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New platyrrhine tali from La Venta, Colombia

Two new primate tali were discovered from the middle Miocene of South America at La Venta, Colombia. IGM-KU 8802 is similar in morphology to *Callicebus* and *Aotus*, and is allocated to cf. *Aotus dindensis*, while IGM-KU 8803, associated with a dentition of a new cebine primate, is similar to *Saimiri*. Both tali differ from the other known fossil platyrrhine tali, *Dolichocebus* and *Cebupithecia*, and increase our knowledge of the locomotor diversity of the La Venta primate fauna.

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Introduction

Two new platyrrhine tali were discovered at La Venta, Colombia, by the Japanese/American field team working in conjunction with INGEOMINAS (Instituto Nacional de Investigaciones Geologico-Mineras) during the field season of 1988. These two fossils add to the rare but growing number of postcranial remains of extinct platyrrhines from the Miocene of South America (Stirton, 1951; Gebo & Simons, 1987; Anapol & Fleagle, 1988; Ford, 1990). They represent the first new primate postcranials to be described from La Venta in nearly four decades. Here we: (1) describe the two new tali; (2) compare them with examples of living and extinct taxa, and (3) briefly discuss their functional and phylogenetic implications.

Descriptions

IGM-KU 8802 (Figure 1) was discovered within the Monkey Unit (Fields, 1959; Luchterhand *et al.*, 1986) at locality 9-86A in the area known as El Dinde. It is unassociated with other postcranial or dental remains. Platyrrhines known by dental remains from this locality include *Aotus dindensis* (Setoguchi & Rosenberger, 1987) and *Mohanamico hershkovitzi* (Luchterhand *et al.*, 1986). Other localities within the Monkey Unit of La Venta have

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yielded *Neosaimiri, Cebupithecia, Stirtonia* and *Micodon* (Stirton, 1951; Hershkovitz, 1970; Setoguchi & Rosenberger, 1985; Kay *et al.*, 1987). IGM-KU 8802 is not similar to the talus of *Cebupithecia*, is too small to belong to *Stirtonia*, and is too large for *Micodon*. Although similar in size to *Saimiri*, the fossil is not morphologically similar to the living genus (see discussion below) and so is not attributable to *Neosaimiri*. Given the platyrrhines known so far at La Venta, IGM-KU 8802 may be attributable to *Aotus dindensis* or *Mohanamico hershkovitzi*, (see Kay, 1990 and Rosenberger *et al.*, 1990, for discussion of their systematic relationships), two species of very similar size. Our analysis suggests that an allocation to cf. *Aotus dindensis* is appropriate.

IGM-KU 8802 possesses the following morphological characteristics: talar body robust and moderately high (Table 1, index HT/TL; Table 3) in lateral view; trochlear rims parallel with slight proximal wedging; medial trochlear rim rounded; trochlear surface fairly flat with little grooving along the midline; most proximal part of the trochlea flat and lacks a notch for the flexor groove; talar head and neck very wide (Table 1, index HW/TW; Table 3) and oval in shape, being flattened dorsoplantarly; slight lateral rotation of the talar head relative to the body; and tibial malleolar cup obliquely oriented. The medial side of the talus possesses a relatively large protuberance proximal to the insertion for the posterior talo-tibial ligament. The surface of the protuberance is flat, smooth and facet-like. Table 1 lists several measurements for this specimen and comparative taxa. IGM-KU 8802 is similar in size to tali of moderate-sized specimens of *Saimiri*.

The following combination of features implies extensive use of arboreal quadrupedalism for IGM-KU 8802 (see Gebo, 1988, 1989): a large talar head; a wide, short talar neck (Table 1, Table 3) combined with a moderate talar body height; slight trochlear grooving; a rounded medial trochlear rim; and a more obliquely facing tibial malleolar cup. There are no features indicating extensive climbing or leaping as seen in atelines or *Saimiri*, respectively.

