ANTHROPOLOGY

Apes Among the Tangled Branches of Human Origins

The evolution of apes between 23 and 5 million years ago set the scene for the emergence of the first hominins in Africa.

Terry Harrison

The detailed description of *Ardipithecus ramidus* (*1*) more than lived up to the buzz of anticipation that preceded it in the paleoanthropological community. *A. ramidus* is a purported hominin (the group comprising humans and their extinct relatives after they diverged from our closest living relatives, the chimpanzees) from the Middle Awash region of Ethiopia. The focus of attention has been on how *A. ramidus* may relate to later fossil hominins and to living apes and humans (see the first figure), but to appreciate the place of *A. ramidus* in human origins, we must also view it from the perspective of the hominoids (apes) that lived in the Miocene, 23 to 5 million years ago (see the second figure).

A. ramidus is known from more than 100 specimens, including a remarkably preserved partial skeleton, that date back to 4.4 million years ago (*2*). Several other hominin contenders are known from the late Miocene (7 to 5 million years ago), including *Ardipithecus kadabba*, *Orrorin tugenensis*, and *Sahelanthropus tchadensis*, but our knowledge of

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their anatomy is much less complete. Not all paleoanthropologists (including this author) accept that *A. ramidus* is a hominin or agree with the evolutionary and paleobiological interpretations that have been proposed (*2*), but there is no doubt about its critical importance for understanding human origins (*3*, *4*). The unveiling of *A. ramidus* has required a major rethinking of what the last common ancestor of humans and chimpanzees looked like and which initial evolutionary steps may have characterized the earliest hominins. *A. ramidus* also helps to close the gap between the last common ancestor of humans and chimpanzees (estimated at 7 to 5 million years ago) and the earliest undoubted hominin, *Australopithecus anamensis* (4.2 million years ago) (*5*).

During the early Miocene (23 to 16 million years ago), the precursors of hominoids—the proconsuloids—were a remarkably diverse group of catarrhine primates (the group comprising Old World monkeys and apes, see the first figure) restricted to the tropical forests and woodlands of Africa and the Arabian Peninsula (*6*). Between 17 and 14 million years ago, environments in Africa became drier and increasingly more seasonal. Proconsuloid diversity declined, and cercopith-
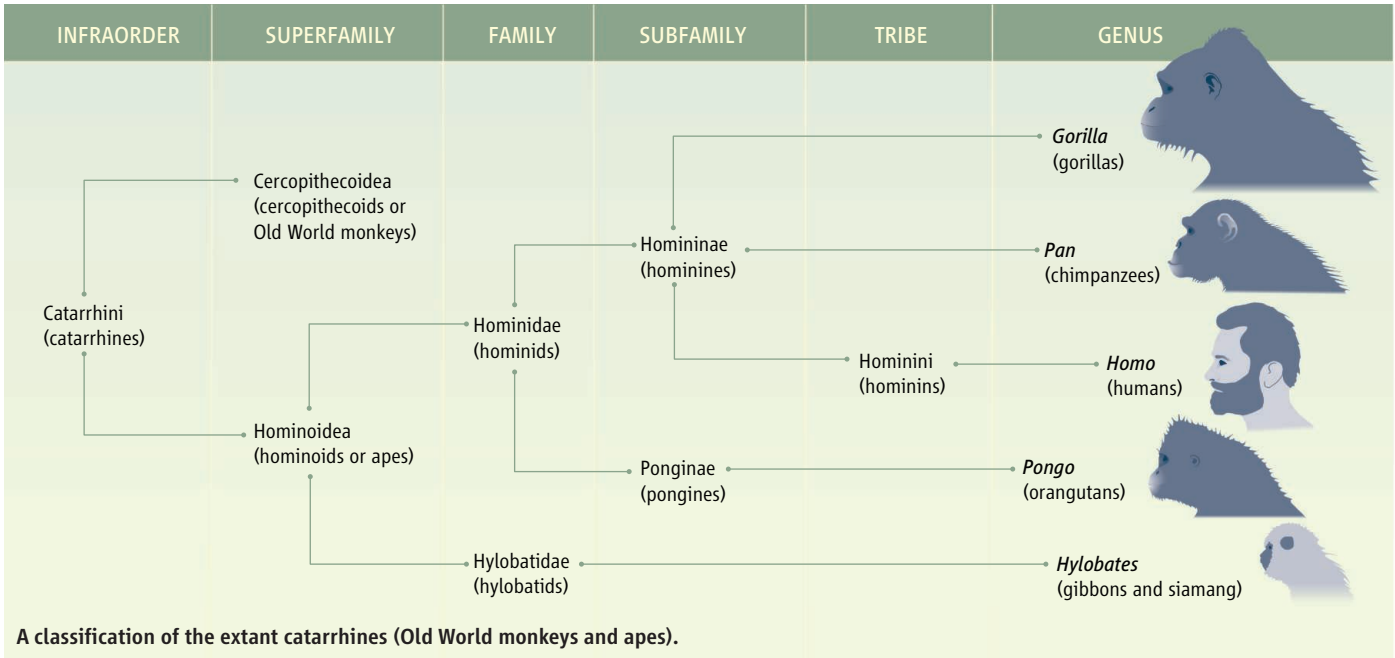
ecoids (Old World monkeys) and early hominoids, such as *Kenyapithecus, Equatorius*, and *Nacholapithecus*, became the dominant taxa (see the second figure). These hominoids and other catarrhines responded to increased seasonality by developing dietary adaptations for eating leaves or for processing hard food items, and by developing a range of specialized locomotor behaviors (*6–8*).

