shelf than in *Hapalops* and V-shaped femoral third trochanter. *E. latifrons* differs from *E. ingens* in its smaller caniniforms; nearly equivalent preorbital and postorbital widths; maxillary extension beyond the caniniform alveolus; larger lateral margin of the humeral deltopectoral shelf; less proximally extended femoral greater trochanter; larger lesser trochanter; and less prominent trochanteric fossa and intertrochanteric crest. Exploration that these differences might be due to sexual dimorphism rather than to specific distinction suggests that it is more prudent to maintain specific status.

Key words. Sloths. Santacrucian. Patagonia. Taxonomy. Synonymy. *Eucholoeops ingens*.

Resumen. SISTEMÁTICA DE *EUCHOLOEOPS* (XENARTHRA, FOLIVORA, MEGALONYCHIDAE) DEL MIOCENO TEMPRANO. EL STATUS DE *EUCHOLOEOPS LATIFRONS*. Esfuerzos previos recientes han esclarecido la sistemática del perezoso megaloníquido *Eucholoeops ingens* de la Formación Santa Cruz (Mioceno Temprano–Medio, ~18 a 15.6 Ma, Edad Santacrucense) de la Patagonia Argentina. En esta contribución se continúa con la revisión de *Eucholoeops* a través del análisis de especímenes previamente asignados a este género en la literatura y en los registros de museos, pero excluidos de los trabajos anteriores. Los análisis comparativos realizados, incorporando especímenes de *Hapalops*, un género muy afín, sugieren que las dos especies de *Eucholoeops*, *Eucholoeops ingens* y *Eucholoeops latifrons* del Santacrucense de la Patagonia Argentina, son válidas. Los caracteres craneales y postcraneales exhiben diferencias consistentes aunque sutiles entre ellos, así como similitudes, que sugieren que son especies diferentes pertenecientes al mismo género. Las similitudes incluyen: un rostro relativamente corto y ancho; ancho preorbital casi igual o mayor que la constricción postorbital; poca o nula extensión maxilar más allá del alvéolo del caniniforme; caniniformes grandes y triangulares; molariformes comprimidos mesiodistalmente; plataforma deltopectoral humeral menos prominente que en *Hapalops* y tercer trocánter del fémur en forma de V. *E. latifrons* difiere de *E. ingens* en sus caniniformes más pequeños; anchos preorbitales y posorbitales casi equivalentes; extensión del maxilar más allá del alvéolo de los caniniformes; margen lateral de la plataforma deltopectoral del húmero más grande; trocánter mayor del fémur menos extendido proximalmente; trocánter menor más grande y fosa trocantérea y cresta intertrocantérea menos prominentes. El análisis de que estas diferencias podrían deberse a un dimorfismo sexual más que a una distinción específica sugiere que es más prudente mantener un estatus específico.

Palabras clave. Perezosos. Santacrucense. Patagonia. Taxonomía. Sinonimia. *Eucholoeops ingens*.

THE TREE SLOTHS, *Bradypus* Linnaeus, 1758 and *Choloepus* Linnaeus, 1758, are small (from ~3 to 8 kg) and almost exclusively arboreal and folivorous mammals. They are the only surviving members of Folivora (Xenarthra, Pilosa), a once abundant and taxonomically, morphologically, and behaviourally diverse clade. These fossil forms include some 100 described genera (see Cartelle *et al.*, 2008; Rinderknecht *et al.*, 2010; McDonald *et al.*, 2013; De Iuliis

et al., 2016; Stinnesbeck *et al.*, 2017) and document considerable diversity in size, substrate preference, and diet (see *e.g.*, Bargo, 2001; Pujos *et al.*, 2007; Bargo & Vizcaíno, 2008; McDonald & De Iuliis, 2008; Vizcaíno *et al.*, 2008; Bargo *et al.*, 2009, 2012; Amson *et al.*, 2014; Toledo *et al.*, 2017). Studies based on osteology generally recognize the monogeneric Bradypodidae, including *Bradypus*, sister group to the remaining sloths, and the much more abundantly represented Megalonychidae, Nothrotheriidae, Mylodontidae, and Megatheriidae (*e.g.*, Gaudin, 2004; McDonald & De Iuliis, 2008; Varela *et al.*, 2019). Other than Megalonychidae, which includes *Choloepus* as its only extant representative, these clades are extinct. The phylogenetic analysis by Casali *et al.* (2022), including the largest morphological data set ever applied to sloths, broadly supported such systematic arrangements. These authors recognized *Bradypus* as sister genus to the remaining sloths, and Mylodontoidea (including Scelidotheriidae and Mylodontidae) and Megatherioidea (including Megalonychidae and Megatheriidae) as the two main sloth clades, with *Choloepus* within Megalonychidae and Megatheriidae including clades that have been traditionally recognized as Megatheriidae and Nothrotheriidae. By contrast, studies based on molecular evidence (Delsuc *et al.*, 2019; Presslee *et al.*, 2019) consider *Choloepus* as closely related to mylodontids and *Bradypus* to Nothrotheriidae and Megatheriidae (*i.e.*, Megatherioidea).

Sloths have been recorded from the late Eocene (Gaudin & Croft, 2015; Pujos *et al.*, 2021) but are first well known from the Early–Middle Miocene Santacrucian South American Land Mammal Age (SALMA; ~18 to 15.6 Ma, Cuitiño *et al.*, 2021) (see MacPhee & Iturralde-Vinent, 1995; Bargo *et al.*, 2012; Gaudin & Croft, 2015). These sloths comprise the earliest abundant representation of their clade and are, thus, highly important in understanding the early history of the group and its subsequent evolution. As noted by several authors, however, only a few of the many named genera (and species assigned to them) may be confidently considered valid, including *Schismotherium* Ameghino, 1887, *Eucholoeops* Ameghino, 1887, *Hapalops* Ameghino, 1887, *Pelecyodon* Ameghino, 1891a, *Nematherium* Ameghino, 1887, and *Planops* Ameghino, 1887 (see Bargo *et al.* 2012, 2019; De Iuliis *et al.*, 2014, 2024; Racco *et al.*, 2018; Gaudin *et al.*, 2023). While it has been long recognized that the taxonomy of most of these Santacrucian sloths is unsatisfactory (see De Iuliis *et al.*, 2024 for an account of the reasons for this situation), several recent analyses (*e.g.*, Racco *et al.*, 2018; Bargo *et al.*, 2019; Gaudin *et al.*, 2023; De Iuliis *et al.*, 2024) have begun to provide improved resolution of the systematics of several of the genera. Among them, *Eucholoeops* has perhaps received the most attention, with De Iuliis *et al.* (2014, 2024) concluding that many of the named species are synonymous with *E. ingens* Ameghino, 1887. The current report continues the analysis of species assigned to *Eucholoeops*, with focus on *E. latifrons* Mercerat, 1891. De Iuliis *et al.* (2024) suggested that, whereas many species are synonyms of *E. ingens*, several specimens support the recognition of at least a second species, *E. latifrons*.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; **FMNH,** Field Museum of Natural History, Chicago, USA; **MACN-A,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; **MLP-PV,** Museo de La Plata, Colección de Paleontología de Vertebrados, La Plata, Argentina; **MPM-PV,** Museo Regional Provincial Padre M. J. Molina, Colección de Paleontología Vertebrados, Río Gallegos, Argentina; **YPM-VPPU,** Yale Peabody Museum, Vertebrate Paleontology, Princeton University Collection, New Haven, USA.

Anatomical abbreviations. Cf, upper caniniform; **cf,** lower caniniform; **L,** left; **Mc,** metacarpal; **Mf,** upper molariform; **mf,** lower molariform, **R,** right.

MATERIALS AND METHODS

Specimens studied

This analysis includes a formal description of MPM-PV 3403, a very well-preserved specimen, noted only briefly in De Iuliis *et al.* (2024), that was recovered from the Santa Cruz Formation (Fig. 1) during expeditions conducted jointly by the Museo de La Plata, Argentina, and Duke University, USA. Other analyzed specimens include MLP-PV 4-2 (the type of *E. latifrons*) and MACN-A 11614, neither of which have been formally described. Finally, MLP-PV 4-10, another undescribed specimen that had previously been unavailable for study (see below), is assigned to *E. ingens*. The *E. ingens* specimens included in this analysis are those for which the skull is reasonably complete, as well as any

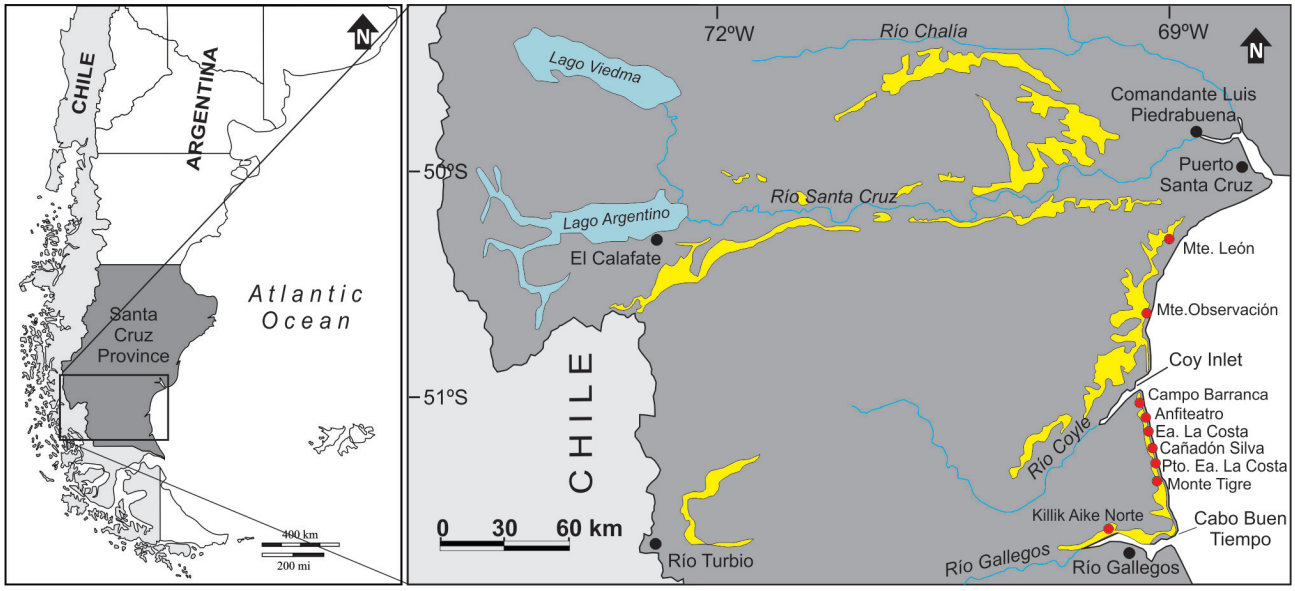

Figure 1. Geographic locations of the fossil localities mentioned in the text that have yielded specimens of ***Eucholoeops***. Depicted in yellow, exposures of the Santa Cruz Formation. Red circles: fossil localities (see Vizcaíno *et al.*, 2012 for information on the localities). Abbreviations: **Ea,** Estancia; **Mte,** Monte; **Pto,** Puesto. Modified from De Iuliis *et al.* (2024).

