

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

Main Manuscript for

An Early Oligocene age for the oldest known monkeys and rodents of South America

Kenneth E. Campbell Jr.¹, Paul B. O'Sullivan², John G. Fleagle³, Dorien de Vries⁴, Erik R. Seiffert⁵

¹Department of Vertebrate Zoology, Natural History Museum of Los Angeles County, Los Angeles, California, 90007, USA

²GeoSep Services, Moscow, Idaho, 83843, USA

³Department of Anatomical Sciences, Renaissance School of Medicine, Stony Brook University, Stony Brook, New York, 11794, USA

⁴Ecosystems and Environment Research Centre, School of Science, Engineering and Environment, University of Salford, Manchester, U.K.

⁵Department of Integrative Anatomical Sciences, Keck School of Medicine of USC, University of Southern California, Los Angeles, California, 90033, USA

*Corresponding authors: Kenneth E. Campbell Jr. (ucayaliken@gmail.com) and Erik R. Seiffert (seiffert@usc.edu)

Author Contributions: KEC, JGF, and ERS collected zircon samples. PBO extracted zircons and performed LA-ICP-MS analyses. ERS ran Bayesian tip-dating analyses. DD compiled ages of caviomorph species. KEC, PBO, and ERS wrote the first draft and JGF and DD contributed to text.

Competing Interest Statement: The authors declare no competing interests.

Classification: Biological Sciences >> Anthropology.

Keywords: *Perupithecus*, *Ucayalipithecus*, Caviomorpha, Amazon Basin, paleobiogeography, zircon dating, tip-dating

This PDF file includes:

- Main Text
- Figures 1 to 3
- Table 1

30 **Abstract**

31 The Santa Rosa fossil locality in eastern Perú produced the first Paleogene vertebrate fauna from the
32 Amazon Basin, including the oldest known monkeys from South America. This diverse paleofauna was
33 originally assigned an Eocene age, based largely on the stage of evolution of the site's caviomorph
34 rodents and marsupials. Here we present new detrital zircon dates that indicate that the maximum
35 composite age of Santa Rosa is 29.6 ± 0.8 Ma (Lower Oligocene), although several zircons from Santa
36 Rosa date to the Upper Oligocene. The first appearance datum for Caviomorpha in South America is
37 purported to be the CTA-27 site in the Contamana region of Perú, which is hypothesized to be ~41 Ma
38 (Middle Eocene) in age. However, the presence of the same caviomorph species and/or genera at both
39 CTA-27 and at Santa Rosa is now difficult to reconcile with a >11 Myr age difference. To further test the
40 Middle Eocene age estimate for CTA-27, we ran multiple Bayesian tip-dating analyses of Caviomorpha,
41 treating the ages of all Paleogene species from Perú as unknown. These analyses produced mean age
42 estimates for Santa Rosa that overlap with the maximum 29.6 ± 0.8 Ma composite date provided by detrital
43 zircons, but predict that CTA-27 is much younger than currently thought (~31-30 Ma). We conclude that
44 the ~41 Ma age proposed for CTA-27 is incorrect, and that there are currently no compelling Eocene
45 records of either rodents or primates in the known fossil record of South America.

46 **Significance Statement**

47

48 The Paleogene dispersals of monkeys and rodents from Africa to South America permanently and
49 profoundly altered the composition of mammalian communities in the Neotropics, but the timing of these
50 colonization events remain uncertain. Through a combination of geochronological analyses (detrital zircon
51 dating of the Santa Rosa fossil locality in eastern Perú) and phylogenetic biochronological analyses (tip-
52 dating age estimation of caviomorph rodents), we demonstrate that the oldest known primates and
53 rodents of South America are unlikely to be older than Early Oligocene in age, and are not Eocene in age
54 as previously postulated. There are no grounds for rejecting the possibility of an earlier arrival for either
55 clade, but at present the fossil record provides no evidence for earlier dispersals.

56

57

58 **Introduction**

59
60 The Santa Rosa local fauna, derived from an isolated riverbank exposure in the Departamento de
61 Ucayali, Perú (Fig. 1), was the first Paleogene vertebrate paleofauna discovered in the low latitude,
62 lowland Neotropics of Amazonia (1). This paleofauna has proven to be extremely rich in terms of
63 numbers of specimens and their diversity. Fish and crocodylian teeth occur in the thousands, whereas
64 amphibians, turtles, lacertilians, birds, bats, notoungulates, xenarthrans, and anthropoid primates form
65 minor components. The most abundant, speciose, and best-studied mammalian groups are the
66 marsupials and caviomorph rodents. Though anthropoids are rare in the Santa Rosa paleofauna, they are
67 of outsized importance as they potentially represent the oldest records of that clade in South America,
68 and their inferred age would constrain scenarios for the timing of the trans-Atlantic dispersal of stem
69 platyrrhines from Africa (2, 3).

70 Three major factors have hindered studies of the Santa Rosan vertebrates. First, it is mostly a
71 microvertebrate paleofauna comprising primarily isolated teeth, the majority of which are only a few
72 millimeters in size. Moreover, there are few mammalian maxillary or mandibular fragments with more than
73 one tooth, which makes associating teeth of different loci within a species' tooth row difficult. Second, all
74 of the identified mammalian taxa present have been new to science at the species level, most at the
75 generic level, many at the family level, and some possibly even at the ordinal level. This makes
76 biogeographic and biostratigraphic correlation difficult, if not impossible, in most cases. Third, there have
77 been no means to date the paleofauna accurately using stratigraphy. The fossil site (Fig. 2) is located in a
78 remote, isolated corner of eastern Perú where access is solely by chartered aircraft and there has been
79 little to no modern geologic work. The regional stratigraphy is poorly exposed and known only
80 rudimentarily.

81 The Santa Rosa local fauna was tentatively assigned an ?Eocene age (1). This age assignment
82 was based on the perceived stage of evolution of the components of the large caviomorph rodent
83 assemblage (4) and the wide variety of primitive marsupials present in the paleofauna (5). Confidence in
84 the ?Eocene age was reinforced by the discovery of an anthropoid primate, *Perupithecus ucayaliensis*,
85 the single known tooth of which (an upper first molar) is very similar to that of the Late Eocene genus

86 *Talahpithecus* from Libya (6). A Late Eocene or Early Oligocene age for the paleofauna was proposed
87 based on study of the Santa Rosa cingulate xenarthrans (7), whereas Shockey et al. (8) suggested that
88 the site's notoungulates supported an "imprecise" late Paleogene age of Early to Late Oligocene. More
89 recently, the surprising discovery of a parapithecoid monkey of African origin (*Ucayalipithecus perdita*) at
90 Santa Rosa (3) provided a Lower Oligocene estimate for the site (31.7 Ma), derived from Bayesian tip-
91 dating analysis.

92 Several years after the discovery of the Santa Rosa locality and the first descriptions of
93 Paleogene vertebrates from lowland Amazonia (1), another international team began paleontological
94 work in the region south of the town of Contamana (07°19' S, 74°56' W), specifically along the Quebrada
95 Cachiyacu, a right bank tributary of the Ucayali River, where Kummel (9) had described a stratigraphic
96 sequence extending from the Cretaceous to the Plio-Pleistocene. This work resulted in the identification
97 of a number of Paleogene sites, which have been estimated to range in age from Middle Eocene to Upper
98 Oligocene (10-15). If this dating scheme is correct, some of the Contamana sites have produced the
99 oldest known caviomorph rodents from South America and constrain the caviomorph dispersal from Africa
100 to have occurred by the late Middle Eocene (~41 Ma). However, a number of the vertebrate taxa reported
101 from these sites appear to be closely related to those that were previously identified in the Santa Rosa
102 local fauna, particularly various species of caviomorph rodents (16) and genera of marsupials.

103 The Shapaja area of Perú, northwest of Contamana in the Departamento de San Martín, has also
104 yielded remains of Paleogene caviomorphs, and — unlike the oldest Contamana localities — fragmentary
105 dental remains of anthropoids as well (17, 18). No geochronological data are available from the Shapaja
106 localities (17). Boivin et al. (18) argued that the Shapaja localities are close in age to, but are likely
107 younger than, Santa Rosa (p. 134). More recently, Antoine et al. (17) presented chemostratigraphies of
108 the Shapaja sections based on $\delta^{13}\text{C}$ analyses of dispersed organic matter and carbonate nodules. They
109 found positive $\delta^{13}\text{C}$ excursions in the section which they correlated with the Oi-1 and Oi-1a events of the
110 earliest Oligocene, and used this evidence to argue that their oldest caviomorph-bearing locality (TAR-20)
111 is Upper Eocene in age, the next-oldest (TAR-21) is close in age to the Eocene-Oligocene boundary, and
112 all others are earliest Oligocene in age.

