Basal Anthropoids from Egypt and the Antiquity of Africa's Higher Primate Radiation

Erik R. Seiffert,[1]* Elwyn L. Simons,[2] William C. Clyde,[3]
James B. Rossie,[4] Yousry Attia,[5] Thomas M. Bown,[6]
Prithijit Chatrath,[2] Mark E. Mathison[7]

Early anthropoid evolution in Afro-Arabia is poorly documented, with only a few isolated teeth known from before ~35 million years ago. Here we describe craniodental remains of the primitive anthropoid *Biretia* from ~37-million-year-old rocks in Egypt. *Biretia* is unique among early anthropoids in exhibiting evidence for nocturnality, but derived dental features shared with younger parapithecids draw this genus, and possibly >45-million-year-old *Algeripithecus*, into a morphologically and behaviorally diverse parapithecoid clade of great antiquity.

The early or early middle Eocene Algerian primate *Algeripithecus* establishes that higher primates have been evolving on the Afro-Arabian land mass for at least 45 million years (*1–3*), but that genus is only known from a few isolated teeth that have precluded meaningful inferences about its adaptations and phylogenetic affinities. Late middle and early late Eocene anthropoid evolution in Afro-Arabia is documented by only a single lower molar of the Algerian anthropoid *Biretia piveteaui* (*4*). The much-better-documented oligopithecids, parapithecids, and proteopithecids first appear around 35 million years ago (Ma) in the Jebel Qatrani Formation of northern Egypt (*5*, *6*).

Recent paleontological work in Egypt's Fayum Depression has resulted in the discovery of a diverse primate fauna at a site called Birket Qarun Locality 2 (BQ-2) (*7*). Here we describe two new species of *Biretia* from that locality—*B. fayumensis* (*8*) and *B. megalopsis* (*9*)—and provide magnetostratigraphic evidence that supports an earliest late Eocene (earliest Priabonian, ~37 Ma) age for these taxa. The character complexes exhibited by the new species support the inclusion of *Biretia* in an expanded parapithecoid clade and reveal new evidence for behavioral diversity and morphological homoplasy among early African anthropoids.

Locality BQ-2 is situated 229 m below Quarry L-41, the next-oldest primate-bearing

---

[1] Department of Earth Sciences, University of Oxford, and Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, UK. [2] Department of Biological Anthropology and Anatomy, Duke University, and Division of Fossil Primates, Duke Primate Center, 1013 Broad Street, Durham, NC 27705, USA. [3] Department of Earth Sciences, University of New Hampshire, 56 College Road, Durham, NH 03824, USA. [4] Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA. [5] Egyptian Geological Museum, Misr el Kadima, Ethar el Nabi, Cairo, Egypt. [6] Erathem-Vanir Geological, 2300 Arapahoe Avenue, no. 236, Boulder, CO 80302, USA. [7] Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA 50011, USA.

*To whom correspondence should be addressed. E-mail: erik.seiffert@earth.ox.ac.uk