associated mandibular and/or postcranial remains and the above-mentioned previously unstudied MLP-PV 4-10 specimen. For those specimens collected in the late 19th and early 20th centuries, we provide (in parentheses), as far as possible, estimated updated locality references based on Vizcaíno *et al.* (2012)

AMNH 9241. *E. ingens* (see De Iuliis *et al.*, 2024) includes an incomplete skull, mandible, and several postcranial elements (vertebrae, ribs, partial pelvis and sacrum, left radius, several carpals and phalanges, right femur, and right navicular). The skull is preserved in two portions. The smaller part corresponds to the rostrum, including the left lacrimal, partial left maxilla, and partial left and right nasals. The maxillary portion preserves the Cf alveolus, with a broken margin, and the vestibular portion of the Mf1-Mf3 alveoli. The other, larger portion of the skull includes much of the skull roof, occiput, and basicranium, although the sphenoidal region is missing. Provenance: Santa Cruz Formation, Río Gallegos, Santa Cruz Province, Argentina.

FMNH P13123. *Hapalops elongatus* Ameghino, 1891a, includes an incomplete skull and mandible and several nearly complete postcranial elements, such as the humerus, radius, ulna, patella, tibia-fibula, astragalus, calcaneum, cuboid. Provenance: Santa Cruz Formation, Felton's Ranch (Killik Aike Norte), Santa Cruz Province, Argentina.

FMNH P13125. *E. ingens* comprises an incomplete skull, partially preserved dentaries, and several postcranial elements. Most of the elements are reconstructed with plaster (see De Iuliis *et al.*, 2014). Provenance: Santa Cruz Formation, Estancia La Angelina (Monte Tigre), Santa Cruz Province, Argentina.

FMNH P13130. *Hapalops ruetimeyeri* Ameghino, 1891a, includes a nearly complete mandible (missing tip of symphysis and of coronoid processes; reconstructed angular processes), humerus, radius, ulna, femur (missing proximal end), and tibia. Provenance: Santa Cruz Formation, Estancia La Angelina, 20 km north of Cape Fairweather (Monte Tigre), Santa Cruz Province, Argentina.

FMNH P13133. *H. elongatus* is a nearly complete and well-preserved skull and mandible, and several postcranial elements, including scapula, humerus, radius, and ulna. Provenance: Santa Cruz Formation, approximately 8 km south of Coy Inlet (Anfiteatro), or approximately 8 km above from the mouth of the Río Coyle, Santa Cruz Province, Argentina, according to different labels.

FMNH P13143. *Hapalops* cf. *H. rectangularis* Ameghino, 1887, includes a mandible (missing tip of R coronoid process and most of L ascending ramus), scapula (missing postero-dorsal portion), humerus (missing proximal third), nearly complete radius, ulna, and tibia (missing proximal epiphysis).

This specimen represents a subadult individual, as evidenced by incompletely fused epiphyses. Provenance: Santa Cruz Formation, approximately 5 km south of Coy Inlet (Campo Barranca), Santa Cruz Province, Argentina.

MACN-A 6413. *E. ingens* (the type of *Eucholoeops curtus* Ameghino, 1894) includes a well-preserved skull bearing fragments of both Cfs, all complete Mfs; jugals are missing. MACN-A 6414 is a left humerus associated with the former specimen (see De Iuliis *et al.*, 2014). Provenance: Santa Cruz Formation, Corriguen-Kaik (Puesto Estancia La Costa), Santa Cruz Province, Argentina.

MACN-A 11614. Assigned to *E. ingens* in MACN catalogue and by Pujos and De Iuliis (2007), includes a skull and left dentary. The skull is missing its right side anteriorly (filled with plaster), and the jugals, ectotympanics, premaxillae, and apical part of Cf, but the remainder is reasonably complete and only slightly distorted. The dentary is missing the anterior part of the symphyseal region and tip of the coronoid process. Provenance: MACN records do not indicate the locality and stratigraphy for this specimen (see Discussion).

MLP-PV 4-2. The type of *Eucholoeops latifrons* Mercerat, 1891, consists of a skull that is reasonably well preserved, although it is missing its basicranial region, the right Mf2, premaxillae, and jugals. It preserves the L Cf and Mf1-Mf3 completely, and the L Mf4 and the R Cf, Mf1, Mf2, and Mf4 broken at the level of their alveolar margin. Provenance: Santa Cruz Formation, Monte León, Santa Cruz Province, Argentina.

MLP-PV 4-10. Assigned to *E. ingens* according to the MLP catalogue, consists of the anterior half of the skull, preserving all teeth, although the Cfs are broken. Provenance: Gobernación de Santa Cruz, Argentina.

MPM-PV 3401. The neotype of *E. ingens* De Iuliis, Pujos, Toledo, Bargo, and Vizcaíno, 2014, includes a nearly complete and well-preserved skull and mandible, a R humerus and several L manus elements (see De Iuliis *et al.*, 2014). Provenance: Santa Cruz Formation, Puesto Estancia La Costa, Santa Cruz Province, Argentina.

MPM-PV 3403. Assigned here to *E. latifrons*, a very well-preserved skull and several postcranial elements, but lacking mandible. Skull nearly undistorted, with only its posterodorsal part shifted slightly to the right; missing ectotympanics, L occipital condyle, premaxillae, jugals, and R Cf1 and Mf1 and Mf2; several vertebrae, some nearly complete (*e.g.*, atlas, axis, lumbar, sacral, caudal); R scapula missing coracoacromial arch; R humerus, missing part of entepicondyle and medial part of trochlea; R radius, missing its proximal articular surface and small portion of its diaphysis; R ulna; sacrum; R femur, missing its entepicondyle; R tibia, missing small length of diaphysis and posteroproximal surface, including nearly all of its articular facets; R fibula, missing its distal epiphysis. Provenance: Santa Cruz Formation, Puesto Estancia La Costa, Santa Cruz Province, Argentina.

MPM-PV 3451. *E. ingens* includes a nearly complete skull and a L radius (see De Iuliis *et al.*, 2014). Provenance: Santa Cruz Formation, Puesto Estancia La Costa, Santa Cruz Province, Argentina.

MPM-PV 15046. *E. ingens* is a nearly complete skull, with all teeth, and a fragmentary pelvis (see De Iuliis *et al.*, 2014). Provenance: Santa Cruz Formation, Monte Tigre, Santa Cruz Province, Argentina.

MPM-PV 15086. *E. ingens* includes a nearly complete skull and the L zygomatic arch preserving the ascending process (see De Iuliis *et al.*, 2024). The skull's dorsal surface is flattened. The L Cf, the Mf1 alveoli, L and R Mf2-Mf4, and the R ectotympanic are preserved, as are the mesial part of the L Cf and its alveolus, though they are displaced slightly laterally. This specimen preserves other elements as well (*e.g.*, an incomplete distal femoral epiphysis, a fragmentary distal L fibula, and fragments of vertebrae and ribs still embedded in the sediment). Provenance: Santa Cruz Formation, Monte Tigre, Santa Cruz Province, Argentina.

YPM-VPPU 15110. *Hapalops indifferens* Ameghino, 1887, includes the anterior part of the skull (region posterior to the pterygoids is missing), nearly complete mandible, missing the tip of the symphyseal spout and of the coronoid processes and the L angular process, fragments of vertebrae and ribs, a partial L ulna, several metacarpals, a nearly complete L femur, both calcanei, several metatarsal, phalanges, and unguals. Provenance: Santa Cruz Formation, approximately 16 km south of Coy Inlet (Cañadón Silva), Santa Cruz Province, Argentina.

YPM-VPPU 15160. *H. elongatus* includes a nearly complete skull, R and L humeri, R ulna, R calcaneum, and several metapodials and phalanges. Provenance: Santa Cruz Formation, Coy Inlet, Santa Cruz Province, Argentina.

YPM-VPPU 15314. *E. ingens* (see De Iuliis *et al.*, 2024), comprises a nearly complete mandible with all its teeth preserved but missing the tip of both coronoid processes and the R angular process; the L angular process is preserved but displaced dorsally. Fragments of vertebrae are preserved as well. Provenance: Santa Cruz Formation**,** approximately 16 km south of Coy Inlet (Cañadón Silva), Santa Cruz Province, Argentina**.**

YMP-VPPU 15520. The type of *Hapalops ponderosus* Scott, 1903, includes a nearly complete and reasonably well-preserved skull, particularly its L side; teeth are preserved, but the R cf is broken; nearly complete L humerus, R femur, partial proximal R tibia, and L calcaneum are preserved. Most elements are reconstructed with plaster. Provenance: Santa Cruz Formation, approximately 16 km south of Coy Inlet (Cañadón Silva), Santa Cruz, Argentina.

YPM-VPPU 15523. The type of *Hapalops longiceps* Scott, 1903, includes the skull and mandible and most postcranial elements, including vertebrae and ribs, nearly complete L humerus, both radii, L ulna, pelvis and sacrum, both femora, both tibiae, R fibula, L astragalus, L calcaneum, several carpal, metacarpal, tarsal, and metatarsal elements, phalanges, and unguals. The skull is distorted but nearly complete, although several portions are reconstructed (*e.g.*, parts of the premaxillae, L zygomatic arch, and L pterygoid); the mandible is well preserved and nearly undistorted, with minor reconstruction (*e.g.*, to the symphysis, tips of the coronoid processes, and R angular process). Most of the postcranial elements are heavily reconstructed with plaster. Provenance: Santa Cruz Formation, approximately 13 km south of Coy Inlet (near Estancia La Costa), Santa Cruz Province, Argentina.

YPM-VPPU 15597. *H. elongatus*, includes a skull and mandible, both nearly complete and well preserved, a proximal fragment of R ulna, nearly complete L radius, and R tibia (the latter missing portions of its distal articular surface). Provenance: Santa Cruz Formation, Felton's Estancia (Killik Aike Norte), 15 km west-northwest of Río Gallegos, Güer Aike Department, Santa Cruz Province, Argentina.