113 The confusing mix of conflicting biochronological signals from the Paleogene mammal-bearing
114 sites of Perú would ideally be resolved through robust geochronological analyses. Here we present new
115 data from detrital zircon U-Pb geochronology that indicate that the maximum age of the Santa Rosa site
116 is Lower Oligocene (29.6 ± 0.08 Ma), with the youngest grain from the locality dating to 25 ± 1.67 Ma (Upper
117 Oligocene). This new evidence forces a reanalysis of the rodent-bearing localities of Contamana and
118 Shapaja, several of which have strong biochronological ties to Santa Rosa but, as noted above, are
119 purported to be Eocene in age. In the absence of reliable geochronological data from these sites, we
120 provide an independent, unbiased, and objective test of the proposed ages of the Contamana and
121 Shapaja caviomorph-bearing sites by employing Bayesian tip-dating (=BTD) analyses (19-21) of an
122 unmodified caviomorph morphological matrix (22) that was originally compiled by several of the
123 researchers who have argued in favor of Eocene age estimates for some of the Contamana and Shapaja
124 caviomorph-bearing sites. The results of these BTD analyses suggest that there are no known
125 caviomorphs of Eocene age in the fossil record of South America, and that all of the caviomorph-bearing
126 sites of Contamana and Shapaja are likely to be either Lower Oligocene in age or younger.

127

128 **Results**

129

130 **LA-ICP-MS detrital zircon analyses.** Results of all zircon analyses are provided in *Tables S1-4* and
131 Cenozoic grains are summarized in Fig. 3. Of the 440 zircon grains analyzed, out of 110 zircon grains
132 analyzed per sample, 114 date to the Cenozoic. Only two grains date from the Paleocene and only 20
133 date from the Eocene. Of the other Cenozoic-aged zircon grains, 25 date to the Upper Oligocene and 67
134 date to the Lower Oligocene.

135 Following the law of detrital zircon chronology — i.e., a sedimentary rock cannot be older than the
136 youngest zircon grain it contains — the maximum depositional age (MDA) for the Santa Rosa deposits is
137 25 ± 1.67 Ma, or Upper Oligocene, based on youngest single grain (YSG) analyses of the detrital zircons
138 from the four samples analyzed (specifically from Spot 4, see Fig. 2). However, as noted by Herriott et al.
139 (23), detrital zircon analyses are always complicated by uncertainty, with YSG analyses often producing
140 results indicating a younger age than results derived from analyses of youngest statistical populations

141 (YSP). To derive the age of the YSP we used the program IsoplotR (24), which resulted in a composite
142 age for the four samples of 29.6 ± 0.08 Ma (Fig. 3). Results for the YSP analyses for each of the four
143 samples using IsoplotR are presented in *Figs. S3-6*.

144 The results from both types of analyses, YSG and YSP, falsify the postulated ?Eocene age
145 assigned to the Santa Rosa local fauna by Campbell et al. (1). Given that there are no significant
146 statistical differences among the four samples analyzed, we prefer to recognize the YSP age of 29.6 ± 0.08
147 Ma, or Lower Oligocene, as the best maximum age for the Santa Rosa deposit.

148

149 **Ages of the Paleogene caviomorph-bearing sites of Perú, as inferred from Bayesian tip-dating**

150 **analysis.** BTM analyses of the full caviomorph matrix of Marivaux et al. (22), with all species from the
151 Santa Rosa, Contamana (=CTA), and Shapaja (=TAR) localities assigned a broad post-Paleocene (56-0
152 Myr; i.e., effectively “unknown”) age prior, returned mean ages of 29.5 Ma for Santa Rosa (n=7 species),
153 30.3 Ma for CTA-27 (n=4 species), 27.0 Ma for CTA-29 (n=1 species), 28.7 Ma for the Shapaja localities
154 (n=6 species), 26.0 Ma for CTA-61 (n=3 species), and 21.8 Ma for CTA-32 (n=4 species) (*Fig. S7*). The
155 29.5 Ma BTM estimate for Santa Rosa is remarkably close to both the 29.6 ± 0.08 Ma YSP estimate from
156 detrital zircons, and to the mean 30.25 Ma estimate derived for the two Santa Rosa anthropoids that were
157 included in an entirely independent BTM analysis of a primate matrix (3). Our analyses correctly predicted
158 that *Pozomys ucayaliensis* from CTA-29 is younger (27.0 Ma) than the rodents from the underlying level
159 CTA-27 (mean of 30.3 Ma), and provide an independent age estimate for CTA-29 that is ~16.5 Myr
160 younger than that provided by “biotite” grains from the same layer (presumably reworked, see discussion
161 below) that yielded a $^{40}\text{Ar}/^{39}\text{Ar}$ date of 43.44 ± 2.5 Ma.

162 The ranges of mean estimates provided by our various BTM analyses (Table 1 and *Tables S5-*
163 *S9*) are largely in agreement with age estimates that had previously been proposed for the Shapaja and
164 younger Contamana localities. The 29.1-28.6 Ma estimates for the Shapaja localities are consistent with
165 the Lower Oligocene age favored by Boivin et al. (18), who argued that the sites were likely to be close in
166 age to Santa Rosa, but perhaps slightly younger. The 26.3-23.8 Ma (Upper Oligocene) age estimates for
167 the younger Contamana site CTA-61 are consistent with the 26.56 ± 0.07 Ma date from a detrital zircon (at

168 level CTA-08SA) that was collected 4 m below the fossil-bearing layer. The 22.7-20.8 Ma estimates for
169 CTA-32 (i.e., Lower Miocene, but potentially very close to the Oligocene-Miocene boundary of 23.03 Ma)
170 are younger than the Upper Oligocene age proposed by Boivin et al. (14), but they are also the estimates
171 with the most uncertainty. Only the BTM estimates of 31.0-29.8 Ma and 27.4-26.4 Ma for the older
172 Contamana localities (CTA-27 and CTA-29, respectively) are strongly at odds with the Middle Eocene
173 ages previously proposed for these sites (10, 11).

174 We estimated the marginal likelihoods of the two competing hypotheses for the age of CTA-27
175 and CTA-29 (Middle Eocene versus Lower Oligocene) by running two stepping stone analyses in
176 MrBayes 3.2.7 (25) – one in which CTA-27 and CTA-29 were fixed to the youngest bound (40.9 Ma) of
177 the age range favored by Antoine et al. (10), and one in which it was fixed to the mean age recovered by
178 our BTM analysis of the full data set (30.3 Ma). In both analyses, Santa Rosa, Shapaja, and the younger
179 Contamana localities were fixed to the mean age estimates from our BTM analysis of the full data set as
180 described above. The resulting estimated marginal likelihoods for the Middle Eocene (-10005.28) and
181 Lower Oligocene (-9994.64) hypotheses for the age of CTA-27 and CTA-29 differ by 10.64 units, and the
182 resulting $2 \times \log_e \text{BF}$ (BF, Bayes factor) test statistic of 21.28 indicates “very strong” (26) evidence in favor
183 of rejecting the Middle Eocene estimate.

184

185 **Discussion**

186 **Questioning the Middle Eocene age estimate for the earliest caviomorph rodents.** The first rodent-
187 bearing Paleogene faunas from Perú that were potentially older than that of Santa Rosa were recovered
188 from several localities along the Quebrada Cachiyacu near the town of Contamana. These sites produced
189 a number of isolated rodent teeth and an assortment of fragmentary vertebrate fossils (10, 11). The first
190 sites to be reported were interpreted to be Middle Eocene in age (10) based on three criteria: $^{40}\text{Ar}/^{39}\text{Ar}$
191 dates on biotites, mammalian biochronology, and an associated palynoflora “characteristic of the Middle
192 Eocene to Early Oligocene.” Each of these justifications requires reassessment in light of the new
193 geochronological evidence from Santa Rosa and the results of our BTM analyses, which support a much
194 younger (Lower Oligocene) age for the oldest Contamana localities (CTA-27 and CTA-29).

195 First, site CTA-29 — which, importantly, yielded the caviomorph species *Pozomys ucayaliensis*
196 (13) that has also been identified at Santa Rosa (16) — was dated to 43.44 ± 2.5 Ma based on $^{40}\text{Ar}/^{39}\text{Ar}$
197 step heating of single biotite grains ($n = 3$) derived from a “tuffaceous silt located 47 m above the
198 fossiliferous level” comprising CTA-27 (10). However, in defiance of the Law of Superposition (i.e., in
199 undeformed stratigraphic sequences, the oldest strata will always be at the bottom of a sequence), and
200 without explanation, locality CTA-27 was assigned an age of 41.6-40.94, or late Middle Eocene. We infer
201 that the authors were possibly taking into account the large standard deviation about the mean (± 2.5 Myr)
202 in the $^{40}\text{Ar}/^{39}\text{Ar}$ date to make the argument that the underlying stratum was younger. There is no evidence
203 that overturning of the beds exposed along the Quebrada Cachiyacu has taken place, and on their
204 depiction of the Cachiyacu Anticline of Kummel (9) (Maquia Anticline of Antoine et al. (10), their SOM fig.
205 S5), the authors did not indicate any overturned beds.

