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Dryopithecinae

Subfamily of Hominidae including species close to the common ancestors of the modern great apes and humans. The subfamily Dryopithecinae was originally named by W.K. Gregory and M. Hellman in 1939 to accommodate the then known Miocene apes. In a major revision in 1965, E.L. Simons and D.R. Pilbeam again used it as a catchall taxon to include the three main groups of Miocene ape that were recognized as subgenera of the single genus *Dryopithecus*: *D. (Proconsul)*, *D. (Sivapithecus)*, and *D. (Dryopithecus)*. At that time, the genus *Ramapithecus* was identified as a hominid and separated from *Sivapithecus*. *Ramapithecus* and *Sivapithecus* have since been synonymized and placed in the orangutan clade, Ponginae, while *Proconsul* and *Dryopithecus* have been placed in different families, Proconsulidae and Hominidae, respectively. In the early 1990s, Dryopithecinae was used yet again as a "dustbin" category to include three tribes: Afropithecini, Kenyapithecini, and Dryopithecini. The first two are very similar to each other, and they may form a monophyletic group, but it seems most likely that what was termed Dryopithecini is distinct and more closely related to the living great apes and humans than are the first two tribes. Therefore, it is here returned to subfamily rank, while the two other tribes are included in the more conservative Kenyapithecinae.

In this concept, the genus *Dryopithecus* remains central to the subfamily Dryopithecinae. Several species of this genus are now accepted in the Middle to Late Miocene (ca. 13–8? Ma) of Europe, from Spain through France, Germany, Austria, Hungary, and into Georgia. These forms share thin molar enamel and a rather conservative subnasal region (almost as in gibbons, Old World monkeys, and *Proconsul*, but with a slight angulation and narrowing of the incisive canal), combined with robust limb bones somewhat more derived in the direction of modern apes than those of kenyapithecines or earlier catarrhines. The browridge is not very well developed, although D. Begun has suggested that it is

stronger in some specimens, which may indicate moderate klinorhynchity (downward flexion of the face or the cranial base), foreshadowing the Homininae.

Some Asian fossils have been included in *Dryopithecus*, mainly on the basis of apparently thin molar enamel. It is not clear whether *D. wuduensis* from Gansu Province in China (ca. 9–6 Ma) or *D. simonsi* from the Pakistan Siwaliks (ca. 10–8 Ma) belong to this genus or to another, as no facial or postcranial remains are known. The name *Hylopithecus hysudricus* was given in 1927 to some dental fragments from the Siwaliks that may conceivably belong to a similar form, and this genus might be used for the Asian "*Dryopithecus*" if a new name should prove necessary.

Three other fairly well-known genera may also be included in the Dryopithecinae, depending upon interpretations of their phyletic position. *Graecopithecus freybergi* is a European form known from only four Greek Late Miocene localities, apparently dating between 10 and 8 Ma. It is represented by numerous jaws and parts of two male faces. These are robust, with strong browridges, prominent glabella, and squarish muzzles, in some ways reminiscent of gorillas. The subnasal region is also gorillalike, which may be ancestral for Homininae and perhaps Ponginae as well. The teeth have extremely thick molar enamel, and the male canines appear to be reduced in height if not diameter. *Graecopithecus* has been proposed variously as an ancestor or relative of *Australopithecus*, *Gorilla*, or all hominines, as well as the sister taxon of *Dryopithecus*. Several of these views may be mutually acceptable, if the taxon is slightly more derived than *Dryopithecus*, in the direction of Homininae. Direct links to *Gorilla* or *Australopithecus* are less likely, but ultimate ancestry is a possibility. Comparison with the *Samburupithecus* maxilla from Kenya might prove interesting as well, as these populations are roughly contemporaneous. Here, *Graecopithecus* is tentatively classified as the most conservative known member of Homininae, but it might easily be the most derived dryopithecine instead.

Another European species, *Oreopithecus bambolii*, is slightly younger and more autapomorphic. Known from a series of Late Miocene lignite deposits in Tuscany and Sardinia (Italy) dating to ca. 9–6 Ma, *Oreopithecus* combines highly distinctive teeth with a conservative but hominidlike skull and derived hominid postcrania. Although it has also been suggested to be either the sister taxon to Cercopithecoidea or a direct human ancestor, it now is broadly accepted to show strongest links to modern apes in its postcranium. It is, in fact, the most "modern" Miocene ape below the neck, with closest similarities to the postcranial elements of *Dryopithecus* reported from Spain in the mid-1990s. On the other hand, its lophodont dentition (adapted presumably to a leafy diet) and generally conservative skull (with a few possibly hominid features), as well as the badly crushed condition of most specimens, urge caution in proposing a close link to *Dryopithecus*. For the moment, it is placed in its own subfamily within Hominidae, but it could instead be included in the same subfamily as *Dryopithecus*, perhaps as a distinct tribe (in this case, the rules of priority would require the subfamily to be named *Oreopithecinae*).

Finally, the south Chinese Late Miocene *Lufengpithecus* (ca. 9–7 Ma) is also represented by mostly crushed cranial remains but lacks postcranial elements. It probably had thin molar enamel and a conservative skull (with wide interorbital distance, no clear frontal sinus, weak browridges, and fairly simple incisive canal complex); the lower anterior dentition is somewhat pitheciinlike, with tall incisors and heavy canines; the I^2 is quite small compared to I^1 . The weak brow and small lateral incisor are ponginelike, but the other features are less derived. *Lufengpithecus* could conceivably be classified in the Dryopithecinae, Kenyapithecinae, or even Ponginae, once it becomes better known.

Dryopithecinae

† *Dryopithecus*

?† *Lufengpithecus*

?† *Hylopithecus*

??† *Oreopithecus*

??† *Graecopithecus* (more probably in Homininae)

†extinct

See also Ape; Asia, Eastern and Southern; Asia, Western; Australopithecus; Dryopithecus; Europe; Graecopithecus; Griphopithecus; Hominidae; Hominoidea; Kenyapithecus; Lu-fengpithecus; Oreopithecus; Ponginae; Priority; Skull; Teeth. [E.D., P.A.]

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