1 # Community Ecology of the Middle Miocene Primates of La Venta,

2 # Colombia: the Relationship between Ecological Diversity, Divergence

3 # Time, and Phylogenetic Richness

4

6

7

8 Brandon C. Wheeler

9 Interdepartmental Doctoral Program in Anthropological Sciences

10 Stony Brook University

11 Stony Brook, NY 11794-4364 USA

12 Phone: 1-631-675-6412

13 Fax: 1-631-632-9165

14 E-mail: bcwheeler43@gmail.com

15

16

17 Size of the manuscript:

18 Word count (whole file): 4,622

19 Word count abstract: 229

20 3 tables & 8 figures

21

22 Originally submitted to *Primates* on July 15, 2009

23 Revision submitted on November 26, 2009

24

25

26

Abstract

It has been suggested that the degree of ecological diversity that characterizes a primate

community correlates positively with both its phylogenetic richness

and the time since the members of that community diverged (Fleagle and Reed 1999). It is

therefore questionable whether or not a community with a relatively recent divergence time

but high phylogenetic richness would be as ecologically variable as a community with

similar phylogenetic richness but a more distant divergence time. To address this question,

the ecological diversity of a fossil primate community from La Venta, Colombia, a Middle

Miocene platyrrhine community with phylogenetic diversity comparable to extant

platyrrhine communities but a relatively short time since divergence, was compared with

that of modern neotropical primate communities. Shearing quotients and molar lengths,

which together are reliable indicators of diet, for both fossil and extant species were plotted

against each other to describe the dietary "ecospace" occupied by each community.

Community diversity was calculated as the area of the minimum convex polygon

encompassing all community members. The diversity of the fossil community was then

compared to that of extant communities to test if the fossil community was less diverse

than extant communities while taking phylogenetic richness into account. Results indicate

that the La Ventan community was not significantly less ecologically diverse than modern

communities, supporting the idea that ecological diversification occurred along with

phylogenetic diversification early in platyrrhine evolution.

Key words: New World monkeys; Ecospace; Primate communities; Dietary diversity;

Primate evolution

Introduction

Studies of primate communities over the past decade have used multivariate "ecospace" to describe the ecological diversity that characterizes a given community (e.g., Fleagle and Reed 1996; Godfrey et al. 1997; Gilbert 2005; see also Novack-Gottshall 2007). A community's ecospace can be defined as the space it takes up on multivariate axes which represent a variety of ecological variables (including diet, locomotor and positional behavior, activity pattern, and body size) and describe the niche of each species present in the community (see Fleagle and Reed 1996). Such analyses have demonstrated a positive relationship between the ecological diversity of a primate community and the degree of phylogenetic richness in that community (Fleagle and Reed 1999). Similarly, primate communities whose members share a more ancient common ancestor tend to be more diverse than those communities whose members share a more recent ancestor (Fleagle and Reed 1999). Specifically, Neotropical primate communities, whose members diverged relatively recently (20 Ma) (Hodgson et al. 2009), are much less ecologically diverse than Old World primate communities (Fleagle and Reed 1999), whose members share a more ancient common ancestor (80-90 Ma for African and Asian communities: Eizirik et al. 2004; 40 to 65 Ma for the Malagasy communities: Yoder and Yang 2004).

To date, studies correlating ecological diversity in primate communities with either phylogenetic diversity or time since divergence have not compared the ecological variation of fossil primate communities with that of living communities. Such a comparison is especially apt when examining the affect divergence time has on platyrrhine communities because there is little variation in average time since divergence among most New World primate communities due to the fact that most modern subfamilies appeared relatively early in platyrrhine evolution

74   (Rosenberger et al. 2009). The fossil community from La Venta, Colombia (see Fleagle et al.

75   1997) demonstrates a degree of phylogenetic richness (i.e., number of taxa) comparable to

76   modern communities (Rosenberger et al. 2009), with many taxa attributable to extant subfamilies

77   (Fig. 1), yet with a time since divergence roughly one third that of modern platyrrhines. The

78   positive relationship between ecological diversity and divergence time of primate communities

79   (Fleagle and Reed 1999) predicts that the fossil primate community at La Venta would be less

80   ecologically diverse than modern platyrrhine communities. However, because the phylogenetic

81   richness of the primate community from La Venta is comparable to many modern platyrrhine

82   communities, it is questionable whether the degree of diversity of the La Ventan primates would

83   be less than that of modern primate communities with a similar degree of phylogenetic diversity,

84   despite their shorter divergence time.

85   This study addresses this question by first examining how phylogenetic richness affects

86   ecological diversity (as determined by variation in dental measurements related to diet and body

87   size) in modern neotropical communities. The degree of ecological diversity of the La Ventan

88   fauna is then compared to that of the modern communities while taking the number of taxa

89   present in the community into account. It was predicted that modern communities with greater

90   phylogenetic richness would be more ecologically variable than less rich communities, and that

91   the La Ventan community would be less ecologically diverse than modern communities given its

92   degree of phylogenetic richness. This comparison of the La Ventan fossil community to modern

93   communities provides insight into whether ecological diversity has remained relatively static

94   since the divergence of the major extant platyrrhine clades, or if ecological diversity continued to

95   increase even after the initial adaptive radiation.