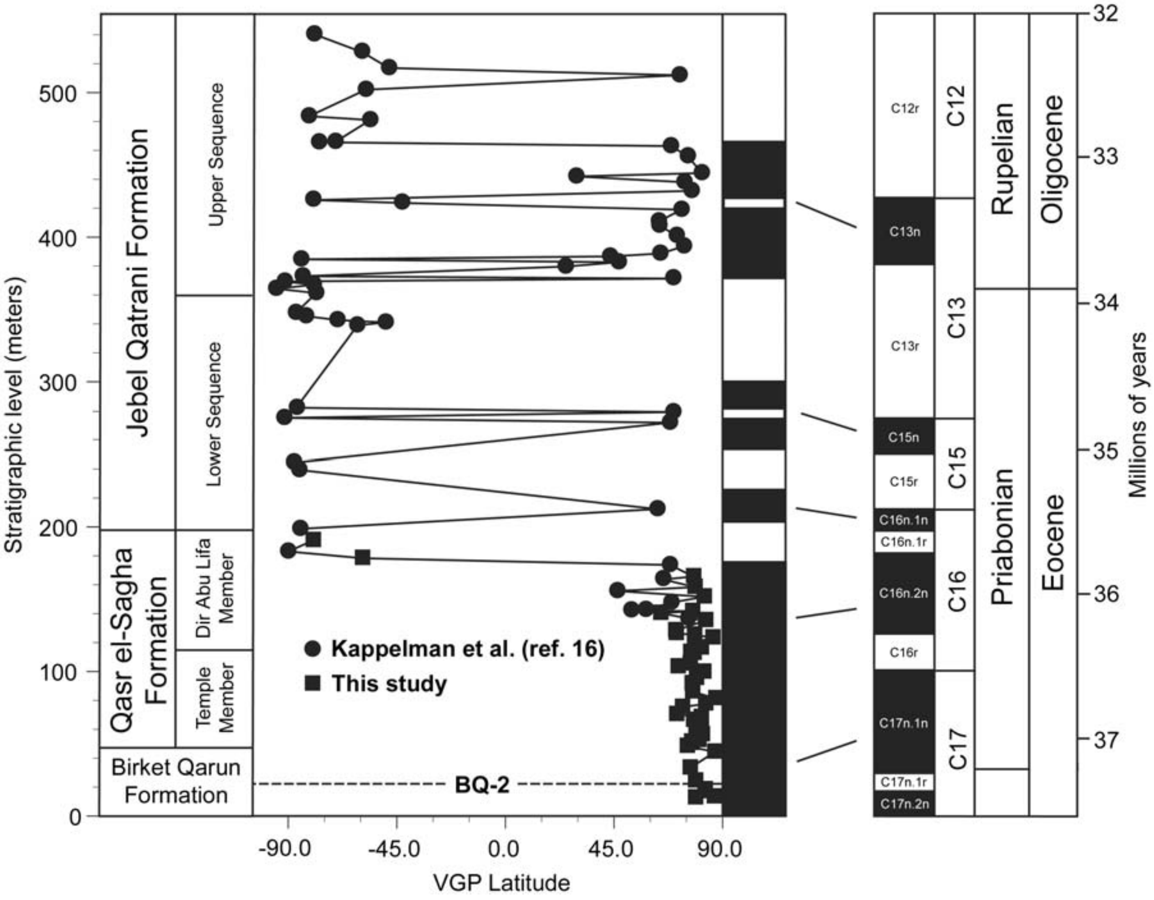

Fig. 1. Fayum magnetostratigraphy and preferred correlation with the GPTS. Paleomagnetic data are from this study (squares) and Kappelman *et al.* (*16*) (circles). The time scale is from Ogg and Smith (*18*). VGP, virtual geomagnetic pole. Three or more oriented samples from 53 sites were demagnetized progressively, using a combination of alternating field and thermal demagnetization (figs. S1 and S2 and methods in the supporting online material). The long normal-polarity zone at the base of the section likely correlates to Chron C16n and part of C17n. Chron C16r may be missing due to an erosional unconformity at the Temple/Dir Abu Lifa contact. The upper part of the section matches Kappelman *et al.*'s (*16*) preferred correlation (their correlation 1), but other correlations are possible. BQ-2 correlates to C17n.1n (early Priabonian, ~37 Ma) in our preferred correlation.

locality in Egypt, and has also produced remains of strepsirrhine primates (*7*), proboscideans, hyracoids, herodotiines, ptolemaiids, creodonts, anomaluroid and hystricognathous rodents, chiropterans, and insectivores. The primary fossiliferous horizons at BQ-2 occur in intraclastic ironstone pebble and cobble conglomerate beds that are about 5 to 15 cm thick; the new anthropoid specimens were collected either by quarrying or dry-screening these sediments. Sedimentary structures preserved at BQ-2 provide strong evidence for a fluvial origin of these deposits. This horizon was originally placed in the Birket Qarun Formation by Beadnell (*10*) but was more recently assigned to a new (Umm Rigl) Member of the Qasr el-Sagha Formation by Gingerich (*11*). We include the Umm Rigl Member in the top of the Birket Qarun Formation, because the lithology of this unit does not correspond with that of the estuarine and lagoonal facies preserved in the overlying Temple and Dir Abu Lifa Members of the Qasr el-Sagha Formation (*12*). Retaining these sediments in the Birket Qarun Formation is also consistent with the suggestion that that unit preserves the oldest known Cenozoic coastal deposits in Egypt (*11*, *12*).

BQ-2 is younger than the underlying Gehannam Formation, which preserves late middle Eocene [Bartonian, Zone P14 (*13*)] planktic foraminifera (*14*, *15*). The exact placement of the Eocene-Oligocene boundary in the Fayum area has been a matter of debate (*5*, *11*, *16*), but the Qasr el-Sagha and Birket Qarun Formations are Eocene under all interpretations. Magnetostratigraphic sampling of the Qasr el-Sagha Formation and upper Birket Qarun Formation reveals that these sediments are almost entirely of normal polarity, although a polarity reversal recorded at the top of the Qasr el-Sagha Formation coincides precisely with a reversal recorded at the base of the section that was previously sampled by Kappelman *et al*. (*16*) (Fig. 1 and fig. S3). There are several potential correlations of the Fayum magnetostratigraphy with the geomagnetic polarity time scale (GPTS) (*16*); however, the long normal-polarity zone at the base of the section is likely to include part of Chron C16n under any correlation. Significant erosional unconformities mark the contacts of the Qasr el-Sagha and Jebel Qatrani Formations and the Temple and Dir Abu Lifa Members of the Qasr el-Sagha Formation (*11*, *12*), and may cut out more than 95 m of sediment, suggesting that the lower part of the long normal-polarity zone at the base of the section encompassing BQ-2 represents Chron C17n.1n (*17*). These constraints indicate that BQ-2 is likely to be earliest Priabonian in age or ~37 million years old on the most recent time scale (*18*). Thus, the new species of *Biretia* are probably ~3.5 million years older than the derived parapithecids and propliopithecids from the early Oligocene Fayum Quarries I and M, ~2 million years older than late Eocene anthropoids such as *Catopithecus* and *Proteopithecus* from Quarry L-41 (*5*), and roughly the same age as *Bahinia*, *Myanmarpithecus*, *Amphipithecus*, and *Pondaungia* from the Pondaung Formation in Myanmar, which have also been tied to Chron C17n.1n (*19*).

