

Systematic palaeontology (Vertebrate palaeontology)
A new ground sloth (Mammalia: Xenarthra) from
the Quaternary of Brazil

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Abstract

The record of South-American Pleistocene Megalonychidae is scarce. Of the species described for intertropical Brazil, including *Megalonyx* sp., *Ocnopus gracilis*, *Valgipes deformis*, *Xenocnus cearensis* and *Ahytherium aureum*, only the last, recently described, is valid. The new megalonychid species described here was recovered from the same locality as *Ah. aureum*. The latter is apparently more closely linked to the North-American Pleistocene forms whereas *Australonyx aquae* may be more closely related to the Antillean sloths. The fossil remains of extant taxa recovered in association with the new sloth species suggest that the region, currently within the Caatinga biome, was a mosaic of the Atlantic Forest and Savannah biomes during the final stages of the Pleistocene. **To cite this article:** G. De Iuliis et al., C. R. Palevol 8 (2009).

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Résumé

Un nouveau paresseux géant (Mammalia : Xenarthra) du Quaternaire du Brésil. Le registre des Megalonychidae pléistocènes en Amérique du Sud est rare. Parmi les espèces décrites provenant de la région intertropicale du Brésil, incluant *Megalonyx* sp., *Ocnopus gracilis*, *Valgipes deformis*, *Xenocnus cearensis* et *Ahytherium aureum*, seule cette dernière décrite récemment est valide. La nouvelle espèce de mégalonychidé décrite ici provient de la même localité qu'*Ah. aureum*. Cette dernière espèce semble apparentée aux formes quaternaires d'Amérique du Nord, alors qu'*Australonyx aquae* est plus proche des formes des Antilles. Les restes de fossiles d'espèces disparues retrouvées, associées avec la nouvelle espèce de paresseux suggèrent que cette région, actuellement située au sein du biome de Caatinga, était une mosaïque de biomes de la forêt Atlantique et de la savane durant les derniers stades du Pléistocène. **Pour citer cet article :** G. De Iuliis et al., C. R. Palevol 8 (2009).

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Mots clés : Xenarthra ; Megalonychidae ; *Australonyx aquae* ; Quaternaire ; Brésil

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1. Abbreviations

C	upper caniniform
M	upper molariform
MCN	Museu de Ciências Naturais Pontifícia Universidade Católica de Minas Gerais Brazil
MCL	acronym for paleontological collection of MCN
Mt	metatarsal
SALMA	South American Land Mammal Age

2. Introduction

Although the oldest record of sloths is from the middle Eocene of Antarctica [1], it is generally accepted that the Megalonychidae originated in South America, where it subsequently underwent several radiations that populated North America and the Antilles [15,19]. The record of South American Pleistocene megalonychids is exceedingly scarce compared to that of North America and the Antilles. Mones [11] considered only *Megalonychops carlesi* (Kraglievich, 1930) and *Pseudodiodomus annaratonei* (Ameghino, 1881) from Argentina as valid Pleistocene forms.

Paula Couto [14] recognized *Megalonychops primigenius* (Kraglievich, 1926) and *Megalonychops carlesi* from Argentina and *Megalonychops fontanai* (Kraglievich, 1926) from Uruguay. All these species are poorly known, based on incomplete long bones and some teeth [12,15], with the last two species considered as Miocene by Mones [11]. *Diabolotherium nordenskioldi* (Pujos, De Iuliis, Argot, and Werdelin, 2007) [17], from the Quaternary of Peru, is based on far more complete remains than those of the already mentioned species.

Until recently, remains assigned to Brazilian Pleistocene megalonychids were also very rare, comprising a few isolated and poorly preserved remains from southern Brazil [14,16] and the states of Ceará [16], Minas Gerais [8], and Acre [18]. However, most of these records are based on erroneous identifications (see below). Cartelle et al. [2] described the new Megalonychidae species from the Pleistocene of the State of Bahia, *Ahytherium aureum* (Cartelle, De Iuliis and Pujos, 2008) [3], known from teeth and a nearly entire skeleton. Indeed, it is the most complete South-American Pleistocene megalonychid known, and serves as the basis for comparison with the new species described here.

With regard to the other Brazilian Pleistocene megalonychids alluded to in the previous paragraph, Cartelle et al. [3] demonstrated that *Ocnopus gracilis* (Lund) and *Valgipes deformis* (Gervais, 1874), which were regarded as megalonychids by Hoffstetter [8] on postcranial



Fig. 1. Map showing location of Poço Azul Cave (Nova Redenção County, Chapada Diamantina, Brazil; after Cartelle et al. [2]).
Fig. 1. Carte de situation de la grotte de Poço Azul (comté de Nova Redenção, Chapada Diamantina, Brésil; d'après Cartelle et al. [2]).

remains discovered by P.W. Lund from the State of Minas Gerais during the first half of the 19th century, actually represent the Scelidotheriinae *Valgipes bucklandi* (Lund, Gervais, 1874). Consequently, *Ocnopodinae* (Hoffstetter, 1954) is invalid, as is Hoffstetter's [8] suggestion that *V. deformis* deserved its own suprageneric rank. Also, *Xenocnus cearensis* (Paula Couto, 1977) [16], which was long considered an aberrant megalonychid requiring its own subfamily Xenocninae [16], has as its holotype an unciform of the Megatheriidae *Eremotherium laurillardi* (Lund, 1842), so that the species and its subfamily are rendered invalid [2]. Various teeth recovered from the State of Rio Grande do Sul were assigned by Paula Couto [14] to *Megalonychops primigenius*. However, this is doubtful as the teeth of this species are not known. Simpson and Paula Couto [18] noted the presence of *Megalonyx* sp. in the State of Acre. This seems unlikely as well, given that this genus is known otherwise in North America.