96

Methods

Diversity in the dietary ecology of the Middle Miocene fossil primate community at La Venta (see Kay and Madden 1997 for details regarding the paleoecology of La Venta) is here compared to that of nine modern neotropical primate communities (fig. 2, table 1). Extant communities were chosen such that a range of degrees phylogenetic diversity would be represented (see table 1 for a list of all species present at each site). The fossil community was limited to the five primate species associated with the La Ventan "Monkey Beds" sedimentary deposits (including *Aotus dindensis*, *Cebupithecia sarmientoi*, *Mohanamico hershkovitzi*, *Neosaimiri fieldsi*, and *Stirtonia tatacoensis*) (Fleagle et al., 1997; Hartwig and Meldrum, 2002) plus the one species found in deposits both above and below the Monkey Beds (*Patasola magdalenae*). *Micodon kiotensis* is also associated with the Monkey Beds but was not included as a member of the fossil community because the limited fossil remains of this genus do not allow for detailed analysis regarding its ecology (Rosenberger et al. 2009) and the specimens ascribed to this genus may actually be deciduous teeth of another La Ventan primate species such as *Neosaimiri* (Fleagle et al. 1997; Fleagle pers. comm.). The Monkey Beds date to slightly less than 13 Ma (Madden et al. 1997; Flynn et al. 1997; but see Takemura et al. 1992 for slightly older dates for younger La Ventan deposits) and are thought to represent a short enough period of time (approximately 15 ky; Kay and Madden 1997) that it is likely that the species found in this deposit co-existed.

Ecological diversity was determined through analysis of variation in shearing quotients (SQ) and length of the lower first molar (M_1), which respectively are indicative of diet (Kay 1975) and body size (Gingerich et al. 1982). Shearing quotients are a measure of the development of the molar shearing crests; low (negative) SQ values indicate rounded molar

6

121   cusps and are associated with largely frugivorous diets while high (positive) values indicate

122   high-crested molars and are associated with largely folivorous (at large body sizes) or

123   insectivorous (at small body sizes) diets (see Kay 1975; Ungar and Kay 1995). These

124   measurements have been published for both fossil and extant taxa (Anthony and Kay 1993;

125   Fleagle et al. 1997; Meldrum and Kay 1997; Currie Ketchum 2002) and are perhaps the only

126   diet-related variables that are measurable for all species concerned, given that some fossil taxa

127   are represented exclusively by dental remains. Measurements are species averages (see table 2

128   for values of all measurements used) and were not measured for the specific populations used in

129   this study.

130   The M_1 length and SQ for each species were plotted against each other on a bivariate plot

131   to determine the dietary "ecospace" occupied by each primate assemblage (fig. 3). Following

132   Fleagle and Reed (1996), ecological diversity for each community was calculated as the area of

133   the minimum convex polygon (MCP) that encompasses the position of all species of that

134   community on the bivariate plot. MCPs were made from bivariate scatter plots made in

135   Microsoft Excel. The scale of each plot was standardized (as in fig. 3) so that the MCP area for

136   each community was directly comparable to those of all other communities. MCP areas were

137   calculated by importing each plot into Adobe Illustrator 12.0, dividing each MCP into multiple

138   triangles, and summing the areas of all constituting triangles. One mm of M1 length was given a

139   value of 3.175 cm in Adobe Illustrator, while 10 SQ units were given a value of 2.25 cm

140   Phylogenetic diversity for each community was measured using three methods: 1) the

141   number of species, 2) the number of genera, and 3) the number of subfamilies which make up the

142   community. Traditional (conservative) species designations were used following Fleagle (1999).

143   Based on Schneider (in Schneider and Rosenberger 1996), the following five subfamilies of

144 extant platyrrhines were recognized for the current study: Callitrichinae, Aotinae, Cebinae,

145 Atelinae, and Pitheciinae. Some researchers break the Platyrrhini down into additional (smaller)

146 groups, but only these five subfamilies were used because they are now widely accepted as

147 natural groupings (reviewed in Rylands et al. 2000; Rylands and Mittermeier 2009). The six

148 fossil taxa constituting the Miocene community were considered to be stem or crown members

149 of these subfamilies (fig. 1). Based on Fleagle and Kay (1997), *Cebupithecia sarmientoi* is

150 placed within the Pitheciinae and *Patasola magdalenae* is placed with the Callitrichinae. Based

151 on Rosenberger et al. (2009), *Aotus dindensis is placed within the Aotinae*, *Neosaimiri fieldsi* is

152 placed within the Cebinae, *Stirtonia tatacoensis* is placed within the Atelinae, and *Mohanamico*

153 *hershkovitzi* is placed within the Callitrichinae. It should be noted that the status of *Mohanamico*

154 is disputed, with Kay (1990) arguing that it is likely a pithecine. However, whether one places

155 this species within the callitrichines or the pithecines does not affect the current analysis because

156 it does not change the number of species, genera, or subfamilies present in the Monkey Beds

157 community.

