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A platyrrhine talus from the early Miocene of Peru (Amazonian Madre de Dios Sub-Andean Zone)

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ABSTRACT

The earliest platyrrhines have been documented from the late Oligocene of Bolivia (Salla) and from the early and early middle Miocene of middle and high latitudes (central Chile and Argentinean Patagonia). Recent paleontological field expeditions in Peruvian Amazonia (Atalaya, Cusco; Upper Madre de Dios Basin) have led to the discovery of a new early Miocene locality termed MD-61 ('Pinturan' biochronological unit, ~18.75–16.5 Ma [millions of years ago]). Associated with the typical Pinturan dinomyid rodent *Scleromys quadrangulatus*, we found a well-preserved right talus of a small-bodied anthropoid primate (MUSM-2024). This new platyrrhine postcranial element displays a combination of talar features primarily found among the Cebidae, and more especially in the Cebinae. Its size approximates that of the talus of some living large marmosets or small tamarins (Cebidae, Callitrichinae). MUSM-2024 would thus document a tiny *Saimiri*-like cebine, with the body size of a large marmoset. Functionally, the features and proportions of MUSM-2024 indicate that this small primate was arboreal and primarily quadrupedal, agile, with frequent horizontal leaping and vertical clinging in its locomotor repertoire. This small talus is the first platyrrhine fossil to be found from Peru and the earliest primate fossil from northern South America. This new early Miocene taxon could be a stem cebid, thereby providing new evidence on the existence of some long-lived clades of modern platyrrhines.

Introduction

Neotropical areas are today among the major hotspots of mammal diversity (Grenyer et al., 2006). In South America, the forests of the great Amazonian Basin shelter the most diversified platyrrhine primate communities (Perez, 1997; Garber et al., 2009; Ramdarshan et al., 2011). However, from a historical perspective, the early evolutionary stages of primates in northern South America (including Amazonia) have proven to be elusive, except for the late middle Miocene of Colombia (La Venta) and the late Miocene of western Brazil (Kay and Frailey, 1993; Kay and Cozzuol, 2006; Negri et al., 2010). The primate-bearing localities from La Venta in central Colombia are particularly famous for having yielded a wide array of crown platyrrhines ('Monkey Beds', Stirton, 1951; Luchterhand et al., 1986; Setoguchi and Rosenberger, 1987; Rosenberger et al., 1991b; Kay, 1994; Takai, 1994; Meldrum and Kay, 1997; Nakatsukasa et al., 1997; Takai et al., 2001). Earlier platyrrhines have been thus far restricted to the late Oligocene locality of Salla, Bolivia (Hoffstetter, 1969; Rosenberger et al., 1991a; Takai and Anaya, 1996; Takai et al., 2000), and to early and early middle Miocene localities at middle and high latitudes (central Chile and Argentinean Patagonia; Bordas, 1942; Fleagle and Bown, 1983; Fleagle et al., 1987; Fleagle and Kay, 1989; Fleagle, 1990; Meldrum, 1990; Flynn et al., 1995; Tejedor, 2002, 2003, 2005a, b). Although the fossil record of New World monkeys has significantly increased

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over the last decades (Tejedor, 2008), it has remained difficult to trace back the origin of major modern clades, inasmuch as the earliest fossil taxa (from Patagonia, Bolivia and Chile) seem to be outside the crown radiation ('stem platyrrhine hypothesis'; Kay et al., 2008; Hodgson et al., 2009; Kay and Fleagle, 2010; Youlatos and Meldrum, 2011; but see Schrago, 2007; Rosenberger, 2010 and references therein, advocating the 'long lineage hypothesis').

Recent geological and paleontological field expeditions in the Amazonian Madre de Dios Sub-Andean Zone of eastern Peru (Fig. 1) have led to the discovery of a new vertebrate locality, designated MD-61 (S12°52.15′; W71°22.03′; ~484 m ASL). In August 2011, our thorough survey of this locality led to the recovery of a complete right talus of a small anthropoid primate. This tarsal bone provides the first documentation of fossil primates from Peru. The aims of this paper are: 1) to comment on the age of this new primate-bearing locality from the Upper Madre de Dios Basin, 2) describe morphologically and compare this new fossil talus with both extinct and extant platyrrhines, 3) determine its possible relationships to crown platyrrhines and eventually to modern higher taxa, and 4) identify osteological talar features that reflect functional attributes related to locomotor behavior of this fossil primate. Most of the metric features for describing and comparing the talar anatomy among primates follow the works of Gebo (1988), Meldrum (1990), Gebo et al. (1991, 2001), and Marivaux et al. (2010, 2011). The specimen described here is permanently housed in the Departamento de Paleontología de Vertebrados of the Museo de Historia Natural de la Universidad Nacional Mayor San Marcos (MUSM), Lima, Perú.

Geological and paleontological settings

The MD-61 locality is situated within the Sub-Andean Zone of the Madre de Dios foreland basin, as a part of the South Amazonian foreland basin system (Fig. 1A; Roddaz et al., 2005, 2010). The southernmost part of the concerned Sub-Andean Zone is structured by the Salvación Syncline, with a thick Phanerozoic sedimentary sequence (Vargas and Hipólito, 1998; Antoine et al., in press). The fossiliferous deposit, located on the right bank of the Río Madre de Dios (Fig. 1A), crops out in the southern flank of the Salvación Syncline nearby Atalaya. Based on sedimentary facies and in the absence of any biostratigraphic constraint, it was originally mapped as part of the Paleocene-Eocene Yahuarango Formation (Vargas and Hipólito, 1998). However, laterally equivalent deposits from the northern flank of the Salvación Syncline, ~25 km more to the north, were shown to document a much longer interval, ranging up to the early middle Miocene period (Antoine et al., in press).