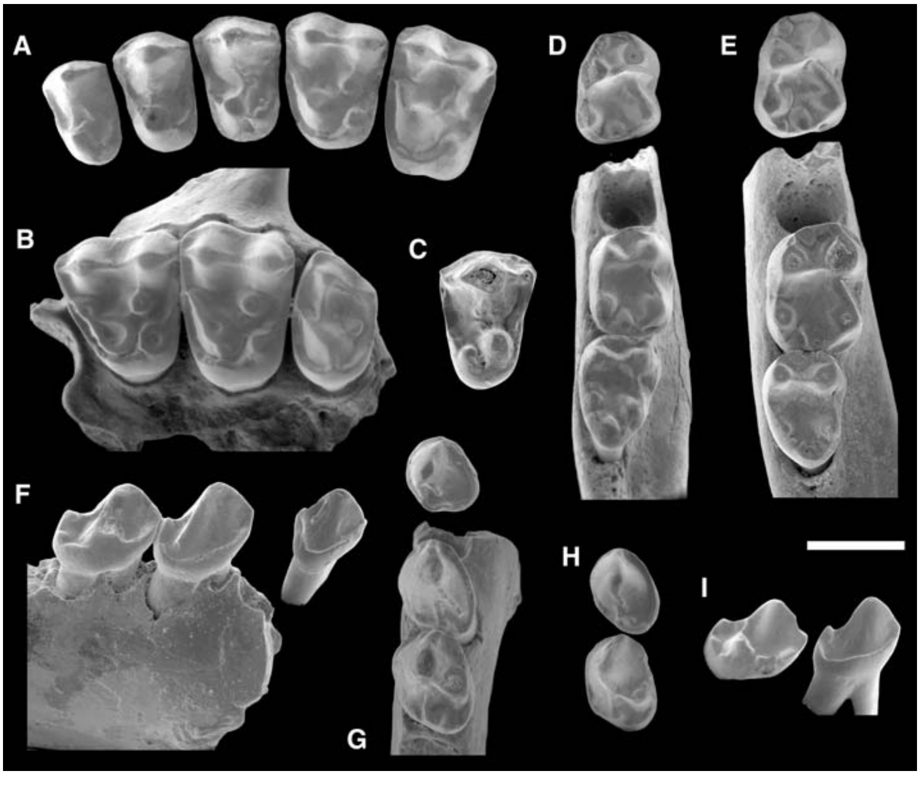

Fig. 2. (**A**) *B. fayumensis*, new species, composite of isolated P2 (DPC 21759C), P3 (DPC 21249E), P4 (DPC 21371A), M1 (DPC 21250D), and M2 (DPC 21539E, reversed). (**B**) *B. megalopsis*, new species, maxilla with M1 through M3 (DPC 21358F). (**C**) *B. megalopsis*, P4 (DPC 22279D). (**D**) *B. fayumensis*, isolated m1 (DPC 21220A) and holotype mandible with m2 and m3 (CGM 83658). (**E**) *B. megalopsis*, isolated m1 (DPC 22442G) and holotype mandible with m2 and m3 (CGM 83661). (**F** and **G**) *B. megalopsis*, mandible with p3 and p4 and alveoli for c and p2 (DPC 21539B) and isolated p2 (DPC 21757E, reversed) in lingual (F) and occlusal (G) views. (**H** and **I**) *B. fayumensis*, isolated p3 (DPC 21296D, reversed) and p4 (DPC 21757D) in occlusal (H) and lingual (I) views. Scale bar, 2 mm.

B. fayumensis is one of the smallest known Fayum anthropoids, with mean body mass estimates of 273 and 160 g, based on extant anthropoid and all primate regressions, respectively, of body mass on m1 area (m, lower molar; M, upper molar) (*20*). The new material provides additional support for the hypothesis that *Biretia* is more closely related to younger parapithecoids (here defined as a clade containing *Arsinoea* and the parapithecids *Abuqatrania*, *Qatrania*, *Apidium*, and *Parapithecus*) than it is to other Paleogene African anthropoids (*4*, *21*). In addition to the centrally placed molar hypoconulids, distolingual foveae, and generalized bunodonty already observable on the type specimen of *B. piveteaui*, *B. fayumensis* shares with the early Oligocene parapithecids *Apidium* and *Parapithecus* a three-rooted and bicuspid P2 (p, lower premolar; P, upper premolar), a distinct paraconule on M1, and well-developed metaconules on M1-2 (Fig. 2). *B. fayumensis* shares other features of the upper dentition exclusively with *Apidium*, such as hypocones on P3 and P4 and a pericone on M2, but lacks the apomorphic lower dental features that unite later parapithecoids, such as an absence of lower molar protocristids (fig. S4). *B. fayumensis* also lacks the well-developed upper premolar paraconules observable in *Apidium* and *Parapithecus*, but does have a trenchant crest coursing labially from the P4 protocone that terminates in a tiny cuspule. A similar crest is observable in the amphipithecids *Myanmarpithecus* (*22*) and *Pondaungia* (*23*) as well as in some Oligocene propliopithecids, but in neither group is there any development of a cuspule at the crest's terminus. Despite the numerous apomorphic characters aligning *B. fayumensis* with younger parapithecoids, this species nevertheless retains a few apparent plesiomorphies, such as a premetacristid on m1, a relatively long and narrow p4, and a distally oriented p3 protocristid, that are not observable in any of the late Eocene parapithecoid or proteopithecid species rep-