158

159 Statistical Analyses

160

161   To examine the relationship between phylogenetic and ecological diversity, a linear

162 regression was used to test if each of the three measures of phylogenetic richness (i.e., number of

163 species, genera, and subfamilies) was a significant predictor of ecological diversity in the extant

164 communities. The area of the MCP of the La Ventan community was then compared to that of

165 the extant communities, taking into account each measure of phylogenetic richness which was

166 significant in the regressions. This was tested by measuring the vertical distance to the regression

167 line (i.e., the residual) on the plot of MCP area against phylogenetic richness for each of the

168 extant communities (fig. 4); a positive value was given to those points above the regression line

169 and a negative value to those below. The La Ventan community was then superimposed on the

170 graph (based on its MCP area and phylogenetic richness) and its vertical distance from the

171 regression line was measured. A special case t-test for comparing a single specimen against a

172 sample (Sokal and Rohlf 1995) was then used to test if the residual of the La Ventan community

173 differed significantly from those of the extant communities. Such a method allows for a test of

174 whether or not the La Ventan community was less diverse while taking phylogenetic richness

175 into account. Linear regressions were conducted using SPSS 15.0. The special case t-tests were

176 conducted by hand.

177

178 **Results**

179

180   Among extant communities, ecological diversity (as measured by MCP area) varied

181 considerably (Table 3) and was positively associated with each measure of phylogenetic

182 richness. Each of the number of species (n=9, R^2=0.537, p=0.025; fig. 5), the number of genera

183 (n=9, R^2=0.564, p=0.020; fig. 6), and the number of subfamilies (n=9, R^2=0.597, p=0.015; fig. 7)

184 were significant predictors of the area of the MCPs. When the La Ventan community is

185 superimposed onto these plots, it consistently falls below the regression line (figs. 5-7).

186 However, the degree to which the La Ventan community falls below the regression line is not

187 significantly different from that of the extant communities, regardless of how phylogenetic

188 richness was measured (number of species: t=-0.167, df=8, p>0.90; number of genera: t=-0.463,

189 df=8, p>0.90; number of subfamilies: t=-1.567, df=8, p>0.10).

190

Discussion

As expected, the greatest diversity in dietary ecospace as measured by the area of the

MCP was found in communities with the greatest degree of phylogenetic richness. This

relationship held whether phylogenetic richness was defined as the number of species, number of

genera, or number of subfamilies present in a given community. Differences in ecological

diversity between the La Ventan fossil community and modern communities, however, were not

significant. It thus seems that much of the ecological diversity that characterizes extant

Neotropical primate communities occurred early in the adaptive radiation of modern platyrrhines

(i.e., from 20 to 13 Ma) and that phylogenetic richness explains the degree of ecological diversity

that characterizes platyrrhine communities to a greater extent than does the time elapsed since

the members of that community diverged (see Fleagle and Reed 1999).

Despite the lack of a significant difference, it appears that some expansion in dietary

ecospace has occurred among New World primates over the last 13 million years (fig. 8). This

increase is related to both greater diversity in M_1 lengths among extant platyrrhines and a slight

increase in SQs at both small and large body size, with the species of La Venta having lower SQs

than many of their extant relatives. This may be indicative of an increased reliance on insectivory

and folivory in some modern taxa relative to the species of the fossil community. However, Kay

and Ungar (1997) found that although SQs of some Miocene catarrhines were low relative to

their modern relatives, dental microwear indicated that the Miocene fauna were as folivorous as

modern catarrhines with relatively high SQs. The authors argued that this may be an example of

the "Red Queen effect" (see Van Valen 1973), in which these folivorous taxa became better

adapted to the niche they already occupied as a means to compete with other contemporaneous

214 folivores. It is possible that a similar phenomenon occurred in the course of platyrrhine

215 evolution; studies of microscopic dental wear in these fossil species would provide insight in this

216 regard. In addition to an increase in SQs, some of the expansion of ecospace that has taken place

217 over the last 13 million years is the result of a greater diversity of M_1 lengths among extant taxa

218 relative to the species of the La Ventan Monkey Beds. If relatively recent platyrrhine

219 communities, such as those which included *Protopithecus* and *Caipora*, were included among

220 modern communities, the dietary ecospace would be considerably larger, as these taxa are up to

221 twice the size of any modern New World primate (MacPhee and Horovitz 2002; Rosenberger et

222 al. 2009).

223   Finally, the lack of a significant difference between La Venta and the extant communities

224 may be due to a type II error. It is possible that if other fossil platyrrhine communities dating to

225 the Middle Miocene were available for examination, a significant difference in ecological

226 diversity between the extinct and extant communities could be found. However, because of the

227 dearth of known fossil platyrrhine communities, this is not possible to test. Results may also

228 change if additional discoveries increase the number of taxa known from the Monkey Beds or

229 what we know about the ecology of the taxa already described. Indeed, a number of additional

230 taxa, including *Lagonimico, Nuciruptor*, *Stirtonia victoriae* (Fleagle et al. 1997), and

231 *Miocallicebus* (Takai et al. 2001) have been found in other La Ventan deposits and may

232 eventually be known from the Monkey Beds, although their addition to the fossil community

233 would not necessarily change the results or conclusion of the current study. Among the species

234 known from other layers, lower dentition is available for three (*Lagonimico, Nuciruptor,*

235 *Stirtonia victoriae*; Fleagle et al., 1997; Meldrum & Kay 1997. While their addition would

236 indeed add somewhat to the fossil community's MCP area, this would also add to its

237 ==phylogenetic richness. Whether or not these species should be considered members of the fossil==

238 ==community awaits further fossil discoveries.==

239

240 **Acknowledgements**

241

248

249 **References**

250

251 Anthony MRL, Kay RF (1993) Tooth form and diet in ateline and alouattine primates:

252   reflections on the comparative method. Am J Sci 293A:356-382.