About 16 to 15 million years ago, apes expanded their geographic range out of Africa to colonize much of Eurasia. This influx of hominoids into Eurasia coincided with the middle Miocene climatic optimum, a phase of global warming that allowed tropical and subtropical mammals to extend their ranges northward. The earliest Eurasian apes, *Griphopithecus* and *Kenyapithecus*, are known from sites in Turkey and central Europe. Like their African contemporaries, they had thick-enameled molars and robust jaws, adaptations for exploiting a broad spectrum of seasonally available foods.

Between 13 and 9 million years ago, hominoid diversity in western and central Europe increased to include *Pierolapithecus*, *Anoiapithecus*, and at least four species of *Dryopithecus* (*9*, *10*). *Pierolapithecus* and *Anoiapithecus* from Spain are probably stem hominids

INFRAORDER	SUPERFAMILY	FAMILY	SUBFAMILY	TRIBE	GENUS

A classification of the extant catarrhines (Old World monkeys and apes).

(great apes and humans, see the first figure). *Dryopithecus* has been inferred to be a stem hominid, an early member of the orangutan lineage, or a stem hominine (African great apes and humans, see the first figure), but the first of these options is the most plausible.

A diversity of hominoids also occurred in Asia during the middle and late Miocene, extending from Indo-Pakistan to Thailand. Of these, *Ankarapithecus*, *Sivapithecus*, *Lufeng-pithecus*, *Khoratpithecus*, and *Gigantopithecus* are all likely to be closely related to the extant orangutan (*11*).

Gradual cooling during the middle Miocene led to greater seasonality in western and central Europe and a shift from subtropical evergreen forests to predominantly deciduous broadleaved woodlands. This shift was accompanied by a dramatic turnover of the mammalian fauna at 9.6 million years ago, termed the Mid-Vallesian Crisis, when most hominoids became extinct (*12*). The highly specialized stem hominid *Oreopithecus* survived on European island refugia until 6 to 7 million years ago. In southeast Europe and southwest Asia, hominoids specialized for dry open woodlands, including *Ouranopithecus* and *Udabnopithecus*, survived well into the late Miocene (10 to 7 million years ago). *Ouranopithecus* probably offers the best evidence of an early hominine in Eurasia, which implies that African great apes extended their range from Africa into southeast Europe and southwest Asia about 10 million years ago.

About 7 to 8 million years ago, uplift of the Tibetan Plateau and increased intensity of the Asian monsoon, together with the global expansion of C_4 grasses, led to a further decline in the diversity of Eurasian hominoids. By 5 million years ago, hominoids had become extinct throughout Eurasia, except for those surviving in the present-day range of Asian hominoids (orangutans and hylobatids, see the first figure), extending from southern China to Southeast Asia.