YPM-VPPU 15562. The type of *Hapalops angustipalatus* Ameghino, 1887, includes the well-preserved ventral part of the skull (much of the dorsal half is missing and filled with plaster), and several postcranial elements, including vertebrae and rib fragments, the R scapula (missing its dorsal margin), fragmentary distal L humerus, R radius (missing a small proximal portion of its diaphysis), carpals, both ulnae, patella, R femur (preserving its proximal and distal ends, medial half of the diaphysis, and the third trochanter), R tibia, R calcaneum, metatarsals, and unguals. Provenance: Santa Cruz Formation, approximately 16 km south of Coy Inlet (Cañadón Silva), Santa Cruz, Argentina.

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889
FOLIVORA Delsuc, Catzeflis, Stanhope and Douzery, 2001
MEGATHERIOIDEA Gray, 1821
MEGALONYCHIDAE Gervais, 1855

Genus ***Eucholoeops*** Ameghino, 1887

Type species. *Eucholoeops ingens* Ameghino, 1887.

Diagnosis (emended from De Iuliis *et al.*, 2024). Much smaller than the Plio-Pleistocene ground sloths but larger than extant tree sloths; shares with other megalonychids large Cf and cf, prominent diastema, anteriorly divergent tooth rows, with Cfs displaced laterally with respect to a line passing through the middle of remaining teeth, and oval to rectangular molariforms; muzzle prominent, short and broad, but less so than in *Ahytherium* Cartelle, De Iuliis, and Pujos, 2008 and *Megistonyx* McDonald, Rincón, and Gaudin, 2013; differing from *Megalonyx* Jefferson, 1799 in possessing caniniforms that are triangular in section and pointed at the tips and a longer mandibular spout; differing from other megalonychids with triangular caniniforms (*e.g.*, *Choloepus* Linnaeus, 1758, *Acratocnus* Anthony, 1916, and *Neocnus* Arredondo, 1961) in having dorsoventrally deep, rather than anteriorly tapered, rostrum; as in megalonychids generally, Mf2 and Mf3 transversely expanded; palatal width across buccinator fossae much less than width at preorbital rostrum; preorbital rostrum width nearly equal to or greater than that of postorbital constriction; posterior surface of lacrimal markedly concave; ectotympanic loosely attached to squamosal; stapedial artery sulcus present on petrosal; humerus with well-developed deltopectoral crest but, in contrast to *Hapalops* species, not as consistently wide distally; compared to *Hapalops*, pectoral crest less

prominent and does not closely approach lesser tubercle; radius is more gracile, with a less markedly mediolateral offset between its proximal and distal portions, less prominent bicipital tuberosity, and less prominent and more gently curved pronator crest compared to *Hapalops* species; femur relatively less wide, particularly proximally, and third trochanter less prominent and with lateral margin widely V-shaped rather than nearly rectilinear; tibia with lateral margin nearly rectilinear rather than curved as in *Hapalops*.

Eucholoeops latifrons Mercerat, 1891: 21.
Figure 2

Synonymy list

Eucholoeops fronto Ameghino, 1891b, in part
Eucholoeops fronto Ameghino, 1894, in part
Eucholoeops ingens Lydekker, 1894, in part
Eucholoeops fronto Scott, 1904, in part
Eucholoeops fronto Dozo, 1994, in part
Eucholoeops cf. *E. fronto* Bargo *et al.*, 2012, in part
Eucholoeops fronto De Iuliis *et al.*, 2014, in part

Diagnosis. Size similar to *E. ingens*; caniniform teeth large and vaguely triangular in section, but less so than in *E. ingens*; in contrast to the condition in the latter, maxilla extends beyond alveolar wall of Cf1 laterally and ventrally, rather than forming a pillar-like sheath surrounding Cf1; premaxillary margins of maxillae form narrower V-shaped notch than in *E. ingens*, and bear a prominent anterior flange for articulation with premaxillae; preorbital rostrum width equal or slightly greater than that of postorbital constriction, differing from *Hapalops* species, in which the preorbital width is clearly narrower, and from *E. ingens* is which the preorbital width is clearly greater; dentary with a less prominent concavity anterior to the cf alveolus than in *E. ingens*; enthesis for *latissimus dorsi*, proximomedially on posterior humeral surface, more prominent than in *E. ingens* but does not extend as far distally; in *E. latifrons*, lateral margin of the humeral deltopectoral shelf larger; femoral greater trochanter does not extend as far proximally in *E. latifrons*, whereas lesser trochanter is more prominent, so that the medial femoral margin between this structure and head is more deeply concave; trochanteric fossa and intertrochanteric crest better developed in *E. ingens*; tibia of *E. latifrons* more robust than that of *E. ingens*; its diaphysis is wider proximally, and its lateral and medial diaphyseal margins converge distally more markedly.

Type material. MLP-PV 4-2

Referred material. MPM-PV 3403, MACN-A 11614

Geographic and stratigraphic occurrence. Santa Cruz Formation (Early-Middle Miocene), Santacrucian SALMA, Santa Cruz Province, Argentina.

TAXONOMIC HISTORY

Mercerat (1891) erected *Eucholoeops latifrons* (type specimen MLP-PV 4-2, Fig. 2; figured by Lydekker, 1894: pl. 59, fig. 3 in ventral view, and pl. 60, fig. 1 in lateral view), and *Eucholoeops lafonei* (type specimen MLP-PV 4-5; figured by Lydekker, 1894: pl. 59, fig. 3; Scott, 1904: pl. 56, fig. 2; De Iuliis *et al.*, 2024: fig. 5). Mercerat (1891) indicated that *E. latifrons* was somewhat larger than half the size of the genotype *E. ingens* and provided several measurements but did not identify any distinguishing morphological features. Similarly, this author noted only that *E. lafonei* was considerably smaller than *E. ingens* and *E. latifrons*. Ameghino (1891b), unable to access and analyse the relevant specimens (see De Iuliis *et al.*, 2014, 2024), suspected that *E. latifrons* was a synonym of *E. fronto* and *E. lafonei* a synonym of *Eucholoeops externus* Ameghino, 1891a. Still without access to the specimens, Ameghino (1894) formally synonymized *E. latifrons* with *E. fronto* and *E. lafonei* with *E. externus*.

Lydekker (1894: pls. 59, 60), without discussion (see De Iuliis *et al.*, 2024), assigned *E. lafonei* and *E. latifrons* to *E. ingens*. Scott (1904) considered *E. fronto* as valid and accepted Ameghino's (1894) synonymy of *E. latifrons* with it, but also considered *E. lafonei* a synonym of *E. fronto*. Dozo (1994) followed Scott (1904) in recognizing MLP-PV 4-2 as *E. fronto*. Similarly, Bargo *et al.* (2012) and Toledo *et al.* (2013), for example, accepted Scott's (1904) taxonomic arrangement in assigning MPM-PV 3403 to *E.* cf. *E. fronto*. De Iuliis *et al.* (2014) also deferred to Scott's (1904) taxonomic scheme in tentatively recognizing *E. fronto*. However, the analyses of De Iuliis *et al.* (2014, 2024) considered *E. fronto*, as well as many other species previously assigned to *Eucholoeops*, as synonyms of *E. ingens* but De Iuliis *et al.* (2024) maintained *E. latifrons* as possibly valid, pending further investigation.

Figure 2. ***Eucholoeops latifrons*** (MLP-PV 4-2, type), skull in **1,** ventral view; **2,** left lateral view; and **3,** dorsal view. Scale bar equals 20 mm. From De Iuliis *et al.* (2024).

DESCRIPTIONS AND COMPARISONS

Skull and Mandible

The basicranium of MLP-PV 4-2, the type of *E. latifrons*, is missing, as are the jugals, but the skull is otherwise nearly complete. Anteriorly, diagenetic dorsoventral compression produced ventral displacement of the nasals, the anterior ends of which are missing. A transverse break is present through the skull, separating it into anterior and posterior moieties, although these regions preserve a contact dorsally and have been glued together. The individual was subadult, as many of the sutures remain open, such as the internasal, nasomaxillary, interfrontal, interparietal, and lambdoid sutures. Ventrally, the intermaxillary suture is open anteriorly but its posterior portion and the interpalatine suture appear to have closed, furnishing data on the sequence of sutural closure in this species.

In dorsal view, the outline of the skull (Fig. 2) resembles that of *E. ingens* (*e.g.*, MPM-PV 3401 and MPM-PV 3451; see De Iuliis *et al.*, 2014, figs. 2 and 3, respectively) except that MLP-PV 4-2 is less expanded anteriorly owing to smaller caniniforms (see below), so that the lateral walls of the maxillae are less concave. Nonetheless, the preorbital constriction dorsally (at the level of the diastema) is wider than the postorbital constriction of the skull, approximately as in better-preserved specimens of *E. ingens* (*e.g.*, MPM-PV 3401, MPM-PV 3451). However, the difference in the pre vs. postorbital constrictions may be exaggerated in MLP-PV 4-2, as the anterior region of the skull appears slightly spread owing to the compression that caused ventral displacement of the nasals. Further, the narrowest width of the postorbital constriction occurs precisely at the position of the transverse break through the skull, and deformation has occurred as, at the narrowest part of the postorbital constriction, the left half of the skull is not as wide as the right side. Moreover, if the widths are considered separately for the left and right sides of the skull (*i.e.*, to the midline of the skull), that at the postorbital constriction is nearly equivalent to that of the postorbital constriction on the right (less distorted) side. Based on the reasonably intact posterior end of the nasals, the nasomaxillary suture in MLP-PV 4-2 was nearly rectilinear and oriented posteromedially, resembling the condition in MPM-PV 3451 and MLP-PV 4-10 (see below), the only *E. ingens* specimens in which the suture is clearly and entirely preserved. The anterior end of the frontals of MLP-PV 4-2 are broken, a condition that, at first glance, lends a sinusoidal course to the suture, but this is an artifact resulting from the breakage.

In lateral view the dorsal profiles of MLP-PV 4-2, MPM-PV 3403, and *E. ingens* MPM-PV 3451 are similar, with a shallow depression present approximately where the temporal lines meet and the sagittal crest begins. Among specimens with a reasonably well-preserved sagittal crest, this structure is best developed in MPM-PV 3401, followed by MPM-PV 3403 and MPM-PV 3451, with the skulls of the last two specimens being very similar in size. The arrangement of the ventrolateral orbital wall foramina is similar in MPM-PV 3451 and MPM-PV 3403. However, in MPM-PV 3403 a ridge of bone extends between the ventral margins of the foramen rotundum and the depression containing the openings of the sphenopalatine and caudal palatine foramina. Based on the preserved portions in this region, this ridge does not seem to be present in MPM-PV 3451 (see Gaudin *et al.*, 2015, fig. 1).