IGM-KU 8802 exhibits a well developed protuberance with a facet-like surface proximal to the main area of insertion of the posterior talo-tibial ligament. We have observed a similar condition in only two genera of living platyrrhines, *Aotus* and *Callicebus* (Figure 1), where the protuberance is also relatively large and sometimes faceted (Table 2). In other platyrrhines the protuberance is not as large, nor is it usually faceted. Dissection of *Aotus trivirgatus* (Field Museum of Natural History #600277) and *Callicebus moloch* (FMNH #60278) reveals that the thick fibrous part of the posterior talo-tibial ligament originates anterior and dorsal to this protuberance, but much thinner connective tissue from the joint capsule sometimes inserts along the surface of the protuberance proximally. The size of the protuberance is probably related to the size of the posterior talo-tibial ligament. We can only envision three possibilities for the smoothing or "faceting" on this surface of the protuberance. The tibial malleolus appears to contact this region of the talus when the foot is fully plantarflexed and slightly abducted, but ligamentous and connective tissue prevents actual bone-on-bone contact. Posterior fibers of the posterior talo-tibial ligament or of the joint capsule may stretch over the distal part of this protuberance. However, the majority of fibers clearly originate distal to, rather than upon or proximal to the protuberance. The tendon of flexor digitorum longus also passes over the proximal part of the the protuberance in plantarflexion. We cannot now determine which of these options are responsible for producing the facet. However, both the large size and smoothing of this feature distinguish the tali of *Aotus* and *Callicebus* from the otherwise similarly shaped tali of *Saimiri* and *Cebus*. Thus, the overall morphology of IGM-KU 8802 and the presence of a

Figure 1. Fossil tali from La Venta, Colombia, compared to tali of *Callicebus torquatus* and *Saimiri sciureus*. Top (dorsal view) and bottom (medial view). Rows one and three: IGM-KU 8802 (left) and *Callicebus torquatus* (right); rows two and four: IGM-KU 8803 (left) and *Saimiri sciureus* (right). Note the black arrows in row three which point to the large medial protuberance in IGM-KU 8802 and *Callicebus*.

Table 1 **Measurements and indices of the fossils and some extant platyrrhine species**

TAXON	N		AL	AW	TL	TW	NL	HW
IGM KU 8802	1		11·10	7·60	6·70	4·94	6·50	5·40
IGM KU 8803	1		10·40	6·68	5·99	4·39	6·20	4·00
Dolichocebus gaimanensis	1		14·76	9·63	8·42	6·35	7·94	—
Cebupithecia sarmientoi	1		15·07	8·85	7·73	5·94	8·11	6·86
Callicebus torquatus	2	mean	12·96	7·29	7·40	4·70	6·75	5·55
		range	12·8–13·12	7·2–7·37	7·2–7·6		6·75–6·76	5·4–5·7
C. donacophilus	3		12·78	7·57	7·63	5·21	6·46	5·30
			12·54–13·1	7·41–7·7	7·15–8·2	4·95–5·67	6·2–6·9	5·0–5·88
C. cupreus	1		13·16	7·45	7·54	5·61	7·24	5·42
Aotus azarae	6		13·89	7·55	7·72	5·18	7·41	5·67
			11·89–14·7	6·33–8·13	6·56–8·45	4·27–5·89	6·49–7·81	4·75–6·16
Aotus lemurinus	3		12·63	7·45	7·41	4·87	6·80	5·21
			12·57–12·73	6·97–8·05	7·03–7·71	4·78–5·03	6·52–7·19	5·08–5·29
Saimiri sciureus	10		11·79	6·82	6·53	4·78	6·30	4·67
			11·04–13·46	6·04–7·73	6·02–7·47	4·18–5·8	5·76–7·13	4·13–5·04
Cebus apella	6		17·71	11·67	10·31	8·49	10·00	7·95
			15·96–19·67	9·72–12·77	9·19–10·99	7·94–9·39	9·33–10·68	7·32–8·67
Callimico goeldii	3		9·65	5·74	5·58	4·15	5·40	4·35
			9·5–9·79	5·51–5·9	5·3–5·76	3·6–4·51	5·2–5·69	4·25–4·51
Saguinus leucopus	3		9·73	6·00	4·97	3·73	5·73	4·10
			9·4–10·1	5·9–6·1	4·6–5·3	3·5–3·9	5·5–5·9	3·9–4·2
S. midas	4		9·73	6·43	5·23	4·20	5·80	4·25
			9·3–10·0	5·9–6·8	4·9–5·6	3·9–4·5	5·3–6·3	4·0–4·4
Pithecia pithecia	6		15·45	10·32	9·42	6·13	8·10	7·22
			14·6–16·1	9·7–10·8	9·0–9·9	5·9–6·3	7·7–8·5	6·8–7·6
Chiropotes satanas	4		17·58	12·73	10·18	6·95	9·85	7·83
			17·4–17·7	12·2–13·1	10·0–10·4	6·7–7·4	9·5–10·1	7·3–8·4
Alouatta palliata	3		21·58	15·53	13·31	8·58	10·78	9·37
			20·1–22·85	15·1–16·3	12·6–14·4	7·9–8·95	9·04–11·8	8·8–9·52
Alouatta seniculus	6		22·65	15·56	13·12	9·71	11·19	9·62
			20·54–24·05	14·7–17·17	11·82–13·9	8·2–10·94	10·4–12·22	9·0–10·3
Lagothrix lagothricha	4		23·18	17·50	15·03	9·33	10·98	10·58
			22·4–24·2	17·0–18·0	13·9–16·2	8·6–9·8	10·6–11·6	10·4–10·8