3. Systematic paleontology

- order Xenarthra (Cope, 1889);
- suborder Tardigrada Latham and Davis in Forster, 1795 = Phyllophaga (Owen, 1842);

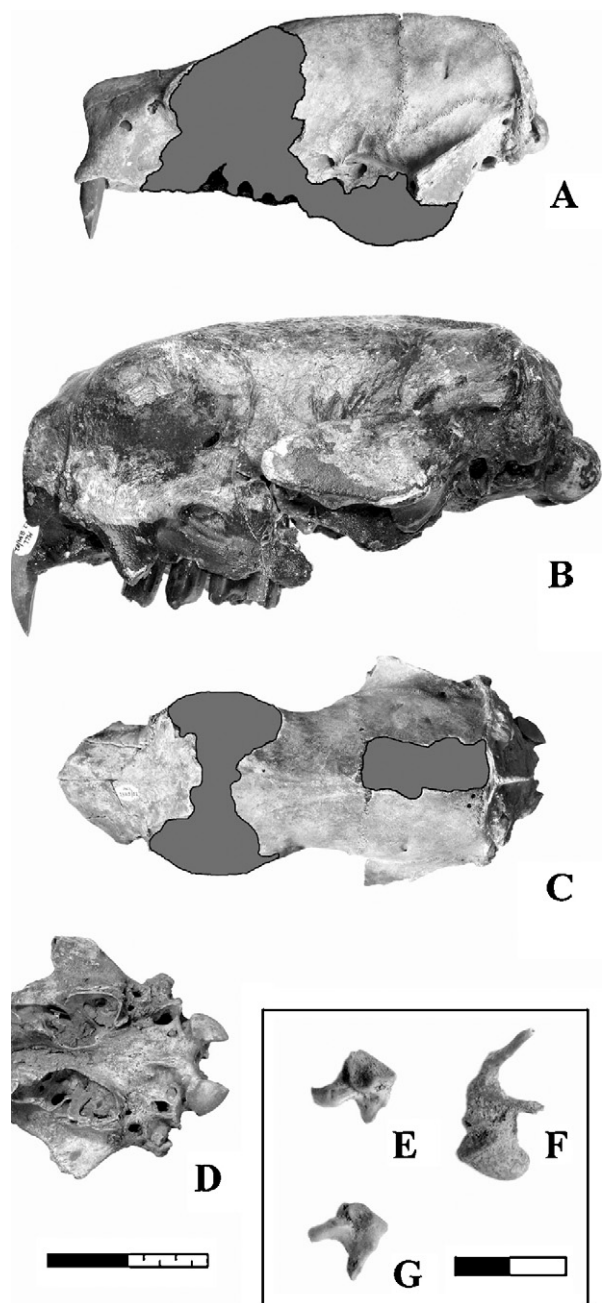


Fig. 2. Skull and ossicles of *Australonyx aquae* gen. and sp. nov. (MCL 23315/01) and *Ahytherium aureum* [2] (MCL 22834/01), both from the Quaternary of Poço Azul (Brazil). A, C–D. Skull of *Australonyx aquae* gen. and sp. nov. in lateral (A), dorsal (C), and ventral (D) views. B. Skull and mandible of *Ahytherium aureum* in lateral view. E–F. Incus (MCL 23315/02) and malleus (MCL 23315/02) of *Australonyx aquae* gen. and sp. nov. G. incus (MCL 22254/02) of *Ahytherium aureum*. Scales: 100 mm for skulls and 10 mm for ossicles.

Fig. 2. Crâne et osselets de l'oreille d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/01) et d'*Ahytherium aureum* [2] (MCL 22834/01), les deux provenant de la grotte quaternaire de Poço Azul (Brésil). A, C–D. Crâne d'*Australonyx aquae* nov. gen. et sp. en vues latérale (A), dorsale

- family Megalonychidae (Gervais, 1855);
- genus *Australonyx* gen. nov.;
- generic diagnosis: as for type species by monotypy;
- species *Australonyx aquae* gen. and sp. nov. (Figs. 1, 2A, 2C–G and 3, Table 1).

Derivatio nominis: the generic name is derived from the ancient Greek *australos*, austral or south, and *onyx*, claw. The specific epithet is derived from the Latin genitive for water. The specific name is in tribute to the team of divers who recovered the holotype from the waters of a flooded cave: Fernando Hiroshi Kuramoto, Luis Augusto Alessio Pedro, Eduardo Valencia, João Paulo Franco and Tulio Schargel.

Holotype: MCL 23315, representing a well-preserved individual including the posterior half the skull and dorsal portion of the rostrum, upper caniniform teeth, much of the axial skeleton, forelimb and hindlimb elements, and many elements of the pes, totaling some 70 elements.

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

Diagnosis: similar in size to *Ah. aureum* but with smaller manus and pes and the long bones of the extremities more robust. Dorsal skull profile nearly linear posteriorly but markedly descending in rostral region. Rostrum relatively elongated, more so than in *Ah. aureum* and less than in *Mesocnus torrei* [11] (Matthew, 1931). Preorbital constriction greater than postorbital constriction, the reverse of the condition in *Ah. aureum*; caniniform teeth rodentiform, resembling but more robust than those of *Ah. aureum* but less so than of *Megalonyx jeffersoni* (Harlan, 1825). Outline of external choana rounded and narrow compared to that of the two species just mentioned. Pterygoid inflated, similar to *M. torrei*. Ectotympanic ring shaped. Forelimb elements longer and curved compared to *Ah. aureum*. Femoral head lacks fovea for *teres* ligament, as in *Ah. aureum* but in contrast to Choloepodinae and Megalocninae.