In ventral view the smaller size of the Cf, particularly distomedially, is apparent. This tooth is also less clearly triangular than that of *E. ingens*. The molariforms, however, are well within the range of variation outlined by De Iuliis *et al.* (2014, 2024) for *E. ingens* in relative size and shape. The sulcus extending the length of the diastema is best defined in MLP-PV 4-2 compared to specimens of *E. ingens*. In the latter this sulcus begins as a triangular depression from the distal Cf alveolar margin and narrows markedly, whereas in MLP-PV 4-2 the triangular portion is less wide, perhaps due to the smaller Cf alveolus and does not narrow as markedly, so that the depression and sulcus are of more nearly uniform width.

In contrast to the condition in *E. ingens*, in which the maxilla wraps as a pillar-like sheath around the Cf without extending anteriorly beyond the Cf (other than forming its alveolar wall) laterally or ventrally, in MLP-PV 4-2 the maxilla extends a short distance anteriorly. Most laterally, in ventral view, this extension has an anteriorly tapered, triangular shape, with its anterior apex aligned nearly directly anterior to the lingual margin of the Cf alveolus. The medial surface of this extension forms the lateral wall of a notch for the lateral ramus of the premaxilla. A well-defined

premaxillary notch is not discernable in *E. ingens*. The medial margin of the maxilla of MLP-PV 4-2 bears a prominent flange that extends anteriorly, reaching the level of the mesial margin of Cf, to form the medial margin of the premaxillary notch. The flange is considerably less prominent in *E. ingens* (see De Iuliis *et al.*, 2014, 2024).

MPM-PV 3403, a nearly complete (missing only the premaxillae and jugals among its main skeletal elements) and undeformed skull (Fig. 3), is also of a subadult, as the internasal, nasofrontal, and interfrontal sutures are largely open. Closure is more advanced than in MLP-PV 4-2, with the lambdoid sutures and, on the ventral surface, the intermaxillary and interpalatine sutures having closed. The nasals, largely complete anteriorly, overhang the maxillae and resemble the condition in *E. ingens* MPM-PV 3451, as do the nearly rectilinear and posteromedially oriented nasomaxillary sutures. The preorbital and postorbital constrictions are nearly equivalent in MPM-PV 3403, as in MLP-PV 4-2 as discerned from the right side of this specimen's skull (see above).

In ventral view the maxilla bears a short triangular anterior extension, with its apex aligned with the lingual alveolar margin of the Cf1 alveolus, as in MLP-PV 4-2. The medial margin of the maxilla is incompletely preserved so that the flange is largely missing, although its preserved portion is appreciably larger than in *E. ingens*. Cf1 is similar in size and shape to that of MLP-PV 4-2, as is the well-defined sulcus extending the length of the diastema. The size and shape of the molariform teeth are, as in MLP-PV 4-2, characteristic of *Eucholoeops*.

Gaudin *et al.* (2015; see figs. 2, 4) reported the presence in an exceptionally well-preserved specimen of *E. ingens* (MPM-PV 3451) of a stapedial artery sulcus extending between the anterior margins of the fenestra ovalis and the fenestra cochleae of the petrosal. De Iuliis *et al.* (2024) noted this sulcus is also present in MPM-PV 3401 and AMNH 9241. A sulcus is not clearly apparent in less well-preserved remains of this species. The petrosal is well preserved in MPM-PV 3403, and a sulcus is present in the same region, but its course differs from that of MPM-PV 3451. In the former the sulcus extends from the anterior margin of the fenestra cochleae but passes well anterior to the anterior margin of the fenestra ovalis.

MACN-A 11614 (Fig. 4) preserves much of the posterior part of the skull but only the left half of the anterior part, including Cf1-Mf4. The anteroventral portion is reasonably undistorted, although the maxilla medial to Cf1 is largely missing. However, the maxilla has a triangular extension anterior to Cf1 as in MLP 4-2 and MPM-PV 3403, although it is displaced slightly laterally. The Cf1, broken just beyond its alveolar margin, is similar in size to those of the two previous specimens and, like them, also vaguely triangular in section. The preorbital constriction is about as wide as the postorbital constriction, as also described above for MLP-PV 4-2 and MPM-PV 3403. The molariforms are also as described above for the other two specimens.

The partial left dentary of *E. latifrons* MACN-A 11641 is missing only its anterior end and the tip of the coronoid process. It is robust, as in *E. ingens* (*e.g.*, MACN-A 4645, MPM-PV 3401, and YPM-VPPU 15314; see De Iuliis *et al.*, 2024). The ventral margin of MACN-A 11641 is regularly convex. In MPM-PV 3401, a bulge is present ventral to cf1, perhaps owing to the large size of the alveolus of this tooth. A less prominent bulge is present in MACN-A 4645 and YPM-VPPU 15314. In the *E. ingens* specimens, a deep sulcus lies just anterior to cf1 to receive the large Cf1 (De Iuliis *et al.*, 2014, fig. 6; 2024, figs. 2, 3). The sulcus is shallower in MACN-A 11641, which is expected, given that Cf1 is smaller. The angular process of this specimen extends posteriorly to about the same level as the articular process, whereas in MPM-PV 3401 and YPM-VPPU 15314, the only specimens of *E. ingens* preserving the former structure completely, it extends well beyond the articular process and is more robust than in MACN-A 11641. The two processes reach about the same level in FMNH P13125, but the angular process of this specimen is incompletely preserved on the right side and largely reconstructed in plaster on the left side (see De Iuliis *et al.*, 2014).

Dentition

The Cfs of *E. latifrons* are large, curved, triangular in section, and worn obliquely, and are similar to those described by De Iuliis *et al.* (2014, 2024) for *E. ingens*. They are smaller than in the latter but still larger than the circular to oval Cfs present in *Hapalops*, the other genus of similarly sized Santacrucian sloths that possess a prominent diastema.

Figure 3. ***Eucholoeops latifrons*** (MPM-PV 3403), skull in **1,** ventral view; **2,** right lateral view; and **3,** dorsal view. Scale bar equals 20 mm.

Figure 4. ***Eucholoeops latifrons*** (MACN-A 11614), skull in **1,** ventral view; **2,** left lateral view; and **3,** dorsal view; left dentary in **4,** lateral view; **5,** medial view; and **6,** occlusal view. Scale bars equal 20 mm.

The angle of the occlusal surface of the Cf differs between MLP-PV 4-2 and MPM-PV 3403. It is oriented vertically in the former, so that the occlusal surface faces distally, whereas in the latter it is oblique, facing distoventrally (see Figs. 2 and 3). The molariforms are oblong, mesiodistally compressed and tend to have rounded rather than angular corners. Mf2 is the largest tooth, followed by Mf3, Mf1, and Mf4. Among the molariforms, Mf1 is proportionately less mesiodistally compressed, and its mesial margin is gently convex. The distal margin of Mf4 may be gently concave. In addition to minor differences among individuals, minor intraindividual differences occur between the left and right molariform. For example, in MLP-PV 4-2 the left Mf1 is slightly more mesiodistally compressed than the right Mf1; in MPM-PV 3403 the left Mf4 is slightly wider transversely and more compressed mesiodistally than the right Mf4. Similar differences exist within and among individuals of *E. ingens* (see De Iuliis *et al.*, 2014, 2024). The lower dentition of *E. latifrons* also strongly resembles that of *E. ingens*, with a large, triangular cf, mesiodistally compressed, oblong mf1 and mf2, and slightly oval mf2, with long axis oriented mesiovestibularly to distolingually. The morphology of the dentition of *Eucholoeops* differs from that of *Hapalops* in several respects. In the latter genus the upper and lower caniniforms are smaller and circular to oval and the molariforms tend to be rectangular or more nearly squared, with angular rather than rounded corners (see *e.g.*, Bargo *et al.*, 2019).

Figure 5. ***Eucholoeops ingens*** (MLP-PV 4-10), anterior portion of the skull in **1,** ventral view; **2,** right lateral view; and **3,** dorsal view. Scale bar equals 20 mm.

In addition to the above descriptions and comparisons among cranial specimens previously assigned to *E. ingens* by De Iuliis *et al.* (2014, 2024) and here to *E. latifrons*, MLP-PV 4-10 (Fig. 5) is addressed. This specimen, assigned here to *E. ingens*, was not discussed previously because it was only recently relocated in the MLP-PV collections. MLP-PV 4-10 preserves only the anterior half of the skull. As in the neotype of *E. ingens* (MPM-PV 3401), the Cf1 alveolus is large, and the maxilla forms a sheath-like pillar around this tooth and does not extend anteriorly. The premaxillary notch also strongly resembles that of the neotype and MPM-PV 15046, widely open and with a small flange. The form of the teeth of MLP-PV 4-10 is as in the other specimens assigned to *E. ingens* (see De Iuliis *et al.*, 2014, 2024) and the preorbital width is greater than the postorbital width.

Scapula

The right scapula of MPM-PV 3403 (Fig. 6.1-6.2), preserved nearly completely, is the only scapula known for *Eucholoeops*, and it is thus compared with scapulae that have been catalogued as *Hapalops* cf. *H. rectangularis* (FMNH P13143; Fig. 6.3) and *H. elongatus* (FMNH P13133; Fig. 6.4). They are largely complete, except that the former's anterior and dorsal margins are eroded and the latter is missing its posterodorsal portion. Among the few differences that may

be noted among the specimens are that the postscapular fossa and posterior margin of the subscapular fossa are more prominent in MPM-PV 3403 than in FMNH P13133 (this region is reconstructed with plaster in FMNH P 13143).

Humerus

The humerus of MPM-PV 3403 (Fig. 7.1–7.3) is nearly complete and well preserved, missing only a small disto-medial part, including the medial half of its trochlea. The subadult ontogenetic stage of the animal is evident in that the head and lesser tubercle are attached though not fully fused to the diaphysis, indicating that the individual had nonetheless likely reached its adult size. The distal epiphysis is fused to the diaphysis. This humerus strongly resembles that of *E. ingens* MPM-PV 3401 (Fig. 7.4–7.6), MACN-A 6414 (associated with MACN-A 6413, as noted in Materials and Methods), and FMNH P13125 (to the extent that these last two specimens, being less complete, permit comparison). MPM-PV 3401 and MPM-PV 3403 are nearly the same size, but the enthesis for the *latissimus dorsi* muscle, on the posteromedial surface of the humerus, is better developed in the latter, despite MPM-PV-3401, based on complete fusion of the diaphysis and epiphysis proximally, being an older individual. In this specimen the distal end of this enthesis is located farther distally, approximately at humeral mid-length, than in MPM-PV 3403. The lateral margin of the deltopectoral shelf is larger, extending farther laterally in MPM-PV 3403 than in MPM-PV 3401 and MACN-A 6414.

