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THE FOSSIL RECORD OF PRIMATE INTELLIGENCE

From the earliest primates to human origins

David R. Begun

Animals collect and process the information they need to survive and reproduce. The means by which they process information is through the capacity of intelligence, which is in turn a function of the brain, its morphology, size, organization, and cytoarchitecture. While the internal organization and cellular interconnectivity of the brains of fossilized animals are invisible to paleontologists, the size and surface morphology of the brain are sometimes preserved, usually only in part, in the form of endocasts (casts, either natural or artificial, of the inside of the brain case). This broad survey of the evolution of intelligence in primates as interpreted from the fossil record of endocasts is primarily focused on the lineages that inform us more directly about the evolutionary events leading to the origin of human intelligence.

Keywords: **primate evolution**, **paleoneurology**, **paleoanthropology**, **hominoids**, **cognition**.

Since it was recognized, the order Primates has been considered especially intelligent in comparison with other animals. Today we recognize in other animals primate-like cognitive capacities, but it is undeniable that primates prioritize cognition and behavioral flexibility over genetically determined behavior.

«It is undeniable that primates prioritize cognition and behavioral flexibility over genetically determined behavior»

EUPRIMATE ORIGINS

The Plesiadapiformes (65 to 37 Ma) is the oldest fossil taxon attributed to the order Primates, but its members lack most of the attributes that define the Euprimates, primates of modern aspect (Bloch et al., 2007). Some have suggested that Plesiadapiformes are more closely related to the Dermoptera (colugos or flying lemurs) (Beard, 1990; Kay et al., 1990) but the current consensus is that they are primitive primates. This incredibly diverse group persisted for more than 25 Ma and ranged from North America to Asia and Europe. Plesiadapiformes evolved from arboreal mammals and have primate-like grasping feet but teeth that resemble those of the earliest mammals and living insectivores, with pointy cusps and sharp crests to pierce and slice the exoskeletons of the insects they eat (Silcox et al., 2015); their teeth are similar, but slightly broader, with more rounded cusps, which may signal a more diverse diet that included fruit and other plant products (sap, for example) as well as insects. It is a subtle difference, but one that may have put primates on the path toward a more diverse and adaptable diet and lifestyle.

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Primates		
Plesiadapiformes		
Euprimates	Strepsirrhini (lemurs, lorises, galagos)	
	Haplorrhini (anthropoids and tarsiers)	Catarrhini (Old World monkeys, apes and humans)
		Platyrrhini (New World monkeys)

Primate taxonomy. A simplified summary of primate systematics.

SOURCE: Created by the author.

The first described fossil Euprimate (from here on referred to as primates), *Adapis parisiensis*, was not at first recognized as a primate but as an artiodactyl (even-toed hooved animals like cattle, sheep, and antelopes). Adapids, the family to which *Adapis* belongs, have slender, flexible limbs and dexterous, gripping hands and feet with nails supporting expanded digital pads, rather than claws. These modern-looking primates appear in the Eocene (56–33.9 Ma) (Godinot, 2015). Early on, once primate fossils were recognized as such, it was noted that, like modern primates, they tend to have relatively large brains, small snouts, and large, convergent eyes. These traits are suggestive of a lower reliance on smell and a higher reliance on vision, compared with other mammals, as well as of enhanced cognitive capacity.

«Brain size begins to increase more dramatically with the evolution of anthropoid primates (monkeys, apes, and humans)»

In seeking to explain the tactile and visual emphasis of the sensory systems in primates, theories have focused on diet and ecology (Cartmill, 1992; Sussman, 1991). Like modern primates, early primates were arboreal, spending most of their time in the trees. There are many challenges in an arboreal habitat. Its 3-dimensionality, the importance of not falling while leaping and moving rapidly among the branches, and the ability to hunt or collect food in the most terminal branches. Hunting, in particular the ability to grab insects using the enhanced 3-D vision, is made possible by overlapping visual fields. The earliest primates evolved in the context of the emergence in abundance of angiosperm vegetation (flowering plants), which not only produce fruit in the terminal branches but also attract insects. The earliest primates were nocturnal (deduced from the large size of the orbits or eye sockets), which imposes special challenges for hunting and negotiating an arboreal milieu (Wu et al., 2022).

These primates already show potential signs of enhanced intelligence in the size and morphology of the brain. Compared with contemporary mammals, the brains of the first primates are absolutely larger with reduced olfactory lobes in relation to overall brain size (Radinsky, 1979). Brain size is generally considered to be a proxy, albeit imperfect, for intelligence (Gibson et al., 2001; Street et al., 2017). Reorganization of cerebral regions often accompanies the attainment of more modern primate grades (strepsirrhine to haplorrhine, basal anthropoid to hominoid, basal hominoid to modern apes, apes to humans), and has also been implicated in the development of enhanced levels of intelligence (Gibson et al., 2001; Radinsky, 1979; Street et al., 2017).