4. Description

In dorsal view, the well-defined nuchal and occipital crests are narrow (Fig. 1C). The sagittal crest is low, probably due to the youth of the individual, and

(C) et ventrale (D); B, crâne et mandibule d'*Ahytherium aureum* en vue latérale. E–F. Enclume (MCL 23315/02) et marteau (MCL 23315/02) d'*Australonyx aquae* nov. gen. et sp. G. Enclume (MCL 22254/02) d'*Ahytherium aureum*. Échelles: 100 mm pour les crânes et 10 mm pour les osselets de l'oreille.

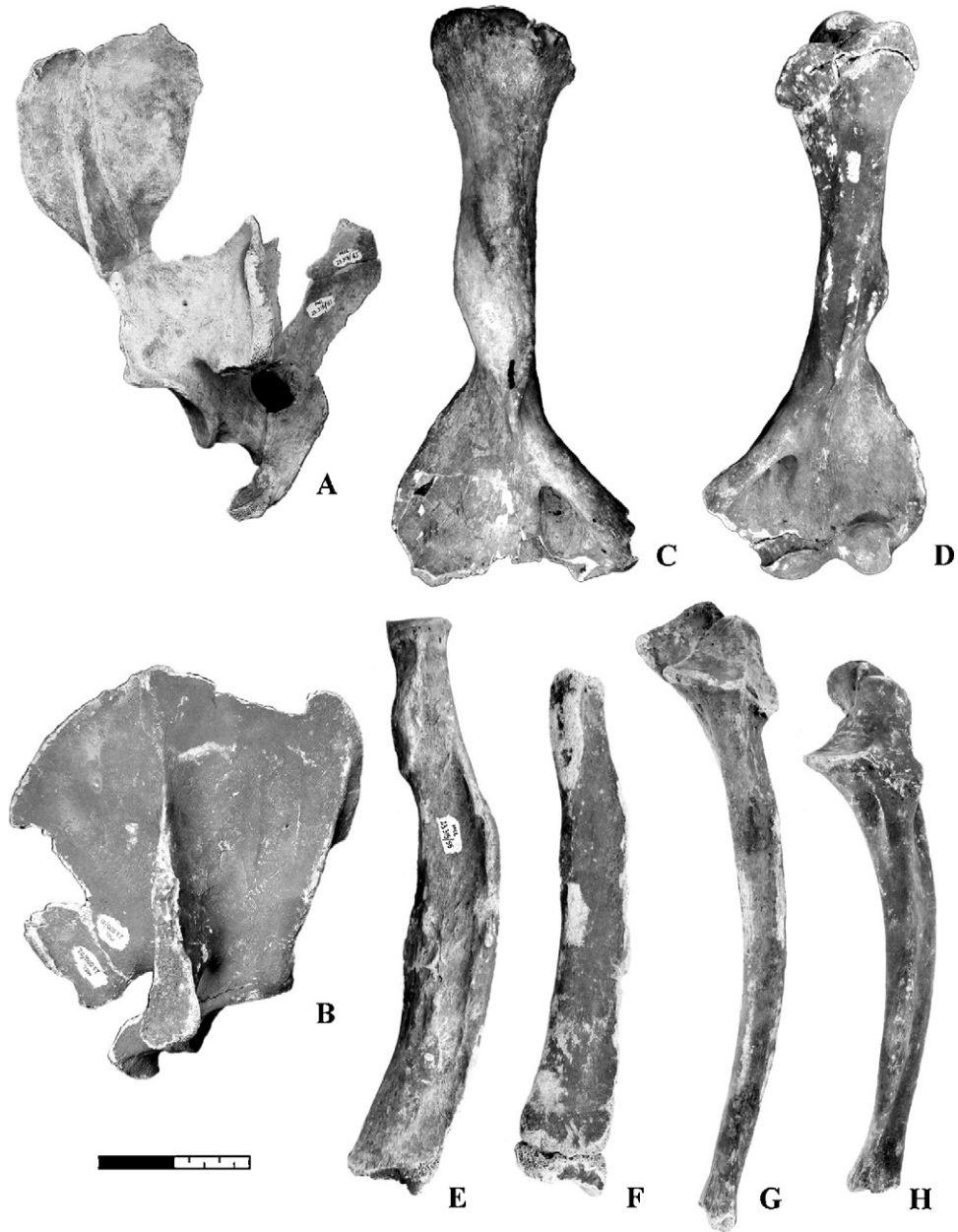


Fig. 3. Long bones of the forelimb of *Australonyx aquae* gen. and sp. nov. and *Ahytherium aureum* [2]. **A–B.** Right and left scapula of *Australonyx aquae* gen. and sp. nov. (MCL 23315/61) and *Ahytherium aureum* (MCL 23000/01), respectively, in lateral view (dorsal towards top); **C–D.** Right and left humerus of *Australonyx aquae* gen. and sp. nov. (MCL 23315/52) and *Ahytherium aureum* (MCL 23004/01), respectively, in anterior view (proximal towards top). **E–F.** Left radius of *Australonyx aquae* gen. and sp. nov. (MCL 23315/55) and *Ahytherium aureum* (MCL 22875/01), respectively, in posterior view (proximal towards top). **G–H.** Left ulna of *Australonyx aquae* gen. and sp. nov. (MCL 23315/54) and *Ahytherium aureum* (MCL 22875/02), respectively, in anterior view (proximal towards top). Scale 100 mm.

Fig. 3. Éléments du membre antérieur d'*Australonyx aquae* nov. gen. et sp. et d'*Ahytherium aureum* [2]. **A–B.** Omoplates droite et gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/61) et d'*Ahytherium aureum* (MCL 23000/01) respectivement en vue latérale (dorsale vers le haut). **C–D.** Humerus droit et gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/52) et d'*Ahytherium aureum* (MCL 23004/01) respectivement en vue antérieure (proximale vers le haut). **E–F.** Radius gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/55) et d'*Ahytherium aureum* (MCL 22875/01), respectivement en vue postérieure (proximale vers le haut). **G–H.** Ulna gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/54) et d'*Ahytherium aureum* (MCL 22875/02) respectivement en vue antérieure (proximale vers le haut). Échelle : 100 mm.