The MD-61 section is 30 m thick (Fig. 1B). It consists of individual or stacked brownish sandstone bodies (deposited in fluvial channels, point bars, stream floods, and/or waning flows; Fig. 1C–D) separated by reddish mudstones with carbonate nodules, further testifying to the presence of a floodplain with frequent subaerial exposure under oxidizing conditions (Fig. 1E). Fossil vertebrate remains are scattered within the lower 5-m thick sand body (Fig. 1B). This early Miocene sequence is unconformably overlain by unconsolidated Pleistocene terrace conglomerates (Fig. 1B).

All identifiable vertebrate remains from MD-61 were recovered by hand-picking, during the 2011 fieldwork. They were isolated and scattered all over the iron-pisolite-rich sand-and-gravel channel (Fig. 1B–C). The corresponding sediments were not screen-washed, as no fossil concentration was recognized within the fossiliferous level. Together with the primate talus, MD-61 yielded several mammalian remains consisting of a fragmentary osteoderm of a small euphractine dasypodid armadillo, an incomplete claw referable to a megatherioid sloth, a dental fragment documenting a medium-sized toxodontid notoungulate, a complete cuboid of

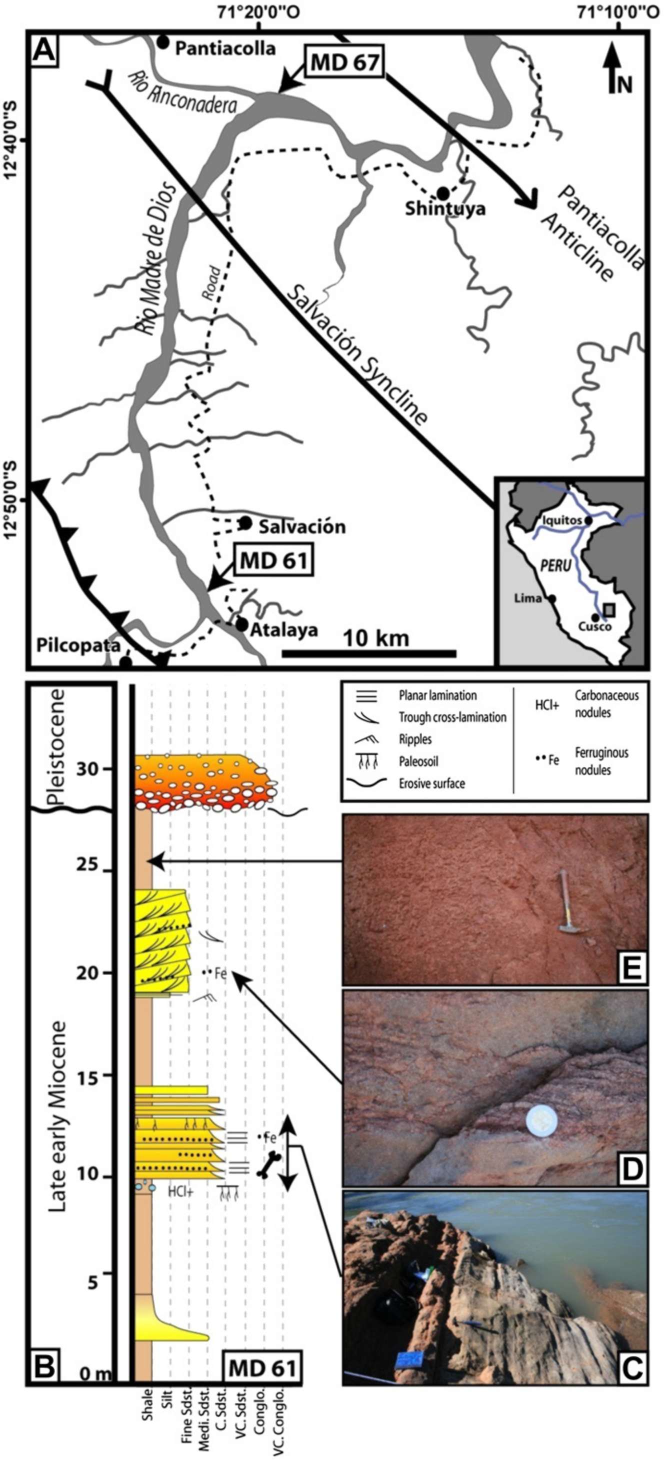

Figure 1. Location map (A) and stratigraphic section of the MD-61 vertebrate locality (B), in the Madre de Dios Sub-Andean Zone of Amazonian Peru. Fossil vertebrates referred to in the text (primate talus and associated mammalian/bird remains) are scattered within the lower 5-m thick stacked medium- to coarse-grained sandstone body (C). The upper sandstone body is characterized by trough cross-stratification outlined by millimetric to centimetric iron-oxide nodules interpreted as point bar deposits (D) and reddish mudstones with carbonate nodules interpreted as fluvial floodplain deposits (E) and have not yielded any vertebrate fossils. This late early Miocene section is unconformably overlain by Pleistocene terrace conglomerates. C, coarse; Conglo., conglomerate; Sdst., sandstone; VC, very coarse.