206 The biotite grains from CTA-29 that provided the 43.44 ± 2.5 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ date were derived from a
207 “reddish brown tuffaceous silt” (10) — which, by definition, means they were derived from a silt, not a tuff.
208 In recognizing this, the silt must have been a water-deposited sediment and not a consolidated volcanic
209 ash, or tuff, and therefore the probability that the silt and its contained biotite grains comprised reworked
210 sediments sourced from older deposits is quite high (by comparison, note for instance that there are 19
211 reworked detrital zircons of Middle and Late Eocene age at Santa Rosa; *Tables S1-4*). Antoine et al. (10)
212 cited Kummel (9) as describing the tuffaceous silt they dated as a tuff. However, Kummel (10, p. 1258)
213 mentioned only one ash, and no tuffaceous silts, in the Tertiary portion of the section along the Quebrada
214 Cachiyacu; that ash was a 2 m thick, massive, nodular, light gray to greenish buff-colored tuff in the
215 Chambira Formation. This deposit was located 294 m below the contact with the Ipururo Formation and
216 255 m above the contact with the Yahuarango Formation (9). Therefore the biotites from the reddish-
217 brown silt dated by Antoine et al. (10), which they cite as coming from the top of the Yahuarango
218 Formation, could not have come from the ash Kummel (9) described. Later, Boivin et al. (14) described
219 the sediments at CTA-27 and CTA-29 as scattered, inframetric, channelized “sands” and sandstone
220 lenses deposited within a low-energy small stream, as opposed to a tuffaceous silt (10). Located in a
221 foreland basin receiving sediments from the Andes, it can safely be assumed that any sands containing

222 biotites were reworked many times before being deposited in the lowlands of the Contamana region. Any
223 radiometric dates derived from reworked biotites do not necessarily, and in all probability do not, reflect
224 the age of deposition of the sandstone lenses.

225 Antoine et al. (10, SOM) correlated CTA-29 with CTA-08SA, the latter a deposit comprising “a
226 coarse altered tuffaceous sand with a mixture of quartz, feldspars, biotite, and white micas, and a
227 carbonate matrix” located on the opposite, or southwest, side of the Cachiyacu Anticline from CTA-29.
228 Antoine et al. (11) later described both CTA-29 and CTA-08SA as “tuffs”, a clear departure from their
229 earlier descriptions; no estimate for the percentage of tuffaceous material present in the sands of the sites
230 was given. Regarding the age of CTA-08SA, Antoine et al. (10) reported “no consistent data” from
231 attempts to date biotites from that site.

232 However, of importance for the dating of the stratigraphy, Antoine et al. (11) later reported ID-TIMS U/Pb
233 ($^{206}\text{Pb}/^{238}\text{U}$) dates on five detrital zircon grains from CTA-08SA. Two of the zircon grains produced ages
234 older than the Cenozoic (264.4 Ma and 903.3 Ma); these are significant only in indicating that the deposit
235 is detrital in origin and definitely not a tuff. The other three zircon grains yielded dates of 34.91 ± 0.20 ,
236 30.04 ± 0.08 , and 26.56 ± 0.07 Ma, or latest Upper Eocene to Lower Oligocene. By themselves, these three
237 dates do not comprise a sample sufficiently large to be treated statistically as a population, nor do they
238 indicate the age of the deposit, but they do suggest a possible maximum depositional age of the deposit.
239 It is therefore striking that the three youngest zircon dates all fall within the range of dates of zircon grains
240 from Santa Rosa, which do form a significant population (Fig. 3).

241 Antoine et al. (11) described undated zircon grains from CTA-08SA as generally sub-rounded and
242 having appearances suggesting that they are mostly detrital in origin, as opposed to a more pristine
243 appearance that would occur in grains from a tuff. The combination of sediments described for CTA-08SA
244 by Antoine et al. (10), and given above, are again consistent with a detrital origin for the deposit, and the
245 authors unequivocally state that the five analyzed zircon grains are detrital in origin, which conflicts with
246 the description of their having come from a tuff. Based on the dates from the zircon grains, Antoine et al.
247 (11) retracted the correlation of CTA-29 with CTA-08SA proposed by Antoine et al. (10). Instead, they
248 proposed a correlation of CTA-29 on the NE flank of the Cachiyacu Anticline with CTA-67, on the SW

249 flank of the Cachiyacu Anticline, the latter being lower in the stratigraphic section than CTA-08SA. CTA-
250 67 was described as comprising a tuff, but no mention was made of attempts to secure a radiometric date
251 from the site. A late Middle Eocene age was assigned to CTA-67 based on unspecified “all available
252 dating proxies,” presumably meaning miscellaneous fossil content.

253 Similarly, Boivin et al. (14) reported locality CTA-61 on the SW flank of the anticline as dating to
254 the Upper Oligocene by radioisotopy when its age was apparently extrapolated from mammalian
255 biochronology and from the dates for detrital zircons derived from CTA-08SA, a deposit stratigraphically
256 lower in the section, but on the same flank of the anticline.

257 Unfortunately, it will probably never be possible to secure an accurate date for CTA-29 and CTA-27
258 because Boivin et al. (14) reported that both localities, amongst others along the Quebrada Cachiyacu,
259 were irremediably lost because of landslides, erosion, or silting caused by flooding events.

260 Regarding the mammalian biochronology used by Antoine et al. (10) to support a late Middle
261 Eocene age for CTA-27, it is notable that, at the time of their publication, no vertebrate fossil from CTA-27
262 was affirmatively assigned to a previously known species. Subsequently, however, one of the caviomorph
263 species from CTA-27 (*Cachiyacuy kummeli*) was identified at Santa Rosa, as was *Pozomys ucayaliensis*
264 (16), which was first described from the Contamana region at the stratigraphically higher CTA-29 level
265 that yielded the 43.44 ± 2.5 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ date. The late Middle Eocene age (i.e., 41.6-40.94 Ma) estimated
266 for the mammalian paleofauna from CTA-27 by Antoine et al. (10) appears to have been initially based
267 primarily on their interpretation of the stage of evolution of fragmentary vertebrate specimens, and it might
268 have been significantly different had the *Cachiyacuy kummeli* and *Pozomys ucayaliensis* specimens from
269 Santa Rosa been known at the time. Similarly, further justification provided by Antoine et al. (10) for CTA-
270 27 being older than Santa Rosa was their interpretation that the caviomorph rodents from CTA-27 were
271 remarkably small compared with those of Santa Rosa (the assumption being that the smaller the
272 individuals comprising a species, the older the species). However, Arnal et al. (16) have since
273 documented that this was not true; some specimens from Santa Rosa are actually as small as, or smaller
274 than, the smallest rodents from Contamana. It is now clear that all of the genera and two of the species
275 recognized from Contamana also occurred in Santa Rosa, thereby demonstrating considerable taxonomic

276 overlap, and thus a similarity in ages, of the sites (16). Boivin et al. (14) acknowledged these similarities,
277 but took the position that they probably reflected biogeographic affinities more than contemporaneity.

278 Regarding the third line of evidence used to support a Middle Eocene age for sites such as CTA-
279 27 — i.e., a continental palynoflora — there is, in fact, no well-dated palynological zonation for western
280 lowland Amazonia, a vast region with many distinct sub-regions. Although it is possible to develop a
281 zonation for a given site, without a well-dated profile from a region near the profile site, if not actually at
282 the site, interpreting an accurate age for the palynological zones is not possible. In the case of the
283 Contamana sites, Antoine et al. (10) correlated what they perceived the pollen zonation of the Contamana
284 sites to be with that of the Llanos of Colombia, thousands of kilometers to the north (27). Further, of the
285 83 palynomorphs identified, 52 were represented by only a single specimen, only 15 were identified to
286 species, and an unspecified number were considered “novel.” Nonetheless, the age inferred by Antoine et
287 al. (10) from the pollen assemblage ranged from 44.8 (Middle Eocene) to 30.9 Ma (Early Oligocene), a
288 span of 13.9 Myr.

289
290 **Age of the Shapaja localities.** Our BTM results are also inconsistent with the latest Eocene and earliest
291 Oligocene ages that Antoine et al. (17) have proposed for the Shapaja localities. Though our analyses do
292 not correctly predict the sequence of the Shapaja localities, the mean estimates for individual species
293 nevertheless range from 31.6 to 20.7 Ma, with composite means for the section ranging from 29.1 to 28.6
294 Ma. The composite mean estimates for the Shapaja section are all very close to those for Santa Rosa,
295 differing by only 0.42 to 1.0 Myr across analyses with both broad (effectively “unknown”) and more
296 restricted age priors. These results are consistent with the close correlation of the Shapaja and Santa
297 Rosa sections originally proposed by Boivin et al. (18).