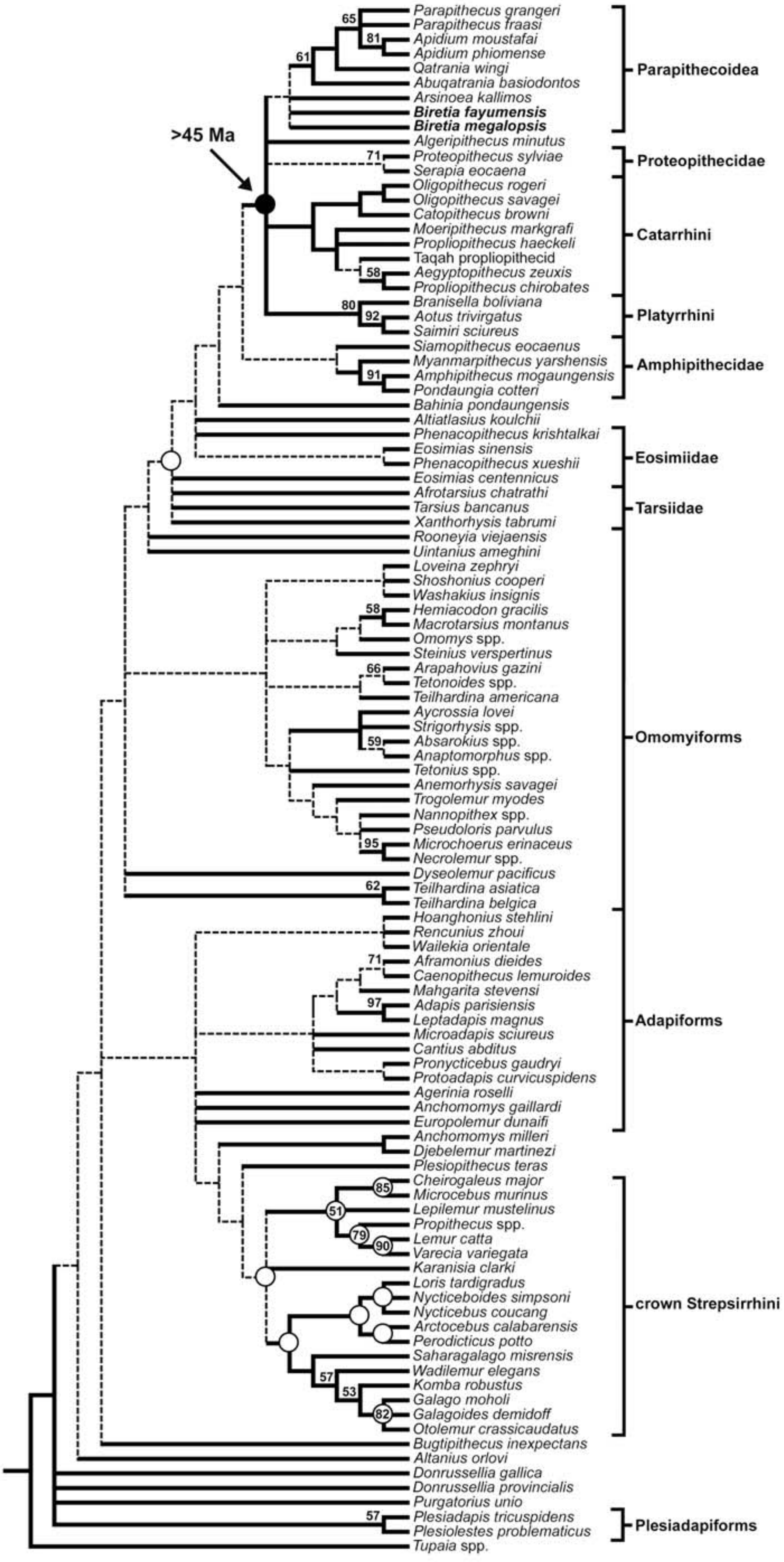

Fig. 3. Strict/Adams consensus tree summarizing all 9992 trees recovered from two parsimony analyses of 360 morphological characters, one in which some multistate characters were ordered and scaled [22 equally parsimonious trees (EPTs), tree length (TL) = 2104.398, consistency index (CI) = 0.2044, retention index (RI) = 0.5890, rescaled consistency index (RCI) = 0.1219] and one in which all characters were unordered (9970 EPTs, TL = 3814, CI = 0.2485, RI = 0.5369, RCI = 0.1346). Solid lines in the cladogram indicate which clades are present in the strict consensus of all 9992 trees; dotted lines indicate which clades are present in the Adams consensus tree, which relocates those taxa that are placed in conflicting positions in the tree, either within or across analyses, to the node held in common by all such conflicting positions. Open circles denote constrained clades supported by Alu SINEs (short interspersed nuclear elements; see supporting online material). Bootstrap support values greater than 50 (derived from analysis of the "ordered/unordered" data set only) are shown above branches. Character support for Parapithecoidea is available in the supporting online material.

resented at L-41 but are present in much more primitive primates such as eosimiids. Regardless of where *Biretia* is placed relative to other Paleogene anthropoids, a considerable amount of dental homoplasy is implied, but parsimony analysis (*24*) consistently aligns the genus with parapithecoids (Fig. 3 and figs. S5 and S6).

B. megalopsis shares with Oligocene parapithecids the same suite of apomorphic upper molar features observable in *B. fayumensis* but is slightly larger than its contemporary, is more bunodont, exhibits variable presence of the m1 premetacristid (a crest that is absent in late Eocene *Arsinoea*, *Abuqatrania*, and *Qatrania*), and shares larger conules and reduced or absent