a rabbit-sized typothere notoungulate, and several rodent teeth. In addition, a distal fragment of a right tibiotarsus unearthed in MD-61 documents unambiguously a crane-sized gruiform bird and testifies to the proximity of water and the occurrence of swamps or extensive wetlands in the area by the time of deposition of the fossiliferous level. Most of the vertebrate remains are of no significance from a biochronological perspective, with the notable exception of the rodent teeth. The latter specimens (right M1, p4, and dp4) document a single taxon, referable to the small dinomyid caviomorph *Scleromys quadrangulatus* (Kramarz 2006), or a close ally. Overall features, such as oblique and curved loph(id)s, partial hypsodonty, M1 with a quadrangulate occlusal contour, p4 with a labially salient posterolophid, and dimensions of the available specimens are only compatible with the small dinomyid from the pre-Santacrucian 'Pinturan' association (18.75–16.5 Ma [millions of years ago]), as discussed in Kramarz and Bellosi (2005), Kramarz (2006), and Kramarz et al. (2010). Moreover, the relevant specimens from MD-61 are much more brachydont than their middle Miocene counterparts from Colombia or Peru (i.e., '*Scleromys schurmanni*' and '*Scleromys colombianus*'; Fields, 1957; Kramarz, 2006; Antoine et al., in press), which further supports a late early Miocene age for the concerned assemblage.

Description and comparisons

MUSM-2024 is a right ankle bone characterized by a well individualized neck, a rounded head showing a plantar navicular facet continuous with the sustentacular facet of the neck, and a hemi-cylindrical trochlea with a small radius of curvature. All of these characters are primarily found in the tali of primates.

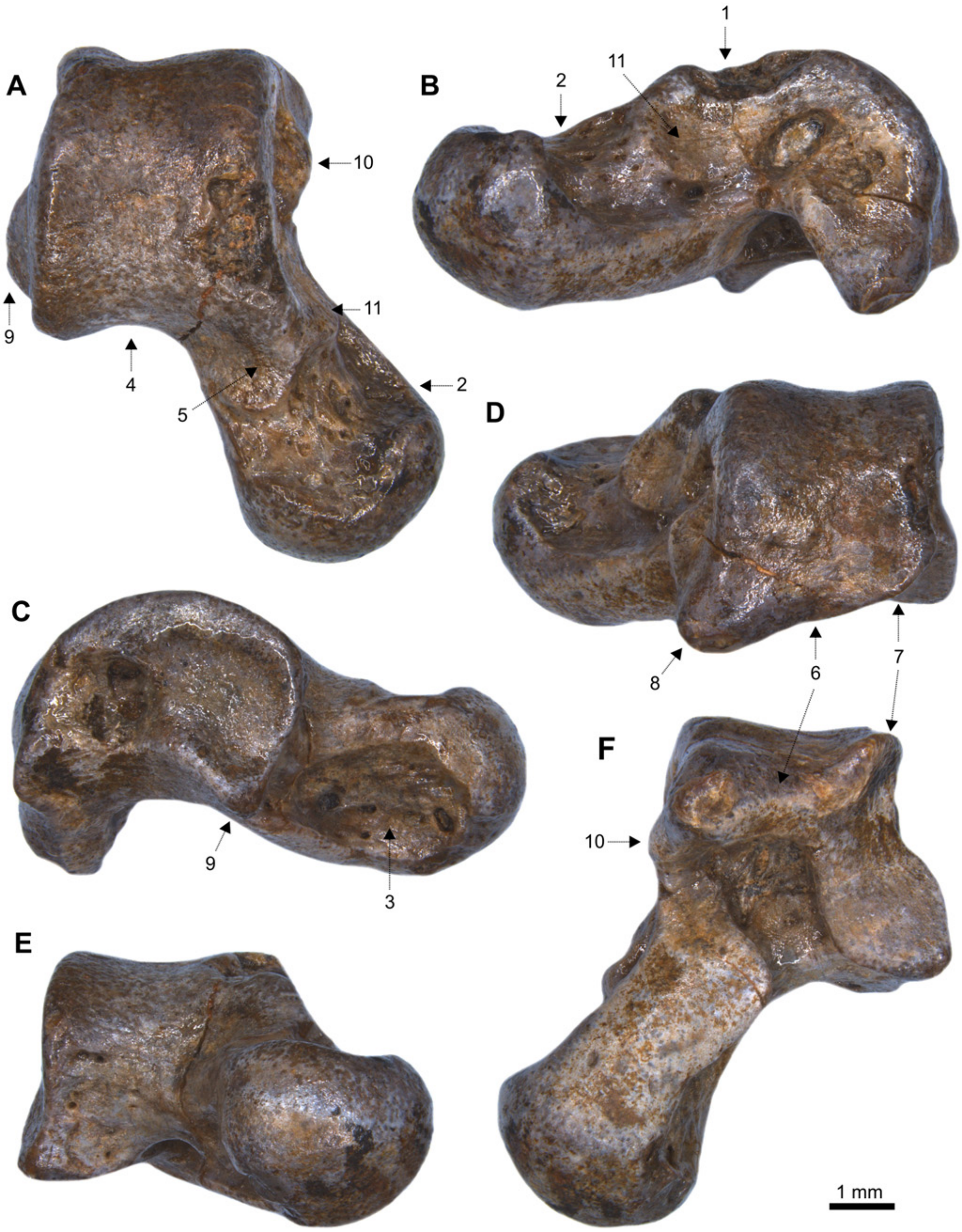

Figure 2. Photographs of MUSM-2024, right talus from MD-61, early Miocene of the Madre de Dios Sub-Andean Zone, Amazonian Peru. Views are dorsal (A), medial (B), lateral (C), proximal (D), distal (E), and plantar (F). These views are the result of the fusion of multi-focus images obtained with an optical stereomicroscope Leica M205C. Arrows and associated numbers denote anatomical features discussed in the text. Scale bar = 1 mm.