298 Antoine et al. (17) note that their placement of the Shapaja localities near the Eocene-Oligocene
299 boundary implies that these faunas include 14 new first appearances in South America (either at the
300 genus, family, or superfamily level), with most of the taxa in question otherwise first known from
301 Deseadan (Upper Oligocene) localities. With the geochronological evidence now available from Santa
302 Rosa, and the biochronological evidence for a close correlation of the Shapaja and Santa Rosa sections,

303 we propose that a more parsimonious explanation for the occurrence of otherwise Deseadan taxa in the
304 Shapaja localities is that those localities are, in fact, Deseadan in age. Given such an age estimate, we
305 suggest that the two positive $\delta^{13}\text{C}$ excursions identified in the Shapaja chemostratigraphies would be
306 better correlated with those that occur at ~26.5 and ~25.5 Ma in the generalized global record (reference
307 28, their Fig. 28.11). We further propose that the positive $\delta^{13}\text{C}$ values identified in the lowest parts of the
308 Shapaja chemostratigraphies more likely represent a zone dating to ~31-30 Ma (magnetochrons Cn10-
309 11) in the generalized global record (28). The Upper Oligocene ages that our proposed
310 chemostratigraphic correlation requires for the stratigraphically higher Shapaja localities are younger than
311 the composite estimates provided by our BTM analyses. However, the same can be said of the multiple
312 zircons of Upper Oligocene age at Santa Rosa (one as young as 25 ± 1.67 Ma) that are younger than that
313 site's composite mean estimate derived from our BTM analyses. Surprisingly given the much older age
314 estimates that have been proposed for both Santa Rosa and Shapaja, it may actually be the case that
315 these localities are not only Deseadan in age, but date to the latter half of the Deseadan, and our BTM
316 analyses are overestimating their ages.

317 Boivin et al. (29) recently described new rodents from the Balsayacu area of the Departamento
318 de San Martín that they interpreted as being intermediate in age between the CTA-27 locality (here
319 considered to be ~31-30 Ma) and those of Santa Rosa and Shapaja (here considered to be younger than
320 ~30 Ma, and possibly Upper Oligocene in age). Given all of the evidence presented here, we anticipate
321 that geochronological and/or phylogenetic biochronological evidence will ultimately place the Balsayacu
322 localities (TAR-55/TAR-55bis, TAR-76 and TAR-77) in the Oligocene as well.

323

324 **Implications for the timing of anthropoid and caviomorph dispersals to South America.** As

325 discussed above, given available evidence we see no compelling justification for the assignment of a
326 Middle, or even an Upper, Eocene age for the oldest rodent-bearing localities of Contamana and
327 Shapaja. However, this conclusion should not be taken to mean that caviomorphs were not present in
328 South America during the Eocene. In fact, a Middle Eocene origin for crown Caviomorpha is supported by
329 our BTM analyses of Marivaux et al.'s (22) matrix, which provided mean estimates for the origin of that

330 clade that extend back to 40.2-39.4 Ma (i.e., late Middle Eocene, Barrancan SALMA). These estimates
331 are remarkably congruent with the independent molecular estimate of 39.9 Ma that Upham and Patterson
332 (30) recovered for crown Caviomorpha when CTA-27 was excluded as a calibration point in their
333 analyses. These results predict that caviomorphs should eventually be found in the currently very meager
334 Late Eocene fossil record of South America.

335 There are no such ancient constraints on the timing of the primate dispersals from Africa to South
336 America, as recent molecular estimates for the origin of crown Platyrrhini generally favor a Late Oligocene
337 or Early Miocene origin of that clade (31-33). Given the absence of anthropoid fossils from CTA-27 and
338 CTA-29, and uncertainty about the precise age of the Santa Rosa and Shapaja anthropoid fossils, we can
339 only state that we see no evidence for this clade having been present in South America prior to ~30 Ma.
340 However, we also have no reason to rule out an earlier dispersal, for instance near the Eocene-Oligocene
341 boundary (3).

342

343 **Materials and methods**

344

345 **Collection of detrital zircons.** In a brief reconnaissance trip to the Santa Rosa locality in 2016 to
346 determine if the site still existed after an 18-year collecting hiatus, we sampled approximately 160 kg of
347 matrix for microvertebrate processing. The matrix came from 11 sites spaced across the face of the ~100
348 m long outcrop. Samples of the fine-grained (i.e., less than 1.0 mm) portion of the matrix from two sites
349 (#2 and near #10) at opposite ends of the outcrop (Fig. 2) were submitted for detrital zircon analysis via
350 LA-ICP-MS. However, as these samples were not collected with detrital zircon analysis in mind, in a
351 subsequent (2019) field season we carefully collected two additional samples from the center of the
352 outcrop (Fig. 2; sites #4 and #7). We submitted the latter samples directly to the laboratory, thereby
353 ensuring that there was no contamination during processing. As the objective of the detrital zircon dating
354 was to determine the maximum age for the deposit, we targeted for dating those zircon crystals that
355 looked to be youngest.

356

357 **LA-ICP-MS detrital zircon analyses.** The LA-ICP-MS methods followed to separate zircons from sample
358 material, and to then produce and process the zircon U/Pb data, are similar to those presented in Bradley
359 et al. (34), Hults et al. (35), and Moore et al. (36). GeoSep Services (GSS; Moscow, ID) performed all
360 zircon laboratory and analytical procedures. Zircons were separated from the four samples collected from
361 the outcrop using a combination of both standard separation procedures along with specific customized
362 procedures described by Donelick et al. (37). This particular process 1) enhances the recovery of all
363 possible grain sizes, while minimizing the potential loss of smaller grains through the use of water table
364 devices and 2) ensures the preservation of complete grains by minimizing grain breakage and/or
365 fracturing associated with traditional methods of isolating individual grains from solid rock samples, or in
366 this case highly consolidated sediment.

367 Isotopic analyses were performed with a New Wave UP-213 laser ablation system in conjunction
368 with an Agilent 7700x quadrupole inductively-coupled plasma-mass spectrometer (LA-ICP-MS) in the
369 GeoAnalytical Lab at Washington State University. For all laser analyses, the beam diameter was 20 μm
370 and the frequency was set at 5 Hz, yielding ablation pits $\sim 10\text{-}12$ μm deep. He and Ar gas were used to
371 deliver the ablated material into the plasma source. Each analysis of 32 cycles took approximately 30
372 seconds to complete and consisted of a 6-second integration on peaks with the laser shutter closed to
373 secure background measurements, followed by a 24-second integration with the shutter open and the
374 laser ablating zircon material. A 25-second delay occurred between analyses. The isotopes measured
375 included ^{202}Hg , $^{204}(\text{Hg} + \text{Pb})$, ^{206}Pb , ^{207}Pb , ^{208}Pb , ^{232}Th , ^{235}U , and ^{238}U . Additional details about
376 the LA-ICP-MS methods appear in the *SI Appendix*.

377
378 **Bayesian tip-dating analyses.** Tip-dating analyses employed the morphological character matrix of
379 Marivaux et al. (22) and were run in MrBayes v. 3.2.7 (25). No modifications were made to the matrix, and
380 the same character ordering scheme was used. The clockratepr prior was calculated using an R script
381 first published in Gunnell et al. (38), which used as input the “allcompat” consensus tree derived from a
382 non-clock Bayesian analysis and the means of the upper and lower bounds of each uniform age prior;
383 extant taxa were fixed at 0 Ma. So as not to bias the calculation of the clockratepr prior, we used the

384 Middle Eocene estimate favored by Antoine et al. (10) for species from CTA-27 and CTA-29, including
385 *Cachiyacuy kummeli* and *Pozomys ucayaliensis*. For two of the tip-dating analyses reported here, the
386 Contamana, Shapaja, and Santa Rosa localities were assigned a broad post-Paleocene (56-0 Myr) age
387 prior, whereas two other analyses employed the YSP age of 29.6 ± 0.08 Ma for Santa Rosa. For each set
388 of age priors, we ran analyses with 1) only the taxa that Marivaux et al. included in their parsimony
389 analysis and 2) all of the caviomorph species in their matrix, including species that were excluded from
390 their parsimony analysis (i.e., *Cephalomys arcidens*, *Cephalomys bolivianus*, *Litodontomys chubutomys*,
391 *Loretomys minutus*, *Plesiosteiomys newelli*, *Soriamys gaimanesis*, and *Ucayalimys crassidens*). We ran
392 an additional analysis of the full data set with more constrained age priors, including a prior for Santa
393 Rosa that disallowed ages older than 30 Ma, but allowed ages as young as the Oligocene/Miocene
394 boundary (see Table S9 for details); this analysis yielded much more constrained 95% HPD intervals for
395 each site than those calculated with the broad 56-0 Myr age prior for the Peruvian localities. Analyses
396 were run for 50 million generations, with the first 25% discarded as burn-in. Resulting minESS values for
397 all parameters were >750 , and the average standard deviations of split frequencies in the final
398 generations of each analysis were <0.009 . Mean tip ages and 95% HPD for the taxa of interest were
399 retrieved using FigTree (39). Stepping stone analyses were also run in MrBayes, for 35 million
400 generations. Other details of the analyses can be found in the original input and output files that have
401 been made available in the Dryad Digital Data Repository (datadryad.org).