postprotocristae on P4-M3 with *Apidium* and *Parapithecus*. As in *B. fayumensis*, the p4 of *B. megalopsis* is also relatively long, and both taxa have more complex p4 talonids (with tall hypoconids, small entoconids, and trenchant oblique cristids and protocristids) than younger parapithecoids. The presence of these features in primitive parapithecoids suggests that this morphology might have been present in the last common ancestor of catarrhines, platyrrhines, proteopithecids, and parapithecoids and was subsequently secondarily simplified in younger parapithecids. The phylogenetic placement of the new *Biretia* species within Parapithecoidea is sensitive to assumptions about ordering and scaling of multistate characters; parsimony analysis with some multistate characters ordered and scaled recovers a *Biretia* clade to the exclusion of parapithecids (fig. S5), whereas the Adams consensus tree derived from an analysis with all characters unordered renders *Biretia* paraphyletic with respect to Parapithecidae (fig. S6).

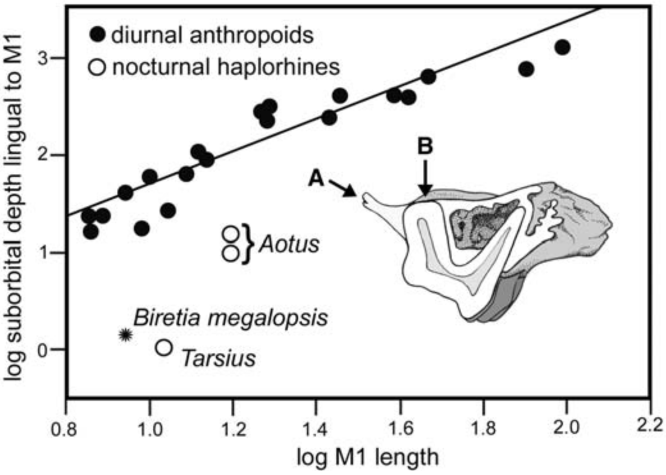

Fig. 4. Bivariate plot of log suborbital depth lingual to M1 versus log M1 length, and least-squares regression line ($Y = 1.633x + 0.049$, $R^2 = 0.882$) for diurnal anthropoids (black circles), compared with extant nocturnal haplorhines (*Tarsius* and *Aotus*) and *B. megalopsis*. All measurements derive from high-resolution computed tomographic (micro-CT) coronal scans taken through the lingual roots of M1. *B. megalopsis* scales in a manner most similar to the nocturnal taxa. The inset line drawing is a mesial view of the *B. megalopsis* maxilla at the level of the M1 lingual root, based on a reconstruction from high-resolution micro-CT scans, to illustrate the lack of a maxillary sinus as well as (A) complete fusion of the bony laminae making up the floor of the orbit and hard palate, and (B) exposure of the lingual root of M1 in the orbit floor.