Furthermore, this new talus exhibits a suite of anatomical features including a steep-sided talofibular facet, a short and shallow talotibial facet, and a mid-trochlear position of the flexor muscle groove (see description of these characters below), which are talar features otherwise found only in extinct and extant anthropoid primates (Gebo, 1986; Beard et al., 1988). Despite the presence of cracks, this new anthropoid talus (MUSM-2024) is complete and undistorted. Only the dorsal aspect of the talar body is slightly damaged in the distal part of the medial trochlear rim, where a single and irregular pit may correspond to a tooth print resulting from peri-mortem predation (Fig. 2B, arrow 1). Interestingly, similar damage is preserved on tali referred to *Carlocebus* (MACN-SC 368 and 271), a fossil platyrrhine from the early Miocene Pinturas Formation in Patagonia (Meldrum, 1990). MUSM-2024 documents a species that was about half the size of its coeval Patagonian primate counterparts (i.e., platyrrhines) for which the talus is known (i.e., *Dolichocebus* (e.g., Reeser, 1984; Gebo and Simons, 1987), *Carlocebus*, and *Soriacebus* (Meldrum, 1990)). One of the most diagnostic characters of MUSM-2024 is the length of the talar neck and head. Indeed, the talar neck represents more than the half of the total length of the talus, and is clearly longer than the trochlea (Table 1). In this latter feature, MUSM-2024 differs substantially from tali of *Dolichocebus* (MACN-CH 362), *Carlocebus* (MACN-SC 271, 368, 304 and 396), *Soriacebus* (MACN-SC 397), and from the Chilean ‘Rio Cisnes talus’ (SGO-PV 974; Tejedor, 2003), which exhibit relatively shorter talar necks (Table 2). In having a long neck, MUSM-2024 differs also radically from the tali of the more recent and extant Pitheciidae and Atelidae, which show moderate to very short (and wide) talar neck, respectively (Fig. 3A–C; Table 2). Ankle bones characterized by long necks are rather found in Cebidae (i.e., Callithrichinae and Cebinae; Fig. 3D–J) and *Aotus* (Fig. 3K). In MUSM-2024, the talar neck narrows proximally and the head is relatively narrow (Fig. 2A). Such conditions of the talar neck and head are primarily observed in tali of stem and crown Cebinae (e.g., *Saimiri* and *Cebus*, *Neosaimiri* from La Venta [IGM-KU 8803, 89030, 89031 and 89199; Gebo et al., 1990; Nakatsukasa et al., 1997]). In anterior view, the head of MUSM-2024 is somewhat ovoid in shape (fairly round but nearly flat dorsally) and slightly rotated dorsolaterally (10–15°; Fig. 2E). In dorsal view, the distal edge of the head, which articulates with the navicular, is strongly curved (Fig. 2A). As in most platyrrhine tali, the navicular facet expands onto the distal lateral and medial aspects of the neck, but not far onto its distal dorsal aspect. In this dorsal region of the neck, the cervical pit is particularly well-marked in MUSM-2024, being deep and very extensive (Fig. 2A–B, arrow 2). Plantarly, the navicular facet is confluent with the sustentacular facet of the talar neck (Fig. 2F). The sustentacular facet is not strictly plantad but it faces slightly medially (obliquely), although without extending far dorsally on the medial margin of the neck. On the lateral aspect of the neck, the site for the attachment of the anterior talocalcaneal ligament appears as a wide and deep excavation (Fig. 2C, arrow 3).

Table 1

Metric features (in millimeters) of MUSM-2024 from MD-61 and body mass estimates (in grams).

Measurements		MUSM-2024 (mm)	Body mass estimates (g)
Talar length	TL	8.14	289.5
Talar neck length	NL	4.69	–
Trochlear length	TRL	3.97	–
Mid-trochlear width	MTRW	3.69	501
Talar width[a]	TW	4.79	254.5
Medial talar height[b]	MTH	4.13	–
Medial talar body height	MTBH	2.72	–
Lateral talar body height[c]	HT	3.58	288.5
Talar head width[d]	HW	3.36	–
Talar head height[e]	HHT	2.95	–
Maximum ectal facet length	EFL	3.32	–
Maximum ectal facet width	EFW	2.01	–
Minimum ectal facet width	MEFW	1.6	–
Talar neck angle[f]	T-Neck-angle (a°)	35	–
Talar head torsion[g]	T-Head-angle (°)	10–15	–
Ectal facet orientation[h]	Ectal-F-angle (°)	50–55	–

T-Neck-angle and talar measurements follow the works of Gebo et al. (2001). The talus was measured with a microscope fitted with a calibrated reticle (Measuroscope Nikon 10). The body mass estimates are from the ‘All Strepsirhine’ bivariate regression equations (with correction factor of + 6.5%) provided by Dagosto and Terranova (1992).

[a] Distance from the most lateral point on the fibular facet (laterally projecting talar process) to the most medial point on the tibial facet.

[b] Perpendicular distance from the most dorsal aspect of the medial trochlear margin to a chord connecting the most plantar point on the medial talar body to the plantar aspect of the talar head.

[c] Perpendicular distance from the most dorsal point on the lateral trochlea margin to the chord defining the most plantar extent of the anterior and posterior aspects of the ectal facet.