402
403
404
405

Acknowledgments

406 We thank the Leakey Foundation and Alison Stenger for financial support of field and laboratory
407 operations. Fanny Cornejo provided crucial logistical support for the 2016 and 2019 field operations, and
408 Alexandra Bustos and Marcelo Tejedor participated in the 2019 fieldwork. Luz Marina Tejada Medina
409 and César Chalcaltana Budiel facilitated coordination with INGEMMET (Instituto Geológico Minero y
410 Metalúrgico of Perú). We thank the members of the indigenous Santa Rosa community for their gracious
411 hospitality and their efforts to facilitate the fieldwork. We thank two anonymous reviewers who provided
412 useful comments that improved the manuscript.

413
414
415
416

References

- 417 1. K. E. Campbell, Jr., The Paleogene Mammalian fauna of Santa Rosa, Amazonian Peru. *Natural*
418 *History Museum of Los Angeles County, Science Series* **40**, 1-162 (2004).
- 419 2. M. Bond *et al.*, Eocene primates of South America and the African origins of New World
420 monkeys. *Nature* **520**, 538-541 (2015).
- 421 3. E. R. Seiffert *et al.*, A parapithecoid stem anthropoid of African origin in the Paleogene of South
422 America. *Science* **368**, 194-197 (2020).
- 423 4. C. D. C. Frailey, K. E. Campbell Jr., Paleogene Rodents from Amazonian Peru: The Santa Rosa
424 Local Fauna. *Natural History Museum of Los Angeles County Science Series* **40**, 71-130 (2004).
- 425 5. F. J. Goin, A. M. Candela, New Paleogene marsupials from the Amazon Basin of eastern Peru.
426 *Natural History Museum of Los Angeles County, Science Series* **40**, 15-60 (2004).
- 427 6. J. Jaeger *et al.*, Late middle Eocene epoch of Libya yields earliest known radiation of African
428 anthropoids. *Nature* **467**, 1096-1103 (2010).
- 429 7. M. Ciancio, A. Carlini, K. Campbell, G. Scillato-Yane, New Palaeogene cingulates (Mammalia,
430 Xenarthra) from Santa Rosa, Peru and their importance in the context of South American faunas.
431 *Journal of Systematic Palaeontology* **11**, 727-741 (2013).
- 432 8. B. J. Shockey, R. Hitz, M. Bond, Paleogene notoungulates from the Amazon Basin of Peru.
433 *Natural History Museum of Los Angeles County, Science Series* **40**, 61-69 (2004).
- 434 9. B. Kummel, Geological Reconnaissance of the Contamana Region, Peru. *Geological Society of*
435 *America Bulletin* **59**, 1217-1265 (1948).
- 436 10. P. Antoine *et al.*, Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of
437 caviomorph origins and biogeography. *Proceedings of the Royal Society B-Biological Sciences*
438 **279**, 1319-1326 (2012).
- 439 11. P. Antoine *et al.*, A 60-million-year Cenozoic history of western Amazonian ecosystems in
440 Contamana, eastern Peru. *Gondwana Research* **31**, 30-59 (2016).
- 441 12. P. Antoine, R. Salas-Gismondi, F. Pujos, M. Ganerod, L. Marivaux, Western Amazonia as a
442 hotspot of mammalian biodiversity throughout the Cenozoic. *Journal of Mammalian Evolution* **24**,
443 5-17 (2017).
- 444 13. M. Boivin *et al.*, Late middle Eocene caviomorph rodents from Contamana, Peruvian Amazonia.
445 *Palaeontologia Electronica* **20** (2017).
- 446 14. M. Boivin *et al.*, Late Oligocene caviomorph rodents from Contamana, Peruvian Amazonia.
447 *Papers in Palaeontology* **3**, 69-109 (2017).
- 448 15. L. Marivaux *et al.*, Neotropics provide insights into the emergence of New World monkeys: New
449 dental evidence from the late Oligocene of Peruvian Amazonia. *Journal of Human Evolution* **97**,
450 159-175 (2016).
- 451 16. M. Arnal, A. Kramarz, M. Vucetich, C. Frailey, K. Campbell, New Paleogene caviomorphs
452 (Rodentia, Hystricognathi) from Santa Rosa, Peru: Systematics, biochronology, biogeography
453 and early evolutionary trends. *Papers in Palaeontology* **6**, 193-216 (2020).
- 454 17. P.-O. Antoine *et al.*, Biotic community and landscape changes around the Eocene–Oligocene
455 transition at Shapaja, Peruvian Amazonia: regional or global drivers? *Global and Planetary*
456 *Change* **202** (2021).
- 457 18. M. Boivin *et al.*, Early Oligocene caviomorph rodents from Shapaja, Peruvian Amazonia.
458 *Palaeontographica Abteilung a-Palaozoologie-Stratigraphie* **311**, 87-156 (2018).
- 459 19. H. Sallam, E. Seiffert, New phiomorph rodents from the latest Eocene of Egypt, and the impact of
460 Bayesian "clock"-based phylogenetic methods on estimates of basal hystricognath relationships
461 and biochronology. *PeerJ* **4** (2016).
- 462 20. H. Sallam, E. Seiffert, Revision of Oligocene '*Paraphiomys*' and an origin for crown
463 Thryonomyoidea (Rodentia: Hystricognathi: Phiomorpha) near the Oligocene-Miocene boundary
464 in Africa. *Zoological Journal of the Linnean Society* **190**, 352-371 (2020).

- 465 21. A. Drummond, T. Stadler, Bayesian phylogenetic estimation of fossil ages. *Philosophical*
466 *Transactions of the Royal Society B-Biological Sciences* **371** (2016).
- 467 22. L. Marivaux *et al.*, Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial
468 rodent colonization of the West Indies. *Proceedings of the Royal Society B-Biological Sciences*
469 **287** (2020).
- 470 23. T. Herriott, J. Crowley, M. Schmitz, M. Wartes, R. Gillis, Exploring the law of detrital zircon: LA-
471 ICP-MS and CA-TIMS geochronology of Jurassic forearc strata, Cook Inlet, Alaska, USA.
472 *Geology* **47**, 1044-1048 (2019).
- 473 24. P. Vermeesch, IsoplotR: A free and open toolbox for geochronology. *Geoscience Frontiers* **9**,
474 1479-1493 (2018).
- 475 25. F. Ronquist *et al.*, MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice
476 across a large model space. *Systematic Biology* **61**, 539-542 (2012).
- 477 26. R. E. Kass, A. E. Raftery, Bayes factors. *Journal of the American Statistical Association* **90**, 773-
478 795 (1995).
- 479 27. C. Jaramillo, M. Rueda, V. Torres, A palynological zonation for the Cenozoic of the Llanos and
480 Llanos Foothills of Colombia. *Palynology* **35**, 46-84 (2011).
- 481 28. F. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, *The Geological Time Scale 2012* (Elsevier,
482 Amsterdam, 2012), pp. 1176.
- 483 29. M. Boivin *et al.*, Eocene caviomorph rodents from Balsayacu (Peruvian Amazonia). *Paläont.*
484 *Zeitschrift* (2021).
- 485 30. N. S. Upham, B. D. Patterson, Evolution of caviomorph rodents: a complete phylogeny and
486 timetree for living genera. *SAREM Series A - Mammalogical Research* **1**, 63-120 (2015).
- 487 31. M. Springer *et al.*, Macroevolutionary dynamics and historical biogeography of primate
488 diversification inferred from a species supermatrix. *PLoS ONE* **7** (2012).
- 489 32. R. Woods, S. Turvey, S. Brace, R. MacPhee, I. Barnes, Ancient DNA of the extinct Jamaican
490 monkey *Xenothrix* reveals extreme insular change within a morphologically conservative
491 radiation. *Proceedings of the National Academy of Sciences of the United States of America* **115**,
492 12769-12774 (2018).
- 493 33. M. Dos Reis *et al.*, Using phylogenomic data to explore the effects of relaxed clocks and
494 calibration strategies on divergence time estimation: Primates as a test case. *Systematic Biology*
495 **67**, 594-615 (2018).
- 496 34. D. Bradley *et al.* (2009) Detrital zircon geochronology of Cretaceous and Paleogene strata across
497 the south-central Alaskan convergent margin. in *U.S. Geological Survey Professional*
498 *Paper 1760-F*, pp 1-36.
- 499 35. C. Hulst, F. Wilson, R. Donelick, P. O'Sullivan, Two flysch belts having distinctly different
500 provenance suggest no stratigraphic link between the Wrangellia composite terrane and the
501 paleo-Alaskan margin. *Lithosphere* **5**, 575-594 (2013).
- 502 36. M. T.E., P. B. O'Sullivan, C. J. Potter, R. A. Donelick, Provenance and detrital zircon
503 geochronologic evolution of lower Brookian foreland basin deposits of the western Brooks Range,
504 Alaska, and implications for early Brookian tectonism. *Geosphere* **11**, 93-122 (2015).
- 505 37. R. A. Donelick, P. B. O'Sullivan, R. A. Ketcham, Apatite fission-track analysis. *Reviews in*
506 *Mineralogy and Geochemistry, Mineralogical Society of America* **58**, 49-94 (2005).
- 507 38. G. Gunnell *et al.*, Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's
508 aye-aye. *Nature Communications* **9** (2018).
- 509 39. A. Rambaut (2009) FigTree Tree Figure Drawing Tool v. 1.3.1. (University of Edinburgh).

