Current events

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Time of origin of primates

Keywords: coalescence models, origin of primates, probability

Journal of Human Evolution (1994) **27**, 443–445

R. D. Martin (1993) recently published an estimate of the time of origin of primates, based on a coalescence model with diversity decreasing backward in time at a constant rate from the present to the origin of the order. This involved the average duration of species, the number of primate species living today, and the number of primate species known as fossils. Martin assumed a fixed species duration of 1 m.y., a modern diversity of 200 primate species, and a primate fossil record of 186 species ranging over the past 55 million years. From this, he estimated the coalescence of his model and the time of origin of primates to be 80 million years before present [Ma]. This seems remarkably early in geological time given that most modern orders of mammals, primates included, have never been found with dinosaurs in the Mesozoic era.

Here we do not wish to question the model Martin (1993) used in deriving an 80 Ma estimate for the origin of primates (other models might be preferable), but rather to evaluate the conclusion probabilistically in the context of his model and his initial assumptions. This can be done by calculating exact probabilities that 186 primate species known as fossils all fall in the interval from 55 Ma to the present, knowing that primates actually began to diversify earlier. Martin's model is shown diagrammatically as a right-angled triangle in Figure 1, where the base of the triangle (abscissa) represents time since the origin of the order. The altitude of the triangle (ordinate) represents postulated standing diversity. Clearly the origin of primates cannot be less than 55 Ma because primates are known this far back in the fossil record. We evaluate the probability that the origin is older than 55 Ma by some increment i, where i ranges from 0 to 25 (i.e., the hypothesized origin ranges from the minimum of $i+55=55$ Ma, where $i=0$, to an origin at $i+55=80$ Ma, where $i=25$).

The model triangle in Figure 1 can be divided into two areas, an area geologically older than 55 Ma (here called A) and an area geologically younger than 55 Ma (here called B), where 55 Ma is the age of the oldest fossil and thus the minimum possible origination time. When $i=0$, the base of the model triangle is $0+55=55$ million years long, the altitude is a diversity of 200 species, and one-half of the product of these two numbers [$0{\cdot}5 \times 55 \times 200=5500$] is the total area of A+B. This is also the total number of primate species estimated to have lived in the past 55 million years. When $i=1$, the base of the model triangle is $1+55=56$ million years long, the altitude is still 200 species, and one-half of the product of these two numbers ($0{\cdot}5 \times 56 \times 200=5600$) is the total area of A+B. This is also the total number of primate species estimated to have lived in the past 56 million years. Estimates of A+B for larger i are listed in Table 1.

It is interesting to know what proportion area B, the area younger than 55 Ma, is to the area A+B of the whole triangle because the ratio B/(A+B) is the probability that a primate

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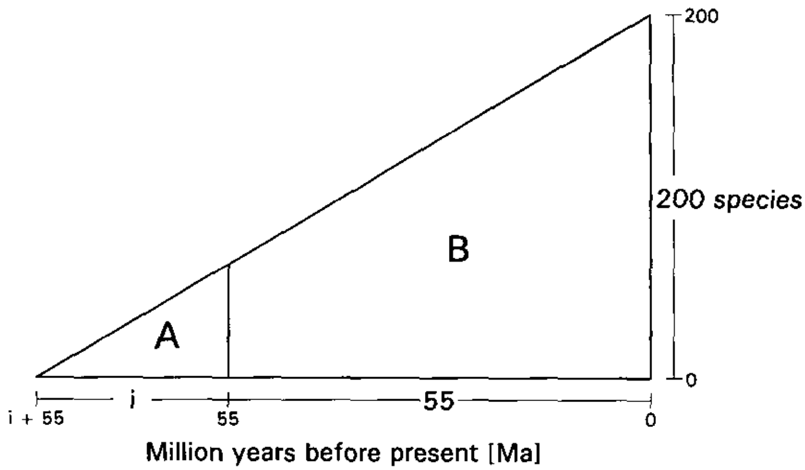

Figure 1. Martin's model of primate coalescence (reading from right to left) or diversification (reading from left to right) scaled to a modern diversity of 200 species on ordinate at right. Diversification started at an unknown time i+55 million years before present. Total area of triangle A+B is divided into proportions A before 55 Ma and B after 55 Ma. A+B, A, and B are calculated for values of i ranging from 0 to 25 (Table 1). B/(A+B) is the probability a primate drawn at random will fall in B and have an age less than 55 Ma.

sampled randomly from A+B will fall in B, that is, the probability that a primate drawn randomly will be younger than 55 Ma. B can be determined by calculating the area of A and subtracting this from A+B. Area A is one-half of the product of base i multiplied by the proportion $i/(i+55)$ of 200 $[0{\cdot}5 \times i \times (i/(i+55)) \times 200]$. Calculated values of A, B, and B/(A+B) are listed in Table 1.