In Africa, the fossil record for hominoids between 13 and 7 million years ago is relatively sparse. This has led some authors to postulate that the hominines initially diverged in Eurasia before migrating back into Africa (*13*, *14*). However, recent discoveries and a growing appreciation of later Miocene hominoid diversity in Africa make this an untenable scenario. The recently described 10-million-year-old *Nakalipithecus* from Kenya is closely related to *Ouranopithecus* but is older and has more primitive teeth, implying that these taxa shared a last common ancestor in Africa (*15*). It has been suggested that *Samburupithecus* (9.5 million years old) from Kenya and *Chororapithecus* (10 to 10.5 million years old)
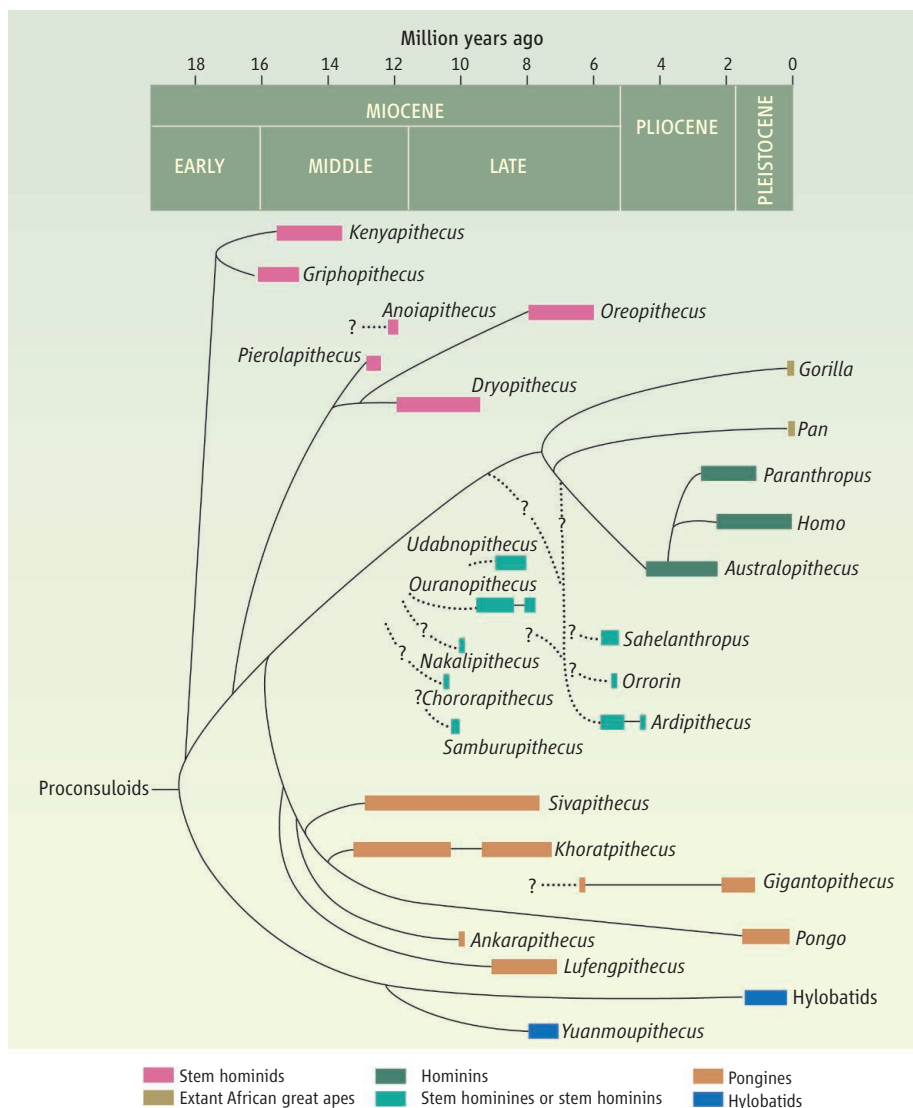
Hominoid relationships. Schematic representation of the inferred evolutionary relationships between Miocene apes, early hominins, and extant hominoids. Solid gray bars represent the known time range of each genus, thin dark lines are inferred relationships between the genera, and thin dashed lines with "?" denote uncertain relationships.

from Ethiopia are related to gorillas, but the evidence is slim, and they are probably stem hominines (*16*). Further recent fossil finds confirm that in the middle and late Miocene, Africa was populated by a multitude of hominoids, but the current material is too scanty to designate additional species (*15*, *17*, *18*).

