

Systematic paleontology (vertebrate paleontology)

A new species of Megalonychidae (Mammalia, Xenarthra) from the Quaternary of Poço Azul (Bahia, Brazil)

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Received 18 January 2008; accepted after revision 20 May 2008

Available online 10 July 2008

Presented by Philippe Taquet

Abstract

The new genus and species *Ahytherium aureum* (Mammalia, Xenarthra, Megalonychidae) from the Quaternary of Poço Azul (Bahia, Brazil) is described. It is the first Brazilian megalonychid known from reasonably complete and well-preserved remains. Purported Brazilian megalonychids described in the past, such as *Ocnopus gracilis* and *Xenocnus cearesis*, are noted as belonging to other sloth clades, and the acceptance by past paleontologists of the existence of ‘strange’ megalonychids in Brazil is shown to be erroneous. *Ahytherium aureum*, in fact, exhibits typical megalonychid morphology. It differs from other known members of Megalonychidae in several characters, including a markedly shortened, but high rostral region, with dorsally inflated frontals, wide zygomatic processes of the frontal, narrow, blade-like and anterolaterally oriented lacrimals, curved, slender and oval caniniforms, gracile humerus with less developed deltopectoral shelf, and relatively distal position of the greater trochanter of the femur. A second specimen from São Paulo state is tentatively assigned to the new genus and species. **To cite this article:** C. Cartelle et al., *C. R. Palevol* 7 (2008).

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Résumé

Une nouvelle espèce de Megalonychidae (Mammalia, Xenarthra) du Quaternaire de Poço Azul (Bahia, Brésil). Un nouveau genre et une nouvelle espèce, *Ahytherium aureum* (Mammalia, Xenarthra, Megalonychidae), provenant des niveaux quaternaires de Poço Azul (État de Bahia, Brésil), sont décrits. Il s’agit du premier mégalonychidé brésilien représenté par un matériel relativement abondant et bien conservé. Les mégalonychidés antérieurement décrits, tels qu’*Ocnopus gracilis* et *Xenocnus cearesis*, appartiennent à d’autres clades. L’acceptation dans le passé de l’existence d’étranges mégalonychidés au Brésil est erronée. *Ahytherium aureum* présente en réalité une morphologie typiquement mégalonychide. Il diffère des autres membres du clade Megalonychidae par plusieurs caractères, dont une région rostrale nettement raccourcie et élevée, des frontaux bombés, un frontal présentant de larges processus zygomatiques, des lacrymaux étroits, en forme de lames et dirigés antérolatéralement, des caniniformes courbes,

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minces et ovales, un humérus gracile montrant un plateau deltopectoral peu développé et une position relativement distale du grand trochanter du fémur. Un second spécimen provenant de l'État de São Paulo est présentement assigné à ce nouveau genre et à cette nouvelle espèce. **Pour citer cet article :** C. Cartelle et al., C. R. Palevol 7 (2008).

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Keywords: Xenarthra; Megalonychidae; *Ahytherium aureum*; Quaternary; Brazil

Mots clés : Xenarthra ; Megalonychidae ; *Ahytherium aureum* ; Quaternaire ; Brésil

1. Introduction

Despite advances in our knowledge of sloth phylogeny, aspects of Megalonychidae systematics remain unresolved. Kraglievich [10] recognized as subfamilies four clades: Megalonychinae, Megalocninae, Orthotheriinae, and Nothrotheriinae. In addition to these, Hoffstetter [8] proposed the subfamily Ocnopodinae for a purportedly odd megalonychid, *Ocnopus gracilis*, and considered *Valgipes deformis* as a megalonychid, but too poorly known to be assigned to any of the then recognized subfamilies. Paula Couto [20] combined these two schemes in excluding the Nothrotheriinae, but including *Ocnopus* and *Valgipes*, and later created the subfamily Xenocninae for his species *Xenocnus cearensis* [21]. Inclusion of the extant *Choloepus* in and exclusion of 'true nothrotheres' (e.g., *Nothrotherium* and *Nothrotheriops*) from the Megalonychidae, essentially following the proposals of Patterson and Pascual [17,18], have increasingly gained widespread support over the past three decades (e.g., [6,14,22,23]). More recently, nothrotheriids have been generally viewed as more closely related to megatherioids ([2,6], for further discussion on the position and definition of this clade).

Under this scheme, megalonychids had come to be recognized as mainly Central American and West Indian, where they are abundantly represented and highly diverse (e.g., *Meizonyx*, *Acratocnus*, *Parocnus*, *Megalocnus*, and *Neocnus*), and from which the oldest certain member of the clade has been recovered [28]. They are reasonably abundant, though much less diverse in North America (e.g., *Megalonyx* and *Pliometanastes*; [7]).

Megalonychids are possibly represented as early as the Eocene of Antarctica (cf. Megalonychidae, [27]). In South America, megalonychids are signaled by isolated remains in the Deseadan of Patagonia [1] and Bolivia [22], but became abundant and represented by nearly complete skeletons in the Santacrucian of Patagonia [24]. Although the clade has a long history in this continent, later remains are scarce so that most subsequent South American megalonychids were poorly

known (e.g., *Pliomorphus*, *Megalonychops*, and *Xenocnus*) or considered somehow odd for megalonychids (e.g., *Ocnopus* and *Valgipes*).

However, recent developments and new discoveries may be changing our concept of megalonychids, particularly of the later South American taxa. For example, Muizon et al. [16], at least, have signaled a possible return to a more traditional view of megalonychid relationships in reporting that Nothrotheriidae may be more closely related to megalonychids than to megatheriids, although these authors have yet to provide a phylogenetic analysis. Muizon and Mc Donald [15] provided a cladogram of nothrothere relationships and some synapomorphies of Megalonychidae. As for South America, Pujos et al. [22] reported the presence of *Diabolotherium nordenskioldi*, an apparently climbing megalonychid from the Peruvian Pleistocene based on relatively well-preserved remains from at least two individuals.