510
511
512
513

514 **Figure captions**

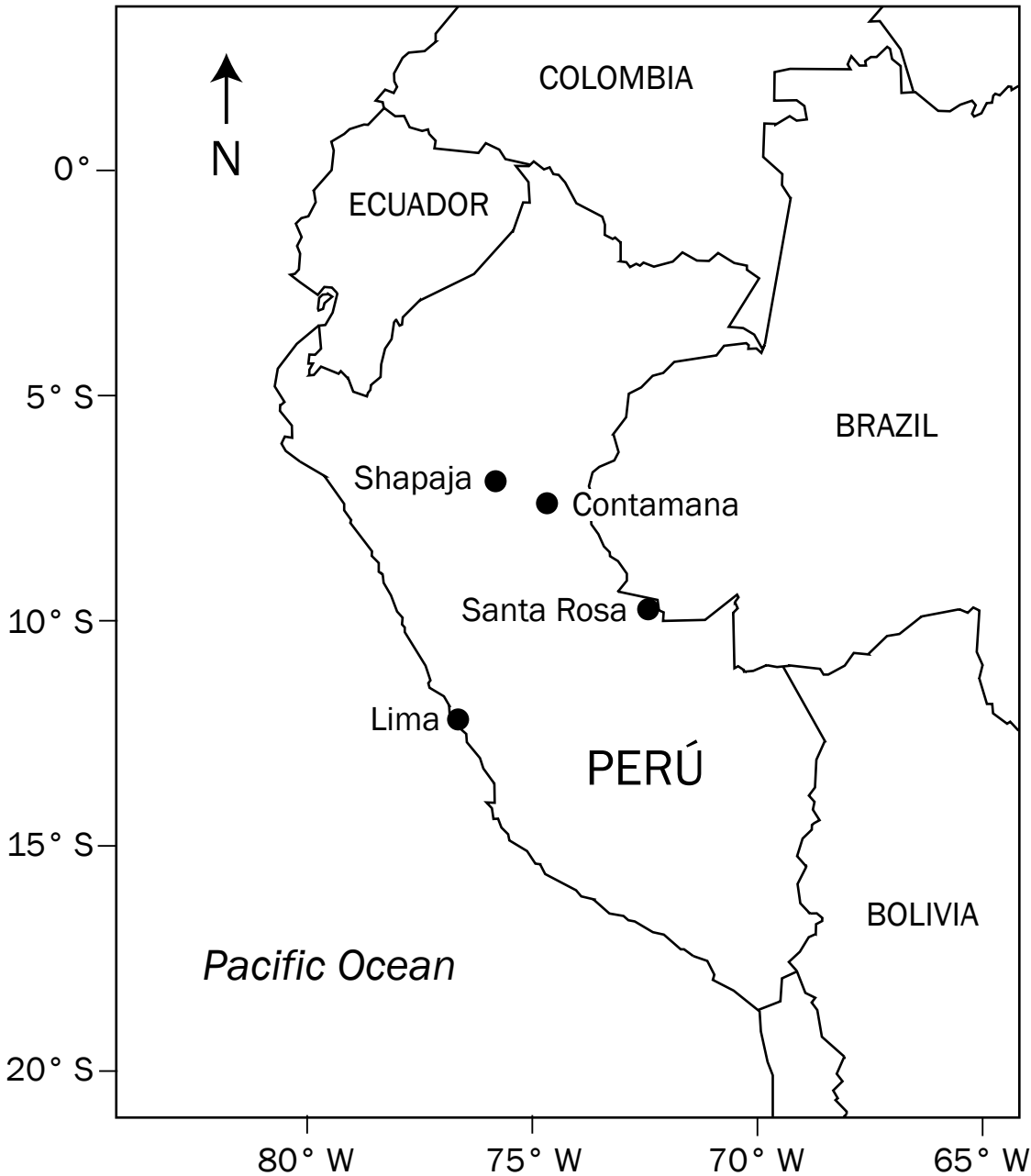
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532

Figure 1. Map of Perú, showing the locations of the Santa Rosa, Shapaja, and Contamana areas.