B/(A+B) is the probability that one primate drawn at random from triangle A+B will fall in B and be younger than 55 Ma. The probability that two primates drawn at random will both fall in B is B/(A+B) for the first, multiplied by B/(A+B) for the second, which is the square of B/(A+B). The probability that all 186 primate species known as fossils will fall in B and be younger than 55 Ma is B/(A+B) raised to the 186th power $[(B/(A+B))^{186}]$. These probabilities are listed in the right-hand column of Table 1. Note that the probability of Martin's hypothesis that primates originated as early as 80 Ma is, by his own model, only 0·000000005 or five chances in a billion.

What is a reasonable time of origin of primates based on Martin's model? Origination at 63 Ma, 8 million years before the first known fossil primates, has a probability of about 0·05, the ordinary level of significance governing rejection in probability and statistics. Thus, accepting Martin's model of diversification, and given what we know about the diversity and geological age of fossil primates, postulated times of origin older than 63 Ma can be rejected. Models of exponential and logistic diversification generally yield coalescence times for the origin of primates lying between 63 and 55 Ma. All lie within the Paleocene epoch of the Cenozoic and all are more probable than the Mesozoic origin postulated by Martin.

Acknowledgements

We thank Mike Foote for reading the manuscript and for numerous discussions of inference based on the fossil record. William C. Clyde, William J. Sanders, and two anonymous reviewers read and improved earlier drafts of this paper.

Table 1 Areas A and B calculated for different values of *i* in the triangle of Figure 1

Increment *i*	Origin (Ma)	A+B	A	B	B/(A+B)	Pr [(B/(A+B))^{186}]
0	55	5500·00	0·00	5500·00	1·00	1·000000000
1	56	5600·00	1·79	5598·21	1·00	0·942406714
2	57	5700·00	7·02	5692·98	1·00	0·795220613
3	58	5800·00	15·52	5784·48	1·00	0·607572436
4	59	5900·00	27·12	5872·88	1·00	0·424476832
5	60	6000·00	41·67	5958·33	0·99	0·273578286
6	61	6100·00	59·02	6040·98	0·99	0·163935170
7	62	6200·00	79·03	6120·97	0·99	0·091977805
8	63	6300·00	101·59	6198·41	0·98	0·048621394
9	64	6400·00	126·56	6273·44	0·98	0·024353528
10	65	6500·00	153·85	6346·15	0·98	0·011616789
11	66	6600·00	183·33	6416·67	0·97	0·005301381
12	67	6700·00	214·93	6485·07	0·97	0·002324201
13	68	6800·00	248·53	6551·47	0·96	0·000982561
14	69	6900·00	284·06	6615·94	0·96	0·000401904
15	70	7000·00	321·43	6678·57	0·95	0·000159554
16	71	7100·00	360·56	6739·44	0·95	0·000061650
17	72	7200·00	401·39	6798·61	0·94	0·000023244
18	73	7300·00	443·84	6856·16	0·94	0·000008572
19	74	7400·00	487·84	6912·16	0·93	0·000003098
20	75	7500·00	533·33	6966·67	0·93	0·000001100
21	76	7600·00	580·26	7019·74	0·92	0·000000384
22	77	7700·00	628·57	7071·43	0·92	0·000000132
23	78	7800·00	678·21	7121·79	0·91	0·000000045
24	79	7900·00	729·11	7170·89	0·91	0·000000015
25	80	8000·00	781·25	7218·75	0·90	0·000000005

i is the hypothesized million-year time increment by which the origin of primates exceeds their first appearance in the fossil record. Probability at right is the probability that all 186 primate species known as fossils would fall within the past 55 million years if they were sampled at random from a clade coalescing at $i+55$ Ma.

Reference

Martin, R. D. (1993). Primate origins: plugging the gaps. *Nature* **363,** 223–234.