[d] Maximum mediolateral width.

[e] Maximum dorsoplantar height.

[f] Medial deviation of the talar neck relative to the anteroposterior axis of the trochlea.

[g] Dorsolateral rotation of the talar head relative to the mediolateral axis of the dorsal trochlea.

[h] Position of the posterior calcaneal facet relative to the talar neck.

The talar body of MUSM-2024 is moderately high in lateral view (Fig. 2C) and is square-shaped in dorsal view (Fig. 2A; Table 2). The medial and lateral rims of the trochlea are rounded, nearly parallel (i.e., the trochlea is not wedge-shaped; Fig. 2A), and display a regular arc of curvature proximally (Fig. 2B–C). There is no strong depression in the distal part of the trochlea (Fig. 2A, arrow 4) and the lateral trochlear rim does not extend far distally as observed in some tali attributed to *Carlocebus* (MACN-SC 304 and 396), and in tali of some callitrichines (e.g., *Callithrix*, *Callimico*, *Saguinus*, and *Cebuella*; Fig. 3E–H) and cebines (*Saimiri* and *Cebus*; Fig. 3I–J). In posterior view, the trochlea is symmetrical and only slightly grooved (Fig. 2D). In having a symmetrical trochlea, MUSM-2024 clearly differs from the tali of some callitrichines (especially *Saguinus*, *Callithrix*, and *Leontopithecus*) and also some *Carlocebus* tali (MACN-SC 304 and 396), in which the lateral rim of the trochlea is noticeably more elevated than the medial rim. Dorsally, the surface of the trochlea extends distally onto the dorsal aspect of the neck, thereby forming a shallow dorsal tibial stop (Fig. 2A, arrow 5). This dorsal facet on the proximal part of the neck is observed in tali of *Carlocebus* and *Soriacebus*, and it is common among modern callitrichines (e.g., *Leontopithecus* and *Saguinus*; Fig. 3D, G) and pitheciines (e.g., *Pithecia*; Fig. 3C). In MUSM-2024, the most proximal part of the trochlea is rather flat, and the groove for the flexor muscle (flexor hallucis longus) is only barely marked (very shallow), being plantad and in a midline position relative to the posterior trochlear facet (Fig. 2D, arrow 6), as it does in the tali of all anthropoid primates. In callitrichines and pitheciines, this groove for the tendon of the flexor muscle is posteroplantarly buttressed by prominent medial and lateral tubercles (Gebo et al., 1990), the medial one being relatively larger and longer (Fig. 3). In MUSM-2024, the lateral tubercle is virtually indistinct (Fig. 2D, arrow 7) and the medial tubercle is moderately developed and projects moderately medially (Fig. 2D, arrow 8). A weakly pronounced and shallow groove for the flexor muscle, associated with a strong asymmetry regarding the development of the buttressing tubercles, are conditions found in aotines (*Aotus*; Fig. 3K) and in cebines (Fig. 3I–J), although in the latter (especially in *Cebus*) the lateral

Table 2
Talar ratios among primates (modified after Gebo et al., 2001).