Table 1
Measurements (mm) of skeletal elements of *Australonyx aquae* gen. and sp. nov. and *Ahytherium aureum*.

Tableau 1

Dimensions en millimètres des éléments du squelette d'*Australonyx aquae* nov. gen. et sp. et d'*Ahytherium aureum*.

Skull	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL23315/01		MCL22834	
Distance between occipital condyle to mesial margin of C alveolus	327		286	
Distance between zygomatic process of frontal to nuchal crest	210 ^a		160	
Width between zygomatic processes of frontal	–		142	
Minimal width at temporal fossa	85		88	
Minimal width of preorbital constriction	79		109	
Height from inion to ventral margin of foramen magnum	88		89	
Width between mastoid processes	122		126	
Width of palate between C	58		64	
Maximal rostral width	60		101	
Maximal height from palate to nasal	60		87	
Distance between lateral margins of occipital condyles	67		78	
Distance between occipital condyle to anterior margin of nasal	330		250	
Scapula	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL 23315/61		MCL 22955	MCL 23000
Greatest length of glenoid fossa	70	80 ^a	72	
Greatest width of glenoid fossa	41	42 ^a	47	
Length between anterior margin of glenoid fossa to vertebral border along scapular spine	–	235 ^a	245 ^a	
Femur	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL 23315/58		MCL 22875	MCL 23033
Length between head and medial condyle along medial surface	375	382	377	
Greatest proximal transverse width	–	134	135	
Transverse width of head	83	74	75	
Anteroposterior depth of head	82	76	77	
Transverse width across epicondyles	150	128	131	
Transverse diaphyseal width proximal to epicondyles and distal to third trochanter	95	81	85	
Tibia	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL 23315/68		MCL 22875	MCL 23085
Length intercondylar spine to middle of astragalar surface	225	207 ^a	–	
Minimal transverse diaphyseal width	61	–	105	
Distal transverse width	108	115	–	
Anteroposterior proximal depth from posterior margin of lateral condyle anterior margin of medial condyle	130 ^a	87	–	
Astragalus	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL 23315/80		MCL 22875	
Anteroposterior length at middle of trochlea between posterior margin and anterior margin of navicular process	80		100	
Transverse width of posterior margin of trochlea	70		70	
Transverse width of anterior margin of trochlea	55		78	
Transverse width of navicular process	40		73	
Dorsoventral height of navicular process	42		51	
Calcaneum	<i>Australonyx aquae</i>		<i>Ahytherium aureum</i>	
	MCL 23315/70		MCL 22875	MCL 23063
Length from posterior margin of tuber calcis to anterior margin of sustentacular facet	198	172 ^a	173	
Transverse width of tuber calcis	143	135 ^a	130	
Transverse width of neck	47	44	56	
Proximal height between dorsal margin of posterior astragalar ectal facet to ventral margin of cuboid process	72	75	67	

^a Estimated data.

would likely have become more prominent with age, as in *Ah. aureum*. Posteriorly it is single, diverging anteriorly into the temporal lines that extend toward the orbital regions, which are not preserved. The postorbital constriction is wider than the preorbital constriction, which is the reverse of the condition in *Ah. aureum*. The frontals, which are fused middorsally, are flattened and descend towards the rostrum (vide [2] Fig. 2B). Based on its preserved portions, the zygomatic processes of the frontal must have been much less prominent than in *Ah. aureum*.

The maxillonasal region or rostrum is longer and narrower than in *Ah. aureum*. In the latter, the distance from the anterolateral margin of the choana to the zygomatic process of the maxilla is one-fifth of the width between the zygomatic processes of the maxillae at the lacrimal foramen. In *Au. aquae* the rostral length is at least half of the width between the maxillary zygomatic processes.

In ventral view (Fig. 2D) the occipital condyles of *Au. aquae* are longitudinally and transversely smaller, but the foramen magnum is higher and wider than in *Ah. aureum*. The carotid and postglenoid foramina are aligned parasagittally. The former lies at the postero-medial angle of the pterygoid, and the latter in the depression between the posterolateral angle of the pterygoid and the ectotympanic. The auditory or Eustachian tube opens anteroventrally between the ectotympanic and entotympanic. The stylostoid foramen lies more anteriorly than in *Ah. aureum*, in which the stylohyal fossa is more nearly circular. The mandibular fossa is larger and flatter than in *Ah. aureum*.

The basioccipital-basisphenoid complex narrows anteriorly abruptly and markedly in *Au. aquae*, whereas in *Ah. aureum* its width remains nearly constant up to the level of the internal choana [2]. These morphologies result from the different form of the pterygoids. In *Ah. aureum* the pterygoids are lamellar, shallowly concave medially and oriented slightly obliquely ventrolaterally. In *Au. aquae* the pterygoids are incomplete, but their base and lateral and medial surfaces are sufficiently preserved to establish that they were strongly inflated, with the medial surfaces markedly convex and converging towards the choana, resembling the condition in *Nothrotherium maquinense* (Lund, 1839), although their incompleteness precludes knowing whether the medial surfaces were fenestrated, as in the latter species. The anterior and posterior limits of the pterygoid coincide respectively with the level of the foramen rotundum and anterior margin of the ectotympanic. The foramen ovale lies on the base of the lateral surface, midway between these limits.