B. megalopsis is unlike other early anthropoids in having an extremely compressed suborbital region, with lingual tooth roots of M1 and M2 exposed in the floor of the orbit (fig. S7), no development of a maxillary sinus lingual to the molars, and complete fusion of the bony laminae forming the floor of the orbit and hard palate medial to M1 and M2. These characteristics are likely related to orbital hypertrophy, because the only other living or extinct haplorhine known to exhibit all of these features in combination is nocturnal *Tarsius* (fig. S8), whose relative orbit size is greater than that of any other living or extinct primate. A plot of suborbital depth (*23*) relative to the length of the first upper molar (Fig. 4) demonstrates that *B. megalopsis* falls far from the regression line for diurnal anthropoids and deviates in a manner most similar to *Tarsius* and *Aotus*, the only extant nocturnal anthropoid. The possibility that *B. megalopsis*'s morphology is due to its small size therefore appears unlikely, because the suborbital depth of like-sized diurnal callitrichid platyrrhines scales in a manner similar to that of other diurnal anthropoids (Fig. 4). Orbital hypertrophy might also account for the fact that there is no evidence for postorbital closure in *B. megalopsis*, because in *Aotus* the jugal and alisphenoid components of the postorbital septum are separated from the maxilla by an enlarged inferior orbital fissure. In the absence of other evidence, we conclude that *B. megalopsis* probably had hypertrophied orbits on a scale equal to or greater than *Aotus* and was, by analogy, presumably nocturnal. Despite *B. megalopsis*'s great antiquity, however, we suspect that identification of this species as a probable nocturnal form is unlikely to be relevant to the origin of anthropoid activity patterns, because the last common ancestor of the clade containing *Bahinia*, parapithecoids, proteopithecids, catarrhines, and platyrrhines would still be reconstructed as having been primitively diurnal (*25*).

The upper molar morphology of >45-million-year-old *Algeripithecus* is remarkably similar to that of *B. fayumensis*, and our phylogenetic analyses consistently nest the former genus deep within the Afro-Arabian anthropoid radiation as either a basal parapithecoid or as a proteopithecid. Either placement would require that a number of key morphological features that parapithecoids and proteopithecids share with platyrrhines and catarrhines [such as full postorbital closure, diurnality, and high-acuity vision (*25*, *26*)] had already appeared by the early Eocene, and probably at small body size (probably 150 to 250 g), because *Algeripithecus* was even smaller than tiny *B. fayumensis*. Although parapithecoids and proteopithecids are generally considered to be stem anthropoids (*27*), our analyses provide no support for that hypothesis (Fig. 3). The lack of phylogenetic resolution among the parapithecoid, proteopithecid, platyrrhine, and catarrhine clades—one of which likely includes >45-million-year-old *Algeripithecus*—leaves open the possibility that crown anthropoid origins may also extend back to the early part of the middle Eocene, as suggested by a recent molecular estimate (*28*).

Finally, our phylogenetic analysis supports the hypothesis that the oldest known crown primate, the African late Paleocene genus *Altiatlasius*, is a primitive stem anthropoid (*27*, *29*). Given the likelihood that crown primates are of Asian (or at least Laurasian) origin (*27*, *29*), *Altiatlasius*'s basal position in anthropoid phylogeny would appear to imply either (i) an immigration into Afro-Arabia independent of the clade that later gave rise to parapithecoids, proteopithecids, platyrrhines, and catarrhines; or (ii) the presence of ancient parallel radiations of anthropoids in Asia and Afro-Arabia (*29*) whose reciprocal monophyly cannot currently be recovered by parsimony analysis because of missing data and rampant morphological convergence. These competing hypotheses appear to us to be equally viable on the basis of available evidence and can be tested with the recovery of additional basal anthropoid taxa from BQ-2 and other, more ancient, horizons in Afro-Arabia.

