applies equally to native and exotic species (*8*), the resource–enemy release hypothesis predicts that high resource availability will help exotic species more than native species (see the figure, right). Consequently, anthropogenic increases in resource availability, ranging from small-scale disturbances to global climate change, may not just facilitate invasion, but facilitate invasion by exotic species in particular. In fact, exotic species tend to outperform native species in high- but not low-resource environments (*17*). Humans may therefore play an even larger role in invasions by exotic species than previously thought.

References

1. J. M. DiTomaso, *Weed Sci.* **48**, 255 (2000).
2. R. M. Keane, M. J. Crawley, *Trends Ecol. Evol.* **17**, 164 (2002).
3. C. E. Mitchell, A. G. Power, *Nature* **421**, 625 (2003).
4. K. Shea, P. Chesson, *Trends Ecol. Evol.* **17**, 170 (2002).
5. R. M. Callaway, E. T. Aschehoug, *Science* **290**, 521 (2000).
6. H. G. Baker, in *The Genetics of Colonizing Species*, H. G. Baker, D. L. Stebbins, Eds. (Academic Press, New York, 1965), pp. 147–172.
7. E. Grotkopp, M. Rejmanek, T. L. Rost, *Am. Nat.* **159**, 396 (2002).
8. M. A. Davis, J. P. Grime, K. Thompson, *J. Ecol.* **88**, 528 (2000).
9. S. J. Dewalt, J. S. Denslow, K. Ickes, *Ecology* **85**, 471 (2004).
10. P. D. Coley, J. P. Bryant, F. S. Chapin, *Science* **230**, 895 (1985).
11. J. P. Grime *et al.*, *Oikos* **79**, 259 (1997).
12. W. J. Mattson, *Annu. Rev. Ecol. Syst.* **11**, 119 (1980).
13. L. H. Fraser, J. P. Grime, *J. Ecol.* **87**, 514 (1999).
14. J. Cebrian, C. M. Duarte, *Funct. Ecol.* **8**, 518 (1994).
15. P. V. A. Fine, I. Mesones, P. D. Coley, *Science* **305**, 663 (2004).
16. E. Hoffland *et al.*, *Plant Cell Environ.* **19**, 1281 (1996).
17. C. C. Daehler, *Annu. Rev. Ecol. Syst.* **34**, 183 (2003).