Internally, the base of the pterygoid (Fig. 2D) bears numerous septate cavities or sinuses communicating via a prominent foramen with the epitympanic recess at the base of the zygomatic process of the squamosal. In *Ah. aureum*, the sinuses in this region are limited to the squamosal over the mandibular fossa and the lateral wall of the adjacent portion of the basisphenoid. Based on the morphology of other species that bear inflated pterygoids, such as *Choloepus didactylus* (Linnaeus, 1758), *N. maquinense* and *M. torrei* [9,13], we may estimate that the height of the pterygoid would be approximately two-third its length, thus projecting beyond the palate as the ventralmost extent of the skull. As in *N. maquinense*, a canal begins within the foramen rotundum that passes dorsal to the base of the pterygoid towards the cranial cavity. In *C. didactylus* the pterygoid, also inflated and septate, communicates with the basisphenoid and basioccipital, which contain sinuses. In *Au. aquae* the sinuses are rudimentary in the basisphenoid and absent in the basioccipital.

The basal portions of the alveoli of M3 and M4 indicate that the tooth rows diverged anteriorly. The distal margin of M4 is midway between the mesial margin of the caniniform and the posterior margin of the occipital condyle. Although incomplete, the length of the molariform tooth row may be estimated, from which we may infer that the length of the diastema was longer in *Au. aquae*, approximately equal to the length of the molariform series, than in *Ah. aureum*. The caniniform alveoli are larger than in *Ah. aureum* but smaller than in *M. jeffersoni*.

The preorbital constriction is nearly equal to the distance between the caniniforms, which is less than the length of the diastema. In *Ah. aureum* the constriction is wider than the distance between the caniniforms, which is greater than the length of the diastema.

Based on the palatal portion preserved between the caniniforms and the morphology of the lateral walls of the maxilla bearing the preorbital constriction, we may infer that the marked constriction of the palate, as observed in some Antillean taxa such as *Microcnus gliriformis* Matthew, 1931 and *M. torrei*, did not occur in *Au. aquae*. Rather, the palate was moderately constricted in this region, with its width less than that between the molariforms.

In lateral view (Fig. 2A) the dorsal skull profile on the parietals is less convex than in *Ah. aureum* (Fig. 2B); on the frontals and nasals it is flattened and descends anteriorly, whereas in *M. jeffersoni* this surface is convex. The orbital fissure, which includes the opening of the optic canal, is posterior to the level of M4 and anterodorsal to the foramen rotundum. The mastoid foramen, visible in

lateral view, lies in the deep fissure between the mastoid and stylohyal processes (Fig. 2D).

The ectotympanic is oval with a sharp ventral projection, whereas that of *Ah. aureum* is more circular and lacks a ventral projection. It is a closed ring in both species, whereas in *Choloepus didactylus* it is U-shaped, open dorsally. The promontory of the petrosal is visible through the external auditory meatus, as well as the oval window, the facial foramen dorsal to it, and the round window below the posterior margin of the ectotympanic.

Left and right mallei and the left incus were recovered from the matrix filling the middle ear cavities (Fig. 2E–G). The malleus has a prominent lateral process, and the manubrium forms an obtuse angle with the neck. The anterior process is short and thin, and the head is longer anteroposteriorly than mediolaterally. The articular surface of the incus comprises two contiguous surfaces. The posterolateral is flat and larger than the concave anteromedial surface. The long process, bearing the lenticular process that articulates with the stapes, is more robust than the short process. In the incus of *Ah. aureum* the body and processes are less robust than in the new species. The long process of the incus is longer and straighter in *Au. aquae*, but curved in *Ah. aureum*. In both species, the concave facet for articulation with the malleus extends as a narrow surface on the proximal portion of the long process. The long and short processes meet in a right angle in *Ah. aureum*, whereas they form an acute angle in *Au. aquae*.

In anterior view the external choana is of nearly equal height and width, and is approximately 1.5 times the diameter of the foramen magnum (Fig. 2D). In *Ah. aureum* the width of the choana, greater than its height, is about three times that of the foramen magnum.

The upper caniniforms are the only teeth preserved (Fig. 2A). They are triangular in section and markedly curved, with concave distal margin. They resemble those of *Au. aureum* (Fig. 2B, [2]) but are rodentiform and more robust, though less so than those of *M. jeffersoni*.

A fairly complete vertebral series was recovered, including the 7 cervical, 13 thoracic, the three lumbar and four sacral, and 16 caudal vertebrae. The last lumbar is fused to the first sacral. There is no doubt that the remains belong to a single individual (even though the skeleton was found disarticulated and together with elements of other sloths species) based on the precision of the articulations between the skull and atlas, the lumbar and sacrum, and the latter with the femur. Several ribs were also recovered that articulate perfectly with their corresponding vertebrae.

There are several notable differences among the vertebrae of *Au. aquae* than in *Ah. aureum*. The lat-

eral vertebral foramina of the atlas of *Au. aquae* are occluded in anterior view by the articular facets for the occipital condyles, whereas the foramina are visible in *Ah. aureum*. The posterior articular facets and the ventral facet for the odontoid process of the axis are contiguous in *Au. aquae*, but separate in *Ah. aureum*. In the axis the articular facets for the atlas are oval with major diameter dorsoventral, whereas in *Ah. aureum* they are circular. The transverse processes of the thoracic vertebrae are more robust and of the lumbar vertebrae anteroposteriorly shorter in *Au. aquae*. The four sacral vertebrae are less robust than those of *Ah. aureum*. In *Au. aquae*, the transverse processes of the caudal vertebrae are relatively thin blades that progressively decrease their mediolateral and anteroposterior dimensions posteriorly. In *Ah. aureum* they are thicker and progressively increase their mediolateral and anteroposterior dimensions posteriorly to the ninth caudal vertebrae, after which the dimensions decrease progressively. This morphology suggests a tail that in life was thick and widest at its midlength.