Table 1—*continued*

TAXON	N		HT	NL/TL	HT/TL	HW/TW	TW/TL
IGM KU 8802	1		5·10	89·55	76·12	114·89	73·73
IGM KU 8803	1		4·74	103·5	79·13	91·11	73·28
Dolichocebus gaimanensis	1		6·91	94·23	82·07	—	75·42
Cebupithecia sarmientoi	1		6·25	104·91	80·85	115·49	76·84
Callicebus torquatus	2	mean	5·55	91·34	74·6	118·08	63·56
		range	5·5–5·6	88·81–93·88	71·43–77·77	114·89–121·27	61·58–65·28
C. donacophilus	3		5·81	84·76	76·37	102·24	68·46
			5·6–6·0	83·42–86·71	68·29–83·92	100·0–103·7	60·97–75·19
C. cupreus	1		6·11	96·14	81·14	96·61	74·5
Aotus azarae	6		6·16	96·07	80·28	109·87	67·15
			5·22–6·58	91·98–100·0	75·97–83·61	98·64–120·78	60·35–70·45
Aotus lemurinus	3		5·59	91·83	75·62	108·68	65·83
			5·52–5·74	86·64–96·12	71·59–78·52	105·19–114·58	62·26–67·99
Saimiri sciureus	10		5·13	96·57	78·59	98·41	73·07
			4·81–5·91	86·88–107·57	73·37–86·54	90·17–105·25	63·54–77·85
Cebus apella	6		8·81	96·62	85·48	93·67	82·45
			7·99–9·99	93·63–105·0	76·88–90·90	92·01–98·41	76·88–86·39
Callimico goeldii	3		4·13	97·08	73·94	105·86	74·15
			3·9–4·35	93·31–99·82	72·71–75·52	98·15–119·44	67·92–78·29
Saguinus leucopus	3		4·03	115·67	81·42	109·88	75·22
			3·9–4·2	109·43–119·57	75·47–84·78	107·69–111·41	73·58–76·08
S. midas	4		4·20	111·27	80·53	101·27	80·43
			4·0–4·3	105·35–126·0	76·78–85·71	97·77–104·76	77·77–84·00
Pithecia pithecia	6		6·43	85·72	68·3	117·74	65·22
			6·0–7·0	81·05–91·39	66·66–70·70	109·68–122·03	59·99–70·00
Chiropotes satanas	4		7·00	96·8	68·81	112·73	68·35
			6·8–7·4	95·0–98·0	65·38–71·84	105·4–121·73	64·42–74·00
Alouatta palliata	3		8·72	81·03	65·68	109·29	64·42
			8·2–9·17	69·87–91·27	61·11–70·86	106·37–111·39	61·80–69·16
Alouatta seniculus	6		8·94	85·34	68·28	99·82	74·25
			8·43–9·39	80·62–91·81	63·33–73·86	90·95–117·07	63·56–86·60
Lagothrix lagothrica	4		9·15	73·26	61·33	113·79	62·27
			8·7–9·8	67·28–77·69	53·7–70·5	106·12–125·58	56·17–69·01

N, sample size; AL, length of talus; AW, width of talus; TL, length of trochlea; TW, width of trochlea; NL, length of neck; HW, width of head; HT, height of talus; NL/TL, length of neck relative to trochlear length; HT/TL, height of talus relative to trochlear length; HW/TW, width of head relative to trochlear width; TW/TL, width of trochlea relative to trochlear length.

