esis, that Plesiadapiformes share a closer relationship to extant flying lemurs (Dermoptera) than to Euprimates (*16*, *17*), has been strongly challenged (*10*, *18–24*) and is not followed here.

12. F. S. Szalay, *Evolution* **22**, 19 (1968).
13. ———, A. L. Rosenberger, M. Dagosto, *Yearb. Phys. Anthropol.* **30**, 75 (1987).
14. P. D. Gingerich, *Nature* **253**, 111 (1975).
15. J. R. Wible, H. H. Covert *J. Hum. Evol.* **16**, 1 (1987).
16. R. F. Kay, J. G. M. Thewissen, A. D. Yoder, *Am. J. Phys. Anthropol.* **89**, 477 (1992).
17. K. C. Beard, in *Mammal Phylogeny: Placentals*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer-Verlag, New York, 1993), pp. 129–150.
18. D. W. Krause, *J. Hum. Evol.* **21**, 177 (1991).
19. R. C. Fox, *J. Vertebr. Paleontol.* **13**, 516 (1993).
20. F. S. Szalay, S. G. Lucas, in *Primates and Their Relatives in Phylogenetic Perspective*, R. D. E. MacPhee, Ed. (Plenum, New York, 1993), pp. 187–226.
21. J. R. Wible, J. R. Martin, in *Primates and Their Relatives in Phylogenetic Perspective*, R. D. E. MacPhee, Ed. (Plenum, New York, 1993), pp. 111–146.
22. J. A. Runestad, C. B. Ruff, *Am. J. Phys. Anthropol.* **98**, 101 (1995).
23. B. Stafford, R. W. Thorington Jr., *J. Morphol.* **235**, 135 (1998).
24. J. I. Bloch, M. T. Silcox, *Am. J. Phys. Anthropol.* **116**, 184 (2001).
25. Supplementary data are available on *Science* Online.
26. K. D. Rose, *Bull. Mus. Comp. Zool.* **147**, 1 (1975).
27. J. I. Bloch, D. C. Fisher, K. D. Rose, P. D. Gingerich, *J. Vertebr. Paleontol.* **21**, 119 (2001).
28. K. C. Beard, J. Wang, *Ann. Carnegie Mus.* **64**, 1 (1995).
29. A. R. Biknevicius, *Am. J. Phys. Anthropol.* **71**, 157 (1986).
30. G. F. Gunnell, *Univ. Mich. Pap. Paleontol.* **27**, 1 (1989).
31. M. T. Silcox, D. W. Krause, M. C. Maas, R. C. Fox, *J. Vertebr. Paleontol.* **21**, 132 (2001).
32. D. Dashzeveg, M. C. McKenna, *Acta Paleontol. Polon.* **22**, 119 (1977).
33. M. C. McKenna, S. K. Bell, *Classification of Mammals Above the Species Level* (Columbia, New York, 1997).
34. The skeleton is referred to Carpolestidae because it has enlarged central incisors, reduced anterior dentition (posterior to I_1), and plagiaulacoid structure of P_4 with correlated specializations of P^{3-4}; to *Carpolestes* because P^3 is polycuspate with a distinct anteroexternal extension, and P_4 is high-crowned, bladelike, and multicuspate; and to *C. simpsoni* because of its reduced dental formula (lacking P_3), its small body size (~100 g), and having P^3 and P_4 of unique size and shape (*35*).
35. J. I. Bloch, P. D. Gingerich, *Contrib. Mus. Paleontol. Univ. Mich.* **30**, 131 (1998).
36. P. D. Gingerich, *Contrib. Mus. Paleontol. Univ. Mich.* **27**, 265 (1987).
37. J. I. Bloch, G. J. Bowen, in *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*, G. F. Gunnell, Ed. (Kluwer/Plenum, New York, 2001), pp. 95–129.
38. G. J. Bowen, J. I. Bloch, *J. Sediment. Res.* **72**, 46 (2002).
39. P. D. Gingerich, in *Early Paleogene Warm Climates and Biosphere Dynamics*, B. Schmitz, B. Sundquist, F. P. Andreasson, Eds. (Geologiska Foreningens Fiorhandlingen, Stockholm, 2000), pp. 57–59.
40. J. I. Bloch, D. M. Boyer, *Univ. Mich. Pap. Paleontol.* **33**, 185 (2001).
41. ———, P. D. Gingerich, G. F. Gunnell, *J. Vertebr. Paleontol.* **22**, 366 (2002).
42. K. C. Beard, in *Origines de la Bipédie chez les Hominidés*, Y. Coppens, B. Senut, Eds. (CNRS, Paris, 1991), pp. 63–90.
43. F. S. Szalay, *Folia Primatol.* **23**, 158 (1975).
44. ———, I. Tattersall, R. L. Decker, in *Approaches to Primate Paleobiology*, F. S. Szalay, Ed. (Karger, Basel, 1975), pp. 136–166.
45. F. S. Szalay, M. Dagosto, *Folia Primatol.* **34**, 1 (1980).
46. E. J. Sargis, *J. Morphol.* **254**, 149 (2002).
47. M. W. Hamrick, *J. Hum. Evol.* **40**, 339 (2001).
48. E. J. Sargis, *J. Zool.* 253, **473** (2001).
49. D. E. Russell, *Mem. Mus. Nat. Hist. Ser. C* **13**, 1 (1964).
50. M. C. McKenna, *Folia Primatol.* **4**, 1 (1966).
51. F. S. Szalay, *Bull. Am. Mus. Nat. Hist.* **140**, 195 (1969).
52. D. T. Rasmussen, *Am. J. Primatol.* **22**, 263 (1990).
53. E. J. Sargis, *J. Zool. London* **253**, 485 (2001).
54. P. Lemelin, *J. Zool. London* **247**, 165 (1999).
55. M. C. Maas, D. W. Krause, S. G. Strait, *Paleobiology* **14**, 410 (1988).
56. F. S. Szalay, G. Drawhorn, in *Comparative Biology and Evolutionary Relationships of Tree Shrews*, W. P. Luckett, Ed. (Plenum, New York, 1980), pp. 133–169.
57. We thank P. Houde for ongoing collaboration on limestone vertebrates; P. Myers for access to comparative collections of mammals in the University of Michigan Museum of Zoology; participants of the 2001 *First-Ever International Conference on Primate Origins and Adaptation* for helpful conversations; M. T. Silcox for access to data used in the phylogenetic analysis; and S. R. Manchester for paleobotanical insights. K. C. Beard, D. C. Fisher, D. L. Fox, P. D. Gingerich, G. F. Gunnell, E. A. Kowalski, D. W. Krause, K. D. Rose, W. J. Sanders, E. J. Sargis, R. Secord, M. T. Silcox, J. Trapani, J. Wilson, I. S. Zalmout, and two anonymous reviewers read and improved the manuscript. J. Klausmeyer and B. Miljour provided technical advice on illustrations. Artwork in Figs. 2 to 5 is by D.M.B. Research was supported by a grant from the National Science Foundation (BCS-0129601) to G. F. Gunnell, P. D. Gingerich, and J.I.B.

