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Dental Variability in *Saimiri* and the Taxonomic Status of *Neosaimiri fieldsi*, an Early Squirrel Monkey from La Venta, Colombia

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Neosaimiri fieldsi, *from the South American middle Miocene locality of La Venta, is represented by a relatively complete mandible and dentition that strongly resembles that of extant* Saimiri. *Comparison with a large sample of mandibles of* Saimiri *indicates that this specimen cannot be distinguished from modern populations on the basis of any reportedly diagnostic feature, such as cingulid development, molar length ratio, trigonic/talonid ratio, or mandibular depth. The fossil is best considered an extinct species of the modern genus* Saimiri *until further material indicates otherwise.*

KEY WORDS: *Neosaimiri fieldsi*; *Saimiri fieldsi*; taxonomy; dentition; *Aotus dindensis*.

INTRODUCTION

The taxonomy of the fossil platyrrhine *Neosaimiri fieldsi* Stirton, 1951, from the Miocene deposits of La Venta, Columbia, has been in doubt since the species was first diagnosed (Stirton, 1951). Authorities tend to agree that the type specimen, a fragmentary lower jaw, is closely allied with *Saimiri*, the living squirrel monkeys (Hershkovitz, 1970; Simons, 1972;

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Szalay and Delson, 1979; Rose and Fleagle, 1981; Delson and Rosenberger, 1984), a point confirmed by recent discovery of postcranial remains (Meldrum *et al.*, 1990). However, its status as a distinct genus has been assumed (Hill, 1960) rather than independently analyzed. The discovery of more new fossil primates from the La Venta region (Setoguchi and Rosenberger, 1985, 1987; Luchterhand *et al.*, 1986; Kay *et al.*, 1987; Kay, 1989; Hartwig *et al.*, 1990; Gebo *et al.*, 1990), among them a species (*Aotus dindensis*) which cannot be distinguished at the generic level from modern owl monkeys (Setoguchi and Rosenberger, 1987), calls for a more detailed comparison of *Neosaimiri* and modern squirrel monkeys. We reassess the generic status of *Neosaimiri* in the context of a relatively large data set describing the interspecific variability of the comparable and pertinent dental features in extant *Saimiri*.

The possibility of synonymizing the genus *Neosaimiri* has been alluded to several times. In his initial description of the species, Stirton (1951, pp. 327–328) remarked:

> There are many differences between the Columbian fossil *Neosaimiri* and the Recent *Saimiri* mandible available for comparison. Many of the characters should be of generic rank, but this determination on the characters can not be made with only one *Saimiri* mandible.

Hill (1960, p. 320), who followed Stirton's analyses of La Venta primates closely, regarded the evidence for generic separation as "very slender." Delson and Rosenberger (1984) suggested that *Neosaimiri* and *Saimiri* would in fact be lumped into a single genus if classified according to the standards applied to cercopithecoids, perhaps separating the two only at the subgeneric level.

MATERIALS AND METHODS

We compiled qualitative and quantitative observations on a broad sample of modern *Saimiri*. We tested the null hypothesis that there are no significant differences (statistically/morphologically) that place *Neosaimiri* outside the range and pattern of variation found among the living species of *Saimiri*. The two leading authorities on the taxonomy of *Saimiri* differ in their interpretations, Hershkovitz (1984) recognizing four species and Thorington (1985) two. We divided our sample of 163 individual specimens into the four species recognized by Hershkovitz and several subsets (Table I). This total of seven comparative populations provides the most rigorous arrangement practical in the context of this study.

The type and only known mandible of *Neosaimiri* represents a young individual; it preserves I_2, C, and P_2–M_2 (Fig. 1). We restricted our study

Table I. Taxonomic Division of Genus *Saimiri* Used in This Study, Following Hershkovitz (1984)[a]

Population	Number				Abbreviation
	M	F	?	Total	
S. sciureus sciureus	19	16	2	37	sci
S. s. albigena	15	2	0	17	alb
S. s. macrodon	28	22	3	53	mac
S. boliviensis boliviensis	11	6	1	18	bol
S. b. peruviensis	17	7	0	24	per
S. oerstedi	4	3	0	7	oer
S. ustus	5	2	0	7	ust
Total	99	58	6	163	

[a] M, male; F, female; ?, unknown sex.

to the dimensions of the mandibular corpus and the central cheek teeth, P_4–M_2, which are presumed to be least affected by sexual dimorphism yet clearly demonstrate the *Saimiri* dental pattern. Special attention was given to the development of the molar buccal cingulid (Stirton's "anterolabial cingulum"), for its morphology distinguishes *Saimiri* from all other modern platyrrhines and can distinguish the living genus even on the basis of an isolated lower molar (Kinzey, 1973). Furthermore, paleontologists commonly emphasize cingulid development as a taxonomic character.