As paleontological exploration intensifies across Africa, our knowledge of hominoids in this critical time period will steadily grow. Rather than just a few relictual evolutionary strands surviving to the end of the Miocene and giving rise to modern hominine lineages, as was previously thought, ape diversity in Africa during the late Miocene looks very bushlike. The relationships between *Ardipithecus* and earlier hominids will remain enigmatic until the quality of the fossil evidence

from the late Miocene of Africa improves, but this will eventually prove critical in resolving its affinities to later hominins. The important questions then become: Where did *Ardipithecus* and the other early hominin contenders come from? Are they truly members of the hominin lineage, or simply apes among the tangled branches that constitute the basal hominine bush?

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ECONOMICS

Measuring Subjective Well-Being

Richard Layard

How should human happiness and life-satisfaction be assessed?

What is progress, and how should we measure the well-being of a population? The Organization for Economic Cooperation and Development has held two major conferences on the subject, and last year, President Sarkozy of France established a distinguished commission to report on the same questions (*1*). This major debate reflects the fact that higher national income has not brought the better quality of life that many expected, and surveys in the United States show no increase in happiness over the past 60 years. These surveys rely on questions about subjective well-being, and it is reasonable to ask how reliable survey answers are as measures of the quality of life as people experience it. On page 576 of this issue (*2*), Oswald and Wu carry out an interesting test of this. First they measure subjective well-being in each U.S. state, and then compare it with the average objectively measured wage in the same U.S. state (both variables being controlled for personal factors). The negative correlation of the two variables is remarkably high—as it should be if higher wages are compensating for a lower experienced quality of life (and vice versa). The study will likely stimulate some lively debate across many disciplines, including scientists, economists, sociologists, psychologists, and policy-makers.

But should we really adopt subjective well-being as our measure of the quality of life? Philosophically, many would say "yes," as they have ever since the 18th-century Enlightenment. But, practically, can subjective well-being really be measured well enough to be used in policy analysis? Is what

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people say about their subjective state well enough correlated with the inner reality?

The science is, of course, very young, but it is well enough developed for us to say "yes." In the typical question, an individual is asked, "Taking all things together, how happy are you?" The possible answers range from 0 (extremely unhappy) to 10 (extremely happy). To evaluate the information con-

tent in the answers to such questions, we can examine whether these answers are well enough correlated with other relevant factors. They are in fact well-correlated with at least five relevant sets of variables: the reports of friends; the plausible causes of well-being; some plausible effects of well-being; physical functioning, such as levels of cortisol; and measures of brain activity.

When a subject's friends are asked about the subject's happiness, the answers correlate well with the subject's own report. (Were it not so, human society would find it hard to function.)

Moreover, questions on happiness and life satisfaction have now been asked in hundreds of routine population surveys, and in multiple regressions within countries, the following causal factors are always important: physical health, family status, employment, income, and age. This is true both in cross-section studies and in panel studies that include an individual fixed effect. Moreover, the sizes of the effects are remarkably similar in widely different studies done within different countries (*3*).

Similarly, responses on life satisfaction can be used to explain behavior such as quitting one's job and exiting from marriage. They can also, as Oswald and Wu show, be used to measure quality-of-life differences across the United States in a way that is consistent with the pattern of wage differences.

Answers about happiness are also well correlated with measurements of bodily function, such as amounts of salivary cortisol, fibrinogen stress responses, blood pressure, heart rate, and (in some cases) immune system responses to a flu vaccination. These correlations hold across individuals, as in the famous cross-sectional study of British Whitehall civil servants (*4*), and also in some cases within the same individual over time.

Finally, there are reported correlations with brain activity across individuals, and within individuals over time. The best known of these is the correlation of positive affect with activity in the left dorsolateral prefrontal cortex (PFC) and negative affect with activity in the right dorsolateral PFC (*5*). This area of work is in its infancy but, if successful, it will reinforce the view that subjective experience is an objective reality. Because this is so often questioned, it is worth repeating the findings of Coghill (*6*), who applied the same very hot pad to