Supporting Online Material
www.sciencemag.org/cgi/content/full/298/5598/1606/DC1
Table S1 and S2
Reference

9 September 2002; accepted 23 October 2002

Genetic Evidence for an East Asian Origin of Domestic Dogs

Peter Savolainen,[1]* Ya-ping Zhang,[2] Jing Luo,[2]† Joakim Lundeberg,[1] Thomas Leitner[3]

The origin of the domestic dog from wolves has been established, but the number of founding events, as well as where and when these occurred, is not known. To address these questions, we examined the mitochondrial DNA (mtDNA) sequence variation among 654 domestic dogs representing all major dog populations worldwide. Although our data indicate several maternal origins from wolf, >95% of all sequences belonged to three phylogenetic groups universally represented at similar frequencies, suggesting a common origin from a single gene pool for all dog populations. A larger genetic variation in East Asia than in other regions and the pattern of phylogeographic variation suggest an East Asian origin for the domestic dog, ~15,000 years ago.

Archaeological finds from Mesolithic sites around the world indicate that the dog was the first domestic animal (*1*). Its origin from wolves is well established from genetic as well as behavioral and morphological data (*1–3*), but apart from this, available clues give no clear picture of its origin. Interpretation of the archaeological record is problematic because of the difficulty in discriminating between small wolves and domestic dogs (*4*, *5*); however, the earliest finds believed to be from domestic dogs are a single jaw from 14,000 years before the present (yr B.P.) in Germany (*5*, *6*) and an assemblage of small canids from 12,000 yr B.P. in Israel (*7*, *8*). This indicates an origin from Southwest Asia, where the first farm animals are believed to have originated (*9*), or Europe. On the other hand, one osteological feature diagnostic of dogs is also found among Chinese wolves, suggesting an East Asian origin (*4*, *10*). On the basis of the morphology and size of early archaeological finds, an origin from the large North Eurasian or North American wolves seems unlikely (*10–12*). An origin from several different wolf populations could explain the extreme morphological variation among dog breeds. To determine whether dogs were domesticated in one or several places, and the approximate place and time of these events, we examined the structure of mtDNA sequence variation among domestic dogs worldwide.

We analyzed the genetic variation in 582 base pairs (bp) of mtDNA in 654 domestic dogs from Europe, Asia, Africa, and Arctic America and in 38 Eurasian wolves (*13*, *14*) (tables S1 and S2; fig. S1). It has previously been shown that domestic dogs originate from at least four female wolf lines (*2*, *15*). Phylogenetic analysis of our data assigned the dog sequences into the same four phylogenetic groups (clades A, B, C, and D) and to a fifth "group," clade E, consisting of an isolated haplotype (Fig. 1 and fig. S2) (*14*). These groups were interspersed by wolf sequences and were approximately equidistant from a cenancestor of all wolves and dogs. Therefore, we conclude that the domestic dog population originates from at least five fe-

---

[1] Department of Biotechnology, Royal Institute of Technology (KTH), 10691 Stockholm, Sweden. [2] Yunnan Laboratory of Molecular Biology of Domestic Animals, and Laboratory of Molecular Evolution and Genome Diversity, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China. [3] Department of Virology, Swedish Institute for Infectious Disease Control, 17182 Solna, Sweden.

*To whom correspondence should be addressed. E-mail: savo@biotech.kth.se

†Present address: Department of Biology, University of Konstanz, 78457 Konstanz, Germany.

charge) yearly, whereas precipitation (less evaporation) contributes ~0.5 m (~60%). The recent observation that water levels rose in May 2002 from the levels in April by ~1.25 m before the monsoon confirms that surface water bodies recharge the aquifer. Infiltrating surface water receives heavy loadings from the untreated waste of the ~17,600 inhabitants of the 16-km^2 area. Hence this water contains high concentrations of dissolved carbon, as would water that infiltrates from rice paddies and through organic-rich pond and river sediments.