The scapula is missing its anterodorsal portion and the coracoacromial bridge (Fig. 3A). The markedly concave glenoid fossa is oval. Its minor diameter is mediolaterally oriented and it is longer than the diameter of the circular coracoscapular foramen. The scapular spine slopes gently anteriorly. In *Au. aquae* the glenoid fossa and the margin of the scapular spine are narrower and the secondary scapular spine is longer than in *Ah. aureum* (Fig. 3A–B). The diameter of the coracoscapular foramen of *Ah. aureum* is about half that of *Au. aquae*.

The humerus of *Au. aquae* (Fig. 3C) is nearly complete, missing only its distal epiphysis. Its gracile, nearly cylindrical diaphysis widens and flattens distally, as is usual in sloths. The nearly semispherical head projects farther proximally than the greater tuberosity, which in turn projects farther and is more robust than the lesser tuberosity. Although the general morphology is similar in *Ah. aureum*, the tuberosities project less proximally and are less prominent, so that the head is widely exposed in anterior view in this species (Fig. 3C–D).

Anteriorly, the humeral diaphysis of *Au. aquae* bears a prominent deltopectoral shelf (see [5]) limited laterally and medially by the deltoid and pectoral crests, respectively (Fig. 3C). The proximal half of the deltoid crest projects strongly laterally and then curves medially to meet the pectoral crest at the distal third of the humerus, beyond which the diaphysis expands transversely. The deltoid crest is more robust proximally than distally, the reverse of the condition for the pectoral crest.

The deltopectoral shelf is larger and more robust in *Au. aquae* than in *Ah. aureum*, although its surface is

less elaborate; for example, the median ridge extending proximally from the distal end of the shelf, probably for insertion of the *brachioradialis* or *cephalohumeralis* muscles (see [5]) is prominent in *Ah. aureum* but barely perceptible in *Au. aquae* (cf. Fig. 3C–D). Distally beyond the shelf, the humerus flattens anteroposteriorly and widens mediolaterally, with the medial margin thicker than the lateral. An ample entepicondylar foramen lies medially. Its diameter exceeds the width of the osseous bridge than defines it.

Both radii and ulnae were recovered, all missing their distal epiphysis. The neck of the radius (Fig. 3E) is constricted. Distally beyond the bicipital tuberosity the diaphysis is of nearly constant width, with the medial border anteroposteriorly deeper than the lateral surface. The lateral margin and posterior surface are concave. The ulnar diaphysis (Fig. 3G) is markedly bowed medially and posteriorly. The olecranon process is short and robust. Its proximal end is transversely wider and projects posterolaterally more markedly than in *Ah. aureum*. In the latter species the shafts of both the radius and ulna are less curved than in *Au. aquae* (Fig. 3E–H).

The concave articular surface of the ulna for the humerus forms a right angle with that for the radius. Beyond the proximal articular surfaces, the diaphysis of the ulna is of nearly constant width. Although the ulna of *Ah. aureum* is shorter, its diaphysis, distal to the proximal articular surfaces, is more robust.

The femur of *Au. aquae* (Fig. 4A) is similar to that of *Ah. aureum* but shorter and more robust (Fig. 4B). The greater trochanter lies farther proximally but less laterally in *Au. aquae*. As in the first species the head does not bear a fovea for the *teres* ligament. According to MacPhee et al. [9], this structure is present in Megalocninae and Choloepodinae. Distally, the patellar facet is longer and narrower in the new species, whereas it is nearly square in *Ah. aureum*. This also applies to the form of the lateral articular surface, which in *Au. aquae* is trapezoidal and more strongly convex. The patellar trochlea is separate from both the medial and lateral articular condyles in *Au. aquae* and *Ah. aureum*.

The tibia of *Au. aquae* (Fig. 4C) is more robust than that of *Ah. aureum* (Fig. 4D). Its lateral margin forms an acutely tapered edge. The lateral part of its posterior surface is deeply concave. The transverse width of the distal articular surface is slightly greater than half that of the proximal articular surface. In *Ah. aureum*, these surfaces are of nearly equal width (Fig. 4D).

The calcaneum of *Au. aquae* (Fig. 4E) has the typical axe-shaped morphology characteristic of megalonychids. It is longer and more robust than that of

Ah. aureum, although the articular surfaces are larger in the latter species (Fig. 4F). The astragalus (Fig. 4G) of the new species is a third smaller than that of *Ah. aureum*. Although the astragal morphology of the two species is similar, clear differences exist in the more concave navicular facet and more pronounced proximomedial protuberance between the navicular and tibial facets in *Ah. aureum* (Fig. 4H). Also, the articular surface for the fibula is nearly tangential to the ectal calcaneal facet in *Au. aquae*, whereas they are clearly separated in *Au. aureum*.

Metatarsals II, III (Fig. 4I), and IV, as well as some phalanges, were recovered. These elements are less robust in *Au. aquae* than in *Ah. aureum*, which contrasts with the more robust long bones in the new species. The most notable difference in these elements occurs in metatarsal III (Fig. 4I–J), in which the proximal articular facets are discontinuous in *Au. aquae* but continuous in *Ah. aureum*. The facet for the ectocuneiform is subtriangular and deeply concave. The plantar surface bears a projection that, in distal view, spans nearly half the articular surface for the proximal phalanx. In *Ah. aureum* the facet for the ectocuneiform outlines a parallelogram and the plantar projection, though narrower, is longer than the articular surface. The navicular and cuboid are also preserved. These elements and metatarsals II and IV are morphologically very similar to, but smaller than, those of *Ah. aureum*.