Advances in our understanding of Brazilian megalonychids have been especially noteworthy, spurred by the discovery of new remains and reanalysis of previously recovered specimens. Previously reported records of Brazilian Pleistocene megalonychids are few and consist essentially of isolated and generally poorly preserved remains from widely scattered localities.

Paula Couto's ([19] p. 297) comment succinctly summarizes the circumstances in this country, as well as South America as a whole: "Megalonychidae seem to have been richer in genera, species and individuals than the other known families of the order Edentata during Mio-Pliocene times. The contrary seems to have happened during Pleistocene times, at least in South America, when the Megatheriidae and the Mylodontidae, among the Pilosa (Tardigrada and Vermilingua), were by far dominant in the South America fauna." Brazilian Pleistocene remains described as megalonychid (excluding the nothrotheriid *Nothrotherium maquinense*) include: *Ocnopus gracilis* (Lund) (Ocnopodinae) and *Valgipes deformis* Gervais, 1874 (apparently so peculiar that Hoffstetter [8] believed it deserved its own subfamily) from Minas Gerais; *Megalonychops primigenius* Kraglievich, 1926 from Rio

Grande do Sul [19]; *Xenocnus cearensis* (also perceived as odd and deserving its own subfamily, the Xenocninae) from Ceará [21] and *Megalonyx* sp. from Acre [25]. The recovery of new remains from several Pleistocene localities allowed some authors [2,4] to demonstrate that remains attributed to *Ocnopus* and *Valgipes* do not represent odd megalonychids. Indeed, they are not Megalonychidae at all, but Scelidotheriinae, with *Ocnopus* a junior synonym of *Valgipes*. Further, analysis of the holotype of *X. cearensis* reveals that it does not represent a megalonychid astragalus, but a left unciform of the Panamerican megatheriine giant ground sloth *Eremotherium laurillardii*. We therefore formally synonymize *X. cearensis* with *E. laurillardii* (see Discussion). Finally, the abundant material reported here demonstrates the presence of a new Pleistocene Brazilian megalonychid species that presents, in contrast to the longstanding perception of the existence of odd megalonychids in Brazil, rather typical megalonychid morphology.

Abbreviations: C, c – upper and lower caniniforms, respectively; M, m – upper and lower molariforms, respectively, MCL – Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte; MNRJ – Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MZ-USP – Museu de Zoologia do São Paulo, São Paulo, Brazil, SALMA, South American Land Mammal Age.

2. Systematic paleontology

Order Xenarthra Cope, 1889

Suborder Tardigrada Latham and Davis in Forster, 1795 = Phyllophaga Owen, 1842

Family Megalonychidae Gervais, 1855

Genus *Ahytherium* gen. nov.

Synonymy: (?) *Iporangabradys* Santos, 1991 Nomen nudum.

Generic diagnosis: as for type species by monotypy.

Species *Ahytherium aureum*, gen. and sp. nov. (Figs 2–4, Tables 1–3) = (?) *Iporangabradys collecti* Santos, 1991 Nomen nudum.

Derivatio nominis: *Ahy*, from old Tupi-Guarani, a group of languages spoken by Brazilian indigenous peoples, meaning sloth; *therium* from the ancient Greek, meaning savage beast; and *aureum*, from the Latin, meaning golden.

In 2008, the Pontifícia Universidade Católica de Minas Gerais (PUC Minas) celebrates 50 years of dedicated activity and service to society. The specific epithet *aureum* pays homage to the University's golden jubilee and acknowledges the efforts of its professors, staff, and alumni in creating this rich history.



Fig. 1. Map showing location of Poço Azul Cave (Nova Redenção County, Chapada Diamantina, Brazil).

Carte de situation de la grotte de Poço Azul (Comté de Nova Redenção, Chapada Diamantina, Brésil).

Holotype: nearly complete skull and mandible, MCL 22834 (Figs 2–3, Tables 1–3).

Referred material: MCL 22875, which includes several postcranial elements (e.g. a vertebrae, femur, tibia, fibula, and pes) (Fig. 4, Tables 2–3).

Type locality and age: Quaternary deposits (Lujanian SALMA, Poço Azul, municipality of Nova Redenção, Bahia State, Brazil, Fig. 1).

Diagnosis: more gracile and smaller than *Megalonyx jeffersonii*. Rostral part of skull markedly inflated dorsally and width between zygomatic processes of frontal greater than between paraoccipital processes. External choana wider than high. Lacrimals oriented anterolaterally and narrow. Maxillary zygomatic process located dorsal to M1. Length between C1 and M4 nearly equal to length between M4 and occipital condyles. Margin of dentary ventral to molariforms wide and markedly convex. Mandibular symphysis anteriorly short and narrow, and with concave ventral margin. C1s narrow, oval in section, and larger than similarly shaped c1s. Scapular spine subdivides lateral scapular surface into approximately equal halves. Humerus with prominent greater and lesser tubercles, the former more proximal than the latter and nearly reaching the level of the head. Humeral diaphysis approximately cylindrical, with prominent anterior crests and deltopectoral shelf, and transversely expanded at its distal third. Proximal epiphysis wider than distal