The humerus of *Hapalops* (Fig. 8) strongly resembles those described for *Eucholoeops*, with the most consistent difference being in shape and size of the deltopectoral shelf, as may be appreciated in anterior and lateral views. In both genera the distal extension of the humeral deltopectoral shelf is similar. However, in *Hapalops* the shelf is more robust as it begins tapering more distally —in other words, the shelf is wider for a greater length, owing to the deltoid and pectoral crests being parallel to each other for a greater length. This seems to be in part due to the pectoral crest being more nearly rectilinear, with a less marked lateral deflection. Also, this crest is more prominent proximally, almost reaching the lesser tubercle, as observed in *H. elongatus* (FMNH P13133, Fig. 8.1; YPM-VPPU 15545, see Scott, 1903, pl. 41, fig. 4), *H. ruetimeyeri* (FMNH P13130,

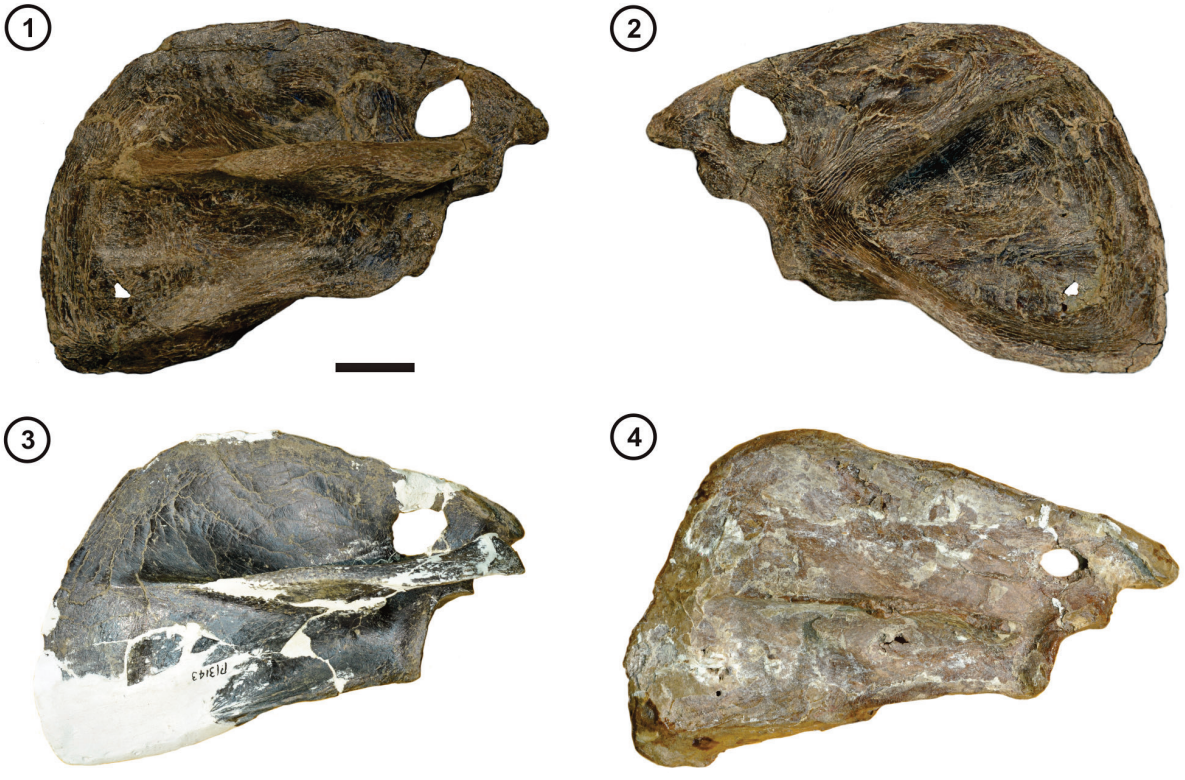

Figure 6. ***Eucholoeops latifrons*** (MPM-PV 3403), right scapula in **1,** lateral view; and **2,** medial view. ***Hapalops*** cf. ***H. rectangularis*** (FMNH P13143), right scapula in **3,** lateral view. ***Hapalops elongatus*** (FMNH P13133), right scapula in **4,** lateral view. Scale bar equals 20 mm.

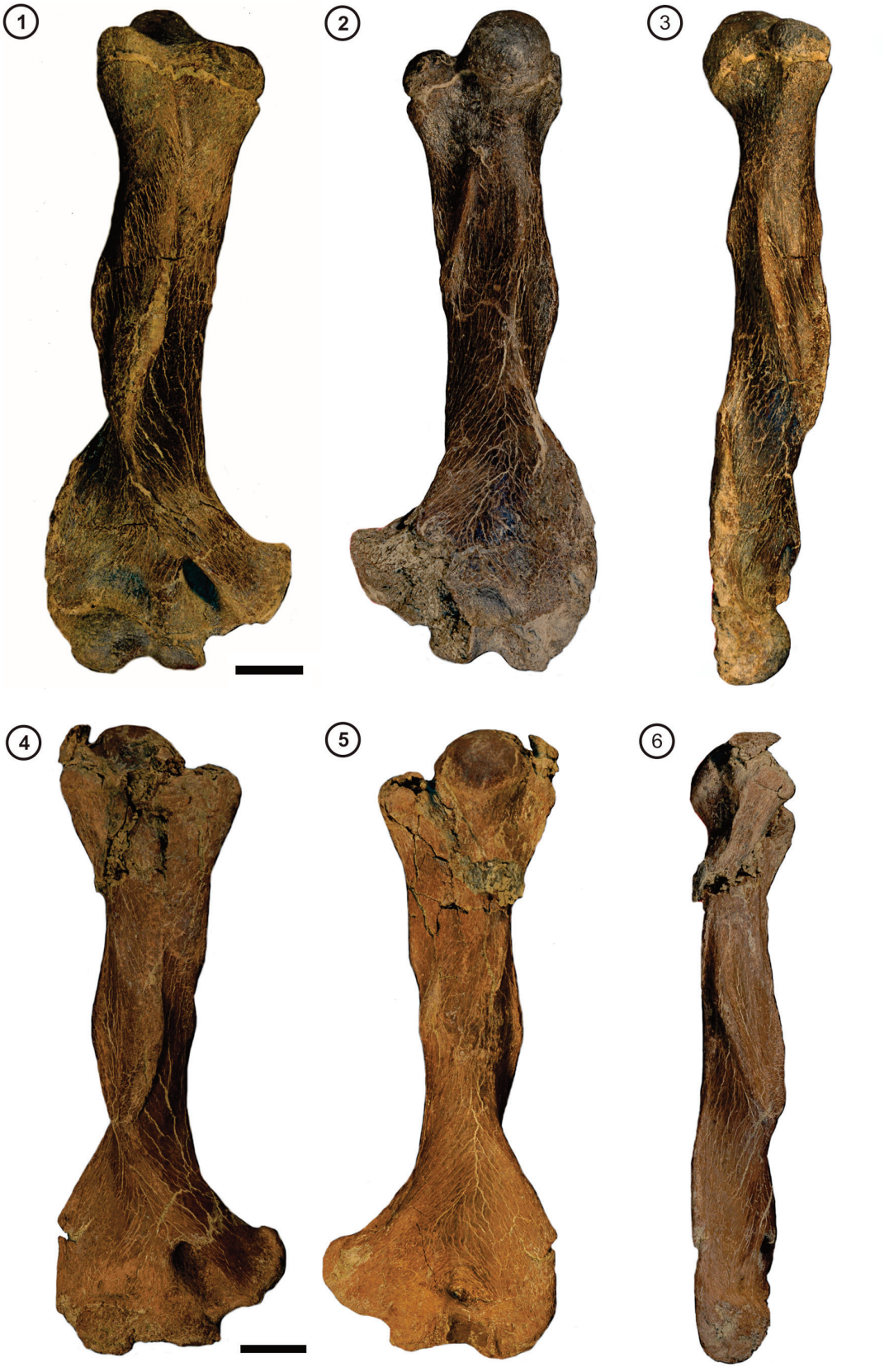

Figure 7. ***Eucholoeops latifrons*** (MPM-PV 3403), right humerus in **1,** anterior view; **2,** posterior view; and **3,** lateral view. ***E. ingens*** (MPM-PV 3401), right humerus in **4,** anterior view; **5,** posterior view; and **6,** lateral view. Scale bars equal 20 mm.

Figure 8. ***Hapalops elongatus*** (FMNH P13133), right humerus in **1,** anterior view; and **2,** lateral view. ***Hapalops ruetimeyeri*** (FMNH P13130), right humerus in **3,** anterior view; and **4,** posterior view. Scale bars equal 20 mm.

Fig. 8.3), *H. longiceps* (YPM-VPPU 15523; see Scott, 1903: pl. 32, figs. 2, 2a) and *H. ponderosus* (YPM-VPPU 15520). The distal end of the shelf differs also in projecting more prominently anteriorly, as may be appreciated in lateral (Figs. 7.3, 7.6, and 8.2) and medial views.

Radius

The radius of *E. latifrons* (MPM-PV 3403, Fig. 9.1, 9.2) is reasonably well preserved although missing its head, most of its neck, and a small portion just proximal to the pronator tuberosity. As noted by Toledo *et al.* (2013) for Santacrucian

Figure 9. ***Eucholoeops latifrons*** (MPM-PV 3403), right radius in **1,** anterior view; and **2,** posterior view. ***Eucholoeops ingens*** (MPM-PV 3451), left radius in **3,** anterior view; and **4,** posterior view. ***Hapalops longiceps*** (YPM -VPPU 15523), left radius in **5,** anterior view; and **6,** posterior view. ***H. ruetimeyeri*** (FMNH P13130) right radius in **7,** anterior view; and **8,** posterior view. Scale bars equal 20 mm.

sloths generally, the diaphysis is robust. It is nearly cylindrical in section proximally but distally flattened anteroposteriorly and widened mediolaterally. The radius is sigmoidal, with its proximal and distal epiphyses offset (in the mediolateral plane) rather than longitudinally aligned so that the lateral diaphyseal margin is concave. MPM-PV 3403 strongly resembles the radius of *E. ingens* (*e.g.*, MPM-PV 3451, Fig. 9.3, 9.4, FMNH P13125, AMNH 9241; the first of these specimens was mistakenly attributed to MPM-PV 3401 in De Iuliis *et al.*, 2014, p. 235), except that the lateral margin is somewhat angled rather than smoothly concave, but this appears to be due to distortion. The bicipital tuberosity of these *Eucholoeops* species is less prominent than in *H. longiceps* and *H. ruetimeyeri* (YPM VPPU 15523 and FMNH P13130, respectively, Fig. 9.5–9.8; the former specimen is illustrated, though inaccurately, by Scott, 1903: pl. 32, fig. 3; AMNH 9250 of *H. ruetimeyeri* is illustrated by Scott, 1904, pl. 42, fig. 6), *H. elongatus* (FMNH P13133), and *H. angustipalatus* (YPM VPPU 15562). Except for the latter, the diaphysis of the *Hapalops* species is more notably offset.