The observed arsenic mobility appears related to recent inflow of carbon through either organic carbon–driven reduction or displacement by carbonate. The distinctly older radiocarbon ages of DOC relative to DIC and methane imply that mobilization is not driven by detrital organic carbon. Water budgets indicate that the advent of massive irrigation pumping has drawn relatively young water into the aquifer over the last several decades, as may be typical of Bangladesh (*19*). Thus, irrigation pumping may affect arsenic concentrations, but not by the oxidation of sulfides as has been proposed. The low arsenic concentrations from the deeper aquifer indicate that deep wells may provide a source of clean water, an option that is already being implemented on an ad hoc basis (*20*). However, the apparent relation of arsenic mobility to inflow of organic carbon raises concerns about the appropriate depth of new drinking-water wells and their position relative to irrigation wells.

References and Notes

1. D. G. Kinniburgh, P. L. Smedley, Eds., *Arsenic Contamination of Groundwater in Bangladesh* (British Geologic Survey Report WC/00/19, 2001) (www.bgs.ac.uk/arsenic/Bangladesh).
2. A. H. Smith, E. O. Lingas, M. Rahman, *Bull. WHO* **78**, 1093 (2000).
3. C. F. Harvey, *Environ. Sci.* **8**, 491 (2001).
4. R. Nickson *et al.*, *Nature* **395**, 338 (1998).
5. P. L. Smedley, D. G. Kinniburgh, *Appl. Geochem.* **17**, 517 (2002).
6. T. R. Chowdhury *et al.*, *Nature* **401**, 545 (1999).
7. D. Das *et al.*, Bore-hole soil-sediment analysis of some As affected areas, in *Proc. Int. Conf. on Arsenic in Groundwater: Cause, Effect and Remedy*, Calcutta, December 1995.
8. See supporting data on *Science* Online.
9. F. H. Khan, *Geology of Bangladesh* (University Press, Dhaka, Bangladesh, 1991).
10. J. M. McArthur *et al.*, *Water Resour. Res.* **37**, 109 (2001).
11. N. E. Keon *et al.*, *Environ. Sci. Technol.* **35**, 2778 (2001).
12. D. B. Senn, H. F. Hemond, *Science* **296**, 2373 (2002).
13. C. A. J. Appelo *et al.*, *Environ. Sci. Technol.* **36**, 3096 (2002).
14. D. K. Nordstrom, in *Minor Elements 2000: Processing and Environmental Aspects of As, Sb, Se, Te, and Bi*, C. Young, Ed. (Society for Mining, Metallurgy, and Exploration, Littleton, CO, 2000), pp. 21–30.
15. S. L. Goodbred Jr., S. A. Kuehl, *Geology* **27**, 559 (1999).
16. C. J. Yapp, H. Poths, *Geochim. Cosmochim. Acta* **50**, 1213 (1986).
17. M. J. Whiticar, *Chem. Geol.* **161**, 291 (1999).
18. No rivers flow from the area during the dry season, so pumped groundwater that is not evaporated or transferred into rice fields or ponds must re-infiltrate back into the aquifer. Thus, the drawdown (the net change in aquifer storage) during this period is controlled by the rate of evapotranspiration and transfer of groundwater with rice fields and ponds. The drawdown due to evapotranspiration, estimated by applying the Penman-Monteith equation to local meteorological data collected by the Bangladesh Water Development Board, is consistent with this water budget, increasing from 1.1 cm/day in January to 2.2 cm/day in March. Although no regional gradient is evident from the measured hydraulic heads, strong lateral flows controlled by the position of irrigation wells and recharge areas may create complex pathways for invading water. Applying Darcy's law to interpolated hydraulic heads and hydraulic conductivity estimated from pump tests gives an average lateral component to groundwater velocity of 1.7 cm/day, similar to the vertical component.
19. C. F. Harvey, *Science* **296**, 1563 (2002).
20. W. H. Yu, C. M. Harvey, C. F. Harvey, *Water Resour. Res.*, in press.
21. Supported by NSF grant EAR-0001098, NSF graduate fellowships, a grant from the Alliance for Global Sustainability, and National Institute of Environmental Health Sciences grant P30ES02109.

Supporting Online Material
www.sciencemag.org/cgi/content/full/298/5598/1602/DC1
Materials and Methods
References

5 August 2002; accepted 21 October 2002

Grasping Primate Origins

Jonathan I. Bloch* and Doug M. Boyer

The evolutionary history that led to Eocene-and-later primates of modern aspect (Euprimates) has been uncertain. We describe a skeleton of Paleocene plesiadapiform *Carpolestes simpsoni* that includes most of the skull and many postcranial bones. Phylogenetic analyses indicate that Carpolestidae are closely related to Euprimates. *C. simpsoni* had long fingers and an opposable hallux with a nail. It lacked orbital convergence and an ankle specialized for leaping. We infer that the ancestor of Euprimates was primitively an arboreal grasper adapted for terminal branch feeding rather than a specialized leaper or visually directed predator.