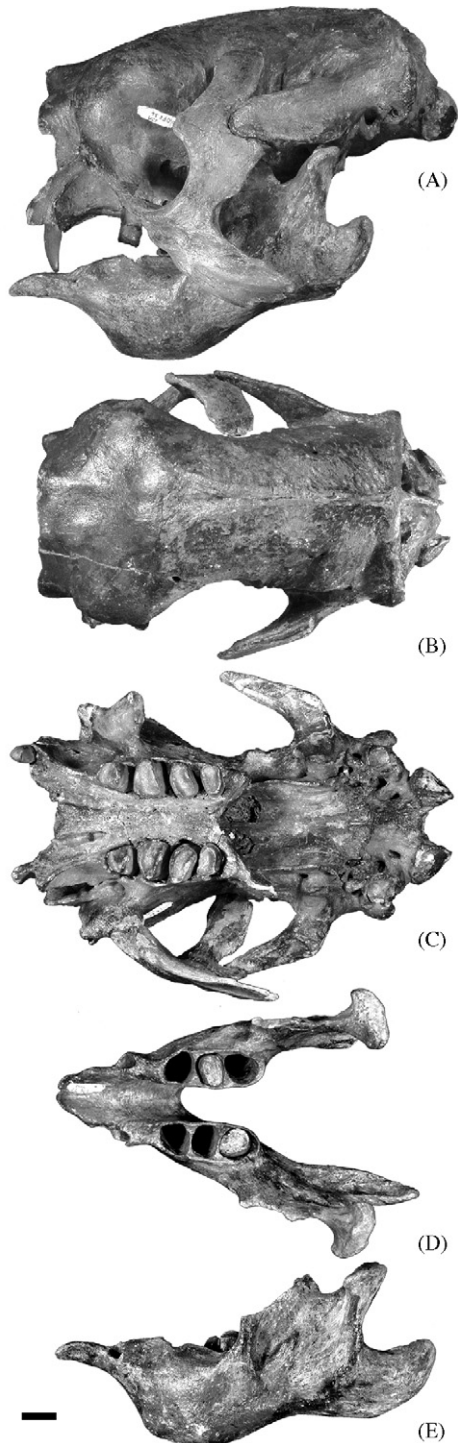


Fig. 2. Skull (MCL 22834–01) and mandible (MCL 22834–02) of *Ahytherium aureum* gen. et sp. nov., from the Quaternary of Poço Azul (Brazil). **A**, Skull and mandible in lateral view (reversed from the original); **B**, skull in dorsal view; **C**, skull in ventral view; **D–E**, mandible in occlusal and lateral views, respectively. Scale: 20 mm. *Crâne* (MCL 22834–01) et mandibule (MCL 22834–02) d'*Ahytherium aureum* nov. gen. et sp., du Quaternaire de Poço Azul (Brésil). **A**, Crâne

articular surfaces. Ulna with short olecranon process, mediolateral narrow and longitudinally curved, producing concave anterior and lateral surfaces. Radius narrow and curved, anteriorly convex, and tapered lateral margin; width of anterior surface narrower at proximal third, and distal two-thirds of nearly constant width. Femur with semicircular head, with greater trochanter relatively distal in position, third trochanter relatively weak, and distal articular surfaces not contiguous. Tibia short with anterolateral margin strongly tapered. Astragalus with separated ectal and sustentacular surfaces. Calcaneum with tuber calcis strongly compressed. Pedal digits 1 and 5 rudimentary, 2–4 narrow and unguis bearing, and 3 larger than 2.

3. Description (Figs. 2 and 3, Tables 1–3)

The well-preserved skull MCL 22834/01 is missing small parts of the mesial alveolar walls of the caniniforms, left zygomatic arch, and the pterygoid blades (Fig. 2A and C). The degree of sutural fusion indicates an adult individual. In dorsal view, the rugose, posteriorly slanting occiput is convex on either side of the prominent external occipital crest (Fig. 2B), which continues from the sagittal crest but does not reach the margin of the foramen magnum. The nuchal crest projects more markedly than the sagittal crest (Fig. 2B). The latter subdivides near the frontoparietal suture into the weakly developed temporal lines. Each curves anterolaterally to reach the postorbital process of the frontal, which bears a pronounced eminence (Fig. 2A). The width across this region is greater than between the paraoccipital processes. The rostrum is short and wide, with the preorbital constriction wider than the postorbital constriction (Fig. 2A–C, Table 1).

In lateral view, the dorsal border outlines a gentle arc between the nuchal crest and frontal eminence, but is depressed at the nasals (Fig. 2A). The brevity of the rostrum is clearly appreciated in this view. The large, nearly hemispherical zygomatic process of the frontal projects abruptly laterally, and the narrow, blade-like lacrimal is oriented anterolaterally.

The foramina in the sphenoidal region and temporal fossa are well preserved (Fig. 3). A small, possibly alveolar, foramen lies posteroventral to the posterior opening of the infraorbital canal. As in most xenarthrans, a single depression contains the openings of the optic canal and

et mandibule en vue latérale (à l'envers par rapport à l'original); **B**, crâne en vue dorsale; **C**, crâne en vue ventrale; **D–E**, mandibule en vues occlusale et latérale, respectivement. Échelle : 20 mm.

Table 1

Measurements of skulls and mandibles of *Ahytherium aureum* gen. and sp. nov., from the Quaternary of Poço Azul (Brazil) in mm (* = estimated data; + = alveolar)

Dimensions des crânes et mandibules d'Ahytherium aureum gen. et sp. nov., du Quaternaire de Poço Azul (Brésil) en mm (= mesure estimée, + = alvéolaire)*