References and Notes

1. M. Godinot, M. Mahboubi, *Nature* **357**, 324 (1992).
2. M. Godinot, M. Mahboubi, *C. R. Acad. Sci. Paris Ser. II* **319**, 357 (1994).
3. F. Mebrouk, M. Mahboubi, M. Bessedik, M. Feist, *Geobios* **30**, 171 (1997).
4. L. de Bonis, J.-J. Jaeger, B. Coiffait, P.-É. Coiffait, *C. R. Acad. Sci. Paris Ser. II* **306**, 929 (1988).
5. E. L. Simons, D. T. Rasmussen, T. M. Bown, P. Chatrath, in *Anthropoid Origins*, J. G. Fleagle, R. F. Kay, Eds. (Plenum, New York, 1994), pp. 179–202.
6. E. L. Simons, E. R. Seiffert, P. S. Chatrath, Y. Attia, *Folia Primatol. (Basel)* **72**, 316 (2001).
7. E. R. Seiffert, E. L. Simons, Y. Attia, *Nature* **422**, 421 (2003).
8. Systematic paleontology: Primates Linnaeus 1758, Anthropoidea Mivart 1864, Parapithecoidea Schlosser 1911, Genus *Biretia* de Bonis *et al*. 1988 (*4*). *Biretia fayumensis*, new species. **Diagnosis.** Differs from other Paleogene anthropoids in combining the following features: small size (mean estimate of 273 g based on m1 area), bunodont molar morphology, p3 protocristid oriented toward cristid obliqua, small metaconid and absence of paraconid on p4, small paraconid and buccally placed cristid obliqua terminus on m1, distolingual foveae on m1 and m2, centrally placed hypoconulids on m1 through m3, three-rooted P2 with small protocone, hypocones on P3 through M2, small paraconule on M1, small metaconules on M1 and M2, poorly developed postprotocristae on M1 and M2, and pericone on M2. Differs from *B. piveteaui* in its smaller size. **Holotype.** CGM 83658, mandible with m2 and m3. **Etymology.** Named for the Fayum area in which the species is found. **Locality.** BQ-2, Umm Rigl Member of Birket Qarun Formation, Fayum Depression, northern Egypt. **Description.** See supporting online material.
9. Systematic paleontology: Primates Linnaeus 1758, Anthropoidea Mivart 1864, Parapithecoidea Schlosser 1911, Genus *Biretia* de Bonis *et al*. 1988 (*4*). *Biretia megalopsis*, new species. **Diagnosis.** Differs from Paleogene anthropoids other than *B. fayumensis* in the following combination of features: bunodont molar morphology, small metaconid and absence of paraconid on p4, distolingual foveae on m1 and m2, centrally placed hypoconulids on m1 through m3, hypocones on M1 and M2, well-developed paraconule on M1 and metaconules on M1 through M3, and pericone on M2. Differs from *B. fayumensis* in its larger size (mean estimate of 376 g based on m1 area); in having a distolingually oriented p3 protocristid and a more lingually placed cristid obliqua terminus on m1; in lacking both a postprotocristid on p4 and, variably, a premetacristid on m1; in having larger paraconules and metaconules on M1 and M2; and in exhibiting the variable presence of postprotocristae on M1 and M2. **Holotype.** CGM 83661, partial mandible with m2 and m3. **Etymology.** Combination of *megal*-, Greek for large, and *ops*, Greek for eye. **Locality.** BQ-2, Umm Rigl Member of Birket Qarun Formation, Fayum Depression, Egypt. **Description.** See supporting online material.
10. H. J. L. Beadnell, *The Topography and Geology of the Fayum Province of Egypt* (Survey Department of Egypt, Cairo, 1905).
11. P. D. Gingerich, *Univ. Mich. Pap. Paleontol.* **30**, 1 (1992).

12. T. M. Bown, M. J. Kraus, *U.S. Geol. Surv. Prof. Paper* **1452**, 1 (1988).
13. M. Toumarkine, H. P. Luterbacher, in *Plankton Stratigraphy*, H. M. Bolli, J. B. Saunders, K. Perch-Nielsen, Eds. (Cambridge Univ. Press, Cambridge, 1985), pp. 88–153.
14. A. Strougo, M. A. Y. Haggag, *N. Jb. Geol. Paläontol. Monat.* **1**, 46 (1984).
15. M. A. Y. Haggag, *Rev. Esp. Micropaleontol.* **17**, 27 (1985).
16. J. Kappelman, E. L. Simons, C. C. Swisher III, *J. Geol.* **100**, 647 (1992).
17. Typical sediment accumulation rates through the upper part of the section would place the base of Chron C16n.2n near the Temple Member–Dir Abu Lifa Member unconformity, where Chron C16r may have been lost to erosion. The fluvial sediments preserved at BQ-2, which are bounded above and below by nearshore marine beds, can also be explained by the major sea-level lowstand that occurred near the Bartonian-Priabonian boundary.
18. J. G. Ogg, A. G. Smith, in *A Geological Time Scale 2004*, A. G. Smith, Ed. (Cambridge Univ. Press, Cambridge, 2004), pp. 63–86.
19. M. Benammi *et al.*, *J. Geol.* **110**, 748 (2002).
20. G. C. Conroy, *Int. J. Primatol.* **8**, 115 (1987).
21. K. C. Beard, in *The Primate Fossil Record*, W. C. Hartwig, Ed. (Cambridge Univ. Press, Cambridge, 2002), pp. 133–149.
22. M. Takai *et al.*, *J. Hum. Evol.* **40**, 393 (2001).
23. N. Shigehara *et al.*, *J. Hum. Evol.* **43**, 143 (2002).
24. Materials and methods are available as supporting material on *Science* Online.
25. C. P. Heesy, C. F. Ross, in *Anthropoid Origins: New Visions*, R. F. Kay, Ed. (Kluwer/Plenum, New York, 2004), pp. 665–698.
26. E. C. Kirk, R. F. Kay, in *Anthropoid Origins: New Visions*, R. F. Kay, Ed. (Kluwer/Plenum, New York, 2004), pp. 539–602.
27. E. R. Seiffert, E. L. Simons, C. V. M. Simons, in *Anthropoid Origins: New Visions*, C. F. Ross, R. F. Kay, Eds. (Kluwer/Plenum, New York, 2004), pp. 157–181.
28. E. Eizirik, W. J. Murphy, M. S. Springer, S. J. O'Brien, in *Anthropoid Origins: New Visions*, C. F. Ross, R. F. Kay, Eds. (Kluwer/Plenum, New York, 2004), pp. 45–64.
29. K. C. Beard, *The Hunt for the Dawn Monkey: Unearthing the Origins of Monkeys, Apes, and Humans* (Univ. of California Press, Berkeley, 2004).
30. A. Abd el-Raouf, Z. el-Alfy, F. Imbabi, and the staff of the Egyptian Mineral Resources Authority and Egyptian Geological Museum facilitated work in the Fayum area. We thank F. Ankel-Simons, J. Fleagle, B. Hanson, R. Kay, C. Seiffert, and two anonymous reviewers for commenting on or editing the manuscript; T. Ryan and A. Walker for providing the micro-CT scans of the *B. megalopsis* maxilla; C. Heesy, R. Kay, and C. Ross for commenting on that specimen; C. Beard, M. Godinot, and L. Marivaux for access to fossils and casts; L. Gannon for helping to process the paleomagnetic samples; the Fayum field crews of 2001–2003 for their work at BQ-2; and the team of local workers from Kom Aushim led by M. Hassen Taha. This research was supported by NSF grants to E.L.S, E.R.S., and J.B.R., and by Leakey Foundation grants to E.R.S. This is Duke Primate Center publication no. 800.