All measurements and morphological scores were taken by one of us (M.T.) in a survey of specimens at the Field Museum of Natural History. Trigonid length was measured between the mesial end of the tooth and the line connecting metaconid and protoconid. The difference between this measurement and the maximum length of the tooth determined the talonid length. Width measurements were taken along the intercusp lines. Figure 2 shows schematically the four categories of cingulid development that we employed. We define them as follows:

Type 0 (absent): no buccal cingulid in the ectoflexid (i.e., the sidewall indentation, where the cristid obliqua meets the distal wall of the trigonid).

Type 1 (slight): a small cingulid lodged in the ectoflexid, connecting the walls below the protoconid and cristid obliqua.

Type 2 (moderate): the cingulid extends around the base of the protoconid but is incomplete, possibly broken into two segments.

Type 3 (strong): the cingulid is ledge-like and continuous and may carry small, distinct conules.

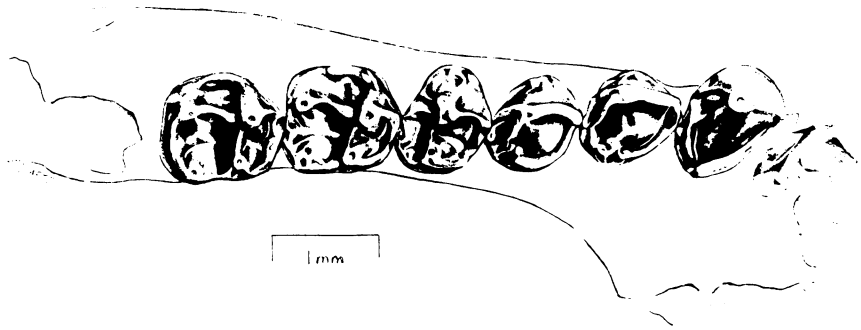


Fig. 1. Occlusal view of left mandibular portion of the type specimen of *Saimiri* (=*Neosaimiri*) *fieldsi*, I_2–M_2. See Table III for dimensions.

RESULTS

Tooth Size

Summary statistics of length and width dimensions of the central cheek teeth are listed in Table II and shown graphically in Fig. 3. There is considerable overlap among all modern populations in the 10 parameters. Furthermore, *Neosaimiri* falls either near the grand mean or within ±1 standard deviation of the mean in nearly all dimensions. It is only in M_2 talonid length that *Neosaimiri* falls slightly outside a standard deviation, but it still lies well within the observed range of values (Fig. 3). *Neosaimiri* may have a slightly narrower M_1 and slightly longer talonids, if any pattern of differences can be extracted from these data. The M_2/M_1 length ratio, cited as characteristic of the fossil by Stirton (1951) and others, is not appreciably different from those of our samples of modern *Saimiri* (Table II).

Cingulid Development

Using our criteria of cingulid development, based expressly on a *Saimiri* model, the $M_{1\text{-}2}$ cingulids of *Neosaimiri* are present but not extensively developed and are categorized as moderate (type 2). Table IV shows the distribution of cingulid classes for sex-pooled samples of all species of *Saimiri*. As noted in Table IV, there are no marked differences among living taxa of *Saimiri* in this character. The well-represented populations (*S. sciureus albigena, S. boliviensis boliviensis, S. s. macrodon, S. b. peruviensis*, and *S. s. sciureus*) are markedly similar to one another.