Ulna

The right ulna of *E. latifrons* MPM-PV 3403 (Fig. 10.1, 10.2) is the only ulna known for *Eucholoeops*. It is stout and tapers distally only slightly so that it remains robust throughout its length. In lateral and medial views this element is nearly straight, with its anterior and, in particular, posterior margins being nearly rectilinear. The ulna of *Hapalops* tapers distally, thereby becoming more noticeably slender, in several specimens (*e.g.*, *H. ruetimeyeri* FMNH P13130, Fig. 10.3, 10.4, and *H. elongatus* FMNH P13133, Fig. 10.5, 10.6, and *Hapalops* sp. MPM-PV 3467, see Toledo *et al.*, 2013, fig. 2), but less so in others (*e.g.*, *H. longiceps* YPM-VPPU 15523). More consistent in this genus is that the ulna's posterior margin is curved, bowing posteriorly;

Figure 10. ***Eucholoeops latifrons*** (MPM-PV 3403), right ulna in **1,** anterior view; and **2,** lateral view. ***Hapalops ruetimeyeri*** (FMNH P13130), right ulna in **3,** anterior view; and **4,** lateral view. ***H. elongatus*** (FMNH P13133), right ulna in **5,** anterior view; and **6,** lateral view. Scale bars equal 20 mm.

its anterior margin also curves, but less strongly. In *E. latifrons* MPM-PV 3403 the ulna is also nearly straight in anterior and posterior views, whereas in *Hapalops* diaphyseal bowing varies from markedly (*H. elongatus* FMNH P13133, *H. longiceps* YPM-VPPU 15523) to moderately (*H. angustipalatus* YPM-VPPU 15562) bowed, to nearly unbowed (*H. elongatus* YPM-VPPU 15160).

Femur

Nearly or reasonably complete femora (Fig. 11.1, 11.2) are known for *E. latifrons* (MPM-PV 3403) and *E. ingens* (FMNH P13125, Fig. 11.3, 11.4, and AMNH 9241, Fig. 11.5, 11.6,). MPM-PV 3403 belongs to a younger individual as the head is incompletely fused to the diaphysis, whereas closure is complete in AMNH 9241. There is considerable

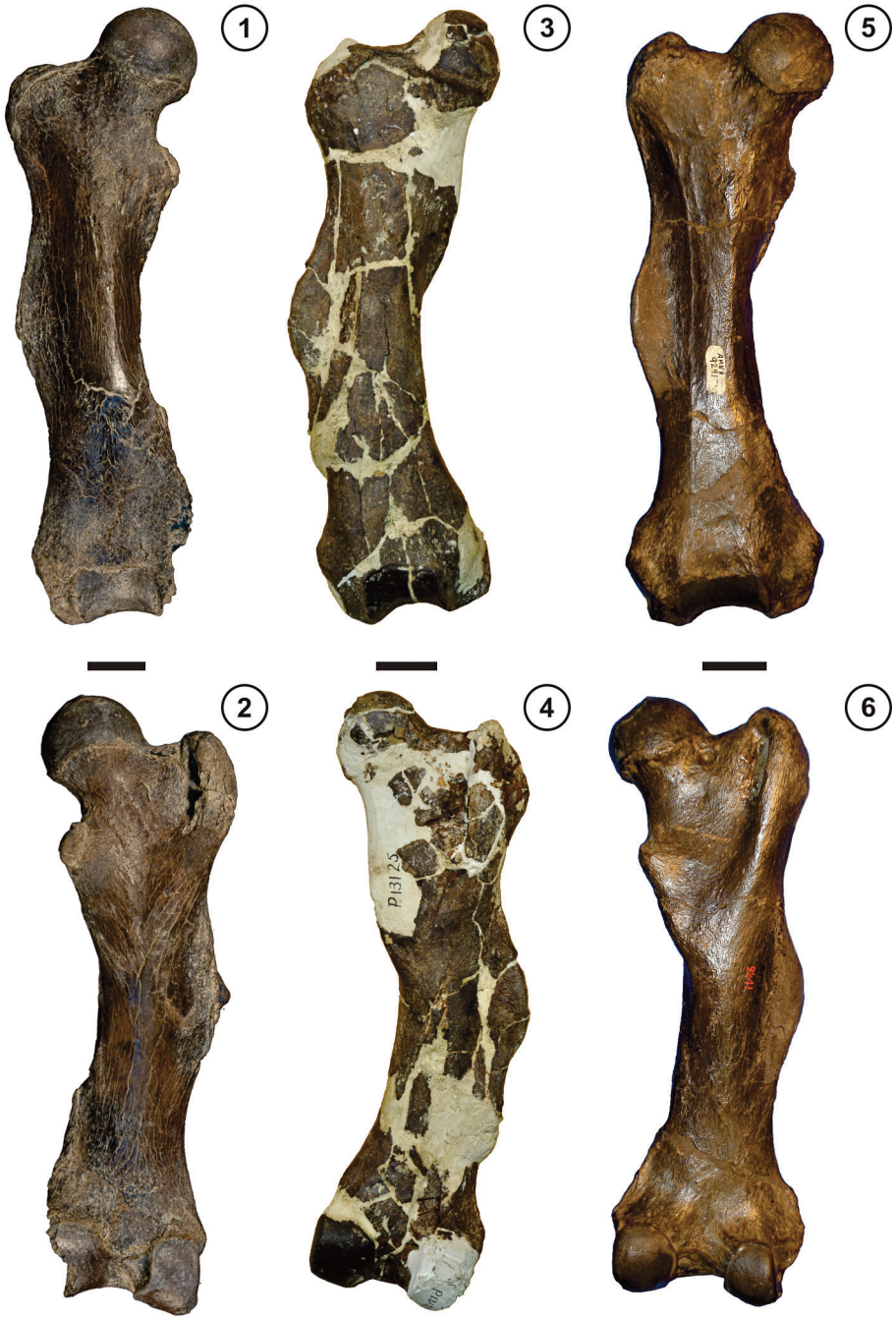

Figure 11. ***Eucholoeops latifrons*** (MPM-PV 3403), right femur in **1,** anterior view; and **2,** posterior view. ***E. ingens*** (FMNH P13125), right femur in **3,** anterior view; and **4,** posterior view. ***E. ingens*** (AMNH 9241), right femur in **5,** anterior view; and **6,** posterior view. Scale bars equal 20 mm.

similarity between AMNH 9241 (for the most part better preserved than FMNH P13125) and MPM-PV 3403 in overall proportions, position, and shape of the head and neck. MPM-PV 3403 and FMNH P13125 are very similar in size, shape, and position of the third trochanter (which is reconstructed in AMNH 9241). Differences include that the greater trochanter reaches farther proximally in FMNH P13125, and the lesser trochanter is larger in MPM-PV 3403 so that the medial margin of the neck is shorter and more strongly concave. In posterior view the trochanteric fossa is more ample, and the intertrochanteric crest is better defined in AMNH 9241. Although there is breakage to the entepicondyle, the medial articular condyle is apparently contiguous with the patellar trochlea, as is the lateral articular condyle, so that *E. latifrons* is like *E. ingens* in this respect.

In *Hapalops* the femur tends to be relatively wider, particularly proximally, than in *Eucholoeops*, so that it has a squatter, more robust appearance (Fig. 12). Among *Hapalops* species, the femur of *H. indifferens* (YPM-VPPU 15110) most resembles that of *Eucholoeops*, compared to *H. longiceps* (YPM-VPPU 15523; so far as may be discerned, as this element is heavily reconstructed in plaster), *H. ponderosus* (YPM-VPPU 15520), and *H. angustipalatus* (YPM-VPPU 15562). The proximal projection of the greater trochanter varies, being more like that of *E. latifrons* in *H. indifferens* and *H. angustipalatus*, and more like that of *E. ingens* in *H. ponderosus* and *H. longiceps*. The size of the lesser trochanter and contour of the medial margin of the neck of *E. latifrons* resembles more the conditions in the *Hapalops* species, except for *H. indifferens*, which resembles more that of *E. ingens*. A consistent difference between the femora of *Eucholoeops* and *Hapalops* is that the third trochanter is more pronounced in the latter. It projects more prominently laterally and is more extensive proximodistally, with its lateral margin being nearly straight. In *Eucholoeops* the lateral margin of the trochanter forms a wide V-shape.