Table 2 Features of the medial protuberance in selected taxa

Genus			Size of protuberance				Faceted	
			None	Small	Medium	Large	Yes	No
Aotus	N	14	0	3	6	5	5	9
	%		0	21	43	36	36	64
Callicebus	N	7	0	1	4	2	2	5
	%		0	14	57	29	29	71
Saimiri	N	9	4	4	1	0	0	9
	%		44	44	11	0	0	100
Cebus	N	25	5	18	2	0	3	22
	%		20	72	8	0	12	88
IGM-KU 8802						×	×	
IGM-KU 8803				×				×
Cebupithecia						×	×	
Dolichocebus					×			×

faceted protuberance indicate that the fossil is best allocated to the *Aotus-Callicebus* tribe, Aotini (e.g., Rosenberger, 1988 or see Rosenberger *et al.*, 1990, for a more recent revision of higher level platyrrhine classification).

IGM-KU 8803 (Figure 1) was discovered, in association with a mandible of a new cebine being described by Rosenberger, Setoguchi, and coworkers at a new locality, Masato site, above the Monkey Unit in Fields (1959) upper redbeds. This locality is younger than the El Dinde area, but still within the middle Miocene, Friasian Land Mammal Age.

IGM-KU 8803 is small compared to IGM-KU 8802 (Figure 1) but larger than *Callimico* or large species of *Saguinus* and smaller than *Saimiri*, which is concordant with the mandibular evidence. Table 1 lists several measurements for comparison. IGM-KU 8803 differs from KGM-KU 8802 in possessing: a relatively long talar neck (Table 1, index NL/TL) which narrows proximally; a narrower talar head (Table 1, index HW/TW; Table 3) which is fairly round and more laterally rotated; a more tightly curved (rather than posteriorly flaring) posterior medial tubercle; sharper trochlear rims; a tibial malleolar cup which is more in line with the medial side of the talar body; a less laterally flaring process of the fibular facet; and a small non-faceted medial protuberance. In its overall appearance, IGM-KU 8803 is unlike callitrichines, atelines, and the pitheciines *Pithecia, Chiropotes* and *Cacajao* (Table 3). Although morphologically most similar to *Saimiri*, IGM-KU 8803 lacks one feature normally found in this genus, a depression in the middle of the distal trochlea. Thus, we believe IGM-KU 8803 is most like the cebines, *Saimiri* and *Cebus*, and is probably best allocated to the Cebinae. The talar features noted above suggest a strong predominance of arboreal quadrupedalism rather than extreme leaping or climbing (Gebo, 1988, 1989). The longer talar neck, sharper trochlear rims and the more in-line position of the tibial malleolar cup imply more frequent leaping for IGM-KU 8803 than for IGM-KU 8802. We infer that the locomotor pattern of this new cebine resembled *Saimiri*, a quadrupedal-leaper (Fleagle & Mittermeier, 1980).

Discussion

Although slightly smaller than living members of this group, the talus of IGM-KU 8802 closely resembles that of *Aotus* and *Callicebus*. Like these aotins, IGM-KU 8802 has a

Table 3 **Distribution of talar features in living platyrrhines**

	Aotini	Cebinae	Callitrichinae	Pitheciini	Atelinae
Relative length of neck NL/TL	Moderately short 84·76–96·14	Moderately long 96·57–96·62	**Long** 97·08–115·67	Moderately short 85·72–96·8	**Very short** 73·26–85·34
Relative height of talar body HT/TL	Moderately high 74·6–81·14	**High** 78·59–85·48	Moderately high 73·94–81·42	Low 68·3–68·81	**Very low** 61·33–68·28
Relative width of talar body TW/TL	Long and narrow 63·56–74·50	Short, squared 73·07–82·45	Short, squared 74·15–80·43	Long and narrow 65·22–68·35	Long and narrow 62·27–74·25
Relative width of talar head HW/TW	Wide 96·61–118·08	**Moderately narrow** 93·67–98·41	Wide 101·27–109·88	Wide 112·73–17·74	Wide 99·82–113·79
Medial protuberance	**Medium to large sometimes faceted**	Small not faceted	Small not faceted	Small not faceted	Small not faceted
Flexor groove and tubercles	Shallow groove, small tubercles	Shallow groove, small tubercles	Prominent groove, moderate sized tubercles equal in size	Prominent groove, moderate tubercles, **medial more prominent**	Prominent groove medium-large tubercles medial slightly more prominent

Bold print indicates features unique (but not necessarily derived) for the taxon.

moderately short talar neck (Table 1 and Table 3), a moderately high talar body, and a moderately wide talar head. Although these features may be found singly in other groups of platyrrhines (Table 3), this combination is restricted to aotins. In addition, the strongly developed and "faceted" medial protuberance of the fossil particularly resembles *Aotus*. This makes it highly unlikely that IGM-KU 8802 can be assigned to the other platyrrhine of the same approximate size from the El Dinde site, *Mohanamico hershkovitzi*. *Mohanamico hershkovitzi* has been interpreted as a primitive pitheciine (e.g., Kay, 1990) or a callitrichine (Rosenberger *et al.*, 1990), but IGM-KU 8802 does not share the combination of talar features characterizing those groups (Table 3).