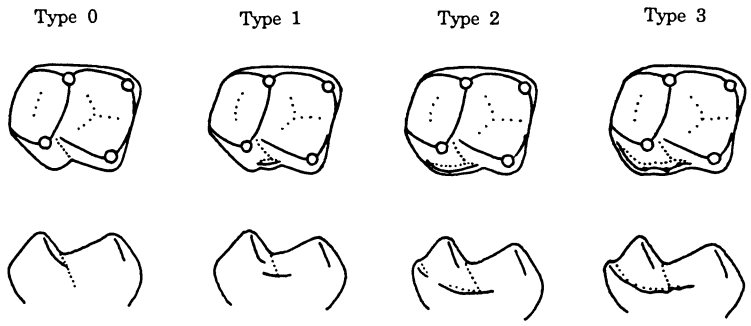


Fig. 2. Occlusal view (upper) and buccal view (lower) of schematic buccal cingulid types in modern *Saimiri* left lower molars. See text for description of each type.

The mean values for both sexes indicate that, according to our intragenic scale, a "typical" *Saimiri* molar also has moderately developed cingulids, which are best expressed on M_1. About 85% of all individual cases range from none to moderately developed cingulids, and in only 10–15% of any given population is the cingulid very strongly developed. Although cingulids tend to be more pronounced in males than in females (Table V), the differences between the sexes are not significant. The morphology of M_1 and M_2 of *Neosaimiri* follows the same symmetric pattern (type 2-2 in Table V) found most often in living *Saimiri*, with moderately developed cingulids on both teeth. Stirton (1951) had argued that the fossil was distinctly more developed in this character, but this observation was based on comparison with only one mandible of *Saimiri*. Thus cingulid development fails to discriminate among living species, and *Neosaimiri* again falls within their range of variation.

CONCLUSIONS

Discussions of *Neosaimiri* have repeatedly emphasized the strong morphological resemblances shared with *Saimiri* (Hershkovitz, 1970; Simons, 1972; Szalay and Delson, 1979), but most have not commented on the validity of the genus in spite of Stirton's (1951) own reservations. Perhaps this reflects the presumption that primates of Miocene times should be sufficiently distinct morphologically from their modern relatives to warrant generic separation.

Table II. Summary Statistics for Mandibular Premolar and Molar Dimensions (mm) in Populations of Modern *Saimiri* and for the Fossil[a]

	P_4		M_1		M_2		M_2/M_1,
Taxon	M–D	B–L	M–D	B–L	M–D	B–L	M–D
alb	2.39	2.92	2.92	2.95	2.60	2.78	0.89
bol	2.14	2.83	2.62	2.81	2.47	2.53	0.94
mac	2.29	2.81	2.87	2.88	2.61	2.65	0.91
oer	2.27	2.73	2.69	2.57	2.49	2.44	0.93
per	2.33	2.74	2.70	2.80	2.51	2.54	0.93
sci	2.24	2.65	2.78	2.79	2.56	2.61	0.92
ust	2.24	2.76	2.76	2.84	2.57	2.70	0.93
Neosaimiri	2.20	2.80	2.85	2.70	2.70	2.60	0.95

[a] See Table I for sample sizes and abbreviations.

Table III. Mandibular Depth and Width Dimensions (mm) Taken Below M_2 in Populations of Modern *Saimiri* and the Fossil[a]

	Depth		Width	
Taxon	Mean	Range	Mean	Range
alb	8.40	(7.0–9.9)	2.94	(2.5–3.4)
bol	7.74	(5.9–9.4)	2.92	(2.5–4.4)
mac	7.89	(6.5–10.1)	2.86	(2.4–3.6)
oer	7.07	(6.4–7.9)	2.71	(2.4–2.9)
per	7.37	(5.8–8.8)	3.02	(2.6–3.8)
sci	7.14	(5.8–9.0)	2.80	(2.3–3.6)
ust	7.23	(6.8–7.9)	2.80	(2.5–3.0)
Total	7.62	(5.8–10.1)	2.88	(2.3–4.4)
Neosaimiri	8.10		3.30	

[a] See Table I for abbreviations.