Skull	MCL 22834						MZ-USP 06
Distance between the occipital condyle and the mesial margin of C1 alveolus	286						315*
Distance between the zygomatic process of frontal and the nucchal crest	160						167
Width between the zygomatic processes of frontal	142						121*
Minimal width at the temporal fossa	88						93
Height frominion to ventral margin of foramen magnum	89						101*
Width between the mastoid processes	126						129*
Width of palate between M1s	33						33
Width of palate between M2s	25						27
Width of palate between M4s	27						31
Distance between the lateral margins of occipital condyles	78						75*
Mandibles	MCL 22834	MCL 22866	MCL 22867	MCL 22868	MCL 22873	MCL 22869	MCL 22872
Length from the mesial margin of c1 (or its alveolus) to the posterior margin of the angular process	210	204*	—	—	—	—	—
Height of ramus at m1	66	60	60	52	58	67	52
Length of diastema between the distal margin of c1 (or its alveolus) and the mesial margin of m1	21	24	20	27	15	19	18
Width of diastema	57	51	46	48	50	50	48*
Alveolar length of the tooth row (m1–m3)	—	—	—	—	—	—	—
Length between the mesial margin of c1 (or its alveolus) and the distal margin of m3	92	99	93	90	88	87	83
Upper and/or lower tooth (mesiodistal/vestibulolingual)	MCL 22834		MCL 22869		MCL 22873		MCL 22872
C1	14/10		—		—		—
M1	17/16		—		—		—
M2	17/23		—		—		—
M3	14/22		—		—		—
M4	12/19		—		—		—
c1	12/10		10/9		18/8 ⁺		18/6
m1	16/22 ⁺		17/21		18/21		15/17
m2	17/21		16/20		15/20		16/18
m3	21/20		17/20		16/18		17/18

orbital fissure ventrally on the orbital wall. The foramen rotundum also lies in the depression, but is more ventrally located, as is the foramen ovale (Fig. 3). The distance between the orbital fissure and foramen rotundum is about equal to the distance between the latter and the foramen ovale.

The right zygomatic arch is well preserved (Fig. 2A–C). The short and robust zygomatic process of the squamosal is nearly parallel to the dorsal skull border (Fig. 2A–B). It is not fused anteriorly with the squamosal process of the jugal bone. The orbital portion is rounded and ventrally demarcates the orbit and bears two pro-

cesses that are about equally developed, one projecting posterodorsally and the other posteroventrally.

In ventral view, the transverse plane through the distal molariforms divides the skull into approximately equal halves (Fig. 2C). The palate is narrow between the molariforms, but expands markedly anteriorly to the M1s towards the C1s, these two teeth being separated by a diastema that is just longer (40 mm) than half the length of the molariform series (72 mm) (Table 1). The anterior margin of the palate is semicircular, with a concavity oriented posteriorly. The internal choana is slightly higher (50 mm) than wide (40 mm). The basicranium, includ-

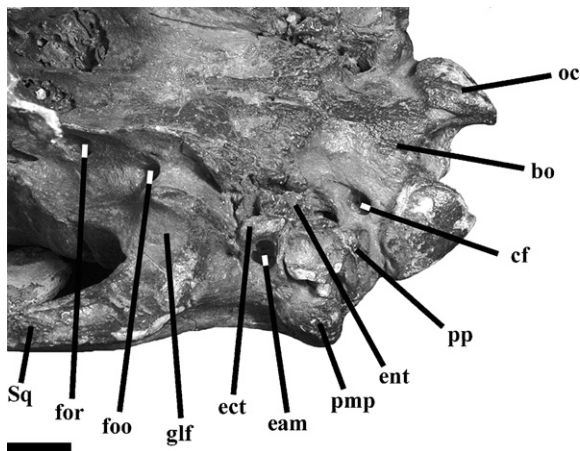


Fig. 3. Basicranium of *Ahytherium aureum* gen. and sp. nov. from the Quaternary of Poço Azul (Brazil) in lateroventral view. Abbreviations: bo, basioccipital; cf, condyloid foramen; eam, external auditory meatus; ect, ectotympanic; ent, entotympanic; foo, foramen ovale; for, foramen rotundum; glf, glenoid fossa; oc, occipital condyle; pmp, pars mastoidea of the petriotic; pp, paraoccipital process; sq, squamosal. Scale: 20 mm.

Base du crâne d'Ahytherium aureum nov. gen. et sp. du Quaternaire de Poço Azul (Brésil) en vue latéro-ventrale. Abréviations : bo, basioccipital ; cf, foramen condyloïde ; eam, trou auditif externe ; ect, ectotympanique ; ent, entotympanique ; foo, foramen ovale ; for, foramen rotundum ; glf, fosse glénoïde ; oc, condyle occipital ; pmp, pars mastoïde du périoïque ; pp, processus paraoccipital ; sq, squamosal. Échelle : 20 mm.

ing the basioccipital, petrosal, tympanics, and mastoid, is illustrated and labeled in Fig. 3. The ectotympanic is oval and projects slightly more ventrally than the entotympanic (Fig. 3).

In anterior view the external choana is considerably wider (105 mm) than high (85 mm), and the maxillae extend farther anteriorly than the nasals. The lacrimals, already noted as narrow, expand anterolaterally (152 mm) to project farther laterally than the processes of the frontals, which bear at this point the marked eminence described above (145 mm).

In addition to the mandible of the holotype (MCL 22834, Fig. 2A and D–E, Tables 1–3) are five other specimens that are reasonably well preserved. The symphyseal region anterior to the caniniforms is preserved only in the holotype, which lacks, however, the coronoid process and a small part of the right angular process (Fig. 2D–E). The coronoids, though, are preserved almost entirely in MCL 22866. In dorsal view, the symphyseal region is a narrow trough, semicircular in section, that extends anteriorly to the caniniforms as a triangular spout and is approximately double the length of the diastema between c1 and m1 (Fig. 2D, Table 1). The posteroventral symphyseal margin lies at or slightly

anterior to m2. The tooth rows between the molariforms are nearly parallel, with the caniniform on each side situated slightly vestibularly to the row (Fig. 2D). The angle formed between the horizontal rami of the dentaries at the symphysis is 45° (Fig. 2A and E). The distance between the condyles (95 mm) is nearly equal to the length of the tooth rows (c1–m3) (Fig. 2D and E, Table 1).

In lateral view, the symphyseal spout projects anterodorsally, with a concave ventral margin (Fig. 2A and E). The ventral surface of the horizontal ramus is transversely wide and convex. The base of the coronoid process bears a deep masseteric fossa. The pterygoid fossa, on the medial surface of the angular process, is well demarcated and rugose. The coronoid process extends farther dorsally than the mandibular condyle and is considerably raised relative to the occlusal surfaces of the lower teeth and of the symphysis (Fig. 2A and E).