10.1126/science.1114851

PALEONTOLOGY

Shaking the Earliest Branches of Anthropoid Primate Evolution

Jean-Jacques Jaeger and Laurent Marivaux

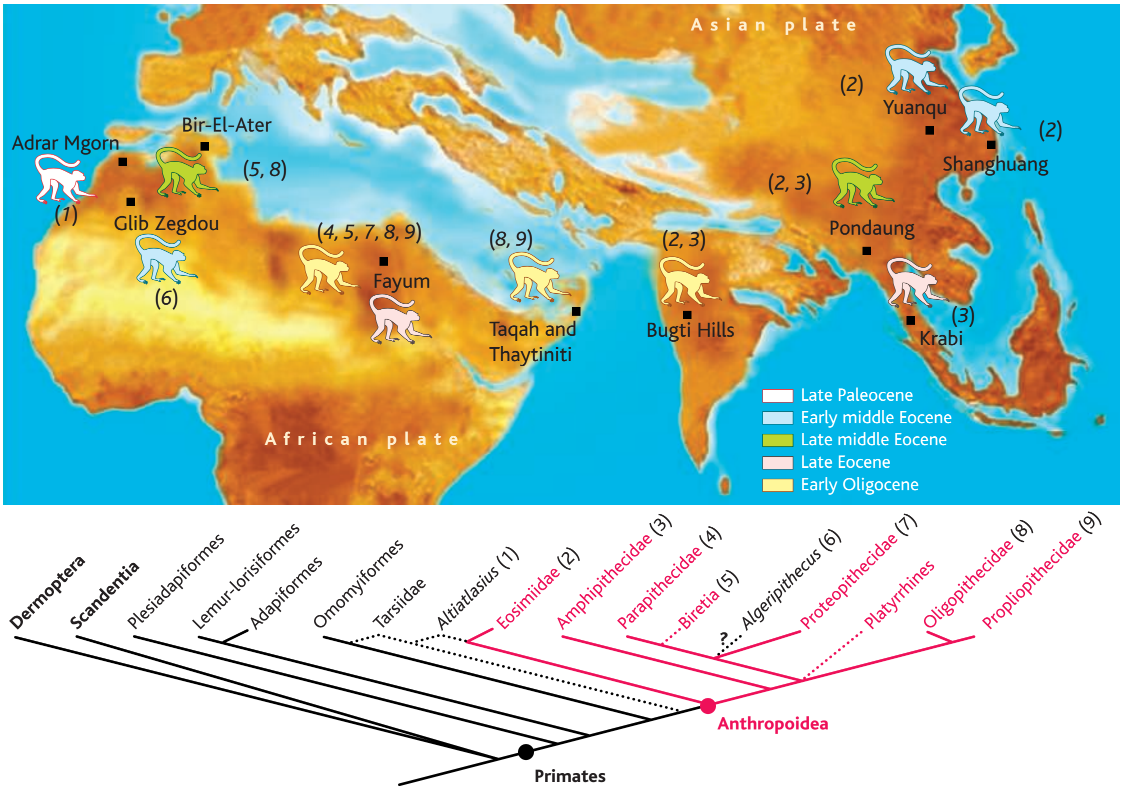
Although chimpanzees are our closest living relatives, humans also share many important anatomical and biochemical characteristics with a large group of extant and fossil primates that taxonomists have named "anthropoids." All living humans, apes, baboons, macaques, leaf monkeys, and New World monkeys, together with numerous fossil anthropoids, share a common ancestor that originated in either Africa or Asia, both continents having yielded primitive fossil representatives of this group (see the figure). In Africa, mostly through the work of Simons and his team in the Fayum desert in Egypt, numerous distinctive taxa of primitive anthropoids have been described from sediments dated at between 35 and 32 million years old (*1*). Not only did Simons discover *Aegyptopithecus*, the ancestor of later and more derived anthropoids (catarrhines, which includes the Old World monkeys), but he also recovered and described a diversity of more primitive anthropoid taxa, some of which appear to be endemic to North Africa while others are considered to be closely related to New World monkeys (*2*). Therefore, for several decades, North Africa was considered as the center of anthropoid origin and early diversification. But this classical Fayum record begins abruptly, at about 35 million years ago, when an ecologically diverse anthropoid community was already in place. Very little was known about earlier African anthropoids dating from closer to the beginning of the African anthropoid radiation.

The authors are at the Laboratoire de Paléontologie, Institut des Sciences de l'Évolution, Université Montpellier II, F-34095 Montpellier Cedex 05, France. E-mail: jaeger@isem.univ-montp2.fr, marivaux@isem.univ-montp2.fr

Now, on page 300 of this issue, Seiffert *et al.* (*3*) describe the most complete known remains of the earliest African anthropoids from the oldest fossiliferous level of the Fayum desert, Birket Qarun Locality 2 (BQ-2), precisely dated from 37 million years ago. These anthropoids are represented by two distinct and small species of the genus *Biretia* (*4*) whose body masses have been estimated to be 273 and 376 g, respectively. Their dental morphology agrees with what had been predicted for a common ancestor of later African anthropoids. It is also one step more evolved than that of any contemporaneous Asian anthropoid. The smaller of these two new species (*Biretia fayumensis*) is similar to a contemporaneous Algerian species (*Biretia piveteani*) from the Bir-El-Ater locality, which is known from a single tooth (*4*). But the larger of these new species, *Biretia megalopsis*, whose dentition is very similar to that of the smaller one, displays a surprising and unexpected specialization. Its ocular orbits are strongly enlarged, being similar in size and morphology to those of *Tarsius*, a modern small-bodied nocturnal primate from Southeast Asia, suggesting that *Biretia* displayed a nocturnal activity pattern as well.