Stirton (1951, p. 327) referred to certain features of the fossil, in differentiating it from *Saimiri*, that he emphasized were of generic rank. Many of these would still be difficult to quantify and compare objectively (e.g., ". . . premolars not as elongate obliquely in *Neosaimiri* as in *Saimiri* . . ."), while others (". . . only remnant of anterolabial cingulum on M_1 in *Saimiri*, not prominent on *Neosaimiri* . . ."; "M_2 relatively smaller than M_1 in *Saimiri* but of equal size in the fossil . . .") have dissolved with a better appreciation of variability within *Saimiri*, as Stirton anticipated. In our estimation none of the other characters emphasized by Stirton and subsequent authors [i.e., cusp acuity, basin constriction (Delson and Rosenberger, 1984); arcade shape, incisor conformation (Hershkovitz, 1970; Simons, 1972)] would

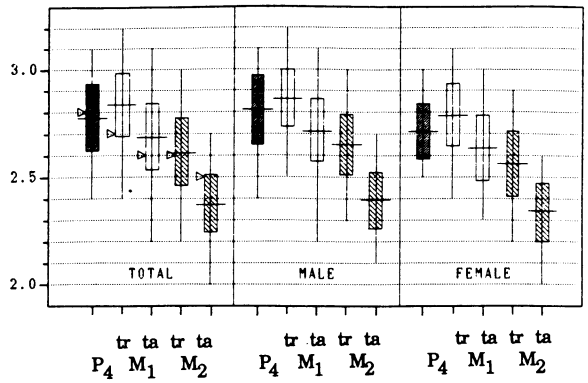
Table IV. Relative Frequencies of Cingulid Types in Sex-Pooled Populations of Modern *Saimiri*

	S. s. albigena				*S. b. boliviensis*				*S. s. macrodon*			
Type	M_1	%	M_2	%	M_1	%	M_2	%	M_1	%	M_2	%
0	4	24	4	24	3	20	8	53	4	8	8	16
1	7	41	4	24	4	27	3	20	5	10	17	34
2	6	35	8	48	6	40	4	27	30	60	17	34
3	0	0	1	6	2	13	0	0	11	22	9	18
Total	17		17		15		15		50		50	
	S. oerstedi				*S. b. peruviensis*				*S. s. sciureus*			
0	4	57	5	83	2	9	5	23	4	11	8	22
1	2	29	0	0	1	4	6	27	6	17	5	14
2	1	14	1	17	17	74	10	46	20	55	18	50
3	0	0	0	0	3	13	1	4	6	17	5	14
Total	7		7		23		22		36		36	
	S. ustus											
0	4	57	5	71								
1	0	0	0	0								
2	3	43	2	29								
3	0	0	0	0								
Total	7		7									

Table V. Relative Frequencies of Cingulid Type Combinations in Males and Females of Modern *Saimiri*[a]

Type	M + F		M		F	
M_{1-2}	*N*	%	*N*	%	*N*	%
0-0	23	15.0	12	12.8	11	20.0
0-1	2	1.3	2	2.1	0	0.0
0-2	0	0.0	0	0.0	0	0.0
0-3	0	0.0	0	0.0	0	0.0
1-0	11	7.2	7	7.4	4	4.3
1-1	8	5.2	2	2.1	6	10.9
1-2	5	3.3	5	5.3	0	0.0
1-3	0	0.0	0	0.0	0	0.0
2-0	8	5.2	4	4.3	3	5.5
2-1	25	16.3	15	16.0	8	14.5
2-2	45	29.4	30	31.9	15	27.3
2-3	4	2.6	2	2.1	2	3.6
3-0	1	0.7	0	0.0	1	1.8
3-1	0	0.0	0	0.0	0	0.0
3-2	9	5.9	7	7.4	1	1.8
3-3	12	7.8	8	8.5	4	7.3
Total	153		94		55	

Premolar & molar width (all species)

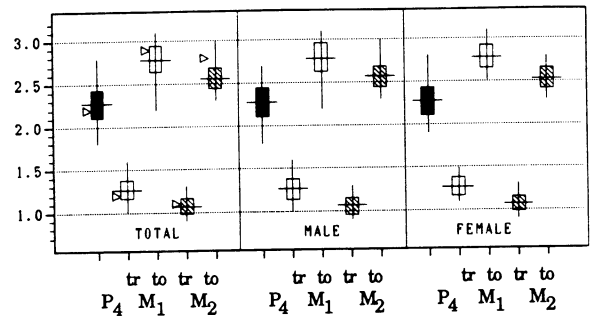


a.