Extant primates are distinct from other eutherian mammals in having large brains, enhanced vision brought about in part by optical convergence, the ability to leap, nails on at least the first toes, and grasping hands and feet (*1*, *2*). Several adaptive scenarios have been proposed to explain these specializations: (i) "grasp-leaping" locomotion (*3*), which predicts simultaneous evolution of grasping and leaping; (ii) visually directed predation (*4*), which predicts simultaneous evolution of forward-facing orbits

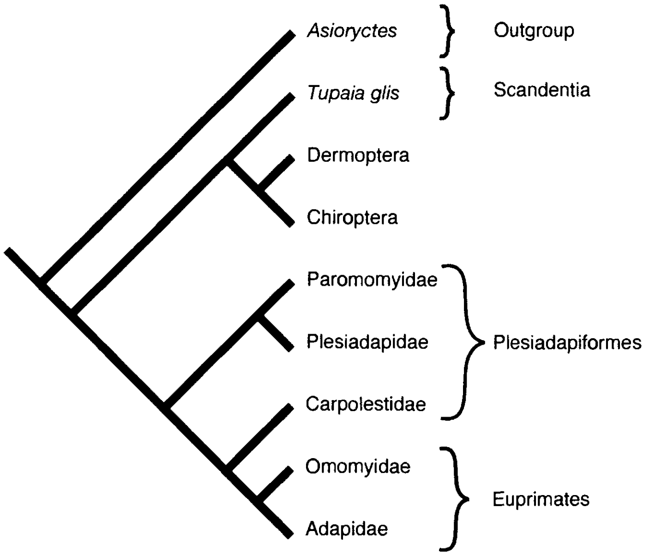

Fig. 1. Hypothesis of phylogenetic relationships among select archontans, illustrating phylogenetic position of Carpolestidae based on cladistic analysis of 65 postcranial characters (*25*). Many fossil archontans were excluded from the analysis because postcranial skeletons for these groups have not yet been described. Cladistic analysis yielded a single most-parsimonious cladogram generated by an exhaustive search algorithm and rooted with *Asioryctes*: tree length = 117, consistency index = 0.75, retention index = 0.67. All characters were unordered. As for previous cladistic analyses (*10*), the topology supports a plesiadapiform-euprimate link, whereas the cladogram based on postcranial data presented here specifically allies Carpolestidae with Euprimates (Omomyidae plus Adapidae). Unambiguous synapomorphies supporting a carpolestid-euprimate link include morphology of distal humerus (character 10), a nail on the hallux (character 21), a sellar joint between metatarsal I and the entocuneiform (character 50), and lateral torsion of the distal metatarsal I (character 65).

Museum of Paleontology, University of Michigan, 1109 Geddes Road, Ann Arbor, MI 48109–1079, USA.
*To whom correspondence should be addressed. E-mail: carpo@umich.edu

and grasping; and (iii) terminal branch feeding on nectar and flowers (*5*, *6*), which allows that grasping evolved independently of other traits. The lack of well-preserved skulls and skeletons of the earliest primates has precluded testing of these hypotheses. Here we describe newly discovered postcrania of a carpolestid plesiadapiform, *Carpolestes simpsoni*; provide evidence that at least this plesiadapiform lacks characteristics indicative of both dermopteran-like gliding and euprimate-like leaping, but has features associated with euprimate-like pedal grasping; and investigate the implications for early primate evolution.

Primates of modern aspect [Euprimates of Hoffstetter (*7*)] first appeared in the fossil record during the Paleocene-Eocene transition [~55 million years ago (Ma)] of North America, Europe, and Asia (*8*, *9*). A recent phylogenetic analysis (*10*) of dental, cranial, and postcranial characters indicates that plesiadapiforms are the sister group to Euprimates and are most appropriately considered primates not related to flying lemurs (Dermoptera), as previously suggested (*11–24*). Our cladistic analysis based on new postcranial data discussed here (*25*) also supports this conclusion (Fig. 1).

Carpolestidae appeared in the early Paleocene of North America and survived through the latest Paleocene in North America and Asia (*26–28*). Carpolestids are small and are recognized by distinctive dental specializations for eating nuts, seeds, invertebrates, and fruit (*29*). Although carpolestids are generally considered plesiadapoid plesiadapiforms (*26*, *30*, *31*), some authors have included carpolestids within Euprimates based on the similarity of carpolestid molars to those of fossil tarsioids (*32*, *33*).

A partially articulated skeleton of *C. simpsoni* (*34*, *35*) was found in a freshwater limestone (*36–38*) from the base of the Willwood Formation in the Clarks Fork Basin near Powell, Wyoming, and is of middle Clarkforkian age, between 55.7 and 55.4 Ma (*39*). It is the most complete carpolestid skeleton known (Fig. 2), and is the only specimen for which dental-postcranial associations are documented (*40*). The bones in the *C. simpsoni* skeleton, all from a single individual, were distinguished from those of the other mammals in the accumulation (three rodents, three paromomyids, one marsupial, and two insectivores) on the basis of their spatial distribution on a single bedding plane, size, age (adult), and morphology (*40*, *41*).

The skeleton of *C. simpsoni* includes a virtually complete skull and left dentary, 19 vertebrae, forelimbs with partial right and left manus, hindlimbs with partial right and left pedes, and some ribs. *C. simpsoni*, like other plesiadapiforms, has a humerus with a spherical capitulum; a femur with a distally positioned and medially extended lesser trochanter, postero-