Early primates with well-preserved brain cases include adapids and omomyids, which resemble modern lemurs and lorises, and early tarsiiforms, the ancestors of living tarsiers. The oldest of these skulls have brains that are smaller relative to overall body size than in living prosimians, but toward the end of their geological range early primates had reached the lower ranges of living prosimian relative brain sizes (Godinot, 2015). Increase in brain size over time is common in mammalian lineages and can be explained by what has been called an *arms race*, in which there is selection for increases in intelligence in predators to outwit their prey and selection in prey species to better detect the presence of predators (Ward et al., 2004). Brain size begins to increase more dramatically with the evolution of anthropoid primates (monkeys, apes, and humans). This is accompanied by a shift to diurnal (daytime) activity and the emergence of social groups (Godinot, 2015). Daytime activity is inferred from the size of the orbits, which are smaller than in nocturnal species, while sociality is inferred from dimorphism in body and canine size. However, as important as social intelligence is in living anthropoids, especially catarrhines (Old world monkeys, apes, and humans), social complexity does not seem to predict brain size so well as diet and socioecology (López-Aguirre et al., 2022).


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Epoch	Ma	Taxa originating
Paleocene	65–56	Plesiadapiformes
Eocene	56–34	Strepsirrhini, Adapidae, Omomyidae, Tarsiidae, Anthropoidea
Oligocene	34–23	Parapithecidae, Propliopithecidae (*Aegyptopithecus*), stem hominoids (*Afropithecus*, *Ekembo*), Cercopithecoidea
Miocene	23–5.5	Hominidae, Homininae, Hominini, Ponginae, *Cercopithecinae*, Colobinae
Pliocene	5.5–2.5	*Ardipithecus*, *Australopithecus*
Pleistocene	2.5–0.01	*Homo*, *Paranthropus*

Chronology of primate evolution. Epochs of the Cenozoic period with their ages and the primate taxa that originate in each. Ma refers to *mega-annum*, or millions of years.

SOURCE: Created by the author.

Ekembo's skull (in the picture) has an average brain size within the range of present-day monkeys and gibbons. *Ekembo* is monkey-like in overall adaptation, with subtle but definitive ape attributes. It was likely at least as intelligent as living Old World monkeys, and probably had a similar flexibility of foraging, ranging, and social behaviors.

«Our knowledge of ape evolution really begins with *Ekembo,* a primitive hominoid known from localities in Kenya»

ANTHROPOIDS

Anthropoids, a primate suborder, include Old and New World monkeys, apes, humans, and their fossil relatives. Most fossil strepsirrhines are extinct by the time anthropoids become common in the fossil record (the earliest anthropoids are very rare before about 40 Ma). The best samples of early anthropoids come from the Fayum deposits in Egypt. Several early anthropoid genera are known with relatively well-preserved crania (Godinot, 2015).

The Fayum anthropoids include a diversity of primitive haplorrhines and catarrhines (Godinot, 2015). They were arboreal, some being primarily frugivorous and others more insectivorous. Most appear to have been diurnal and sexually dimorphic in body and canine size, suggestive of extant anthropoid-like social complexity. They are generally larger than most Eocene prosimians. We have endocasts of the primitive anthropoids *Proteopithecus* and *Parapithecus* and the primitive catarrhines *Catopithecus* and *Aegyptopithecus* (Godinot, 2015). The more primitive taxa have small brains and large olfactory lobes, while *Aegyptopithecus*, which is younger and more modern-looking in cranial morphology, has reduced olfactory lobes but brains at the low end of the modern prosimian range. In sum, the earliest anthropoids retain the ancient and current primate pattern of arboreality and frugivory and signal a change toward diurnal and social behavior with subtle changes in brain size and morphology that may be suggestive of some enhancements in intelligence.

HOMINOIDS

The Hominoidea, a superfamily of the Anthropoidea, includes apes, humans and their fossil relatives. While not the oldest hominoid, our knowledge of ape evolution really begins with *Ekembo*, a primitive hominoid known from localities in Kenya ranging in