The upper dentition is known from numerous implanted or isolated specimens that allow characterization of all the teeth and an appreciation of intraspecific variation (Table 1). Only the right C1 is missing from the holotype (Fig. 2C). C1 is curved in lateral view, oval in section, concave distally, with an obliquely worn apical surface, and occludes mesially to c1 (Fig. 2A). The trapezoidal M1 and subtriangular M2–M3 have longer lingual than vestibular surfaces. The suboval M4, the smallest molariform, has a longer vestibular than lingual surface (Fig. 2C). Implanted in the maxilla, the molariforms outline a gentle, lingually convex arch.

The lower teeth are also well known. Several mandibles (MCL 22869, MCL 22872, and MCL 22873) nearly or completely preserve the dentition. Isolated teeth are also preserved. The holotype MCL 22834 has only the right m2 and left m3 implanted (Fig. 2A and D–E, Table 1). Like its counterpart in the upper jaw, c1 is caniniform, but smaller and its oblique apical wear facet faces mesially. In section m1 is triangular, with a shorter lingual margin as base and apex vestibularly, m2 is rectangular, with a shorter lingual margin, and is the smallest molariform, and m3 is suboval (Fig. 2D and E, Table 1).

MCL 22875 preserves most of the vertebrae (the last few caudal vertebrae are missing) and the pelvic girdle. There are 16 thoracic, 4 sacral and, probably, 23–25 caudal (17 are actually preserved) vertebrae.

On the lateral surface of the scapula, the scapular spine is well developed and widens anteriorly into the acromial process. The acromial arch, the bony bridge between the acromial and coracoid processes typical of tardigrades, is not preserved in any of the five scapulae available for study. The posterior margin bears a well-developed crest that demarcates the subscapular

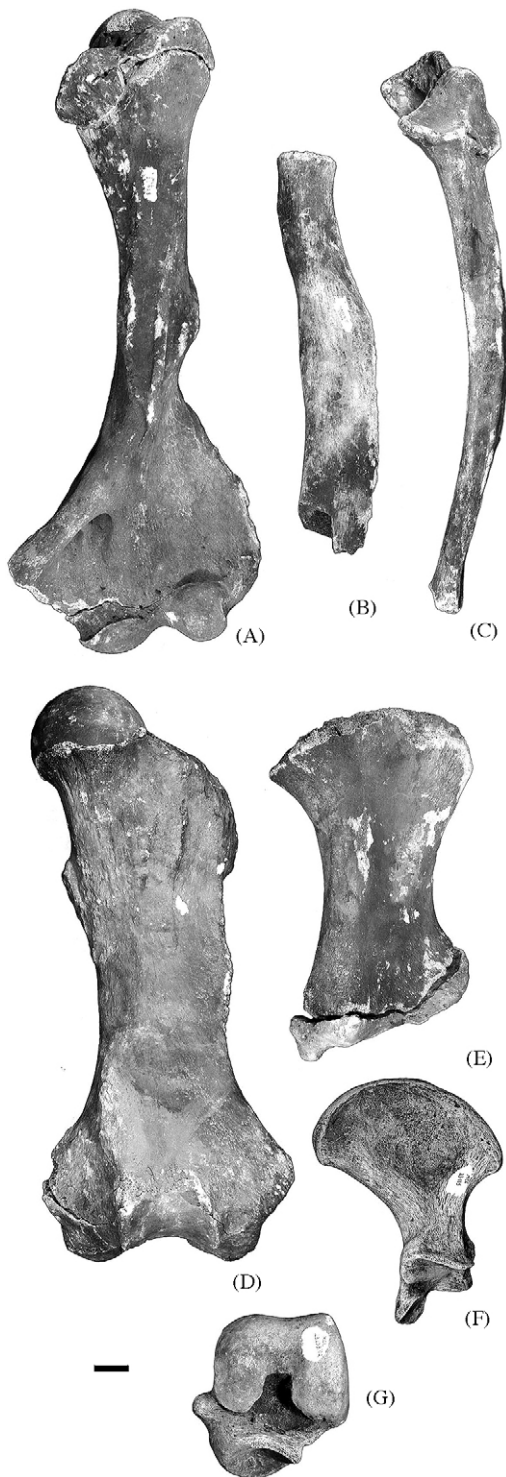


Fig. 4. Postcranial elements of *Ahytherium aureum* gen. and sp. nov, from the Quaternary of Poço Azul (Brazil). **A**, Left humerus (MCL 23004-01) in anterior view; **B**, right radius (MCL 23029) in anterior view; **C**, left ulna (MCL 23019) in anterior view; **D**, left femur (MCL 23033-01) in anterior view; **E**, left tibia (MCL 22875-93) in anterior

fossa posteriorly. The glenoid fossa is anteroposteriorly suboval, with a more extensive posterior rather than anterior margin. The coracoscapular foramen lies midway between the proximal margin of the base of the scapular spine and the anterior margin of the glenoid fossa.