Unfortunately, in the smaller new species this bony area below the orbit is not preserved. The enlarged orbits of *Biretia megalopsis* conflict with the classical notion that the earliest anthropoids were diurnal primates with well-developed stereoscopic and color vision (*5*), and with the oldest Asian fossil record. Seiffert *et al.* (*3*) consider this species as a specialized, early branch of African anthropoids, because no later Fayum anthropoid displays such a character. For these authors, *Biretia* suggests an ancient evolutionary history in Africa that allowed enough time for some anthropoids to develop such specialized adaptations. Alternatively, all of the Algerian and Egyptian anthropoids of this age may have shared enlarged orbits, because their similar dental characters suggest that they are closely related. But such a specialized adaptation would then exclude these fossils from the ancestry of their later Fayum relatives. Nevertheless, the dental morphology of these fossils undoubtedly documents an early stage of African anthropoid evolution, pinpointed by some uniquely shared specialized characters.

In addition to the description of these two new species, Seiffert *et al.* (*3*) present the results of an outstanding cladistic analysis using 360 morphological characters of 102 extant and fossil primate taxa, which supports some interesting hypotheses. The two new Fayum species appear as the sister groups of a well-known extinct anthropoid family, the Parapithecidae, which is only known from North Africa. They derive, according to that cladistic analysis, from an older Saharan primate, *Algeripithecus*, which was described several years ago on the basis of a couple of teeth (*6*), as the earliest (more than 45 million years old) and most primitive African anthropoid. In addition, both new Fayum species and *Algeripithecus* are considered as related to a late Paleocene (60 million years ago) Moroccan primate, *Altiatlasius*, known only from a dozen isolated teeth (*7*). According to that result, the anthropoids would have had a very long evolutionary history on the African continent, and this ancient origin is supported by several molecular analyses that suggest similar antiquity for the branching events between extant anthropoid lineages. Unfortunately, these older African putative "anthropoids" are extremely fragmentary, and many of their morphological characters remain undocumented. Needless to say, this hinders efforts to obtain a strong and accurate phylogenetic tree, and convergent evolution is a common pitfall of cladistic analyses.



Early anthropoids. (**Top**) Paleogeographic reconstruction of South Asia and North Africa at the mid-Paleogene showing the fossiliferous localities that have yielded fossil anthropoid primates [map adapted from (*18*)]. (**Bottom**) Current consensus of anthropoid primate phylogeny. [Adapted from (*3*, *9*)]

Another interesting result of the analysis of Seiffert *et al*. (*3*) is the phylogenetic position of the Asian anthropoids, Eosimiidae and Amphipithecidae. For many years, their anthropoid nature was controversial, but with a recently enriched fossil record, amphipithecids are now recognized as stem anthropoids and as the sister group of the African anthropoids (*8*, *9*). The less specialized eosimiids appear now as the sister group of all anthropoids, pointing to an Asian origin of anthropoids (*10*). The phylogenetic results reported by Seiffert *et al.* closely mirror those that have recently been published by others (*9*), and this present phylogenetic framework appears to be the current consensus of primate phylogeny.

This marks the end of a long controversy and opens the way for deeper understanding of the phylogenetic relationships among these earliest Asian and African anthropoids. However, a major gap in our knowledge remains, both in Asia and in Africa, regarding the anthropoid faunas of the early and middle Eocene (57 to 40 million years ago), a time interval that is believed to correspond to a period of active intercontinental exchange of land mammals (*11*). The Eosimiidae, the oldest and most primitive anthropoids currently known, were originally described from the middle Eocene of China [45 million years ago (*12*)] and have subsequently been discovered in Myanmar in a 37-million-year-old dated locality (*13*), and recently also in Pakistan (*9*) from a more recent layer (32 million years ago), thereby testifying to their wide stratigraphic and geographic range. As stem anthropoids, they are now recognized as phylogenetically related to the African ones, but they have not yet been discovered in Africa. According to Beard (*10*) and Seiffert *et al.* (*3*), the earliest African anthropoids immigrated from Asia at a very early date, probably before the late Paleocene.