Sub-epochs	Taxa	Distribution	Attributes
Early Miocene (23–16 Ma)	*Ekembo* *Afropithecus* *Proconsul*	Kenya Kenya Kenya, Uganda	Monkey-like skeleton (limbs of equal length, horizontal spine, long lower back, narrow thorax), coccyx (no external tail), generalized frugivore dentition, baboon-sized brains.
Middle Miocene (16–11.6 Ma)	*Griphopithecus*, *Nacholapithecus*, *Kenyapithecus* *Equatorius* *Pierolapithecus* *Dryopithecus*	Central Europe/Turkey Kenya Kenya, Turkey Kenya Spain Spain, France, Austria	Evolves from more *Ekembo*-like to early phases of orthogrady/suspension; thick enamel & robust jaws (hard object feeding) in older taxa, thin enamel, more gracile jaws (soft fruit frugivory) in the last two; no direct evidence of brain size, but evidence of extended life history.
European late Miocene (11.6–5.3 Ma)	*Danuvius* *Hispanopithecus* *Rudapithecus* *Ouranopithecus* *Graecopithecus*	Germany Spain Hungary Greece Greece, Bulgaria	Suspensory, orthograde apes with modern ape body plan, terrestriality in Balkan taxa, more gracile jaws/teeth (soft frugivory) in Europe, robust jaws/teeth (hard objects), canine reduction in Balkan taxa; extended life history and *Pan*-sized brains (*Rudapithecus*).
African late Miocene (11.6-5.3 Ma)	*Sahelanthropus* *Orrorin* *Ardipithecus*	Tchad Kenya Ethiopia	Bipedalism, terrestriality, canine reduction, variable gnathic robusticity, *Pan*-sized brains.

Chronology of the Miocene radiation of apes and the attributes associated with their diversity and evolution. Taxa are listed in chronological order within each sub-epoch. The table does not include many taxa not discussed in the text, particularly Asian great apes, which are not well known from their crania. Attributes unique to great apes and humans, including locomotor and brain characters, evolve in the Miocene.

SOURCE: Created by the author.

age from about 19 to 17 Ma (McNulty et al., 2015). *Ekembo* is the first fully modern catarrhine. Most of the bones of its skeleton are known, revealing a body-plan much like that of living monkeys with one major exception, a coccyx in the place of a tail. Tailessness is a derived character that is considered a hallmark of the Hominoidea, possibly forcing hominoids into greater degrees of manual dexterity to compensate for the absence of the tail as a balancing mechanism in the trees. The skull of *Ekembo* has a relative brain size within the range of living monkeys and gibbons (Begun & Kordos, 2004). Overall, *Ekembo* is monkey-like in overall adaptation, with subtle but definitive ape attributes. It was likely at least as intelligent as living Old World monkeys, and probably had a similar flexibility of foraging, ranging, and social behaviors.

Afropithecus overlaps with the latter part of the temporal range of *Ekembo* (Leakey & Walker, 1997). Postcranially *Afropithecus* is indistinguishable from *Ekembo*. Craniodentally *Afropithecus* is distinct in

«Dietary breadth was probably the key to the success of the hominids that first dispersed into Eurasia»

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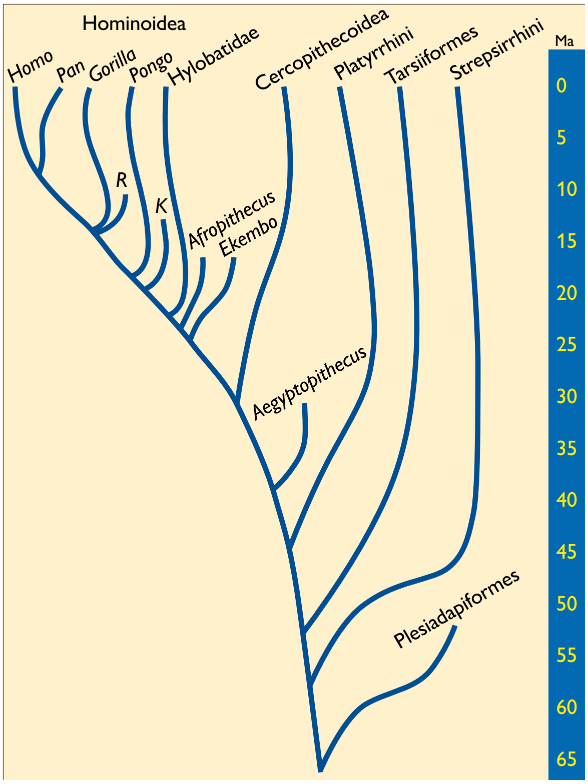
Craniodentally, *Afropithecus* (in the picture) is distinct in having a massive face associated with large chewing muscles indicating a powerfully developed set of jaws and teeth for crushing and grinding.



A simplified phylogeny of the Primates with a focus on the Hominoidea.
R=Rudapithecus, K= Kenyapithecus

SOURCE: Created by the author.

having a massive face associated with large chewing muscles indicating a powerfully developed set of jaws and teeth for crushing and grinding. *Afropithecus* also has specializations of its front teeth that probably allowed it to tear through any protective covering. *Afropithecus* was likely capable of exploiting a wider variety of resources than *Ekembo*, which may have allowed its descendants to disperse north into Saudi Arabia and then Europe (Begun, 2014a, 2015b). It is in Eurasia that modern hominids (great apes and humans) evolve.