Tibia

The tibia of *E. latifrons* (MPM-PV 3403, Fig. 13.1, 13.2) is missing a small portion of its diaphysis and proximolateral epiphysis. That of *E. ingens* (FMNH P13125, Fig. 13.3, 13.4) is also nearly complete, missing only small proximolateral and distomedial portions. The diaphysis of these elements

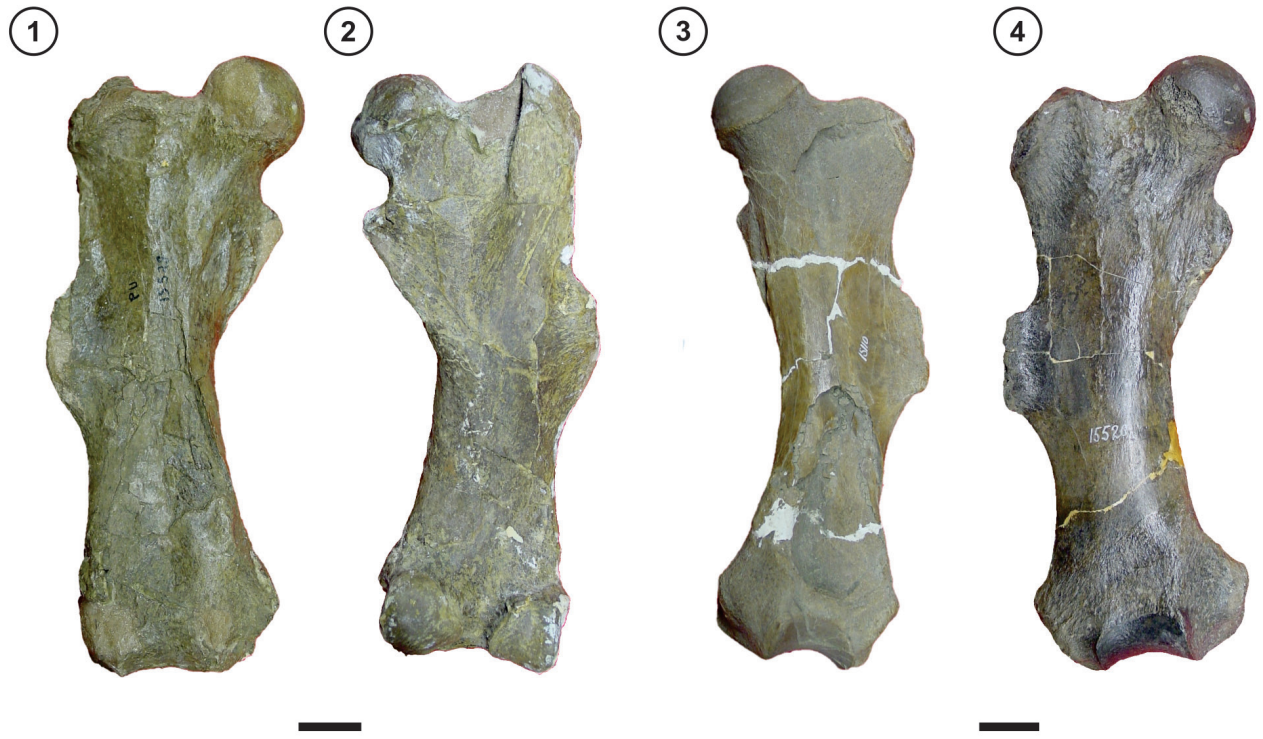

Figure 12. ***Hapalops longiceps*** (YPM-VPPU 15523, type), right femur in **1,** anterior view; and **2,** posterior view. ***H. indifferens*** (YPM-VPPU 15110), left femur in **3,** anterior view. ***H. ponderosus*** (YPM-VPPU 15520, type), left femur in **4,** anterior view. Scale bars equal 20 mm.

is similar in being nearly rectilinear (Fig. 12). MPM-PV 3403 is more robust than FMNH P13125, with its diaphysis being proximally wider and its lateral and medial margins more notably convergent than in FMNH P13125. In both these specimens the lateral and medial diaphyseal margins are nearly rectilinear and converge slightly distally, so that the diaphysis is narrowest distal to its mid-length. The tibia of several *Hapalops* species (*e.g.*, *H. elongatus*, FMNH P13123 and YPM-VPPU 15597, *H. longiceps*, YPM VPPU 15523, *H.* cf. *H. rectangularis*, FMNH 13143, and *H. ruetimeyeri*, FMNH P13130) resembles that of *E. ingens* in being less robust. In some cases (*e.g.*, FMNH P13123, Fig. 13.5, 13.6), it differs

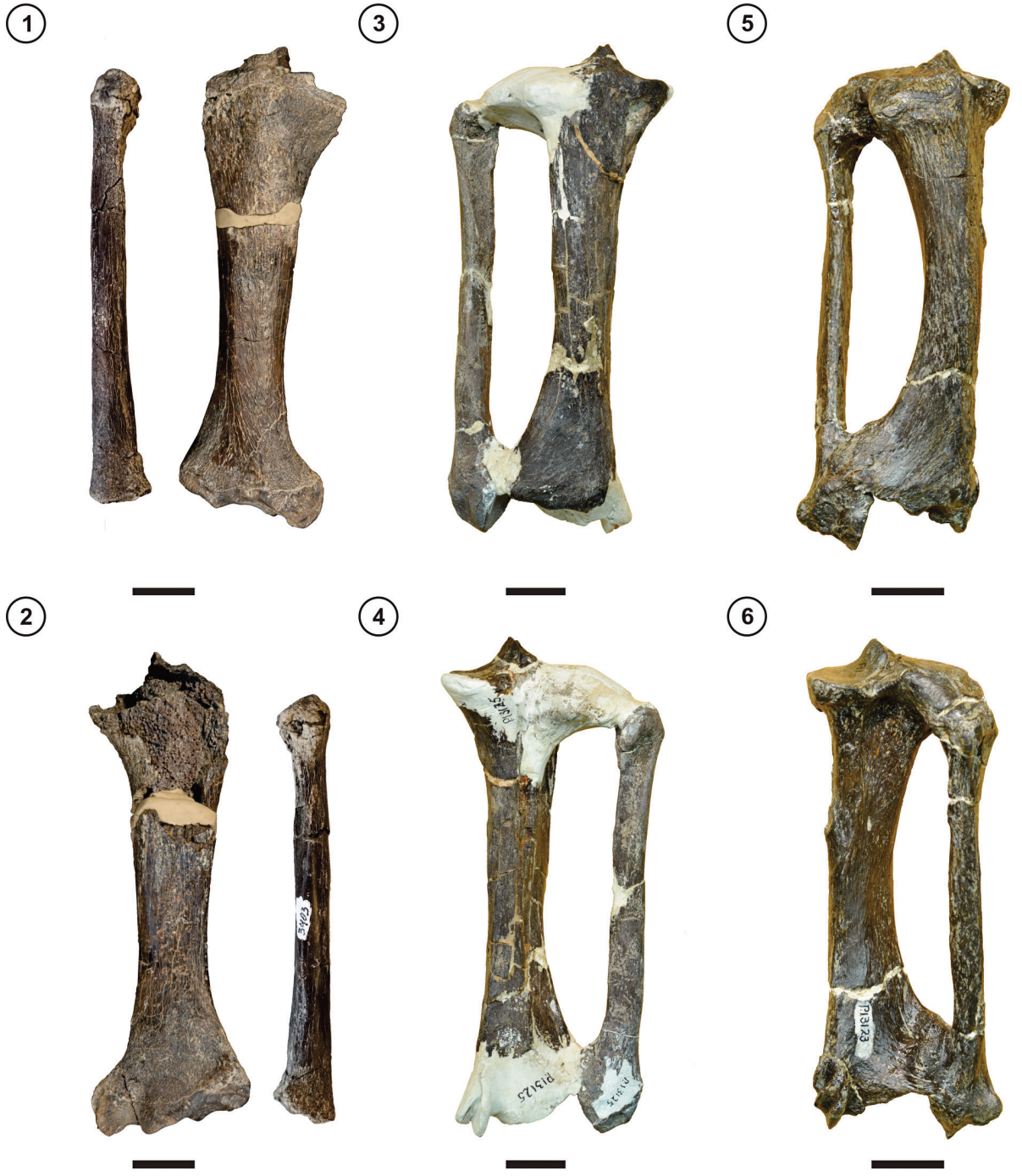

Figure 13. ***Eucholoeops latifrons*** (MPMN-PV 3403), right tibia and fibula in **1,** anterior view; and **2,** posterior view. ***E. ingens*** (FMNH P13125), right tibia and fibula in **3,** anterior view; and **4,** posterior view. ***Hapalops elongatus*** (FMNH P13123), right tibia and fibula in **5,** anterior view; and **6,** posterior view. Scale bars equal 20 mm.

from the tibia of *E. ingens* and *E. latifrons* in that the diaphysis appears medially bowed, owing largely to its markedly concave lateral margin and nearly rectilinear medial margin; in others (*e.g.*, YPM-VPPU 15523 and YPM-VPPU 15597), the bowed appearance is less marked. Further, the diaphysis is narrowest near the diaphyseal mid-length, so that the proximal and distal halves of the tibia appear more nearly symmetric. The diaphysis of *H. longiceps* (YPM VPPU 15523, see Scott, 1903: pl. 33, fig. 3), however, differs from these *Hapalops* species and *Eucholoeops* in that the diaphysis is nearly rectilinear, with unbowed margins, so that diaphyseal width remains nearly constant throughout its length. Further, it is relatively shorter compared to its width, so that it has a stocky appearance.

Fibula

The fibula of *E. latifrons* (MPM-PV 3403; Fig. 13.1, 13.2) lacks its distal epiphysis and bears marks of an unfused closure, evidence of belonging to a young individual. The diaphysis is straight with parallel sides. The proximal epiphysis is stout and bears an inclined flat facet for the tibia. The fibula of *E. ingens* (FMNH P13125; Fig. 13.3, 13.4) resembles that of *E. latifrons* in possessing a straight diaphysis, with rectilinear and subparallel sides and a nearly crescent-shaped cross-section. The proximal epiphysis bears the facet for the tibia, which is reconstructed with plaster, and a marked ridge for the biceps femoris. The distal epiphysis is stout. Its malleolus is robust but not as triangular and well-developed as in *H. longiceps* (YPM-PV 15523) and *H. elongatus* (YPM-PV 13123; Fig. 13.5, 13.6). Distomedially the fibula bears two adjacent facets. The lesser and more proximal, for articulation with the tibia, is reconstructed with plaster. The larger and more distal facet, for articulation with the astragalus, is flat, massive, and crescent-shaped. MPM-PV 15086, a partial left fibula of *E. ingens*, preserves a fragment of a rectilinear, slender diaphysis and its isolated left distal epiphysis, which bears a small proximal tibial facet and a large, reniform facet for the astragalus. The fibular malleolus is similar to that of FMNH P13125.

DISCUSSION

The skull and mandibular characteristics of *E. ingens* were determined by De Iuliis *et al.* (2014, 2024) based mainly on its neotype, MPM-PV 3401, and MPM-PV 3451. In comparing these specimens with those previously described as new species and several others in museum collections that had never been formally described, these authors concluded that *Eucholoeops latirostris* Ameghino, 1891a, *E. fronto*, *E. externus*, *E. lafonei* Mercerat, 1891, and *E. curtus* were synonyms of *E. ingens* (see De Iuliis *et al.*, 2024: table 3 for a taxonomic synopsis of *Eucholoeops*). In doing so, these authors provided an appreciation of the metric and morphological variation in this species. Further, as part of their analysis, they suggested that several features in the type specimen of *E. latifrons* —MLP-PV 4-2; synonymized by Ameghino (1894) with *E. fronto*, an action accepted by Scott (1904)— differentiated it from *E. ingens*. However, De Iuliis *et al.* (2024) were unable to provide thorough comparative descriptions of MLP-PV 4-2, MPM-PV 3403, and MACN-A 11614, with those that they had assigned to *E. ingens*. As noted in Materials and Methods, no locality and stratigraphic information is available for MACN-A 11614. However, MACN records do indicate that it was collected by Carlos Ameghino. While this strongly suggests that it is Santacrucian, this supposition cannot be entirely confirmed. Even so, we have assigned it with a high degree of confidence to *E. latifrons* based on its morphological characteristics, noted in Descriptions and Comparisons.