If the talus is correctly assigned to *Aotus dindensis*, the fossil species differs from extant *Aotus* in being smaller and having a slightly more square-shaped (relatively wide and short) talar body. The locomotion of *Aotus* and *Callicebus* has been described as primarily quadrupedal with some leaping (Kinzey, 1977, 1981; Wright, 1981). IGM-KU 8802 indicates a similar pattern but its smaller body size and more square-shaped talar body might indicate more frequent leaping than in extant aotins.

IGM-KU 8803 is most similar to the living Cebinae, although again it is smaller than either *Saimiri* or *Cebus*. The combination of a moderately long talar neck, a high talar body, a narrow talar head, and relatively short and wide talar body is found only in cebines. However, it is possible, if not probable, that these are also primitive traits for platyrrhines in general. The most likely locomotor pattern for IGM-KU 8803 is that of a quadrupedal-leaper, with a greater emphasis on leaping compared to IGM-KU 8802.

Both IGM-KU 8802 and 8803 are different from other known fossil platyrrhine tali. The pitheciine, *Cebupithecia sarmientoi*, also from La Venta, is much larger than either of them (Stirton & Savage, 1951; Stirton, 1951). Although the dental evidence clearly demonstrates that *Cebupithecia* is a pitheciine, its talus differs from the two living pitheciine species we measured, *Pithecia pithecia* and *Chiropotes satanas* (Table 1, Table 3). *Cebupithecia* has a relatively longer talar neck and a higher, more squared-shaped talar body. In these features, *Cebupithecia* is more like cebines or aotins than pitheciines, but its overall pattern is unlike any living platyrrhine group or any of the known fossils. *Cebupithecia* also exhibits a relatively large medial protuberance which is smoothed, another resemblance to aotins. The significance of these characters is difficult to interpret. *Cebupithecia* may be the most primitive known pitheciine, retaining shared primitive resemblances with aotins and cebines. Alternatively, its unusual morphology could reflect a unique, derived (for pitheciines) locomotor pattern. The talar features which distinguish *Cebupithecia* from other pitheciines indicate that leaping was relatively more frequent, as is also indicated by other postcranial features (Davis, 1987, 1988; Meldrum & Fleagle, 1988; Fleagle & Meldrum, 1988; Ford, 1990). We reconstruct *Cebupithecia*'s locomotor behavior as frequent quadrupedalism and leaping but, in contrast to Fleagle & Meldrum (1988), we see no talar features indicative of vertical clinging.

The early Miocene *Dolichocebus gaimanensis* is older than the Colombian material (Kraglievich, 1951; Fleagle & Bown, 1983; Fleagle, 1985). The skull and dentition of this species share similarities with the cebines, and particularly *Saimiri* (Rosenberger, 1979; Fleagle & Rosenberger, 1983). The talus of *Dolichocebus* is also most similar to that of aotins and cebines, having a relatively long neck and a moderately high and squared body. The medial protuberance is of medium size, larger than generally found in living cebines (Table 2). *Dolichocebus* differs from IGM-KU 8802 in its greater size, relatively higher talar body and smaller medial protuberance, and differs from IGM-KU 8803 in its greater size and

shorter neck. The locomotor profile of *Dolichocebus* would be similar to *Saimiri* and *Cebus*, emphasizing quadrupedalism and leaping.

Although the postcranial record of fossil platyrrhines is sparse compared to the catarrhine record, the new material described here adds to our understanding of the platyrrhine radiation. IGM-KU 8803, attributed to a new cebine genus provides additional evidence of a small, *Saimiri*-like monkey at La Venta. IGM-KU 8802, which we attribute to *Aotus dindensis*, is the first evidence of postcranial material from an aotin and indicates a similar locomotor pattern. The reconstructed locomotor patterns of *Dolichocebus gaimanensis, Cebupithecia hershkovitzi, Aotus dindensis*, and the new cebine from La Venta emphasize quadrupedalism with moderate to high frequencies of leaping. Since quadrupedalism/leaping represents the primitive locomotor pattern of the platyrrhines (Gebo, 1989), none of the fossil species has departed dramatically from this ancestral form of locomotion.

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