253 Aquino R (1978) La fauna primatológica en áreas de Jenaro Herrera. Proyecto de Asentamiento

254   Rural Integral en Jenaro Herrera, Boletín Tecnico 1:1-20

255 Currie Ketchum C (2002) Mandibular and dental measurements as predictors of diet in extant

256   and fossil platyrrhines. Master's Thesis, Arizona State University.

257 Eizirik E, Murphy WJ, Springer MS, O'Brien SJ (2004) Molecular phylogeny and dating of

258   early primate divergences. In: Ross CF, Kay RF (eds) Anthropoid origins: new visions.

259   Kluwer Academic, New York, pp 45-64

260 Fishkind AS, Sussman RW (1987) Preliminary survey of the primates of the Zona Protectora and

261   La Selva Biological Station, Northeast Costa Rica. Primate Conserv 8:63-66

262 Fleagle JG (1999) Primate adaptation and evolution. Academic Press, San Diego

263 Fleagle JG, Kay R (1997) Platyrrhines, catarrhines, and the fossil record. In: Kinzey WG (ed)

264   New World primates: ecology, evolution and behavior. Aldine de Gruyter, New York, pp

265   3–24

266 Fleagle JG, Kay RF, Anthony MRL (1997) Fossil New World monkeys. In: Kay RF, Madden

267   RH, Cifelli RL, Flynn JJ (eds) Vertebrate paleontology in the Neotropics: the Miocene

268   fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C., pp 473-

269   495

270 Fleagle JG, Reed KE (1996) Comparing primate communities: a multivariate approach. J Hum

271   Evol 30:489-510

272 Fleagle JG, Reed KE (1999) Phylogenetic and temporal perspectives on primate ecology. In:

273   Fleagle JG, Janson C, Reed KE (eds) Primate communities. Cambridge University Press,

274   New York, pp 92-115

275 Flynn J, Guerrero J, Swisher C (1997) Geochronology of the Honda Group. In: Kay RF, Madden

276   RH, Cifelli RL, Flynn JJ (eds) Vertebrate paleontology in the Neotropics: the Miocene

277   fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C., pp 44-59

278 Gilbert CC (2005) Dietary ecospace and the diversity of euprimates during the Early and Middle

279   Eocene. Am J Phys Anth 126:237-249

280 Gingerich PD, Smith BH, Rosenberg K (1982) Allometric scaling in the dentition of primates

281   and prediction of body weight from tooth size in fossils. Am J Phys Anth 58:81-100

282 Glanz WE (1990) Neotropical mammal densities: how unusual is the community on Barro

283   Colorado Island, Panama. In: Gentry AH (ed) Four Neotropical Rainforests. Yale

284   University Press, New York, pp 287-313

285   Godfrey LR, Jungers WL, Reed KE, Simons EL, Chatrath PS (1997) Subfossil lemurs:

286   inferences about past and present primate communities in Madagascar. In: Goodman SM,

287   Patterson BD (eds) Natural change and human impact in Madagascar. Smithsonian

288   Institution Press, Washington, pp 218-256

289   Green KM (1978) Primate censusing in northern Colombia: a comparison of two techniques.

290   Primates 19:537-550

291   Hartwig WC, Meldrum DJ (2002) Miocene platyrrhines of the northern Neotropics. In: Hartwig

292   WC (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 175–188

293   Hodgson JA, Sterner KN, Matthews LJ, Burrell AS, Jani RA, Raaum RL, Stewart CB, Disotell

294   TR (2009) Successive radiations, not stasis, in the South American primate fauna. Proc

295   Natl Acad Sci 106:5534-5539

296   Johns AD (1986) Effects of habitat disturbance on rainforest wildlife in Brazilian Amazonia.

297   World Wildlife Fund, Washington

298   Kay RF (1975) The functional adaptations of primate molar teeth. Am J Phys Anth 42:195-215

299   Kay RF (1990) The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini,

300   Anthropoidea). J Hum Evol 19:175-208

301   Kay RF, Madden RH (1997) Paleogeography and paleoecology. In: Kay RF, Madden RH, Cifelli

302   RL, Flynn JJ (eds) Vertebrate paleontology in the Neotropics: the Miocene fauna of La

303   Venta, Colombia. Smithsonian Institution Press, Washington, D.C., pp 520-550.

304   Kay RF, Ungar P (1997) Dental evidence for diet in some Miocene catarrhines with comments

305   on the effects of phylogeny on the interpretation of adaptation. In: Begun DR, Ward CV,

Rose MD (eds) Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations. Plenum Press, New York, pp 131-151

MacPhee RDE, Horovitz I (2002) Extinct Quaternary platyrrhines of the Greater Antilles and Brazil. In: Hartwig WC (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 189-200

Madden R, Guerrero J, Kay R, Flynn J, Swisher C, Walton A (1997) The La Ventan stage and age. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C., pp 499-519

Meldrum D, Kay R (1997) Postcranial skeletons of La Ventan platyrrhines. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C., pp 459-472

Mendes Pontes AR (1999) Environmental determinants of primate abundance in Maracá island, Roraima, Brazilian Amazonia. J Zool 247:189-199

Novack-Gottshall PM (2007) Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. Paleobiology 33:273-294