5. Comments and discussion

The sympatry of two megalonychid species in the same region in the center of the State of Bahia is surprising not only because of the rarity of Pleistocene records of this clade, but also in the likely behavioural differentiation of the two species. The new species is stockier and more robust, but with smaller and gracile manus and pes compared to *Ah. aureum*. Unlike *Megalocnus rodens* (Paula Couto, 1967), neither of the Brazilian species was plantigrade. Manipulation of pedal elements indicates that the pes of *Au. aquae* had a lower degree of pedal flexion and extension, but was capable of greater torsion compared to *Ah. aureum*. The different morphologies suggest that *Au. aquae* had a greater capacity for displacement, with mass preferentially supported on the lateral surface of the pes during locomotion. The relatively large size of *Au. aquae* and its short metacarpus, metatarsus, and phalanges suggest that arboreal habits were unlikely.

The pterygoid is blade like in *Thalassocnus natans* (Muizon & McDonald, 1995), Megatheriinae [4], *Acraetocnus odotrionus* (Anthony, 1926 [13]), *Neocnus*

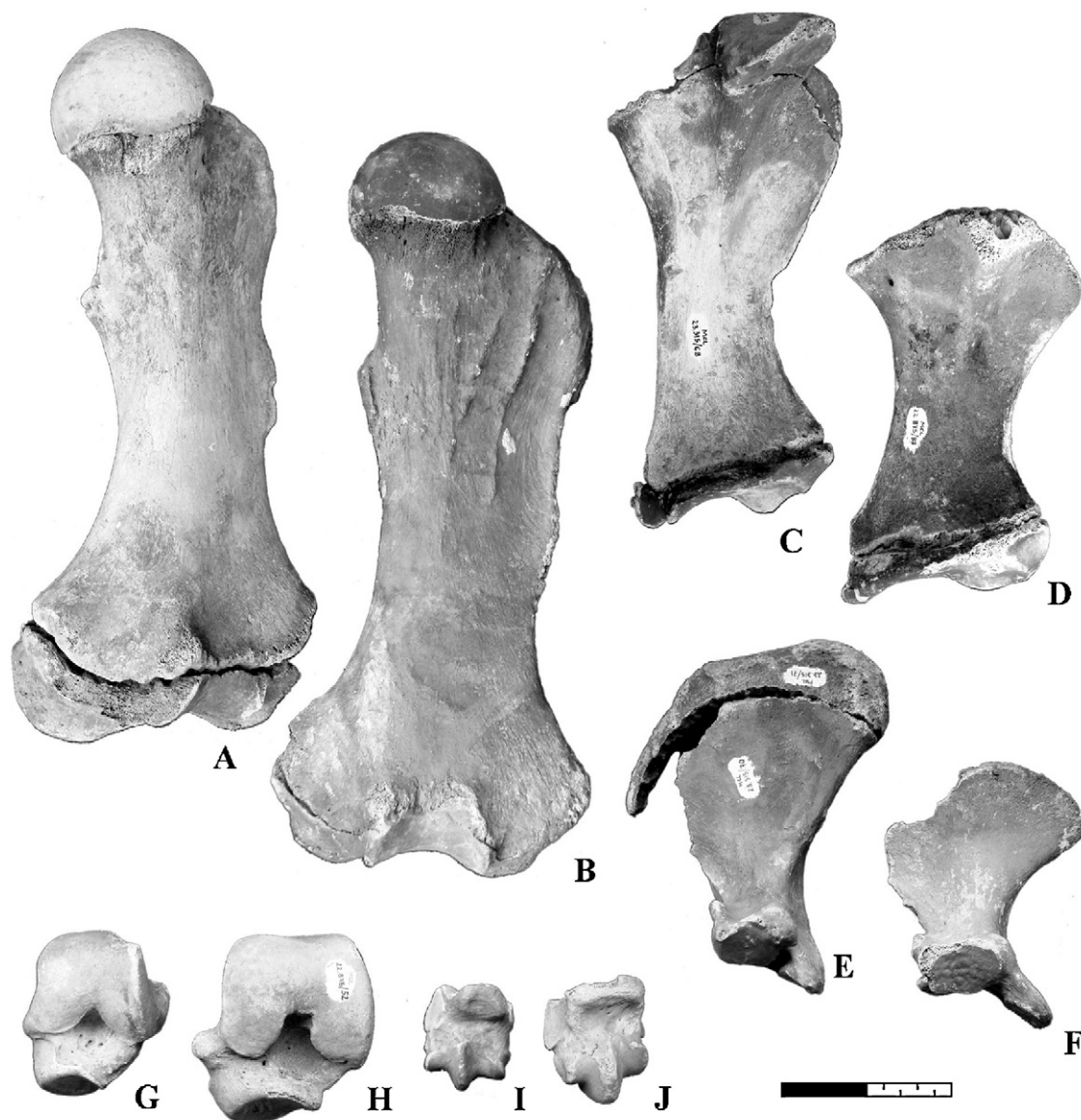


Fig. 4. Hindlimbs elements of *Australonyx aquae* gen. and sp. nov. and *Ahytherium aureum* [2]. **A–B.** Left femur of *Australonyx aquae* gen. and sp. nov. (MCL 23315/58) and *Ahytherium aureum* (MCL 23033/01), respectively, in anterior view (proximal towards top). **C–D.** Right tibia of *Australonyx aquae* gen. and sp. nov. (MCL 23315/68) and *Ahytherium aureum* (MCL 22875/88), respectively, in posterior view (proximal towards top). **E–F.** Left calcaneum of *Australonyx aquae* gen. and sp. nov. (MCL 23315/70) and *Ahytherium aureum* (MCL 22875/51), respectively, in dorsal view (posterior towards top). **G–H.** Left astragalus of *Australonyx aquae* gen. and sp. nov. (MCL 23315/80) and *Ahytherium aureum* (MCL 22875/52), respectively, in dorsal view (posterior towards top). **I–J.** MtIII of *Australonyx aquae* gen. and sp. nov. (MCL 23315/87) and *Ahytherium aureum* (MCL 22875/62), respectively, in plantar view (proximal towards top). Scale 100 mm.