The oldest hominoids from Europe are hominids (orangutans, chimpanzees, bonobos, gorillas, humans, and their fossil relatives), with modern-looking thickly enameled teeth with broad flat cusps. Like *Afropithecus,* European apes such as *Griphopithecus* had broad diets and were able to exploit resources ranging from soft fruits to more embedded foods with outer coverings such as shells or tough peels, as well as buried foods such as roots. Dietary breadth was probably the key to the success of the hominids that first dispersed into Eurasia. Dietary breadth, enabled by masticatory adaptations, may have been accompanied by changes in cognition related to ecological and dietary flexibility. Once in Eurasia, middle Miocene hominids disperse widely, occupying the region between Central Europe and the equator. Multiple taxa arise with various adaptations, but they are all united by enhanced attributes for food processing. Where known, middle Miocene apes show adaptations toward a shift to more forelimb dominated positional behavior, but they were not yet suspensory or orthograde (see below) (Nakatsukasa & Kunimatsu, 2009). They may have been engaged in more vertical climbing and hoisting activities but not suspension below branches, as in extant non-human hominoids. There are no crania known for middle Miocene apes, but by the late Miocene there is evidence of modern great ape brain sizes and developmental biology.

At about 12.5 Ma, more modern apes appear in Europe. The best known is *Pierolapithecus*, from an 11.9 Ma site near Barcelona (Alba, 2012). *Pierolapithecus* was orthograde (having a more vertically oriented backbone, as in living apes, as opposed to the more horizontally oriented backbones of monkeys and most early and middle Miocene apes (Moyà-Solà et al., 2004). Its hands are large, with long, curved fingers, suggestive of some degree of suspension. *Pierolapithecus* and other late middle Miocene apes from Europe have teeth closely resembling those of living chimpanzees and probably had a similar diet, heavy in soft fruits but with sufficient breadth to weather lean periods by exploiting other resources. In the late Miocene, more modern-looking apes appear, the best known of which is *Danuvius*, from the earliest late Miocene (Böhme et al., 2019). *Danuvius* differs from *Pierolapithecus* in having thick enamel, but like *Pierolapithecus*, it was orthograde, with evidence of powerfully grasping hands. The hindlimbs of *Danuvius* indicate that it was bipedal in the trees, with powerfully grasping feet. Bipedalism in *Danuvius* may be a precursor to human bipedalism (Böhme et al., 2019).

«The fossil record of attributes related to intelligence reaches its pinnacle in late Miocene apes»

We know little about the brains of middle Miocene apes. Late Miocene apes from Europe such as *Rudapithecus* in Hungary and *Hispanopithecus* in Spain are known from partial skeletons that reveal a modern, orthograde and fully suspensory body plan. *Rudapithecus* is also known from three partial crania including two with braincases. From these we know that *Rudapithecus* had a brain within the range of living chimpanzees after accounting for the differences in body size between the two (Begun & Kordos, 2004; Gunz et al., 2020). Since brain tissue is among the most metabolically expensive, expanded brain size is very likely to be associated with selection for multiple behaviors and abilities that enhance survival and reproductive success. That *Rudapithecus* had achieved this level of encephalization, which is difficult to explain in the absence of a survival and reproductive benefit, suggests a pattern of behavior approaching the level of complexity of modern great apes. Indirect evidence of the evolution of enhanced cognitive capacity in apes comes from body size and especially dental development (Kelley, 2004; Ward et al., 2004). In *Sivapithecus* (a South Asian great ape related to orangutans) and *Rudapithecus*, dental evidence indicates that both taxa developed at rates comparable with living great apes, which take longer to reach maturity than do living Old World monkeys (Kelley, 2004; Smith et al., 2019). The fossil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ape *Afropithecus* also appears to be characterized by slower growth, though not to the degree seen in the late Miocene taxa (Smith et al., 2003).

CONCLUSIONS

The evolutionary history of the primates is characterized by a diversity of adaptations to an arboreal lifestyle, increasing reliance on visual cues over olfaction and an ever greater dependance on enhanced cognitive capabilities related to resource acquisition and processing, social interactions, and ecological diversity. All extant primates, but especially anthropoids, are exceptional in their levels of intelligence in comparison with most mammals. Impressive cognitive achievements characterize various branches of all anthropoids, including tool use in *Cebus* monkeys and the extraordinary exploits of many Old World monkeys (food washing, stream-baths, incredible behavior flexibility, and their ability to adapt to the presence of humans). Different primates have evolved their own versions of cognitive exceptionalism. But the fossil record of attributes related to intelligence reaches its pinnacle in late Miocene apes, which had achieved modern great ape body plan, reproductive biology, and probably cognition. These apes, broadly ancestral to hominins, set the stage for cognitive evolution in humans. The hominin fossil record shows consistent increases in brain size over time, correlated with the development of progressively more complex and elaborate extra-somatic survival strategies, human culture.

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