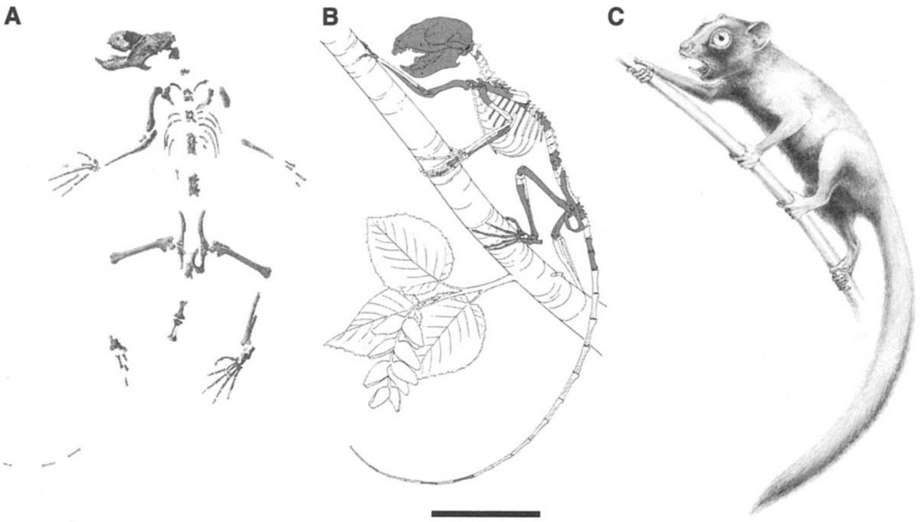

Fig. 2. Skeleton (**A**) and reconstructions (**B** and **C**) of *C. simpsoni* based on University of Michigan Museum of Paleontology (UM) 101963. Documentation of dental-postcranial associations in this specimen has been published elsewhere (*40*). Bones not shaded gray in (B) were not recovered. *C. simpsoni* was a committed arborealist capable of grasping small-diameter supports with both its hands and feet, similar to some euprimates and arboreal marsupials (*3*, *52*). Bar: 5 cm.

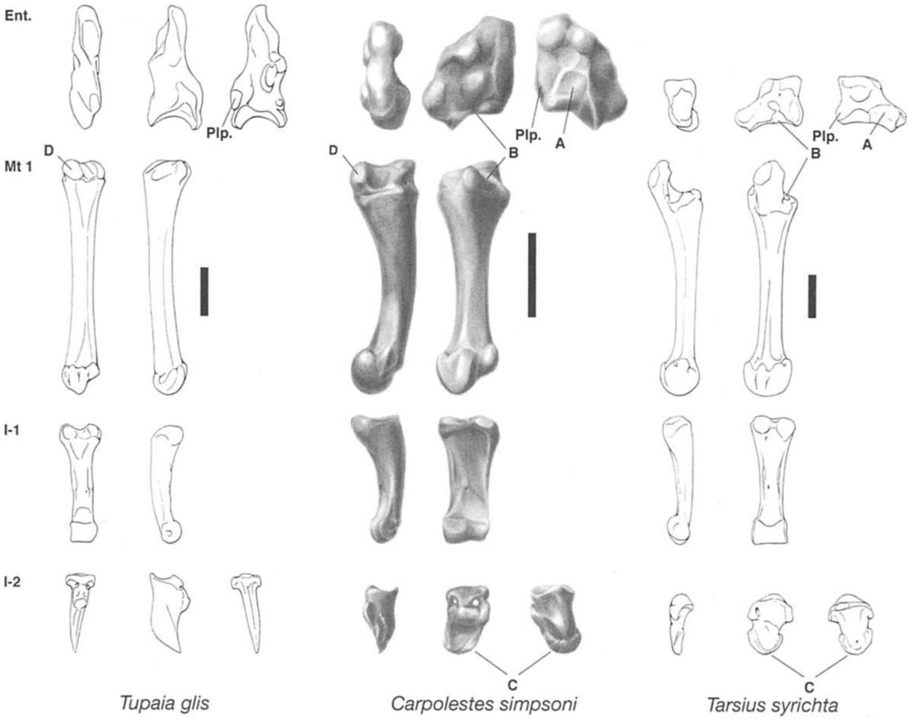

Fig. 3. Left hallux of *C. simpsoni* compared with those of extant euprimate *Tarsius syrichta* and extant tree shrew *Tupaia glis*. Entocuneiform (from left to right) is in ventral, lateral, and medial views; the metatarsal and proximal phalanx are in ventral and lateral views; and the distal phalanx is in ventral, lateral, and medial views. Euprimate traits present in the hallux of *C. simpsoni* include a medial expansion of the distal facet on the entocuneiform (**A**) for articulation with the first metatarsal that forms a saddle-shaped, or sellar joint (**B**), and a distal phalanx that supported a nail instead of a claw (**C**). Primitive traits, also seen in the tree shrew, include a first metatarsal with a peroneal process that is not enlarged (**D**). The distal, relative to the proximal, end of the hallucal metatarsal of *C. simpsoni* is laterally rotated about 90° compared with the condition in that of tupaiids. Similarities to euprimates are reflective of *C. simpsoni* having a divergent and opposable hallux. Similarities to tree shrews (and not to euprimates) are reflective of *C. simpsoni* not being a specialized leaper. The size of the hallux is normalized to the length of the metatarsal. Abbreviations: Ent., entocuneiform; Plp, plantar process of entocuneiform; Mt., metatarsal; I-1, proximal phalanx, first digit; I-2, distal phalanx. Bars: 2 mm.

proximally extended articular surface of the head, and shallow patellar groove; a tibia with an ungrooved distal articular surface that is wider than deep anteroposteriorly; an astragalus with an elliptical head, and short neck; a short calcaneum with a distally positioned peroneal process; an innominate with a cranially positioned ischial spine, and a cranially buttressed, elliptical acetabulum; and terminal phalanges II to V mediolaterally compressed and dorsoventrally high. These characteristics are consistent with the hypothesis that *C. simpsoni*, like other plesiadapiforms, was a committed arborealist, adapted in part for locomotion on large-diameter tree trunks like extant claw-climbing callitrichids (*42–45*). In contrast, and unlike in other plesiadapiforms, both the structure of the joint between the entocuneiform and the hallucal metatarsal, and the structure of the hallucal distal phalanx of *C. simpsoni* are similar to those in animals capable of strong grasping for locomotion on small-diameter terminal branches.