The humerus is represented by two complete elements and more than 13 specimens in various states of preservation (Fig. 4A). The diaphysis is elongated and tubular, except at its distal third, where it widens transversely and is flattened (Table 2). The greater tuberosity, larger and more proximally projecting than the lesser tuberosity, nearly reaches the level of the head. The anterior surface of the diaphysis bears a prominent deltopectoral shelf (De Iuliis [3] provides a detailed discussion of this structure in *Megatheriinae* ground sloths) that is widest at about the humeral midlength due mainly to the marked lateral development of the deltoid crest, which forms the shelf's lateral margin. The medial margin is formed by the pectoral crest, which arises proximally just distal to the bicipital groove, as occurs also in *Megalonyx jeffersonii* [26]. The pectoral crest extends distally and curves slightly medially, contributing to the width of the shelf (Fig. 4A). The crests, both rugose in their distal portions, converge and meet distally. A third, much shorter and nearly median, but markedly developed crest, probably for insertion of the brachioradialis or cephalohumeralis muscles, is present on the shelf where the pectoral and deltoid crests converge. A prominent notch on the lateral surface of the humerus, just distal to the most lateral excursion of the deltoid crest, continues distally into the gently rounded supinator ridge. Mediolaterally, the humerus bears a single entepicondylar foramen in seven of the eight preserved humeri. In the eighth, MCL 23004 (Fig. 4A), a partition divides the opening into separate foramina, an example of intraspecific variation, perhaps isolating the passages of the brachial artery and median nerve. Two humeri preserve the distal articular surface. The capitulum, for the radius, is anteroposteriorly more extensive than the trochlea, for the ulna.

In the radius, out of which three are preserved, (Fig. 4B, Table 2), the neck is relatively indistinct, with a weakly projecting bicipital tuberosity. From the tuberos-

view; **F**, left calcaneum (MCL 23065) in dorsal view; **G**, left astragalus (MCL 22875-52) in dorsal view. Scale: 20 mm.

Éléments postcrâniens d'Ahytherium aureum nov. gen. et sp. du Quaternaire de Poço Azul (Brésil). **A**, Humérus gauche (MCL 23004-01) en vue antérieure ; **B**, radius droit (MCL 23029) en vue antérieure ; **C**, cubitus gauche (MCL 23019) en vue antérieure ; **D**, fémur gauche (MCL 23033-01) en vue antérieure ; **E**, tibia gauche (MCL 22875-93) en vue antérieure ; **F**, calcaneum gauche (MCL 23065) en vue dorsale ; **G**, astragale gauche (MCL 22875-52) en vue dorsale. Échelle : 20 mm.

Table 2

Measurements of atlas, pelvis, and forelimb elements of *Ahytherium aureum* gen. and sp. nov., from the Quaternary of Poço Azul (Brazil) in mm (* = estimated data)

Dimensions des atlas, pelvis, ainsi que des éléments du membre antérieur d'Ahytherium aureum gen. et sp. nov., du Quaternaire de Poço Azul (Brésil) en mm (= mesure estimée)*

Atlas	MCL 22875	MCL 22936
Greatest transverse width	132	125
Greatest transverse width across the anterior articular facets	81	74
Greatest dorsoventral width	62	64
Anteroposterior length at midline of the dorsal arch	34	28
Greatest anteroposterior length	56	55
Greatest transverse width across the posterior articular facets	74	73
Scapula	MCL 22955	MCL 23000
Greatest length of the glenoid fossa	80*	72
Greatest width of the glenoid fossa	40*	47
Length between the anterior margin of glenoid and the vertebral border along the scapular spine	235*	245*
Humerus	MCL 23004	MCL 23006
Greatest length between the head and the medial condyle	406	390*
Greatest proximal transverse width	103	110
Greatest proximal anteroposterior depth	83	84
Posterior diaphyseal length	57	65
Greatest distal transverse width	167	175*
Greatest transverse trochlear width	92	—
Ulna	MCL 23022	MCL 23019
Greatest length	350*	360*
Length of the olecranon process	115*	120*
Distal transverse width	33*	34*
Distal anteroposterior depth	45	50
Anteroposterior depth at the coronoid process	80	85
Radius	MCL 23030	
Anteroposterior depth at the coronoid process	345*	
Anteroposterior midshaft width	45	
Pelvis	MCL 22875	
Dorsoventral diameter of the pelvic opening	185	
Greatest transverse diameter of the pelvic opening	268	
Greatest width of posterior end of the pelvis	380	
Anteroposterior diameter of the acetabulum	74	
Dorsoventral diameter of the acetabulum	81	
Length of the fused sacral vertebrae	188	
Transverse diameter of the anterior surface of the centrum (first sacral vertebra)	85	
Height between the centrum and the spinous process (first sacral vertebra)	124	
Transverse diameter of the vertebral canal (first sacral)	54	
Transverse diameter of the posterior surface of the centrum (last sacral vertebra)	70	
Dorsoventral diameter of the posterior surface (last sacral vertebra)	49	
Length of crest formed by fused sacral spinous processes	156	
Height between the centrum and the spinous process (last sacral vertebra)	88	
Dorsoventral diameter of obturator foramen	110	
Dorsoventral diameter ischiatic foramen	98	

ity, the diaphysis expands slightly and deflects slightly medially, with the rest of the diaphysis being of nearly constant width. The lateral diaphyseal margin is thicker than the sharp-edged medial margin, which is slightly

curved longitudinally and slightly concave posteriorly and medially.

Seven incomplete ulnae are preserved. The diaphysis of the ulna is markedly bowed laterally and of nearly

constant thickness throughout most of its length, narrowing slightly at its distal quarter (Fig. 4C, Table 2). The olecranon process is short and the trochlear notch is widely open.

Preserved elements of the manus include three scaphoids, a lunar, trapezoid, magnum, unciform, two fused trapezoid-metacarpal I elements, two metacarpals II, III and IV, and a metacarpal V. The morphology and relationships of these elements are as in other sloths.