Rosenberger AL, Tejedor MF, Cooke SB, Pekar S (2009) Platyrrhine ecophylogenetics in space and time. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates: comparative perspectives in the study of behavior, ecology, and conservation. Springer, New York, pp 69-113

Rylands AB, Mittermeier RA (2009) The diversity of the New World primates (Platyrrhini): an annotated taxonomy. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier

329   KB (eds) South American primates: comparative perspectives in the study of behavior,

330   ecology, and conservation. Springer, New York, pp 23-54

331   Rylands AB, Schneider H, Langguth A, Mittermeier RA, Groves CP, Rodríguez-Luna E (2000)

332   An assessment of the diversity of New World primates. Neotropical Primates 8:61-93

333   Schneider H, Rosenberger AL (1996) Molecules, morphology, and platyrrhine systematics. In:

334   Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of Neotropical

335   primates. Plenum Press, New York, pp 3-19

336   Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological

337   research. W. H. Freeman and Co, New York

338   Stevenson PR (1996) Censos diurnos de mamíferos y algunas aves de gran tamaño en el Parque

339   Nacional Tinigua, Colombia. Universitas Scientiarum 3:67-81

340   Takai M, Anaya F, Suzuki H, Shigehara N, Setoguchi T (2001) A new platyrrhine from the

341   middle Miocene of La Venta, Colombia, and the phyletic position of Callicebinae.

342   109:289-308

343   Takemura A, Takai M, Danhara T, Setoguchi T (1992) Fission-track ages of the Villavieja

344   Formation of the Miocene Honda Group in La Venta, Department of Huila, Colombia.

345   8:19-27

346   Ungar PS, Kay RF (1995) The dietary adaptations of European Miocene catarrhines. Proc Natl

347   Acad Sci 92:5479-5481

348   Van Valen L (1973) A new evolutionary law. Evol Theory 1:1-30

349   Yoder A, Yang Z (2004) Divergence dates for Malagasy lemurs estimated from multiple gene

350   loci: geological and evolutionary context. 13:757-773

351

352

Table 1. The species present in each of the extant communities examined in this study.

subfamily	species	site								
		1	2	3	4	5	6	7	8	9
Pitheciinae	*Cacajao calvus*								x	
	Callicebus cupreus									x
	Callicebus moloch							x	x	
	Chiropotes satanas				x		x			
	Pithecia monachus								x	
	Pithecia pithecia				x					
Atelinae	*Alouatta belzebul*						x			
	Alouatta palliata	x	x							
	Alouatta seniculus			x	x	x		x		x
	Ateles belzebuth			x		x				x
	Ateles geoffroyi	x	x							
	Ateles paniscus				x			x		
	Lagothrix lagothricha								x	x
Cebinae	*Cebus albifrons*			x				x	x	
	Cebus apella				x	x	x	x		x
	Cebus capucinus	x	x							
	Cebus olivaceus					x				
	Saimiri sciureus				x	x	x	x	x	x
Aotinae	*Aotus azarae*									
	Aotus trivirgatus		x					x		x
Callitrichinae	*Cebuella pygmaea*								x	
	Saguinus fuscicollis							x	x	
	Saguinus geoffroyi		x							
	Saguinus imperator							x		
	Saguinus leucopus			x						
	Saguinus midas				x	x				
	Saguinus mystax								x	

1. La Selva, Costa Rica: Fishkind & Sussman 1987; 2. Barro Colorado Island, Panama: Glanz

1990; 3. Magdalena Valley, Colombia: Green 1978; 4. Raleighvallen, Suriname: Fleagle and

Reed 1996; 5. Maraca Island, Brazil: Mendes-Pontes 1999; 6. Pucurui River, Brazil: Johns 1986;

7. Cocha Cashu, Peru: Fleagle and Reed 1996; 8. Jenaro Herrera, Peru: Aquino 1978; 9. Tinigua,

Colombia: Stevenson 1996.

360 Table 2. Dental measurements used in this study.

Species	M_1 length (mm)	SQ*
Alouatta belzebul [2]	7.3	11.5
Alouatta palliata [1]	6.9	10.8
Alouatta seniculus [2]	7.0	12.7
Aotus azarae [2]	3.1	10.9
Aotus dindensis	3.2	4.7
Aotus trivirgatus [1]	3.1	10.9
Ateles belzebuth [2]	5.0	-1.0
Ateles geoffroyi [1]	5.3	-2.5
Ateles paniscus [2]	5.4	-3.5
Cacajao calvus [2]	4.3	-17.2
Callicebus cupreus [2]	3.2	-4.9
Callicebus moloch [1]	3.2	-4.7
Cebuella pygmaea [1]	1.8	0.9
Cebupithecia sarmientoi [1]	3.5	-19.4
Cebus albifrons [2]	4.5	-7.2
Cebus apella [1]	4.8	-11.3
Cebus capucinus [2]	4.5	-7.7
Cebus olivaceus [2]	4.5	-9.6
Chiropotes satanas [1]	3.6	-15.5
Lagothrix lagotricha [1]	5.5	1.9
Mohanamico hershkovitzi [1]	3.2	-14.6
Neosaimiri fieldsi [1]	2.9	-10.3
Patasola magdelenae [1]	2.5	-7.0
Pithecia monachus [1]	4.0	-6.6
Pithecia pithecia [2]	3.5	-4.5
Saguinus fuscicollis [2]	2.1	-7.0
Saguinus geoffroyi [1]	2.6	-7.9
Saguinus imperator [2]	2.5	-11.0
Saguinus leucops [2]	2.4	-9.3
Saguinus midas [2]	2.3	-9.7
Saguinus mystax [1]	2.5	-11.9
Saimiri sciureus [1]	2.9	6.4

361

362 [1] Data from Fleagle et al. (1997). [2] Data from Currie Ketchum (2002). *Methods for calculating

363 shearing quotients (SQs) described in Fleagle et al. (1997).