The entocuneiform of *C. simpsoni* is similar to that of the plesiadapiform *Plesiadapis*, tupaiids, and euprimates (Fig. 3) in having a prominent plantar process that might be related to pedal inversion (attachment for tibialis anterior) but also likely served as a medial wall against which powerful pedal flexors ran (flexor tibialis and flexor fibularis) and thus may be related to pedal grasping (*3*, *46*). The entocuneiform of *C. simpsoni* differs from that of *Plesiadapis* and tupaiids in having a much more convex and medially expanded surface for articulation with the hallucal metatarsal. This surface forms a saddle joint between the hallucal metatarsal and the entocuneiform that would have allowed a high degree of abduction-adduction in the hallux (Fig. 4, A and B, A_1 and B_1). This morphology is characteristic of animals with a widely divergent hallux, but is most similar to that of Euprimates and has been considered the key feature of grasping-related mechanics in that group (*3*). *C. simpsoni* has only a moderate peroneal process, substantially shorter than that of Euprimates, indicating that it lacked stability at this joint, as required for grasp-leaping locomotion (*3*). Both the astragalotibial and astragalocalcaneal joints are capable of a high degree of flexibility, also supporting the interpretation that *C. simpsoni* was not a specialized leaper (Fig. 4, A and B, A_2 and B_2). The distal end of the hallucal metatarsal of *C. simpsoni* is laterally rotated about 90° relative to the condition in tupaiids (Fig. 3), effectively reorienting the hallucal phalanges in opposition to those of the rest of the digits (Fig. 4B). This is a distinct characteristic of mammals with an opposable hallux (like Euprimates and unlike *Plesiadapis* and tupaiids). Whereas pedal digits II to V have the mediolateral compression and tall hooklike morphology of claws adapted for locomotion on large-diameter vertical supports, the distal phalanx of the hallux is mediolaterally extended and dorsopalmarly compressed (Fig. 3). The distal hallucal phalanx of *C. simpsoni* closely approximates that of euprimates (e.g., *Tarsius*), from which we infer that *C. simpsoni* had a nail on its hallux. Thus, the morphology of the entocuneiform, hallucal metatarsal, and hallucal distal phalanx demonstrates that *C. simpsoni* had a divergent and opposable hallux adapted for strong pedal grasping of small-diameter supports, similar to that of euprimates.

As might be expected for an animal with distinct grasping specializations in the foot, *C. simpsoni* also has correlated grasping specializations in the hand. Although the distal phalanges of the thumbs were not recovered, other elements of the hand, including a complete third digit ray, were preserved. A recent study demonstrated that early euprimates, as well as modern strepsirhines and haplorhines, have relatively short metacarpals and long proximal phalanges associated with a prehensile hand (*47*). The study showed that scandentians, dermopterans, and plesiadapiforms (based on a specimen of *Plesiadapis cookei*) lacked these proportions and concluded that the Eocene origin of Euprimates involved a shift in digital ray pattern formation associated with the evolution of grasping. However, many plesiadapiforms, including *C. simpsoni*, differ from *Plesiadapis* in having relatively short metacarpals and long proximal phalanges, comprising interelement proportions similar to those of Euprimates (Fig. 5). We conclude that manual grasping was not an innovation of Euprimates, but was likely present in the common ancestor of this group and Plesiadapiformes (Primates, sensu lato).

Functional interpretations from morphology of other regions of the postcranial skeleton are consistent with those made for the hands and feet. A skeletal restoration of *C. simpsoni* (Fig. 2B) shows that it had relative-