Taxa	N	NL/TL	NL/TRL	NL/MTRW	HT/MTRW	HT/TRL	MTRW/TRL	HW/HHT	HW/MTRW	TW/TL	a°
Fossil taxa											
MD-61 Talus MUSM-2024	1	58	118	127	97	90	93	114	91	59	35
Dolichocebus gaimanensis (MACN-CH 362)	1	54	94	125	109	82	75	–	–	65	32
Soriacebus ameghinorum (MACN-SC 397)	1	58	97	115	88	74	85	107	84	59	39
Carlocebus cf. *carmenensis* (MACN-SC 271)	1	60	101	118	89	76	86	112	84	60	37
Carlocebus cf. *carmenensis* (MACN-SC 368)	1	58	95	115	85	71	83	120	91	66	34
Carlocebus cf. *carmenensis* (MACN-SC 304)	1	56	96	113	85	72	85	121	92	64	37
Carlocebus cf. *carmenensis* (MACN-SC 396)	1	60	94	114	90	75	82	104	82	73	36
Neosaimiri fieldsi (IGM-KU 89030)	1	58	97	116	88	74	84	107	85	59	30
Neosaimiri fieldsi (IGM-KU 89031)	1	55	91	113	95	76	80	105	87	55	37
Neosaimiri fieldsi (IGM-KU 89199)	1	54	88	113	104	81	78	127	95	58	35
Neosaimiri fieldsi (IGM-KU 8803)	1	60	104	141	108	79	73	84	91	64	35
La Venta IGM-KU 8802	1	59	90	132	103	76	74	106	109	68	32
Living taxa											
Cebupithecia sarmientoi	1	54	105	136	105	81	77	110	115	59	35
Cebuella pygmaeus	7	63 (55–69)	114 (94–124)	125 (109–135)	87 (81–91)	79 (70–86)	91 (82–95)	121 (112–136)	86 (82–91)	61 (59–64)	42
Callithrix jacchus	10	66 (60–72)	125 (112–143)	129 (112–145)	89 (82–95)	86 (82–93)	97 (91–104)	124 (111–136)	88 (83–95)	65 (58–74)	40
Callithrix argentata	6	64 (59–67)	124 (114–132)	134 (129–141)	88 (83–92)	81 (78–85)	92 (87–102)	131 (119–140)	94 (87–101)	61 (59–63)	38
Saguinus leucopus	3	59 (59–60)	116 (103–120)	154 (149–157)	108 (103–111)	72 (71–72)	82 (81–85)	120 (118–124)	110 (108–111)	62 (58–65)	37
Saguinus midas	4	60 (57–63)	111 (105–126)	138 (131–150)	100 (95–108)	74 (67–77)	84 (82–84)	117 (114–120)	101 (98–105)	66 (63–69)	34
Saguinus oedipus	20	59 (51–64)	106 (100–122)	121 (102–132)	91 (78–101)	76 (67–84)	88 (80–93)	118 (111–127)	88 (80–95)	65 (60–71)	37
Callimico goeldi	10	60 (54–66)	111 (101–130)	125 (110–141)	85 (81–89)	76 (70–82)	89 (82–94)	125 (119–142)	92 (87–96)	69 (60–75)	38
Saimiri sciureus	10	54 (48–61)	99 (87–103)	133 (112–150)	108 (100–117)	76 (69–86)	85 (80–90)	130 (124–137)	98 (91–120)	58 (53–64)	30
Cebus apella	6	57 (54–61)	97 (94–105)	118 (114–122)	104 (100–106)	86 (77–91)	82 (77–86)	122 (116–133)	94 (92–98)	66 (61–71)	32
Cebus capucinus	5	56 (53–62)	101 (95–103)	146 (139–159)	134 (127–143)	90 (86–97)	67 (60–71)	127 (118–138)	123 (119–132)	70 (68–73)	33
Callicebus torquatus	2	52 (52–53)	91 (89–94)	144	118 (117–119)	82 (80–84)	77 (76–77)	131 (125–136)	118 (115–121)	56 (55–58)	34
Callicebus donaphilus	3	51 (49–53)	85 (83–87)	125 (110–138)	112 (103–121)	83 (73–94)	77 (68–84)	142 (140–146)	102 (100–104)	59 (58–61)	30
Aotus azarae	6	53 (53–55)	96 (92–100)	144 (131–153)	119 (112–126)	77 (73–81)	83 (77–86)	131 (125–139)	110 (99–121)	54 (51–56)	31
Pithecia pithecia	6	52 (50–56)	86 (81–91)	132 (123–141)	105 (95–119)	68 (66–71)	65 (60–70)	135 (129–143)	118 (110–125)	69 (63–72)	35
Alouatta seniculus	5–6	50 (47–51)	85 (81–92)	116 (98–133)	93 (85–107)	68 (63–74)	74 (63–86)	134 (117–147)	100 (91–117)	70 (65–76)	33
Ateles belzebuth	1	45	77	87	95	84	88	104	81	68	35

Talar measurements and corresponding ratios for the talus specimens of *Soriacebus*, *Carlocebus* and *Neosaimiri* were provided courtesy of D. Gebo.

tubercle may appear more distinct. Fossil tali of *Dolichocebus* and *Carlocebus* exhibit a similar morphological pattern of this proximoplantar talar region as that observed in MUSM-2024. In general, the lateral tubercle forms a part of the posterolateral edge of the ectal facet (Fig. 2F, arrow 7). Due to the weak development of the lateral tubercle, the plantar posterior articulation with the calcaneus is less extensive and less curved in MUSM-2024 than in callitrichines (Fig. 3D–H). In MUSM-2024, the ectal facet is moderately long and narrow, and is oriented at roughly 55° to the talar neck. It exhibits a small radius of curvature (well concave), and its lateral margin is only slightly indented near its midpoint, as it does in *Saimiri* (Fig. 3J).

In dorsal view, the lateral side of the talar body of MUSM-2024 is steep (steep-sided talofibular facet), but it flares abruptly laterally in its plantar region, thereby forming a small and triangular lateral talar process (Fig. 2A, arrow 9). The medial side of the talar body is in contrast less steep-sided and possesses a small but well-marked plantar protuberance for the attachment of the posterior fibers of the deltoid ligament (Fig. 2A, arrow 10). This bony protuberance, which extends outward plantarly on the medial aspect of the talar body, is common in the tali of platyrrhines. In aotines (*Aotus*) and in some pitheciines (e.g., *Callicebus*), it can be prominent and faceted. In cebids and atelids, it is small and not faceted (Gebo et al., 1990). In MUSM-2024, the medial protuberance is moderately developed as it is in cebids. This protuberance contrasts with the site for the attachment of the anterior fibers of the deltoid ligament, which appears as a narrow and deep excavation (Fig. 2B). The medial talar facet for the tibial malleolus is well-elevated from the plantar surface, and is oriented obliquely. It is small, shallow and cup-like, somewhat flaring medially, which slightly projects onto the proximal aspect of the neck, thereby forming a medial tibial stop (Fig. 2A, arrow 11).