364

365   Table 3. Phylogenetic richness and minimum convex polygon (MCP) areas for each of the nine

366   extant and one fossil community examined in this study.

site	# species	# genera	# subfamilies	MCP area
La Selva	3	3	2	0.54
BCI*	5	5	4	12.06
Magdalena	4	4	3	3.99
Raleighvallen	7	7	4	15.42
Maraca Island	5	4	2	9.34
Pucurui River	5	5	4	15.63
Jenerro Herera	9	8	5	12.02
Cocha Cashu	9	7	5	16.82
Tiningua	7	7	4	13.35
La Venta	6	6	5	10.36

367   * Barro Colorado Island

Figure captions

369

370 **Figure 1.** Cladistic relationships of the extant platyrrhine subfamilies (based on Hodgson et al.

371 2009) and the placement of La Ventan taxa within those subfamilies. <mark>A= *Aotus dindensis*</mark>; C =

372 *Cebupithecia*; S = *Stirtonia*; N= *Neosaimiri*; M = *Mohanamico*; P = *Patasola*.

373

374 **Figure 2.** The location of La Venta and the nine extant communities examined in this study. 1.

375 La Selva, Costa Rica. 2. Barro Colorado Island, Panama. 3. Magdalena Valley, Colombia. 4.

376 Raleighvallen, Suriname. 5. Maraca Island, Brazil. 6. Pucurui River, Brazil. 7. Cocha Cashu,

377 Peru. 8. Jenaro Herrera, Peru. 9. Tinigua, Colombia.

378

379 **Figure 3.** An example of the method used to calculate ecological diversity for a given

380 community. This figure shows the shearing quotients (SQs) plotted against the lengths of the first

381 molars for the five species found in Barro Colorado, Panama. Ecological diversity was calculated

382 as the area of the minimum convex polygon encompassing all species of the community (see

383 Fleagle and Reed 1996).

384

385 **Figure 4.** An example of the method used to test for differences in ecological diversity between

386 the La Ventan fossil community and the extant communities. The diagonal line is the regression

387 line based on the equation that describes the relationship between the phylogenetic richness (i.e.,

388 the number of taxa) of the extant communities and the area their minimum convex polygons.

389 Vertical lines are the vertical distance (i.e., the residual) of each community from the regression

390   line. The fossil community is superimposed on the graph and is not included in the regression

391   equation.

392

393   **Figure 5.** The relationship between the number of species at a site and the area of the site's

394   minimum convex polygon. The La Ventan community is superimposed onto the graph.

395

396   **Figure 6.** The relationship between the number of genera at a site and the area of the site's

397   minimum convex polygon. The La Ventan community is superimposed onto the graph.

398

399   **Figure 7.** The relationship between the number of subfamilies at a site and the area of the site's

400   minimum convex polygon. The La Ventan community is superimposed onto the graph.

401

402   **Figure 8.** Scatter plot of shearing quotients (SQs) and M_1 lengths (a proxy for body size) for all

403   extant and fossil taxa included in the current study. Extant taxa show a greater degree of

404   variation in SQs at both small and large body size and slightly more variation in M_1 lengths. A=

405   *Aotus dindensis*; C = *Cebupithecia*; S = *Stirtonia*; N= *Neosaimiri*; M = *Mohanamico*; P =

406   *Patasola*.