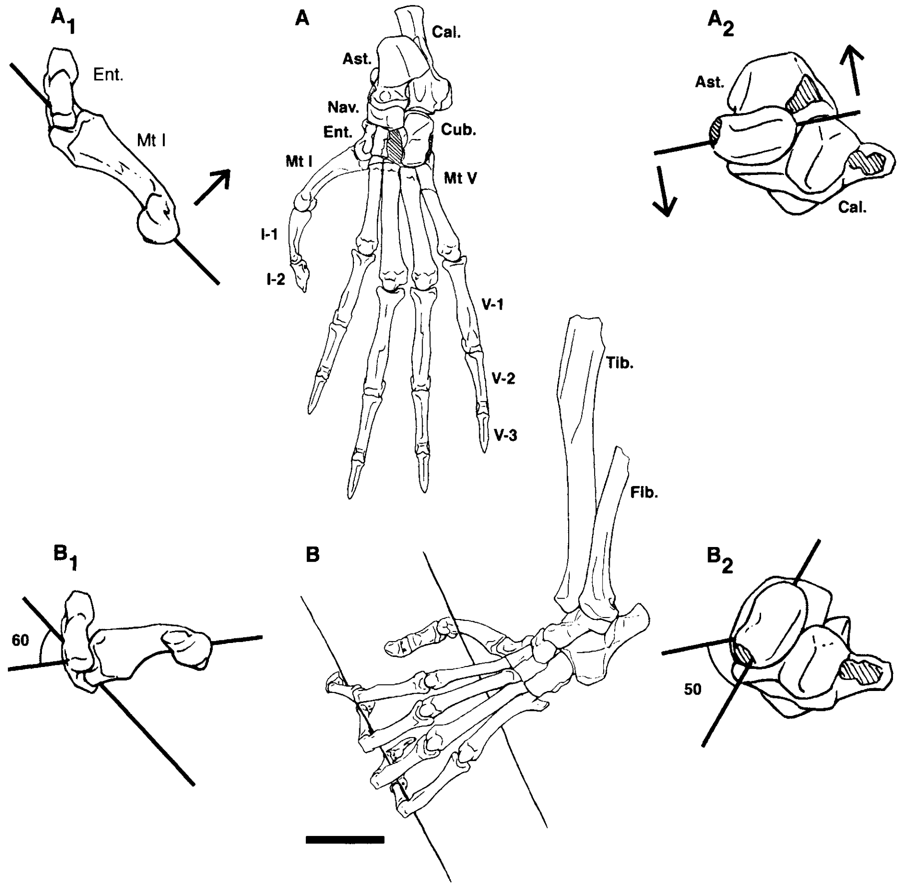

Fig. 4. Functional aspects of left hind foot of *C. simpsoni* interpreted from UM 101963. Hatched areas indicate damaged or missing bone. (**A**) Hind foot, viewed from dorsal aspect, with the hallux adducted (A_1) and the astragalocalcaneal joint everted (A_2). (**B**) Hind foot, viewed from an oblique dorsal aspect, with the hallux abducted about 60° relative to the entocuneiform (B_1) and the astragalocalcaneal joint inverted with about 50° of rotation (B_2). *C. simpsoni* is shown grasping a small-diameter vertical support made of a transparent tube (hallux is shown in plantar orientation). *C. simpsoni* had a divergent and opposable hallux and was capable of pedal inversion. Tarsals are not elongate, in contrast to grasp-leaping euprimates. Abbreviations: Ast., astragalus; Cal., calcaneum; Cub., cuboid; Ent., entocuneiform; Mt., metatarsal; Nav., navicular; Tib., tibia; Fib., fibula; I-1, proximal phalanx, first digit; I-2, distal phalanx, first digit; V-1, proximal phalanx, fifth digit; V-2, middle phalanx, fifth digit; V-3, distal phalanx, fifth digit. Bars: (A and B) 5 mm, (A_1 and A_2, B_1 and B_2) 2.5 mm.

ly long arms (intermembral index = 84), indicating that it was a fairly generalized arborealist. The humerus has a strong deltopectoral crest, indicating a powerful, habitually flexed shoulder. Similarly, a shallow olecranon fossa and abruptly flaring supinator crest on the humerus and a shallow trochlear notch along with a long, anteriorly inflected olecranon process on the ulna indicate habitual flexion of the elbow (*45*). Habitual flexion of the forearms is in this way similar to the condition in modern *Tarsius* and other vertically clinging primates.

C. simpsoni had an anticlinal vertebra in the thoracic region of its vertebral column, indicating that it had a flexible back capable of powerful flexion and extension. On the other hand, low, cranio-caudally long spinous processes, short transverse processes, and broadly spaced, transversely oriented zygapophyses in the lumbar vertebrae indicate that *C. simpsoni*, like vertical-clinging *Tarsius*, had a somewhat stiffer lower back than that of extant callitrichids (*48*). Unlike plesiadapids, *C. simpsoni* had long cervical vertebrae in which the centra are dorsoventrally deep, giving it a long neck like that of extant *Tarsius*. The fibula is robust compared with that of other plesiadapiforms, and both tibia and fibula exhibit deep grooves for tendons of tibialis caudalis and peroneus longus, respectively, making *C. simpsoni* similar to arboreal marsupials. This indicates that stability in the ankle, sacrificed for mobility (Fig. 4, A and B, A_2 and B_2) between joint surfaces, was provided by flexors and extensors that were coopted to resist mediolateral forces and to control inversion and eversion. The cranium of *Carpolestes*, as for all plesiadapiforms for which it is known (*14*, *16*, *36*, *49–51*), lacks the postorbital bar and the convergent, closely spaced orbits of Euprimates.

It has been suggested that "If the first euprimates had grasping feet and blunt teeth adapted for eating fruit, but retained small, divergent orbits like those of *Plesiadapis*. . ." (*2*), the terminal branch feeding hypothesis for primate origins (*5*, *6*, *52*) would be supported. The fossil find presented here is consistent with the hypothesis that early euprimates evolved grasping first and convergent orbits later (*52*) and inconsistent with the visual predation hypothesis (*4*). *C. simpsoni* had feet with strikingly euprimate-like grasping, low-crowned molar teeth adapted for eating fruit, and small and divergent orbits like *Plesiadapis*.

Both arboreal tree shrews (*53*) and didelphid marsupials (*54*) have been presented as living ecological models for early primates. It is plausible that the earliest primates were capable of grasping in a manner similar to that of living arboreal tree shrews like *Ptilocercus* (*3*, *46*, *53*). The specialized euprimate foot, which includes a divergent and opposable hallux with a nail, likely evolved next in a manner similar to that of *Carpolestes*, independent of leaping or orbital convergence. Among living mammals, this stage of primate evolution might be best modeled by arboreal marsupials (*52*, *54*).