However, a later immigration age scenario remains possible, and in such a case, the scarce Moroccan and Algerian earlier anthropoid record will have to be reinterpreted differently on the basis of a more complete fossil record. In the Algerian Bir-El-Ater locality, roughly coeval to the new Fayum locality (BQ-2), *Biretia* has been found in association with two rodent families, anomaluroids and baluchimyines, whose fossil record is well documented in southern Asia (*14*, *15*), together with anthracotheres, a piglike mammalian family of undoubted Asian origins (*16*).

Therefore, African anthropoid ancestors may have immigrated from Asia together with these other Asian mammals just before 37 million years ago (*9*, *17*). But, as suggested by Seiffert *et al*. (*3*), a more complicated scenario is also possible, with several waves of Asian immigrations and exchanges between both continents. To choose between these alternative scenarios, we need a more complete fossil record and to discover new Eocene anthropoid localities in Asia and in Africa.

Understanding the first steps of our own fossil record and deciphering the various immigration events between Asia and Africa is now improving rapidly, and represents a great challenge for future research. Surprisingly, solving this problem may provide a model for the understanding of another critical period of human evolution, the origin and evolution of extant great apes and humans, whose biogeographical background also involves several geographic areas, including Southern Asia and Africa, and also probable multiple immigration events between both continents. The tree of human evolution, when shaken by new discoveries, often changes its branching pattern—a strong argument to stimulate further research in that fascinating field.

References and Notes

1. E. L. Simons, *Yearb. Phys. Anthropol.* **38**, 199 (1995).
2. E. R. Miller, E. L. Simons, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 13760 (1997).
3. E. R. Seiffert *et al.*, *Science* **310**, 300 (2005).
4. L. Bonis de, J.-J. Jaeger, B. Coiffait, P.-E. Coiffait, *C. R. Acad. Sci.* **306**, 929 (1988).
5. C. P. Heesy, C. F. Ross, in *Anthropoid Origins: New Visions*, C. F. Ross, R. F. Kay, Eds. (Plenum, New York, 2004), pp. 665–698.
6. M. Godinot, M. Mahboubi, *Nature* **357**, 324 (1992).
7. B. Sigé, J.-J. Jaeger, J. Sudre, M. Vianey-Liaud, *Palaeontographica* **214**, 31 (1990).
8. L. Marivaux *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 13173 (2003).
9. L. Marivaux *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 8436 (2005).
10. K. C. Beard, *The Hunt for the Dawn Monkey: Unearthing the Origins of Monkeys, Apes, and Humans* (Univ. of California Press, Berkeley, 2004).
11. E. Gheerbrant, *Palaeontographica* **237**, 39 (1995).
12. K. C. Beard, T. Qi, M. R. Dawson, B. Wang, C. Li, *Nature* **368**, 604 (1994).
13. J.-J. Jaeger *et al.*, *Science* **286**, 528 (1999).
14. L. Marivaux, J.-L. Welcomme, M. Vianey-Liaud, J.-J. Jaeger, *Zool. Scr.* **31**, 225 (2002).
15. L. Marivaux *et al.*, *J. Vertebr. Paleontol.* **25**, 214 (2005).
16. S. Ducrocq, *Stuttg. Beitr. Naturkd. Ser. B* **250**, 1 (1997).
17. R. F. Kay, B. A. Williams, C. F. Ross, M. Takai, N. Shigehara, in *Anthropoid Origins: New Visions*, C. F. Ross, R. F. Kay, Eds. (Plenum, New York, 2004), pp. 91–135.
18. R. Blakey, http://jan.ucc.nau.edu/~rcb7/RCB.html.
19. This Perspective is an Instit des Sciences de l'Évolution-Montpellier publication 2005-086.

10.1126/science.1118124