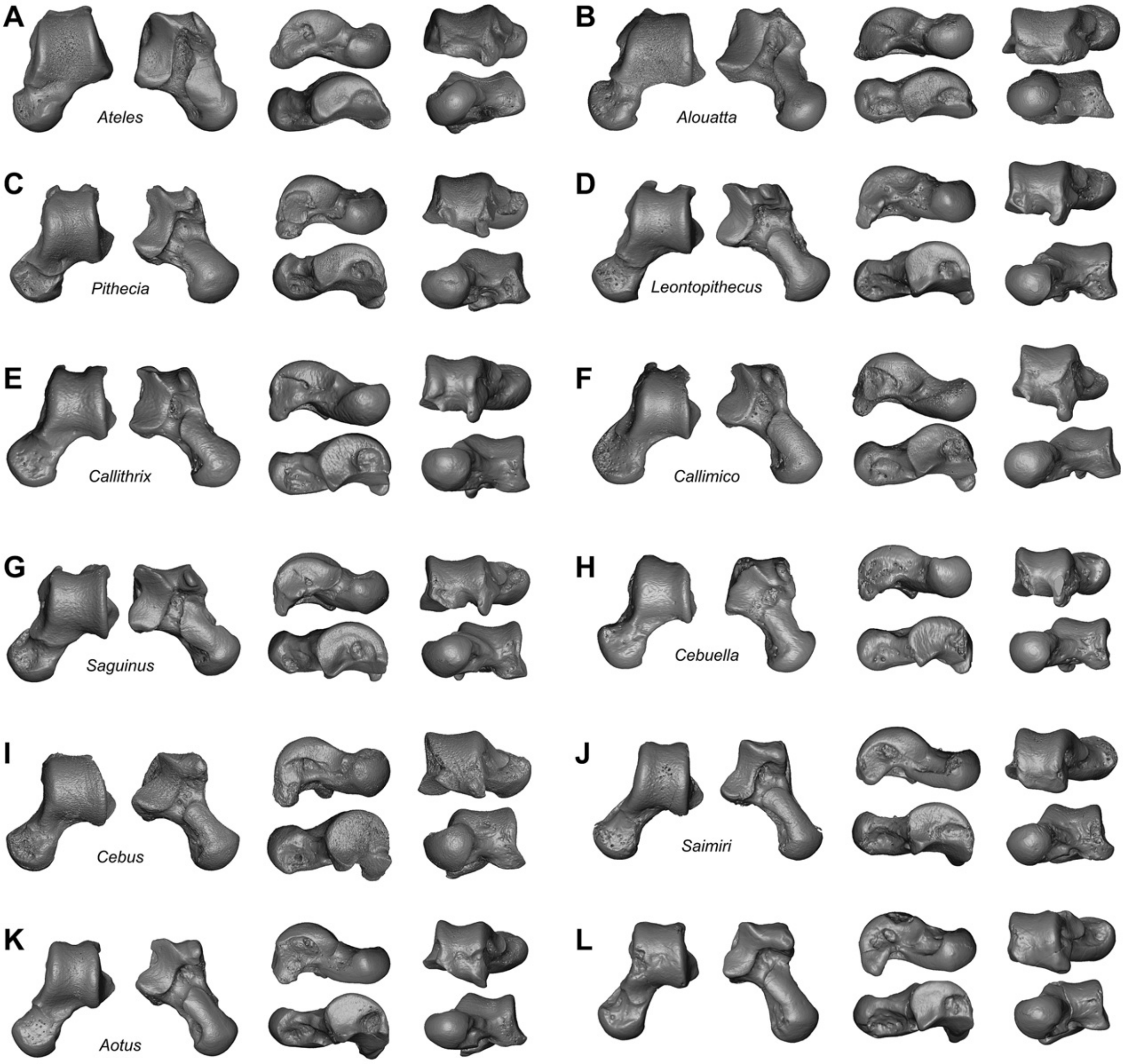

Figure 3. Photographs of left tali of living platyrrhines and of MUSM-2024 (MD-61, early Miocene, Amazonian Peru) obtained with microCT surface reconstructions. All tali are scaled to have equal proximodistal length. A, *Ateles belzebuth* (AS 1028); B, *Alouatta seniculus* (CG 1937-879); C, *Pithecia pithecia* (CG 1998-233); D, *Leontopithecus rosalia* (AS 1847); E, *Callithrix jacchus* (AS 6415); F, *Callimico goeldii* (AS 10332); G, *Saguinus midas* (CG 1998-232); H, *Cebuella pygmaeus* (AS 7162); I, *Cebus albifrons* (UMC-V13); J, *Saimiri sciureus* (AS 7495); K, *Aotus azarae* (AS 1036); L, MUSM-2024. Photographs of MUSM-2024 are reversed. For each talus, the views are as follow (from left to right and top to bottom): dorsal, plantar, medial, lateral, proximal, and distal. (AS, collections from the Anthropological Institute and Museum, Zurich; CG, collections from the Museum National d'Histoire Naturelle, Paris; UMC, collections of the Université Montpellier 2, Montpellier).

Discussion

Early Miocene platyrrhines have thus far been exclusively documented by taxa unearthed from middle and high latitudes of South America (central Chile and Argentinean Patagonia; Bordas, 1942; Fleagle and Bown, 1983; Fleagle et al., 1987; Fleagle and Kay, 1989; Fleagle, 1990; Meldrum, 1990; Flynn et al., 1995; Tejedor, 2002, 2003, 2005a, b). The new platyrrhine tarsal bone described here from the late early Miocene of Peruvian Amazonia represents the first fossil primate to be found in Peru, and also the first early Miocene record of primates in tropical-equatorial areas of South America. The South American fossil record is admittedly still limited but it testifies to the expected widespread distribution of primates in South America at that time. The MUSM-2024 talus from Atalaya (MD-61) was not found in association with other primate postcranial or dental remains. Therefore, any assessment of its phylogenetic affinities rests solely on its morphology. Although some of the talar features characterizing MUSM-2024 may be found in several groups of platyrrhines, the presence of a relatively long talar neck that narrows proximally, a moderately high, short and square talar body, a narrow and fairly rounded talar head, a barely marked proximoplantar groove for the tendon of the flexor muscle, a lateral proximal tubercle weakly developed, and the presence of a small but well-distinct protuberance on the medial aspect of the talar body, are characters primarily found in the Cebinae. Following regressions of talar dimensions against body mass in living primates, MUSM-2024 belonged to a small primate with a body mass ranging from about 250 g to 500 g (estimated from the 'All Strepsirhine' bivariate regression equations based on several linear talar dimensions [TW, MTRW, TL, and HT] provided by Dagosto and Terranova, (1992); Table 1). Therefore, the body size of this early Miocene primate from Peru approximated that of some living large bodied marmosets (i.e., *Callithrix*) or small bodied tamarins (i.e., *Saguinus*), also known as dwarf platyrrhine monkeys (Cebidae, Callitrichinae), from the Neotropics. MUSM-2024 would thus document a tiny *Saimiri*-like cebine, with the body size of a marmoset.