▷ *Neosaimiri*

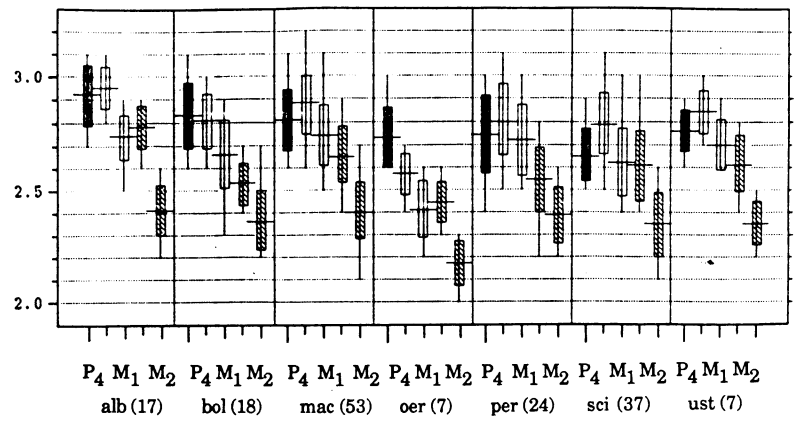
max
x + s.d.
x
x - s.d.
min

Premolar & molar length (all species)



b.

Premolar and molar width (male + female)



c.

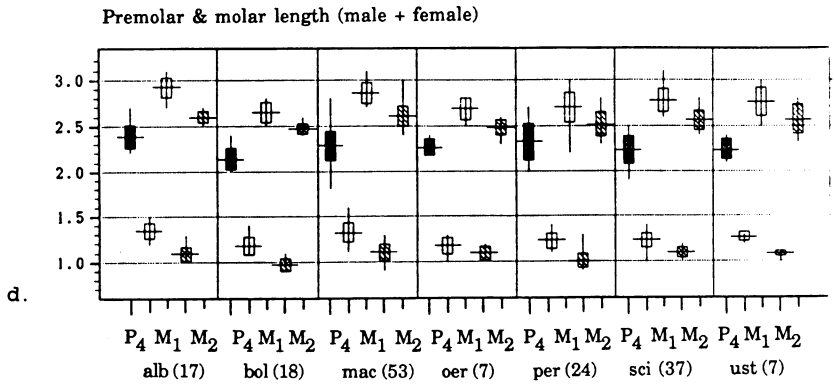


Fig. 3. Bar graphs of measurements (mm) for premolar and molar width and length for modern *Saimiri*, both cumulatively (a, b) and interspecifically (c, d). For each window, the filled box represents P_4, the two open boxes M_1, and the two hatched boxes M_2. The molar widths (a, c) are divided into trigonid (tr) and talonid width, and the molar lengths (b, d) are divided into trigonid and total (to) length. In c and d, the sample size for each population (see Table I for taxonal abbreviations) is indicated in parentheses. The fossil falls within one standard deviation for each parameter except M_2 total length.

qualify today as being of generic rank. Additionally, because the specimen is broken at the symphysis and contains only one incisor crown, it is impossible to reconstruct precisely the dental arcade and incisor battery.

Using conventional methods, our measurements and morphological observations on the central cheek teeth and mandible fail to distinguish the fossil from a suitably large sample of modern specimens of *Saimiri*. Indeed, although there are fundamental questions about the alpha taxonomy of *Saimiri*—Are there two, four, or more species?—none of the features we studied convincingly distinguished any of our samples from one another. We therefore conclude that the available fossil material provides no sound basis for maintaining *Neosaimiri* as a separate genus. Evidently, even in *Saimiri*, where the lower molars have a well marked accessory feature like the cingulid, their rather "simple" morphology offers insufficient variability to segregate species, either horizontally among modern forms or vertically through time.

If the modern forms can be shown to be monophyletic with respect to this fossil, or if they are shown to be composed of two or more valid subgroups, subgeneric distinctions may be useful. Until then, *Neosaimiri fieldsi* is more appropriately synonymized with *Saimiri*. In addition to *Aotus dindensis* (Setoguchi and Rosenberger, 1987), *Saimiri fieldsi* thus becomes

the second example of an extant primate genus to be known from the Miocene beds of La Venta.

ACKNOWLEDGMENTS

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