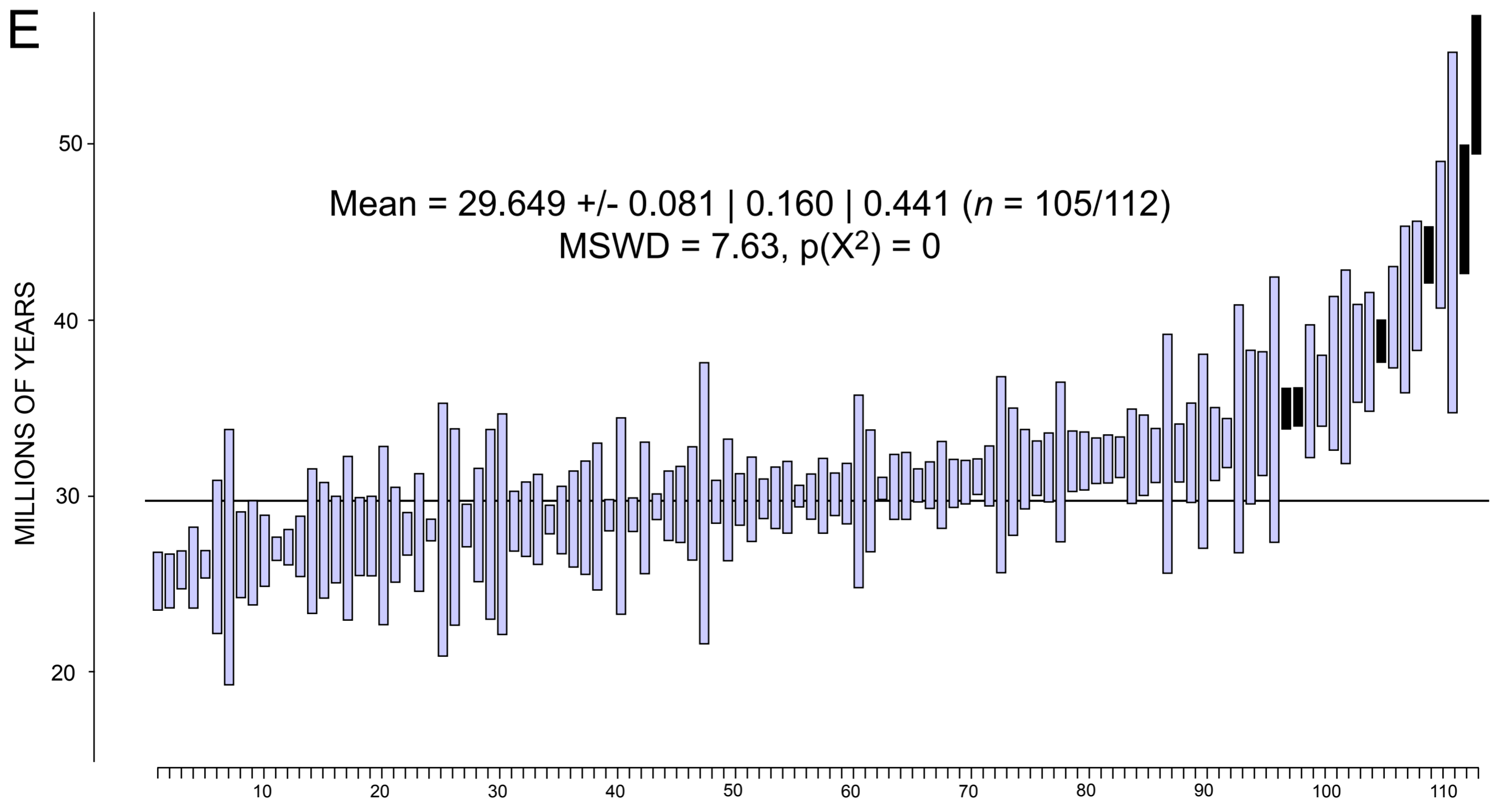
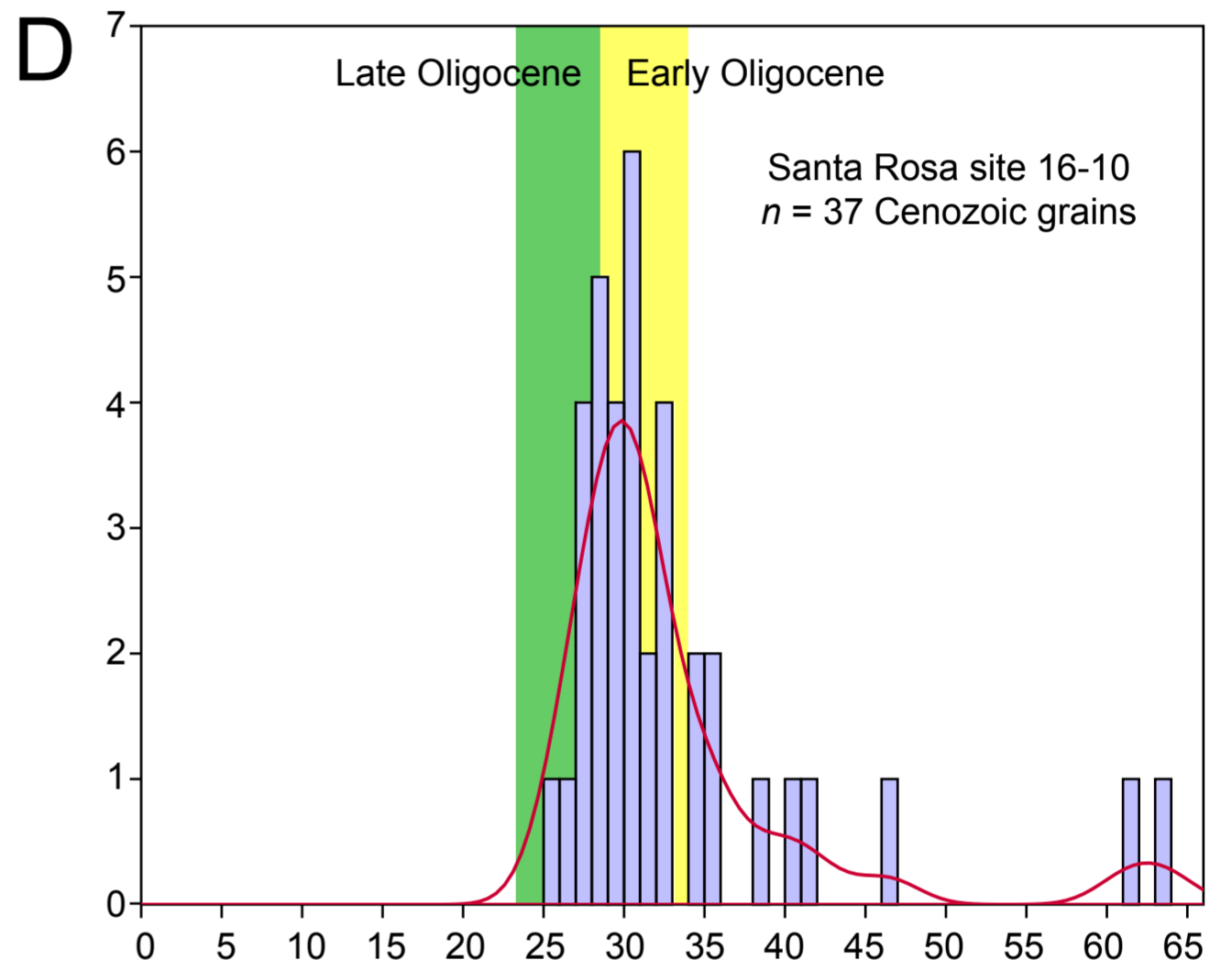
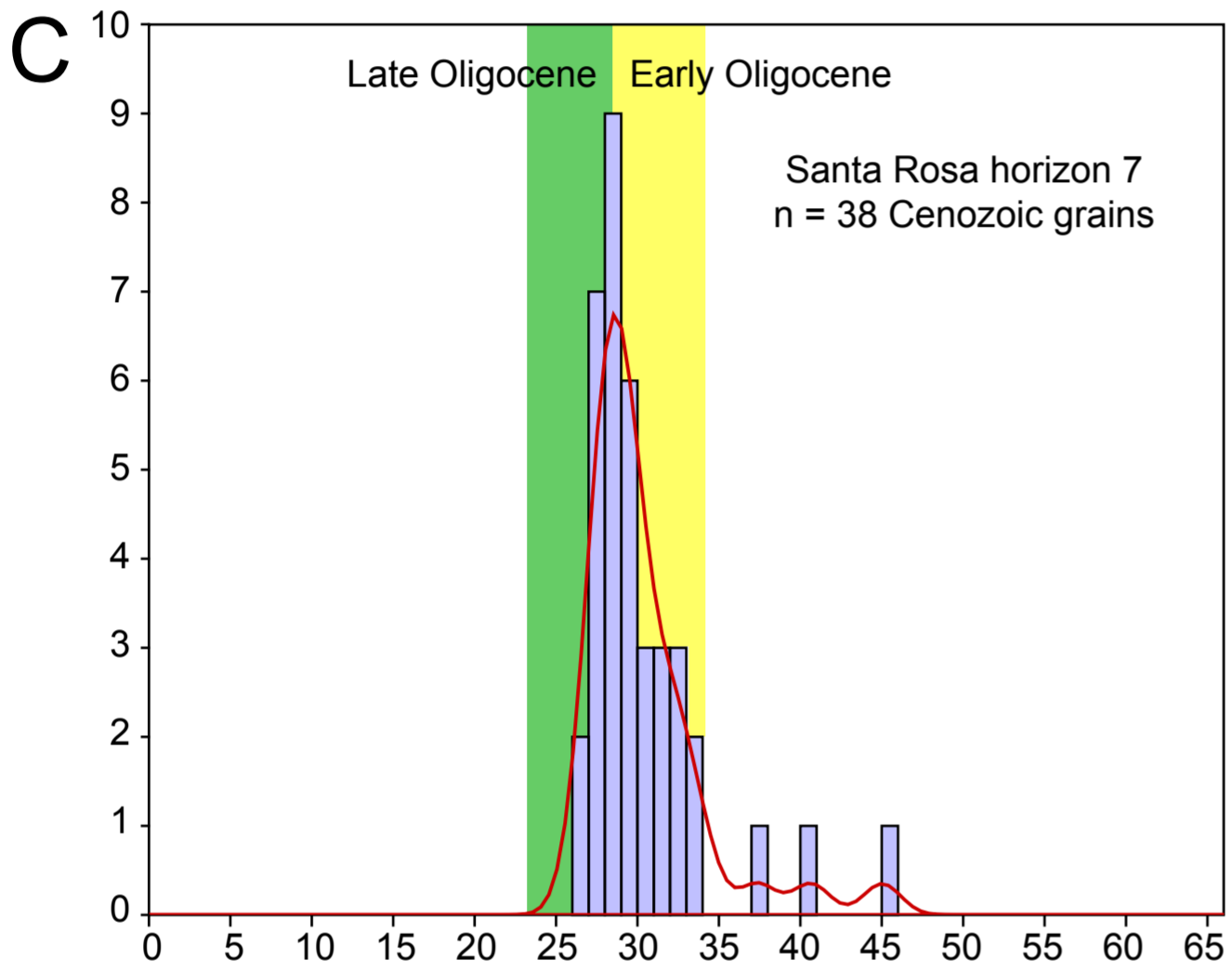
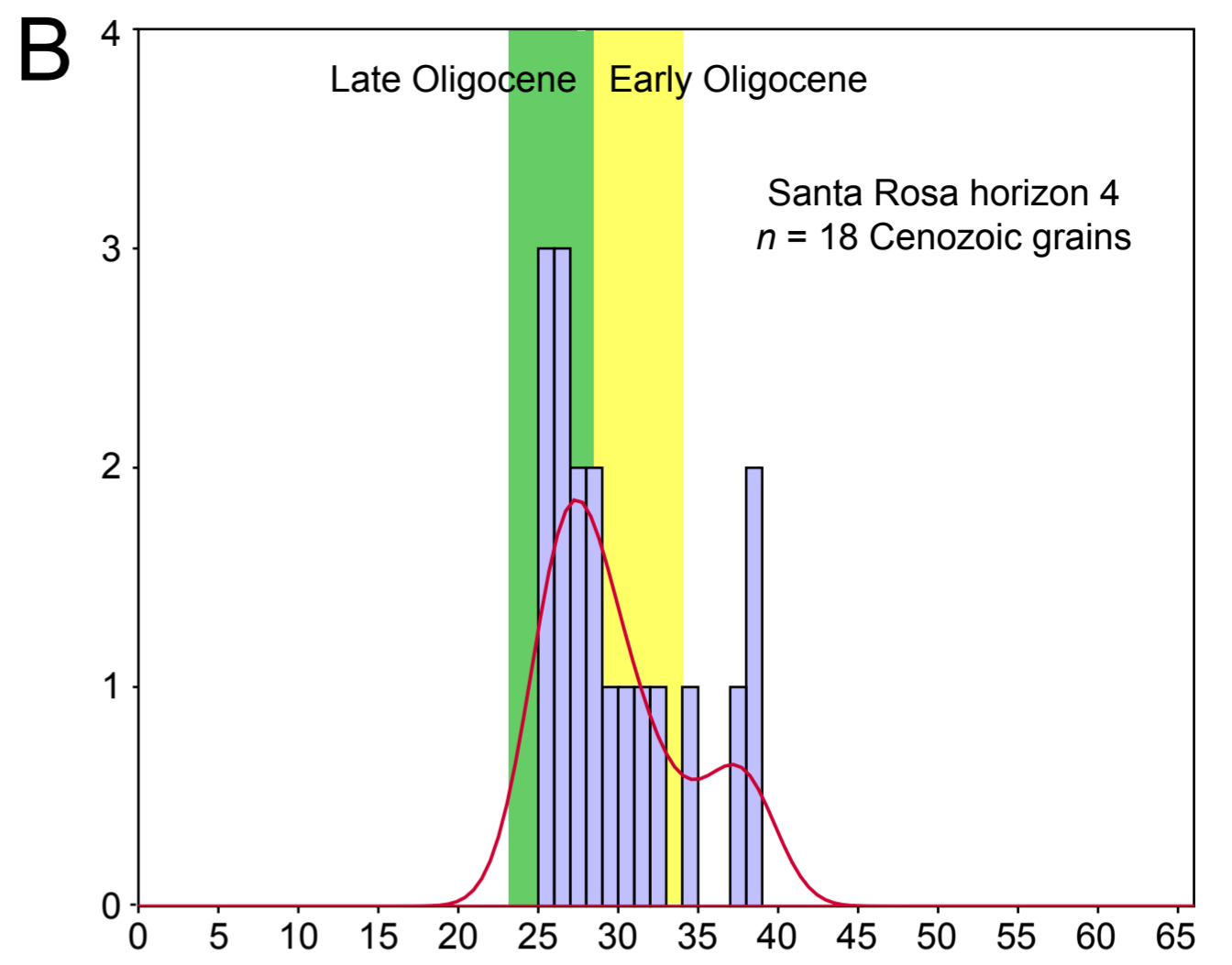
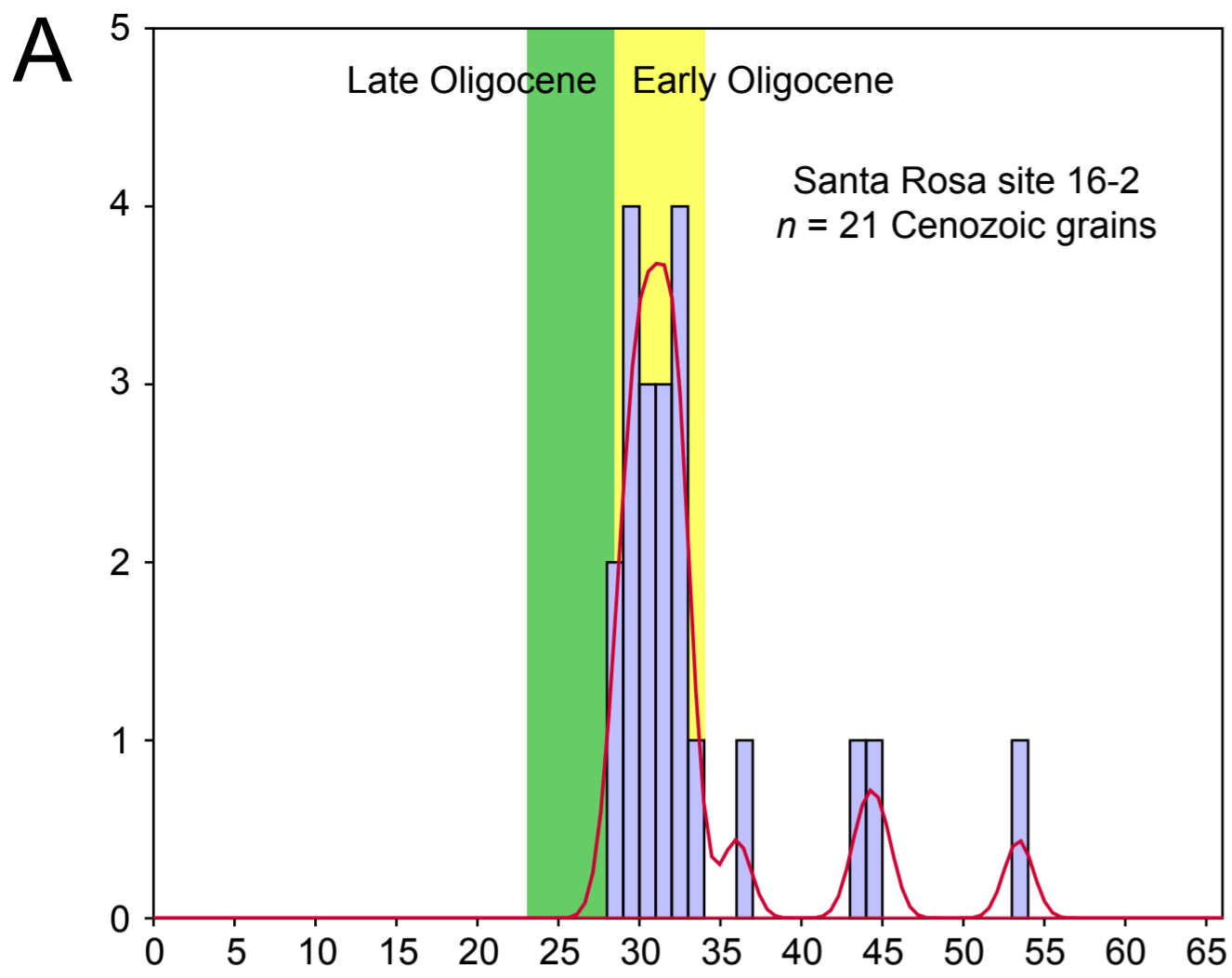
Figure 2. Wide-angle and close-up views of the Santa Rosa outcrop. a) The entire outcrop, showing the isolated upstream exposures (#1 and #2) of the fossil-bearing conglomeratic horizons. The primary portion of the outcrop extends from #3 to #11, and it is ~100 m in length, as shown here, but it is underwater during the rainy season. All of the labeled conglomeratic horizons in this outcrop produce fossils. b,c) The upstream end of the conglomeratic horizons end abruptly at a fault, immediately to the left of #3-#5. The numbered spots indicate various conglomeratic horizons that were sampled individually. The black arrows indicate fault lines. Displacement in this view is slight, but observe left of spot #7, above the arrow. The conglomeratic horizons are thickest at the upstream end (#3-#5) and taper to disappearing downstream of #11. Zircon samples were collected from #2, #4, #7, and near #10. The bench at the top of the exposed sediment marks the contact, the Ucayali Unconformity, between the Yahuarango or Pozo Formation and the Mio-Pliocene Madre de Dios Formation.