Functionally, MUSM-2024 bears a few talar features indicative of some leaping activity. For instance, a long talar neck, a moderately tall talar body, a slight trochlear grooving, and the presence of parallel- and steep-sided medial and lateral trochlear rims and facets, which display a regular arc of curvature proximally, are all features found in some generalized arboreal quadrupedal primates that are frequent leapers (Gebo, 1988). However, in MUSM-2024, the trochlea is not deeply grooved and the rims are not as sharp as those of specialized leapers, where only one primary plane of movement is needed at the talocrural joint to maximize stability during a leap (Gebo, 1988). Indeed, in MUSM-2024 the trochlea is rather flat and its rims are rounded, which probably allowed ankle motions with some degree of mobility at the talocrural joint. In addition, the cup-like malleolar tibial facet on the medial aspect of the talar body probably provided some stability in an inverted foot position. The same is true regarding both the shape and curvature of the ectal facet, which probably allowed a normal degree of subtalar motions, as those characterizing generalized arboreal quadrupedal primates. These talar characteristics indicate that this fossil species was an agile quadrupedal walking primate, probably capable of climbing, although not particularly specialized for this latter activity. MUSM-2024 does not exhibit the talar features observed in highly specialized climbers (e.g., talar body dorsoventrally flat, short and medially deflected talar neck, strongly wedged trochlear surface, reduction or lack of posterior trochlear shelf, small ectal facet with a high radius of curvature; Dagosto, 1983; Gebo, 1986, 1988). Another interesting talar character on MUSM-2024 is the surface of the trochlea, which extends distally onto the dorsal aspect of the neck to form a tibial stop. Such a talar structure indicates the possibility of extreme talocrural dorsiflexion and probably served to limit and stabilize the tibia by restricting its forward progress in vertical clinging posture (Fleagle and Meldrum, 1988; Gebo, 1988; Meldrum, 1990; Youlatos and Meldrum, 2011). In sum, the features and proportions of MUSM-2024 indicate that this small primate was engaged in a form of arboreal quadrupedalism with frequent horizontal leaping. In addition, the possibility of enhanced but stable dorsiflexed foot positions suggests that this small monkey also exhibited some proficiency in the use of vertical supports, a locomotor behavior that is frequently practiced by callitrichines and pitheciines. However, further postcranial elements are needed to better understand the activities and positional behaviors that characterized the locomotor repertoire of this new, small platyrrhine primate from the early Miocene of Peru.

Conclusion

The small talus described here is the first platyrrhine fossil described from Peru and the earliest primate fossil from northern South America. Based on comparative anatomy, the overall morphology of this talus appears most similar to living Cebinae. Interestingly, this *Saimiri*-like cebine had a body size and mode of locomotion that approximated those of a callitrichine or small cebine cebid. However, in the absence of a more comprehensive fossil record for this new platyrrhine taxon, the phylogenetic affinities and locomotion of this small primate are far from being definitive. Nevertheless, despite a limited record for this new taxon, we have shown that its talus differs substantially from the tali of contemporaneous platyrrhine taxa from Patagonia and Chile. This new fossil taxon exhibits undoubted talar affinities with modern Cebidae (Cebinae + Callitrichinae) and, as such, it could be a stem representative of this crown clade. Finally, if we consider that most of the early Miocene Patagonian platyrrhines are not closely related to modern clades (i.e., outside the crown radiation: 'stem platyrrhine hypothesis' (SPH); e.g., Kay et al., 2008; Kay and Fleagle, 2010; Youlatos and Meldrum, 2011), the possibility exists that this small primate from Peruvian Amazonia documents the earliest known crown platyrrhine. Admittedly, this hypothesis would extend the origin of the cebid lineage back to the early Miocene (and possibly earlier) and imply a greater antiquity of the crown radiation as a result. Such an earlier radiation is in fact advocated by Rosenberger (2010, and references therein), who in contrast considers that most of the earliest known fossil taxa (early Miocene Patagonian platyrrhines) are nested within the crown radiation ('long lineage hypothesis' (LLH); e.g., Rosenberger, 2010). Regardless of the phylogenetic position of the early Miocene Patagonian platyrrhines, our discovery provides new evidence for the existence of some long-lived clades of modern platyrrhines. However, such a hypothesis requires further morphological support than current data allow. Our discovery from Peru demonstrates that the low latitudes of South America, notably the forests of the great Amazonian Basin, have played a critical role in the earliest radiation of crown platyrrhines. Given this fact and the great diversity of crown platyrrhines recorded during the middle Miocene in Northern South America (Colombia), further investigation of the late Paleogene – early Miocene tropical-equatorial areas of South America is urgently needed to better understand how New World monkeys evolved through space and time.

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