Analysis of the *E. latifrons* specimens MLP 4-2, MACN-A 11614, and MPM-PV 3403 reveals several minor though consistent differences between this species and *E. ingens*, as well as similarities that suggest they are congeneric as sister species, at least among the contemporaneous sloths of the Santacrucian fauna. Among the latter features are the similarities in dentition (large, triangular caniniforms, mesiodistally compressed and oblong molariforms); relatively short and widened rostrum with preorbital width nearly equivalent to or greater than the postorbital constriction; little or no extension of the maxilla beyond the Cf alveolus; a humerus with a well-developed deltopectoral shelf that does not project as far anteriorly as in *Hapalops* and begins tapering more proximally than in this genus; and a femur with a large third trochanter that is not as prominent as that of *Hapalops* and with a widely V-shaped lateral margin, in contrast to the nearly rectilinear lateral margin of *Hapalops*. Among the differences between *E. latifrons* and *E. ingens* are that: the caniniforms are smaller in *E. latifrons*; the preorbital width is about equivalent to postorbital

width in *E. latifrons* rather than clearly greater as occurs in *E. ingens*; the maxilla extends anteriorly beyond the Cf alveolus in *E. latifrons* rather than forming a pillar-like sheath around this tooth; the lateral margin of the premaxilla bears a prominent flange in *E. latifrons*; the *latissimus dorsi* enthesis is more prominent in *E. latifrons* but extends less distally; in *E. latifrons* the lateral margin of the deltopectoral shelf is larger and the humeral diaphysis is more robust at mid-shaft; the greater trochanter does not extend as far proximally in *E. latifrons*, but its lesser trochanter is more prominent, and the margin between the trochanter and head is more deeply concave so that the medial femoral margin between this structure and head appears more deeply concave; and the trochanteric fossa and intertrochanteric crest are better developed in *E. ingens*.

Several of the anatomical differences associated with the anterior part of the skull and mandible are plausibly due to sexual dimorphism. Indeed, similar differences have been proposed as reflecting sexual dimorphism in other extinct sloth species, such as by Cartelle and Bohórquez (1982), Cartelle and De Iuliis (1995), De Iuliis and Cartelle (1999), McDonald (2006), Miño-Boilini and Zurita (2015), Boscaini *et al.* (2019), McAfee *et al.* (2021), and Varela *et al.* (2022). Differences in features used to support the existence of sexual dimorphism include, for example, the size of the caniniforms, which is generally correlated with a larger, more robust skull with enhanced features (*e.g.*, sagittal and supraorbital crests) or an elongated gracile skull, differences in caniniform wear pattern, slope of the occiput, and larger body size, which is generally evident in dimensions and proportions of limb elements (but see Prothero & Raymond, 2008). Although dimorphism in body size and skull characteristics was proposed for *Eremotherium laurillardi* (Cartelle & Bohórquez, 1982; Cartelle & De Iuliis, 1995) and *Eremotherium eomigrans* (De Iuliis & Cartelle, 1999), body size need not correlate with differences in skull robustness or dental differences. For example, although dimorphism in dental and skull differences was noted for *Paramylodon harlani* and *Lestodon armatus*, body size dimorphism was not (see McDonald, 2006; Varela *et al.*, 2022). Interestingly, a nearly identical difference in the angle of the Cf wear facet, noted above, between MLP-PV 4-2 and MPM-PV 3403 was reported by McDonald (2006, fig. 3A, B) for *P. harlani* and attributed to sexual dimorphism.

Several differences in the features noted in this report would seem to fall among those commonly cited in support of sexual dimorphism. They relate to a size difference of the caniniforms, and features of the maxillae and rostrum apparently related to this difference. On the other hand, the size of the sagittal crest, another commonly cited sexually dimorphic character, is approximately equal in MPM-PV 3451 (*E. ingens*) and MPM-PV 3403 (*E. latifrons*). De Iuliis *et al.* (2024) addressed this issue, particularly with respect to Scott's (1904) conceptualization of dimorphism. This author viewed dimorphism as present in *E. ingens* and *E. fronto* as an explanation for the existence of smaller and larger individuals within each species. De Iuliis *et al.* (2014, 2024) presented evidence suggesting that differences among nearly all the specimens assigned in the literature or museum records to one or the other of these species, as well as several other species, could be explained by intraspecific variation. De Iuliis *et al.* (2024) noted the strong bias in the quantity of recovered remains in favour of the *E. ingens* morphotype compared to the *E. latifrons* morphotype. These authors suggested that an expectation of a more equitable ratio might speak against the view attributing the differences to sexual dimorphism but recognized that a female or male bias has been reported for some mammalian fossil species (see *e.g.*, McDonald & Ray, 1989; Gower *et al.*, 2019). McDonald and Ray (1989; see also Bover *et al.*, 2018) suggested that the male bias in remains of the extinct muskox *Bootherium* may have resulted from preservational bias (the more fragile female skulls were less likely to be preserved), whereas McDonald (2006) noted that the difference in favour of the robust (presumably male) remains of *Paramylodon harlani* may have resulted from greater territorial range of males (leading to their increased entrapment).

In the case of the *Eucholoeops* remains reported here, however, the skulls of *E. latifrons* are as robust (except for anteriorly) as those of *E. ingens*, and the depositional environment of the Santa Cruz Formation was not a tar seep that entrapped individuals. Similarly, body size does not seem to differ between specimens of *E. ingens* and *E. latifrons* —or, at least, the *E. latifrons* specimens fall comfortably within the size range established for *E. ingens*. Also, a difference in the course of the stapedial artery sulcus would not be expected to be sexually dimorphic. Further,

some postcranial differences between these species would seem not to be expected. The larger caniniform and rostrum morphotypes have generally been assumed to belong to male individuals and although there do not seem to be body size differences, some skeletal features of *E. latifrons* suggest stronger musculature, as is evident in the humerus (larger *latissimus dorsi* enthesis and deltopectoral crest) and femur (larger lesser trochanter).

Taken together, the similarities and differences between *E. ingens* and *E. latifrons* are ambiguous with regard to whether they are better viewed as supporting the distinction between these species or as evidence of sexual dimorphism. Viewing them as distinct species may well be a case of 'missing the forest for the trees' because, as noted by Varela *et al.* (2022: 534): "with fossil species badly preserved in the fossil record, where specimens tend to be fragmentary and sample sizes of certain elements are scarce… intraspecific variability due to sexual dimorphism can produce considerably different morphotypes that could be eventually recognised as completely different taxa." While we certainly agree with this assessment, it is also true that the ambiguity produced by the scarce and fragmentary nature of the fossil record obscures other reasons for different morphotypes. In the case under consideration, the specimens are few and fragmentary, and we cannot be confident of the relevance of several of the characters.

There are, for example, only four specimens (three for *E. ingens* and one for *E. latifrons*, and on only one side of the skull for the latter) that clearly preserve a stapedial artery sulcus, and their course differs. However, it is not evident whether this difference is due to variation, be it specific, intraspecific, or intraindividual. It is neither clear the degree to which the cited postcranial differences are relevant. Most of the cranial differences may be suggestive of sexual dimorphism, with the more robust caniniform and rostrum considered as male individuals. However, we would not then expect the more powerful musculature implied by several postcranial features in female individuals. As well, the ratio in quantity of one over the other —there are many remains of *E. ingens* but only three of *E. latifrons*— may have nothing to do with sexual dimorphism in this particular case and, therefore, may not require an explanation. It is worth noting that such differential preservation is not unusual for the fossil sloth record of the Santa Cruz Formation. For example, there are many remains reported for some *Hapalops* species and *E. ingens*, but considerably fewer for *Hyperleptus*, *Analcimorphus*, *Megalonychotherium*, and *Planops*. It may be the case that the quantity of remains reflects the relative abundance of individuals (reflecting population density). Lastly, the difference in angle of the caniniform wear facet reported by McDonald (2006) between males and females of *P. harlani* is mirrored in MLP-PV 4-2 and MPM-PV 3403, which are considered here to be conspecific and therefore perhaps indicates that sexual dimorphism existed in *E. latifrons*.

Given the ambiguities inherent in the remains and characters, we suggest maintaining the two species of *Eucholoeops*, *E. ingens* and *E. latifrons*. While we fully recognize the need to reconsider this decision pending the recovery of additional remains, maintaining these two readily distinguishable morphotypes as species formally recognizes differences that should be evaluated in future studies.

CONCLUSIONS

Analyses of remains assigned to *Eucholoeops* and *Hapalops*, two closely similar Santacrucian sloths, suggest that two species of *Eucholoeops*, *E. ingens* and *E. latifrons*, may be recognized as valid. Comparisons of MLP 4-2 (the type specimen of *E. latifrons*), MPM-PV 3403, and MACN-A 11614 (the last two assigned here to the species) with those assigned to *E. ingens* by De Iuliis *et al.* (2014, 2024) reveal several subtle though consistent differences between these species and similarities that suggest that they are congeneric. Similarities include features of the skull and dentition (*e.g.*, relatively short, wide rostrum; preorbital width nearly equivalent to or greater than the postorbital constriction; little or no extension of the maxilla beyond the Cf alveoli; large, triangular caniniforms, and mesiodistally compressed, oblong molariforms) and postcranial skeleton (*e.g.*, humerus with a well-developed deltopectoral shelf that does not project as far anteriorly and begins tapering more proximally than in *Hapalops*; femur with a V-shaped third trochanter in contrast to the larger third trochanter with a rectilinear lateral margin of *Hapalops*). *E. latifrons* differs from *E. ingens* in, for example, its smaller caniniforms, nearly equivalent preorbital and postorbital widths (in contrast to the markedly greater width of the former as opposed to the latter), the anterior extension of the maxilla

beyond the Cf alveolus, more prominent but less distally extended *latissimus dorsi* enthesis, larger lateral margin of the humeral deltopectoral shelf, less proximally extended femoral greater trochanter, larger lesser trochanter, and less prominent trochanteric fossa and intertrochanteric crest. The possibility that the features set forth here as evidence for a specific distinction between *E. latifrons* and *E. ingens* instead represent sexually dimorphic characters of a single species is considered. However, these features are inconsistent with evidence cited in the literature to support sexual dimorphism in extinct and extant sloths. Therefore, this report suggests that specific status be maintained.

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