Figure 3. Detrital zircon geochronology of the Santa Rosa deposit. A-D) Kernel density estimates (KDEs) of the Cenozoic-aged detrital zircons from four sample sites at Santa Rosa, Perú, illustrate the concentration of the zircons to the Oligocene (Band width = 1; Bin width = 1). For the complete data set for the entire spectrum of zircons from the four sites, see SOM Tables S1-S4. The number of Cenozoic-aged zircons (out of 110 zircons analyzed per sample) is given for each plot. Note that of the 440 zircons analyzed, only 20 date from the Eocene and only 2 from the Paleocene. Of the other Oligocene-aged zircons, 25 date to the Upper Oligocene and 67 date to the Lower Oligocene. E) Plot of zircon ages using IsoplotR.

541
~~542~~
~~543~~
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560







Locality	Ages of all Peruvian localities unconstrained ("unknown")		Age of Santa Rosa constrained to 29.6±0.8 Ma, other Peruvian localities "unknown"		All Peruvian localities further constrained	Previous age estimate	Revised age estimate
	Mean, full dataset	Mean, reduced data set	Mean, full dataset	Mean, reduced data set	Mean, full data set		
CTA-32	21.79 Ma (n=4)	20.81 Ma (n=2)	22.46 Ma (n=4)	22.05 Ma (n=2)	22.74 Ma (n=4)	Upper Oligocene	Upper Oligocene or Earliest Miocene
CTA-61	26.02 Ma (n=3)	24.29 Ma (n=2)	26.33 Ma (n=3)	24.79 Ma (n=2)	23.77 Ma (n=3)	Upper Oligocene	Upper Oligocene
Shapaja	28.71 Ma (n=6)	28.26 Ma (n=6)	29.0 Ma (n=6)	29.13 Ma (n=6)	28.58 Ma (n=6)	Upper Eocene to Lower Oligocene	Lower to Upper Oligocene
Santa Rosa	29.47 Ma (n=7)	29.26 Ma (n=7)	-	-	28.16 Ma (n=7)	Upper Eocene or Lower Oligocene	Lower to Upper Oligocene
CTA-27	30.27 Ma (n=4)	30.23 Ma (n=4)	30.86 Ma (n=4)	30.98 Ma (n=4)	29.78 Ma (n=4)	Late Middle Eocene	Lower Oligocene

Table 1. Age estimates for early caviomorph-bearing localities of Perú, based on BTM analysis of the morphological character matrix of Marivaux et al. (22). Note that the revised age estimates for Shapaja and Santa Rosa (Lower to Upper Oligocene) take into account the evidence from chemostratigraphy (Shapaja) and detrital zircon geochronology (Santa Rosa) which suggest the possibility of an Upper Oligocene age.