Fig. 4. Éléments du membre postérieur d'*Australonyx aquae* nov. gen. et sp. et d'*Ahytherium aureum* [2]. **A–B.** Fémur gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/58) et d'*Ahytherium aureum* (MCL 23033/01) respectivement en vue antérieure (proximale vers le haut). **C–D.** Tibia droit d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/68) et d'*Ahytherium aureum* (MCL 22875/88), respectivement en vue postérieure (proximale vers le haut). **E–F.** Calcaneum gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/70) et d'*Ahytherium aureum* (MCL 22875/51), respectivement en vue dorsale (postérieure vers le haut). **G–H.** Astragale gauche d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/80) et d'*Ahytherium aureum* (MCL 22875/52), respectivement en vue dorsale (postérieure vers le haut). **I–J.** MtIII d'*Australonyx aquae* nov. gen. et sp. (MCL 23315/87) et d'*Ahytherium aureum* (MCL 22875/62), respectivement en vue plantaire (proximale vers le haut). Échelle : 100 mm.

toupeti (MacPhee, White, and Woods, 2000), *Neocnus dousman* (MacPhee, White, and Woods, 2000) [9], *Paulocnus petrifactus* (Hooijer, 1962), several species of *Megalonyx* (see [10]), *Pliometanestes protistus* (Hirschfeld and Webb, 1965) [7], *D. nordenskioldi* or inflated with a pneumatic sinus in *N. maquinense*, *Nothrotheriops shastensis* (Stock, 1925), *Choloepus didactylus* and *Mesocnus*. MacPhee et al. [9] used this character, among others, to distinguish between the clades (traditionally recognized as subfamilies) Megalocninae (inflated pterygoid) and Choloepodinae. Previous attempts to allocate South-American fossil remains to higher level megalonychid clades were highly speculative, given that the only cranial and most postcranial remains known have just recently been recovered and described ([2,17] and in this report), so that diagnostic characteristics were not available. *Ah. aureum* apparently seems more closely linked to the North-American Pleistocene forms (e.g. *Megalonyx*), whereas *Au. aquae* may be more closely related to the Antillean sloths that possess an inflated pterygoid. In dorsal view, for example, the morphology of the skull of *Au. aquae* resembles that of *M. gliriformis*, although the rostrum is more pronounced in the latter. On the other hand, there are differences in cranial proportions that seem to separate the Brazilian species from already recognized megalonychid clades. Clearly, a solution to this problem would be a comprehensive review of megalonychid morphology, followed by phylogenetic analysis. This is in progress by the current authors.

The generic distinction between the two Pleistocene Brazilian species is reasonably clear based on cranial morphology, though the difference is less pronounced based on postcranial elements, other than the strikingly different caudal vertebrae. The more marked cranial differences between *Au. aquae* and *Ah. aureum* occur in dorsal skull profile, differing proportions in the pre- and postorbital constrictions, rostrum length, shape and dimensions of the external choana, condition of the pterygoid, and basicranial morphology.

Remains of extinct and extant species were recovered in association with those of the Brazilian megalonychids. Among the extinct forms are the South-American ungulate *Toxodon platensis* Owen, 1837, the xenarthrans *Catonyx cuvieri* (Lund, 1839), *Nothrotherium maquinense*, *V. bucklandi*, *Eremotherium laurillardii* (Lund, 1842), *Pampatherium humboldtii* (Lund, 1839) and *Glyptodon clavipes* (Owen, 1839), the proboscidean *Stegomastodon waringi* (Holland, 1920), and the carnivoran *Smilodon populator* (Lund, 1842). Among the extant species identified are the marsupial *Didelphis aurita* (Wied-Neuwied, 1826),

the chiropterans *Chrotopterus auritus* (Peters, 1856), *Desmodus rotundus* (Geoffroy, 1810) and *Thyroptera tricolor* (Spix, 1823), the primate *Alouatta guariba* (Humboldt, 1812), the carnivoran *Conepatus chinga* (Molina, 1782), the perissodactyl *Tapirus terrestris* (Linnaeus, 1758), the artiodactyls *Tayassu tajacu* (Linnaeus, 1758) and *Mazama gouazoubira* (Fisher, 1814), and the rodents *Hydrochoerus hydrochaeris* (Linnaeus, 1776), and *Kerodon rupestris* (Wied, 1820). These species comprise a group that currently occupies a habitat that serves as an indicator of the past biome that these species lived in, at least during the end of the Pleistocene.

Among the current Brazilian biomes that might have characterized the fossil locality, today clearly Caatinga, we may exclude those of Amazonia, Campos do Sul, and the Pantanal. Possible biomes are Caatinga, Atlantic Forest, and Cerrado (savanna, with its several physiographic variations). Currently, *T. tricolor* is restricted to the Atlantic forest; *K. rupestris* is characteristic of Cerrado; and *C. auritus* occurs in the Atlantic Forest and Cerrado, as do *A. guariba* and *T. terrestris*. The remaining extant species may occur in all three biomes under consideration [6].

The current distributions of extant species suggest that during the end of the Pleistocene the region under investigation was not dominated by a single biome containing the species noted above, but likely comprised a mosaic of Cerrado and Atlantic Forest, with the latter, on the one hand, dominant in hills, mountains and along water courses, and Cerrado, on the other hand, prominent on lower land and plains. The latter was necessary for sustaining, at least, the large grazing species, which characterize most of the extinct species identified above. The large size of some of these species speaks against their suitability for occupying a closed forest, such as the Atlantic Forest.

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