Supporting Online Material
www.sciencemag.org/cgi/content/full/310/5746/300/DC1
Materials and Methods
SOM Text
Figs. S1 to S8
Tables S1 to S3
References
Movies S1 and S2

24 June 2005; accepted 30 August 2005
10.1126/science.1116569

Selection on Heritable Phenotypic Plasticity in a Wild Bird Population

Daniel H. Nussey,[1,2]* Erik Postma,[1] Phillip Gienapp,[1] Marcel E. Visser[1]

Theoretical and laboratory research suggests that phenotypic plasticity can evolve under selection. However, evidence for its evolutionary potential from the wild is lacking. We present evidence from a Dutch population of great tits (*Parus major*) for variation in individual plasticity in the timing of reproduction, and we show that this variation is heritable. Selection favoring highly plastic individuals has intensified over a 32-year period. This temporal trend is concurrent with climate change causing a mismatch between the breeding times of the birds and their caterpillar prey. Continued selection on plasticity can act to alleviate this mismatch.

Phenotypic plasticity—defined as the ability of a single genotype to alter its phenotype in response to environmental conditions—is an important mechanism by which populations can respond rapidly to changes in ecological conditions (*1*–*3*). Plasticity in life history traits is ubiquitous in animal populations (*1*), with traits often varying within the lifetimes of individuals depending on the conditions they experience (*4*, *5*). It is typically conceptualized and measured using reaction norms: linear functions describing the change in a trait across an environmental gradient (*3*, *6*). Laboratory research has shown that genetic variation for plasticity exists (*7*, *8*) and that heritable plasticity can respond to artificial selection (*2*, *9*).

Given that many species are currently experiencing long-term anthropogenically driven environmental change (*10*, *11*), a better understanding of how natural selection acts on plasticity under altered levels of environmental variation in the wild is imperative. Detailed analyses of within-population variation in life history plasticity are rarely undertaken in naturally occurring populations, because such analyses require data from large numbers of individuals breeding repeatedly across their lifetimes. Recent research using mixed-effects linear models has shown that individuals in two wild vertebrate populations vary in their levels of life history plasticity (*4*, *12*). At present, little is known about the consequences of environmental change for the action of natural selection on plasticity and, ultimately, the ability of populations to continue to respond adaptively to environmental variation. Here we present data from a wild bird population showing temporal trends in natural selection on heritable phenotypic plasticity in the timing of reproduction, which are concurrent with changes in climate and the timing of food availability.

After a warm spring, female passerines often breed earlier than they do after a cold spring (*13*, *14*). This is a result of phenotypic plasticity (*14*, *15*), an individual-level response to temperature. Such a response is considered adaptive because it synchronizes the birds' phenology with the temperature-dependent hatching times and growth rates of the caterpillars they rely on to feed their nestlings (*16*, *17*).

A long-term study of great tits (*Parus major*) in the Hoge Veluwe, one of the Netherlands' largest national parks, has revealed that after recent warming of spring temperatures in

Table 1. Linear mixed-effects model of 2195 laying date observations from 833 female great tits that bred in more than 1 year during the period 1973 to 2004. Estimated covariance (female, female × spring temperature) = 1.16 ± 0.31 (SE).

	Random effects		
Term	Variance	SE	LRT
Year of breeding	9.54	2.55	558.33***
Female	8.05	0.76	226.73***
Female × spring temperature	1.05	0.31	27.07***
Residual	14.97	0.64	
	Fixed effects		
Term	Wald statistic	df	Wald/df
Spring temperature	45.47	1	45.47***
Age	116.91	1	116.91***
Age × spring temperature	7.26	1	7.26**

**P < 0.01. ***P < 0.001.

---

[1] Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 40, 6666 ZG Heteren, Netherlands. [2] Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3JT, UK.

*To whom correspondence should be addressed. E-mail: d.h.nussey@sms.ed.ac.uk