407

408

409 **Figure 1**
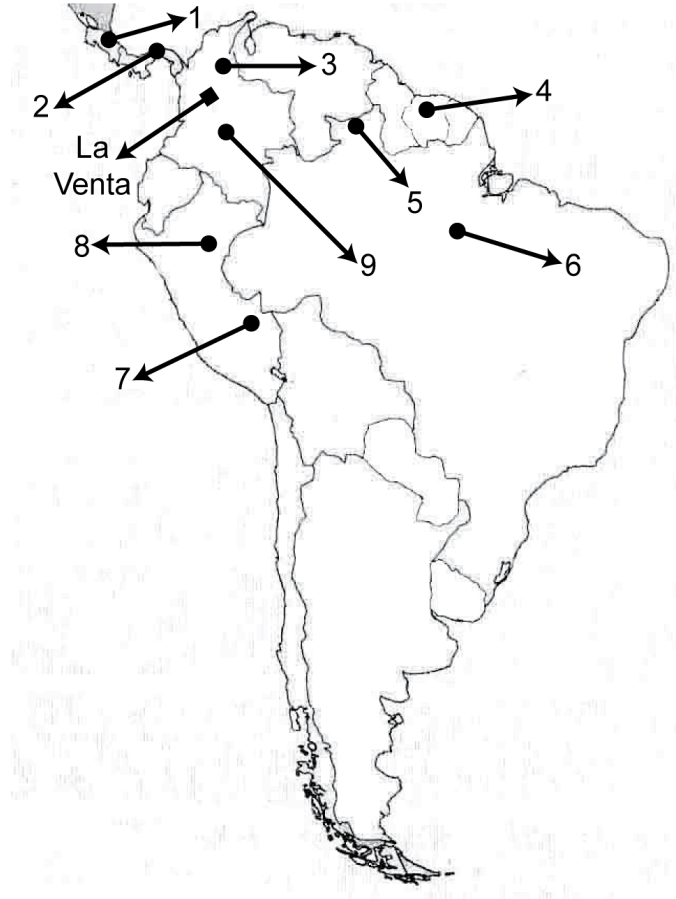
Pitheciines   Atelines   Cebines   Aotines   Callitrichines
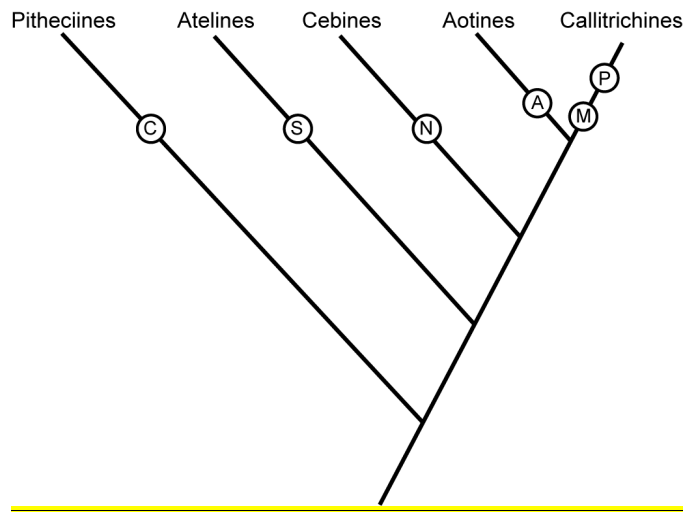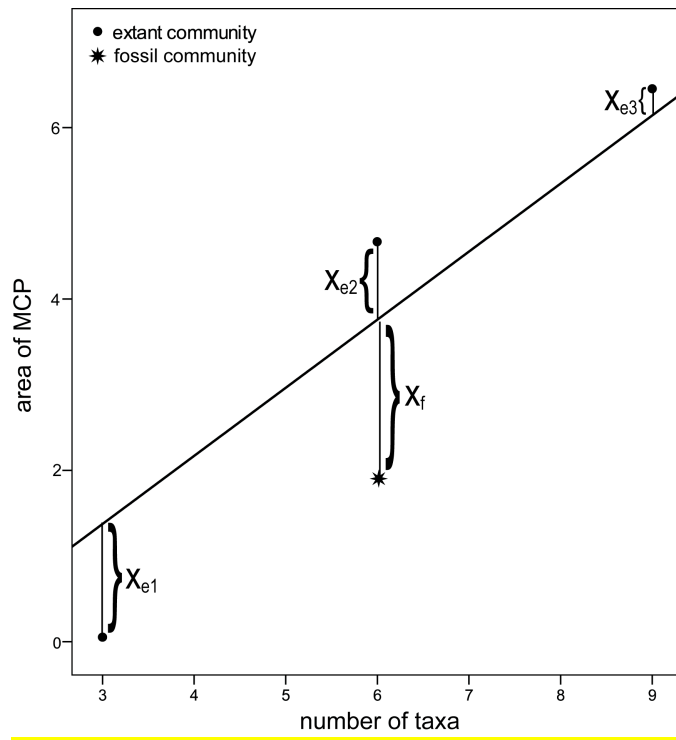