The femur, known from six specimens (Fig. 4D, Table 3), is relatively elongated and narrow, with a nearly

parallelogram outline in anterior view, resembling in these aspects that of *Megalonyx jeffersonii*. The hemispherical head does not have a well-defined fovea. The neck is relatively elongated, but indistinct. The greater trochanter, while well developed and rugose, does not project proximally, in contrast to the condition typical of other sloths. Rather, the proximolateral margin of the femur is gently rounded. The lesser trochanter is distinct, but relatively small. The third trochanter is weakly developed, barely projecting laterally from the midlength of the diaphyseal surface (Fig. 4D). The ect- and entepi-

Table 3

Measurements of hind limb elements of *Ahytherium aureum* gen. and sp. nov., from the Quaternary of Poço Azul (Brazil) in mm (* = estimated data)
Dimensions des éléments du membre postérieur d'Ahytherium aureum gen. et sp. nov., du Quaternaire de Poço Azul (Brésil) en mm (* = mesure estimée)

Femur	MCL 22875	MCL 23033
Length between the head and the medial condyle along the medial surface	382	377
Greatest proximal transverse width	134	135
Transverse width of the head	74	75
Anteroposterior depth of the head	76	77
Transverse width across epicondyles	128	131
Transverse diaphyseal width proximal to epicondyles and distal to third trochanter	81	85
Tibia	MCL 22875	MCL 23085
Length from the intercondylar spine to the middle of the astragalar surface	207*	—
Minimal transverse diaphyseal width	—	105
Distal transverse width	115	—
Transverse proximal width from the margin of the medial condyle to the cnemial crest	—	65
Anteroposterior proximal depth from the posterior margin of the lateral condyle to the anterior margin of the medial condyle	87	—
Fibula	MCL 22875	
Greatest length	215*	
Anteroposterior distal depth across articular facet	61	
Transverse distal width across anterior surface	47	
Astragalus	MCL 22875	
Anteroposterior length at the middle of the trochlea between the posterior and anterior margins of the navicular process	100	
Transverse width of the posterior margin of the trochlea	70	
Transverse width of the anterior margin of the trochlea	78	
Transverse width of the navicular process	73	
Dorsoventral height of the navicular process	51	
Calcaneum	MCL 22875	MCL 23063
Length from the posterior margin of the tuber calcis to the anterior margin of the sustentaculum facet	172*	173
Transverse width of the tuber calcis	135*	130
Transverse width of the neck	44	56
Proximal height between dorsal margin of the posterior ectal facet to the ventral margin of the cuboid process	75	67

condyles are pointed and prominent. Distally, the medial and lateral articular facets are not contiguous with the patellar trochlea.

The patella (of which four are known) is flattened, extended distally, and narrow. The height and width of its articular facet for the femur are about equal and in this region the patella is thicker and wider.

The tibia, known from at least four well-preserved specimens, has a narrow-edged and strongly concave lateral border (Fig. 4E, Table 3). The medial border is thicker and not as markedly concave. Its proximal articular surface is about equal in width and depth. The anterior diaphyseal surface is wide and flattened and bears the anteriorly oriented tibial tuberosity. The distal articular surface for the astragalus is shallowly concave and contiguous laterally with that for the fibula.

The fibula is known from a single specimen, unfortunately missing its proximal articular portion. Its distal portion is robust. The diaphysis is more flattened proximally than distally, where the element expands anteroposteriorly and, more markedly, mediolaterally.

Nearly all the right and left pedal elements of one individual (MCL 22875, Table 3) are known, as well as isolated elements from other individuals.

The strongly compressed, axe-shaped calcaneal tuber is thinner plantarly than dorsally (Fig. 4F). Its articular facets, the cuboidal, ectal and sustentacular, are separated. The latter is the smallest and most distally projecting. A prominent, well-defined crest extends from the medial border of the cuboidal facet to the calcaneum's plantar margin.

The tibial facet of the astragalus is pulley-shaped, but with a relatively shallow groove so that the surface is flattened (Fig. 4G). The surface lateral to this portion is occupied by the fibular facet. An articular surface lies anteriorly and medioplantally and consists of a circular, deeply concave portion medially and a rounded convex portion laterally, also present in most fossil sloths (Fig. 4G). The concavity and the medial part of the convexity articulate with the navicular; the lateral part of the convexity articulates with the cuboid. Distally the concave ectal and nearly circular and flat sustentacular facets are separated, with the former about three times the latter in area.

The cuboid, navicular, ectocuneiform, mesocuneiform, metatarsals and digits II–IV are known completely, and follow the general pattern present in other sloths, with digit V reduced and digits II–IV, at least, bearing three phalanges, the most distal being unguals. The ento- and mesocueiforms, and metatarsal I and its proximal phalanx are co-ossified. The ungual

phalanges are narrow and strongly curved, as also occurs in the homologous elements of the manus.

4. Discussion

During the 1970s, a reasonably complete but deformed megalonychid skull was discovered in a limestone cave in Iporanga (SP), Brazil. This specimen, MZ-USP 06, was analyzed by C. de Paula Couto in an article that was written in 1980, but never published [5]. In this work, the noted Brazilian paleontologist, following the work of Hoffstetter [8] outlined above, tentatively attributed this skull to the species '*Ocnopus gracilis*' given that, again deferring to Hoffstetter's opinion, this species was based on postcranial remains, but its skull was not known. It was, therefore, not unreasonable to attribute the Iporanga skull to the headless 'megalonychid' skeleton.

Dos Santos [5] restudied the skull as part of his Masters dissertation. Doubtful about assigning it to the species of intertropical Pleistocene Megalonychidae then known, "*X. cearensis*" and "*O. gracilis*," which he considered valid, Dos Santos [5] rejected Paula Couto's proposal and chose instead to erect a new species, "*Iporangabradys collecti*". In the light of the above-noted conclusions [2,4] regarding the two purported megalonychid species, Dos Santos [5] bold decision has turned out to be correct, not because his doubt was justified, but because "*X. cearensis*" and "*O. gracilis*" turned out to be invalid.

A Masters dissertation is neither appropriate nor valid for formal erection of a new taxon [9]. Dos Santos' [5] dissertation was produced only in fulfillment of his Masters degree and never formally published, so that the name "*Iporangabradys collecti*" is rendered invalid as a nomen nudum, in accordance with ICZN [9].

