Pliocene primates

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Abstract
The Pliocene fossil record is dominated by Old World monkeys and hominins. Pliocene lemur, loris, tarsier, New World monkey and great ape fossils are non-existent, and very few fossils of galagos and gibbons have been found. All known Pliocene primate fossils can be assigned to modern families; the sivaladapids and pliopithecids, ancient primate groups that survived into the late Miocene, appear to have gone extinct by the beginning of the Pliocene. Given the patchy nature of the Pliocene fossil record, molecular data have been important in revealing the evolutionary history of modern primate radiations, including speciation and dispersal events that occurred during the Pliocene.

Main text
The Pliocene fossil record is dominated by Old World monkeys and hominins. This partially reflects the immense effort that has gone into discovering human origins (and by extension the records of animals, such as Old World monkeys, that lived alongside them), but can also be explained by a number of other geological, taphonomic and ecological factors. The Pliocene is a short epoch, spanning the time between 5.3 and 2.6 Ma. In Madagascar and much of tropical South America, fossiliferous deposits dating to the Pliocene are very rare. This is in contrast to Africa and parts of Eurasia, where Pliocene fossil horizons are well-sampled and have been extensively studied, leading to a good knowledge of the Pliocene hominin and Old World monkey records. These two groups also have multiple taxa that exploit relatively open environments and members with medium to large body masses. These factors predispose to fossilisation, which is usually less likely in smaller animals or those that inhabit tropical forests. The probable rarity in life of some primates may mean that they were statistically less likely to be fossilized compared to more abundant members of their communities, and this could also have contributed to the patterns evident in the Pliocene record.

By the beginning of the Piocene, the sivaladapid adapiforms and the pliopithecids, ancient primate groups that survived into the late Miocene, appear to have gone totally extinct. The Pliocene primate fossils that have been found can all be assigned to modern families, although the record is very patchy. Luckily, we do not have to rely entirely on the fossil record to understand primate evolution: molecular data also help to reveal the evolutionary history of modern primate radiations, including speciation and dispersal events that occurred during the Pliocene.

Lemurs and lorises
Very little is known about Pliocene strepsirhines. There is no Madagascan, and hence lemur, fossil record for much of the past 65 Ma, including the Pliocene (although recent excavation has recovered

some vertebrate and invertebrate material from Eocene and Miocene horizons, so in the future there may be discoveries from other time periods). The only primate fossils known from Madagascar are the 'subfossil' lemurs of the very Late Pleistocene and Holocene. Molecular data suggest that many modern lemur lineages arose in the Miocene, but speciation also occurred in the Pliocene. For example, according to DNA evidence, several *Eulemur* (true lemur) species, widely distributed across Madagascan forests, diversified during the Pliocene (Markolf and Kappeler 2013).

Lorises and pottos (family Lorisidae) are found in the Miocene fossil records of Asia and Africa, but no material has been recovered from Pliocene deposits. Molecular data indicate that some diversification may have occurred within *Nycticebus* (slow lorises) during the Pliocene (Pozzi et al. 2015). Galagos (family Galagidae), however, do have a Pliocene fossil record, and are found at several African sites familiar to students of human evolution, such as Omo (Shungura Formation), Laetoli (Upper Laetolil Beds), and Kanapoi. Material represents two extinct species, *Galago sadimanensis* and *Otolemur howelli*. According to DNA evidence, one extant galago genus, *Sciurocheirus* (squirrel galagos), originated in the Pliocene (the rest emerged in the Late Miocene; Pozzi et al. 2015).

Tarsiers

Although some Miocene tarsier fossils have been found, no fossil tarsiers are known from the Pliocene. Molecular analysis suggests that the main tarsier lineages diversified in the Miocene, but DNA data alongside acoustic evidence have revealed the complexities of their subsequent evolution in the Pliocene. For the Sulawesi clade, this included dispersal across the region, with range expansions and consequent late Pliocene diversification being linked to periodic exposure, due to sea level change, of shelves and land-bridges, as well as lineage divergence promoted by Pliocene tectonic faulting and the associated emergence of lakes (Driller et al. 2015).