410

411
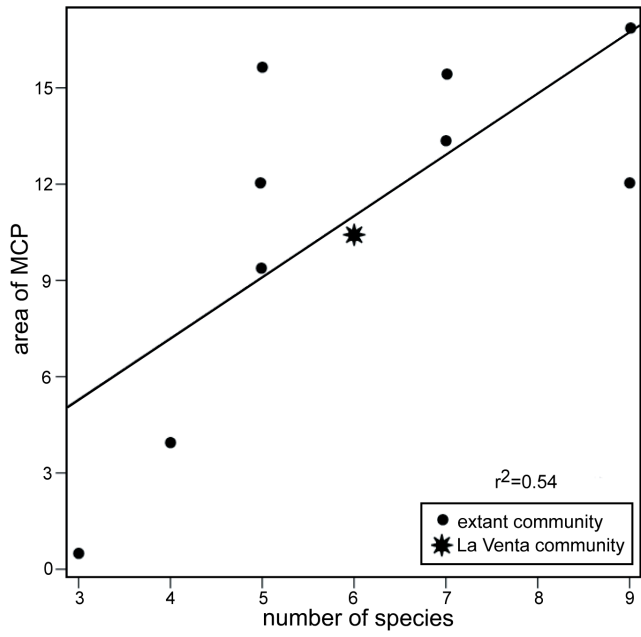
412

413

414   **Figure 2**

421 **Figure 3**
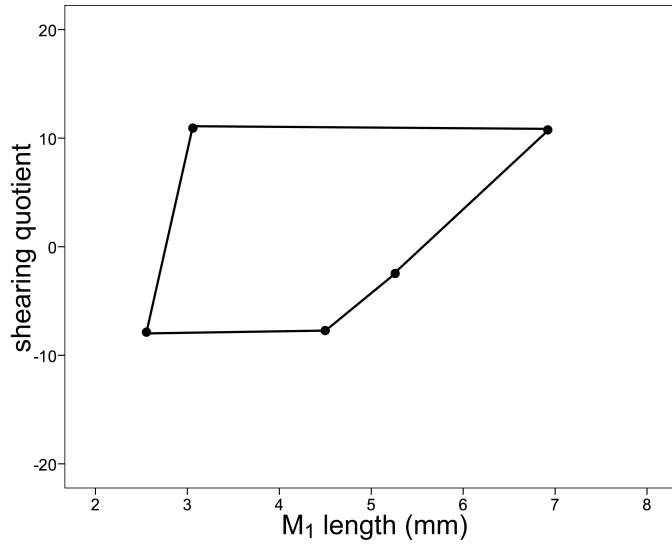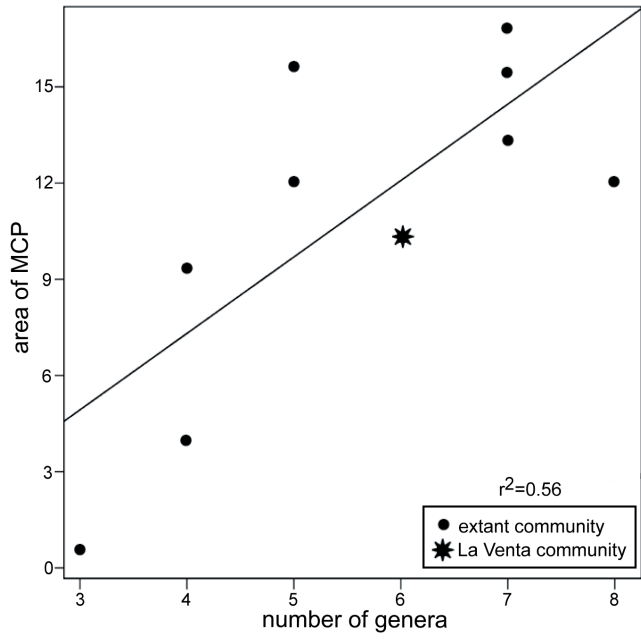

422
423

424 **Figure 4**

425

426

427

428
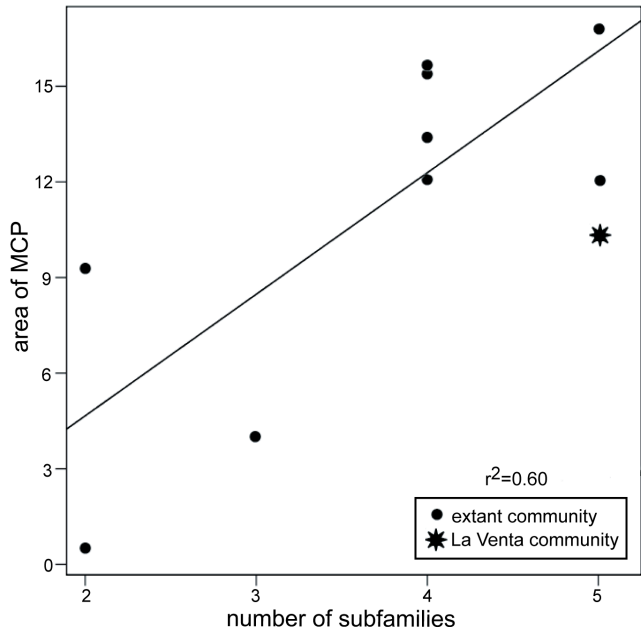
Figure 5

431
432
433
434
435
436

437   **Figure 6**
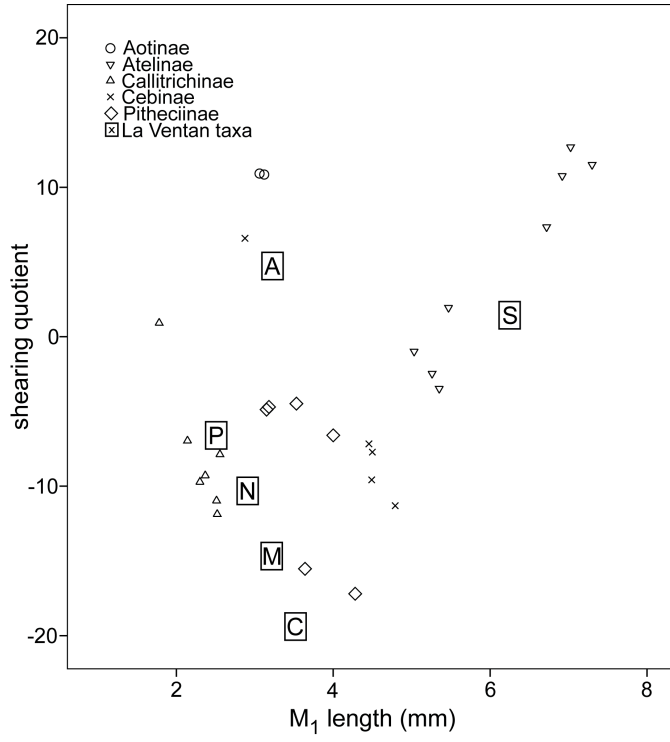
438

439

440

441

442

443

444

445   **Figure 7**

446

447

448

449

450

451 **Figure 8**

452

453

454