MZ-USP 06 is tentatively assigned to the new taxon described here, but there is doubt to this assignment, as the skull is not well preserved, particularly anteriorly and ventrally on the basicranium, two especially diagnostic regions. The present authors are in the process of analyzing another new megalonychid species from intertropical Brazil that differs mainly in these regions from that under consideration here. MZ-USP 06 may belong to this second new species.

The skull of *Ahytherium aureum* (Fig. 2A–C) clearly differs from that of *Megalonyx jeffersonii* (Desmarest, 1822), described by various authors [11–13,26]. The skull is relatively narrower and elongated, particularly in dorsal view, in *Megalonyx*. In *A. aureum* the rostrum is higher, wider and shorter, the ascending ramus of the jugal projects more prominently, the zygomatic process

of the squamosal is more horizontally oriented, and the occiput is more oblique, so that the occipital condyles project more posteriorly. The temporal lines are more widely divergent and strongly curved, and the frontal eminences much more developed. The diastema between C1 and M1 is relatively shorter, so that the rostrum projects less markedly anteriorly to the molariforms. In the upper dentition, the caniniform of *M. jeffersonii* is relatively elongated mesiodistally and more nearly triangular, and the last two teeth are more rectangular. In *M. jeffersonii* the dentaries are more nearly parallel, the mandibular spout shorter and narrower, the condyles narrower (Fig. 2C–E, Table 1). The humeral diaphysis of *A. aureum* is markedly more gracile, the deltopectoral shelf less pronounced, and the distance across the distal epicondyles shorter. The femur of *M. jeffersonii* is more robust and quadrangular in outline, due mainly to a relatively greater proximal width and wider diaphysis, and the greater trochanter projects more proximally. The skull of *Pliomorphus ameghinoi* Kraglievich, 1923 is also lower and more elongated than that of *A. aureum*, including a longer, more slender rostrum. The occiput is oblique, but the external occipital crest reaches the margin of the foramen magnum. The femur of *Pliomorphus mutilatus* Ameghino, 1885 differs in having a proximally projecting greater trochanter, a more pronounced third trochanter, and the lateral tibial condyle and patellar trochlea connected by a narrow isthmus. *Amphiocnus paranense* Kraglievich, 1922 differs in having both tibial articular surfaces of the femur contiguous with the patellar trochlea.

The Caribbean megalonychids are also clearly distinct from *A. aureum*. In *Megalocnus rodens* Leidy, 1868, the skull is considerably lower, narrower, and more elongated, particularly in the rostrum, which is slender and drawn anteriorly with a notable diastema into a rodentiform morphology, a characterization reflected in a first tooth that is incisiform rather than caniniform. The humeral deltopectoral shelf is prominent and laterally projecting, and the femur is markedly expanded proximally. Similarly, the skull of *Mesocnus browni* Matthew, 1931 has a slender, elongated rostrum with a long diastema. Further, the base of the rostrum is strongly constricted, and the humerus has a markedly developed and laterally projecting deltopectoral shelf and nearly equally developed greater and lesser tubercles.

In describing the species *Xenocnus cearensis*, Paula Couto [21] created the new subfamily Xenocninae, which he considered necessary given the aberrant astragalus of *X. cearensis*. The species was based on isolated and fragmentary remains from Itapipoca (Ceará, Brazil),

but diagnosed entirely on MNRJ 2851-V, the holotype, which Paula Couto [21] identified as an astragalus. Three incomplete molariforms, a highly worn symphyseal fragment, and a cuboid were assigned to *X. cearensis*. These specimens, included in the hypodigm, are not diagnostic.

Direct comparison of the holotype (MNRJ 2851-V) with several unciform specimens of the megatheriine *Eremotherium laurillardi*, the Panamerican giant ground sloth, leaves no doubt that MNRJ 2851-V is an unciform of this species rather than the astragalus of a new and aberrant megalonychid. The largely incomplete molariforms assigned to *X. cearensis* may be examples of M5 of *E. laurillardi*. The fragmentary symphysis (MNRJ 3383-V) is not megalonychid: the alveoli of the caniniform teeth converge basally to lie adjacent to one another, a feature that does not occur in megalonychids, and a symphyseal spout is not present. The size and morphology of the cuboid (which similarly lacks megalonychid features) suggest mylodontid affinities.

5. Conclusion

1. Identification of the megalonychid skull MZ-USP 06 from Iporanga, São Paulo, as '*Ocnopus gracilis*' by Paula Couto (in [24]) and Dos Santos as '*Iporangabradys collecti*' is incorrect, for reasons given in the above text.
2. The subfamily Xenocninae and species *Xenocnus cearensis*, defined as a "large and apparently rare and aberrant South American megalonychid with peculiar tarsal and possibly carpal structure" ([21]:146) are rejected. The holotype (MNRJ 2851-V; [21]: Fig. 2), identified by its author as a right astragalus of this species is a left unciform of the Panamerican giant ground sloth *Eremotherium laurillardi*.
3. The new species *Ahytherium aureum* is based on several well-preserved remains from Poço Azul, a submerged cave near Nova Redenção, Bahia, that demonstrate its distinctness from other known Megalonychidae.
4. MZ-USP 06 is tentatively assigned, with reservation, to *A. aureum*.

Acknowledgments

The authors are grateful to the following individuals, institutions and organizations for providing logistic support and funding for the recovery expedition, transport, preparation, and study of the material presented in this report: Didier Dutheil (MNHN, Paris, France) and Dominique Lecuire (Lecuire Production, Paris, France), Fernando and Mauricio Dias and

Tulio Schargel (GrifaMixer, São Paulo, Brazil), Mauro Agostinho Ferreira (PUC Minas, Brazil), Simpliciano Lima (*in memoriam*), R. Seaberg, H.E.R. Blachford, Robert Luke, and the Office of Research and Innovation (George Brown College, Toronto, Canada), Cecav-IBAMA (Brazilian government), Gedeon (Paris, France), Grifa Mixer (São Paulo, Brazil), and Petrobras (Brazil).

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