New World monkeys

There is a dearth of Pliocene platyrrhine fossils, although the Miocene record is becoming increasingly well-known, and there are a number of Quaternary (Pleistocene and Holocene) specimens from Brazil and the Caribbean. The best known and studied Pliocene fossil sites in South America are found at quite high latitudes, with some also being of fairly high altitude. Such sampling bias undoubtedly influences our knowledge of the Pliocene Neotropical primate fossil record, as monkeys were probably confined to more tropical, lower lying regions. Fossil and molecular evidence indicate that the three major clades of modern platyrrhines were established in the Miocene (Kay 2015), but as in other groups of primates, further divergence subsequently occurred. In titi monkeys, for example, the Pliocene saw the split between the donacophilus and moloch groups (Byrne et al. 2016). The Pliocene also witnessed an important dispersal of monkeys northwards into Central America, made possible by the connection through the Isthmus of Panama between the continents of South and North America around 3.5 Ma (Kay 2015). There are currently no fossil data reflecting this dispersal, inferred from molecular data (Kay 2015), and which is part of a much bigger movement of mammals, the Great American Interchange, that occurred when the continents joined in the Pliocene.

Apes

Little is known from the fossil record about most Pliocene apes, with the obvious exception of hominins, which are represented by around eight species from eastern Africa (*Ardipithecus ramidus*, Middle Awash and Gona, Ethiopia; *Australopithecus anamensis*, Kanapoi and Allia Bay, Kenya; *Australopithecus afarensis*, Laetoli, Tanzania plus Hadar and Woranso-Mille, Ethiopia; *Australopithecus deyiremeda*, Woranso-Mille, Ethiopia; *Kenyanthropus platyops*, Lomekwi, Kenya; *Homo* sp. indet., Ledi-Geraru, Ethiopa), central Africa (*Australopithecus bahrelghazali*, Koro Toro, Chad), and southern Africa (*Australopithecus* sp. indet. 'Little Foot' from Sterkfontein Member 2). A further three species are found very close to the Plio-Pleistocene boundary and may have a short latest Pliocene record (*Australopithecus garhi*, Middle Awash, Ethiopia; *Paranthropus aethiopicus*, Omo, Ethiopia and West Turkana, Kenya, and *Australopithecus africanus* from Makapansgat, South Africa). It is clear that hominins underwent an extensive radiation in the Pliocene, although there is no evidence for them outside Africa at that time. No other Pliocene great ape fossils have been formally described, despite the diversity of apes in the Miocene, and the reasonably good record of *Pongo* in the Pleistocene. Intriguingly, there are reports of a 3 – 4 Ma extinct hominoid specimen from Yangyi in Baoshan Prefecture, China (Harrison et al. 2002). The extant African apes have no fossil records at all, except for three isolated teeth from Pleistocene Kenya. Based on mtDNA sequences, it is possible that the two extant species of *Pongo*, *P. pygmaeus* and *P. abelii,* diverged in the Pliocene (Thinh et al. 2010), although estimates from different studies vary widely. Several small ape species, members of the gibbon genus *Hylobates*, also appear to have diverged during the Pliocene, after the four main modern gibbon and siamang clades split in the Late Miocene (Thinh et al. 2010). The fossil record of modern gibbons, however, is sparse, especially from the latest Miocene or early Pliocene, from which only a tiny number of specimens, from Yunnan Province, China, are known (Jablonski and Chaplin 2009).

Old World monkeys

The Old World monkeys have the richest and most diverse fossil record of all Pliocene primates. Specimens have been found in Africa, Asia and Europe, a greater geographic range than cercopithecids occupy even today. A terrestrially-adept colobine, *Mesopithecus*, appears to have been the first Old World monkey to disperse out of Africa, in the Miocene, and is found in Europe and western Asia until the middle to late Pliocene, when it became extinct. In the Pliocene, it was found widely across Europe, reaching as far as Norfolk in the UK (Delson 1994). During this time, *Macaca* was distributed around the Mediterranean, including southern France and the modern Black Sea region. Two other terrestrial monkey species, the relatively large colobine *Dolichopithecus* and the large cercopithecine *Paradolichopithecus* were distributed across a great deal of Europe in the Pliocene. Like *Mesopithecus*, *Dolichopithecus* went extinct in the Pliocene but *Paradolichopithecus* survived into the early Pleistocene (Delson 1994). Although never abundant in the fossil record, co-occurrence of some monkey species has been recorded at several Pliocene sites in Europe.