Although all carpolestids were probably omnivorous, there was a shift in diet to include more fruit in the late Paleocene (*29*), possibly coincident with the evolution of euprimate-like pedal grasping, as documented here. Furthermore, these morphological changes appear to be coincident with a major radiation of angiosperms in the Northern Hemisphere that resulted in an increased diversity of fruits, flowers, floral and leaf buds, gums, and nectars in the late Paleocene (*5*, *6*). Euprimate-like grasping may have evolved as the *Carpolestes* lineage experienced competition with the earliest rodents that immigrated into North America from Asia (*55*) and, probably acting as both pollinators and seed dispersers (*5*), began to exploit a newly forming adaptive zone created by the efflorescence of angiosperms. *C. simpsoni*, the last representative of the *Carpolestes* lineage, became extinct in the latest Paleocene and was replaced at the beginning of the Eocene by the first euprimates (*55*).

Whether *C. simpsoni* and Euprimates acquired a specialized grasping foot from a common ancestor, as suggested by the cladistic analysis of postcranial data (Fig. 1), or through parallel evolution is unknown. Regardless, many striking similarities between Plesiadapiformes and Euprimates seem to indicate a shared arboreal ancestry (*56*). We believe that the postcranium of *C. simpsoni* represents the best morphological model yet known for an early stage in the ancestry of Euprimates on the basis of their shared grasping capabilities and their close phylogenetic relationships (*10*). More complete postcranial fossils of the earliest euprimates and better sampling of the Paleocene fossil record of continents such as Africa, Asia, and India, where euprimates are thought to have originated, are needed to develop a more refined understanding of how leaping and forward-facing orbits might have evolved from a *Carpolestes*-like ancestor.

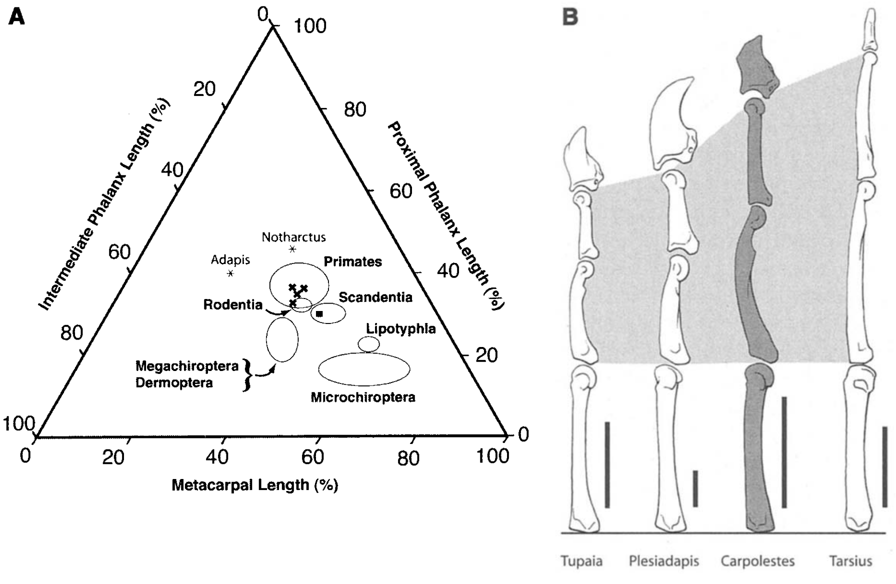

Fig. 5. Ternary plot (**A**) showing relative metacarpal, proximal, and intermediate phalangeal lengths for the third digit ray of the manus [figure modified from Hamrick (*47*)]. Ellipses represent variability in extant taxa. Extant euprimates, as well as Eocene euprimates *Notharctus* and *Adapis*, have relatively short metacarpals and long proximal phalanges indicative of a grasping, prehensile hand (*47*). Comparison of right third digit ray of extant *Tupaia glis*, Paleocene plesiadapiforms *Plesiadapis cookei* and *C. simpsoni*, and extant *Tarsius syrichta* (**B**) show that *P. cookei* had a relatively short proximal phalanx (like *Tupaia*), whereas *C. simpsoni* had a relatively long proximal phalanx, like *Tarsius*. Plesiadapiform proportions, plotted in the Ternary diagram (A), illustrate that *C. simpsoni* and other plesiadapiforms had a grasping hand. Filled square represents *P. cookei*; black crosses represent *C. simpsoni*, micromomyids, and paromomyids. The size of the digit ray is normalized to the length of the metacarpal in (B). Bars: 5 mm.

References and Notes

1. M. Dagosto, *J. Hum. Evol.* **17**, 35 (1988).
2. M. Cartmill, *Evol. Anthropol.* **6**, 111 (1992).
3. F. S. Szalay, M. Dagosto, *J. Hum. Evol.* **17**, 1 (1988).
4. M. Cartmill, *Science* **184**, 436 (1974).
5. R. W. Sussman, P. H. Raven. *Science* **200**, 731 (1978).
6. R. W. Sussman, *Am. J. Primatol.* **23**, 209 (1991).
7. R. Hoffstetter, *Bull. Mem. Soc. Anthropol.* **4**, 327 (1977).
8. P. D. Gingerich, *Univ. Mich. Pap. Paleontol.* **28**, 1 (1989).
9. G. J. Bowen *et al.*, *Science* **295**, 2062 (2002).
10. M. T. Silcox, thesis, Johns Hopkins University (2001).
11. Plesiadapiformes has long been considered an archaic radiation of primates. Evidence in favor of a plesiadapiform-euprimate link was based largely on dental and postcranial similarities (*12–14*), whereas the absence of a postorbital bar and other cranial features in certain plesiadapiforms provided evidence against this hypothesis (*15*). An alternative hypoth-