The Asian Pliocene fossil record contains a large, macaque-like cercopithecine, *Procynocephalus*, found in northern China, which may be synonymous with *Paradolichopithecus* (Jablonski 2002). It is now also extinct. Pliocene macaque fossils are scarce in Asia, but molecular data indicate that the modern *silenus* group diverged around 4.9 Ma, followed by the *fascicularis* and *sinica* groups around 3.2 Ma (Tosi et al. 2003). Several colobine taxa have been found in the Pliocene fossil record of Asia, including *Semnopithecus* from Late Pliocene Burma/Myanmar (Takai et al. 2016), *Trachypithecus* from Java, and, outside the modern primate range, *Parapresbytis* from Mongolia (Jablonski 2002).

DNA evidence suggests that although most major Asian colobine clades diverged in the Miocene, *Trachypithecus – Semnopithecus* may have split in the Pliocene, then hybridised later (Roos et al. 2011); future fossil discoveries will help to untangle the complexities of Asian colobine evolutionary history (Takai et al. 2016).

The Old World monkey record of the African Pliocene is exceptionally well-known and studied. At Hadar alone, four Pliocene species are recognised: the cercopithecines *Parapapio* cf. *jonesi* and *Theropithecus oswaldi darti*, and the colobines cf. *Rhinocolobus turkanaensis* and *Cercopithecoides meaveae*. *Parapapio* is a speciose extinct lineage, comprising several Pliocene taxa from both eastern and southern Africa. Pliocene *Theropithecus* specimens are highly abundant, and at one site, Woranso-Mille, they comprise over 90% of the monkey fossils recovered, in an assemblage that includes four other monkey species (Frost et al. 2014). *Theropithecus* was also palaeobiologically diverse in the Pliocene, with one species, *T. brumpti* (best known from West Turkana and the Omo Shungura Formation) being a large-bodied manual forager exploiting riverine forests, in contrast to the more open-habitat adapted, smaller-bodied and geographically-dispersed *T. o. darti*, which has been found in the Plio-Pleistocene of southern Africa as well as in eastern Africa. The mainly eastern African radiation of large extinct colobines, including *Rhinocolobus*, *Cercopithecoides* and *Paracolobus*, that survived and prospered into the Pleistocene (with exceptional diversity at Koobi Fora, Kenya), became established in the Pliocene. Like *Theropithecus*, *Cercopithecoides* (with hand bones documenting a reduced thumb and thus membership in the clade that includes modern African colobines [Frost et al. 2015]), had a Plio-Pleistocene presence in the southern African record. Two genera forming part of the *Cercocebus* / *Mandrillus* clade, *Procercocebus* and *Soromandrillus*, have been identified from the late Pliocene of Africa, shedding considerable light on the evolutionary history of this previously poorly-understood lineage (Gilbert 2013).

There are some notable but not unexpected gaps in the African Pliocene cercopithecid fossil record. Guenons, with their smaller body masses and mainly forest habitats, are largely unknown from fossils. The same is true for the modern African colobines, also small and forest-living. Molecular analyses have revealed much about their evolutionary history. Arboreal and terrestrial guenon clades split in the Pliocene, followed a little later by further differentiation of some major arboreal lineages (Tosi et al. 2005). After deep colobine splits in the late Miocene, there was extensive speciation in the black and white colobus lineage in the Pliocene, and the three main mitochondrial groups of the highly complex red colobus clade diverged around 3 Ma (Ting 2008). All told, however, and in contrast to the scarce fossil records of many other primate groups at this time, a great deal is known about the spectacular radiation of Old World monkeys that gathered speed in the Pliocene.

See also: Adapid, Divergence dates, Evolution of the Cercopithecidae, Evolution of the Hominoidea, Evolution of the Pliopithecoidea, Evolution of the Modern Strepsirhines, Guenons: arboreal, Guenons: semi-terrestrial, Hominins, Koobi Fora, Madagascar, Miocene primates, Palaeoenvironmental and sea-level change, Plate tectonics and continental drift, Pleistocene primates, Subfossil lemurs.

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