odd composition of Yanaka (1988r). The comet could have been formed in the same cloud as the "standard" comets, but in a different region that had undergone a different chemical evolution. Second, Yanaka (1988r) could have formed in a molecular cloud of different composition and, quite by accident, been dispersed in interstellar space, become an interloper, and been captured by our solar system. This process can be expanded by recourse to a theory of Clube and Napier (*17*, *18*), who proposed that encounters of our solar system with giant molecular clouds have repeatedly depleted the Oort cloud, which was then replenished by new encounters with other molecular clouds. In this case, Yanaka (1988r) could be a lone remnant of a previous episode, while the "standard" comets arise from the latest "catch."

If Yanaka (1988r) originated within the solar system, its deviant composition provides evidence that the solar system was not as uniformly mixed as present theories presume. The region between Uranus and Neptune, where comets are believed to have accreted, spans a radial interval of about 10 astronomical units (AU). This interval is large enough to accommodate significant radial gradients in temperature and composition. If local inhomogeneities or compositional "clumpiness" are superimposed on such gradients, considerable deviations from an average composition could result. Compositional studies of comets can thus give us improved clues about the varying conditions during the time of formation of the solar system.

If they originated in molecular clouds, comets such as Yanaka (1988r) could provide us with the opportunity for a spacecraft rendezvous and thus allow direct sampling of the composition of the interstellar medium. Yanaka (1988r) itself, unfortunately, is not periodic and is now well on its way out of the solar system.

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Miocene Fossil Hominids and the Chimp-Human Clade

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Miocene hominoids from Europe are among the earliest members of the great ape and human clade (the Hominidae). One of these forms, represented by well-preserved cranial remains from Rudabánya, Hungary, sheds new light on the question of the evolutionary relations among living hominids. This new evidence supports the view that humans have a specific evolutionary relation with chimpanzees, to the exclusion of all other apes.

Much has been made recently of the discordance between molecular and morphological methods of reconstructing phylogeny and, in particular, hominoid phylogeny (*1*–*3*). There is an increasing consensus among molecular systematists that the African apes and humans form a clade or lineage distinct from the orang and furthermore that humans and chimps form a clade within the African apes and humans (*4*–*7*). This is contrasted with the morphological evidence, usually thought to favor a clade uniting the African apes to the exclusion of humans (*8*, *9*). This conclusion derived from the morphological evidence is completely dependent on current character state analyses suggesting that *Pan* and *Gorilla* are united by derived characters of the dentition and postcranium not shared by *Homo* or *Australopithecus*. A small number of derived characters shared among *Pan*, *Australopithecus*, and *Homo* are usually considered to be homoplasies and thus of no phyletic significance. One of the strengths of the cladistic approach is that character state analyses can easily be tested with the use of new outgroups to polarize character states, that is, to test hypotheses presenting particular character states as either primitive or derived. When this is done with the use of newly reconstructed fossil material of the early hominid *Dryopithecus*, the polarity of some of the characters used to reconstruct hominid phylogeny changes. The results suggest that *Gorilla* is primitive in a number of characters and, as a consequence, that features shared among *Homo*, *Australopithecus*, and *Pan* formerly concluded to be primitive are in fact derived and thus indicative of a closer evolutionary relation.

Rudapithecus hungaricus is a nomen attributed to a sample of fossil hominoids from the late Miocene locality of Rudabánya, in north-central Hungary (*10*, *11*). This sample includes large portions of two craniofacial skeletons, two additional palatal specimens, four mandibles, numerous isolated teeth, and a number of postcranial elements (Fig. 1). The gnathic material from Rudabánya shares a number of characters with specimens attributed to the four species of the genus *Dryopithecus*. These include high-crowned, narrow, and thick (labiolingually) upper and lower incisors; upper lateral incisors robust at the cervix and lacking pronounced cingula; tall, buccolingually compressed canines that are relatively small compared to the molars and with thick, rounded distal cingula; reduced lower premolar cusp heteromorphy; broad lower third premolars (P_3) often with well-developed mesio-lingual beaks and small metaconids; elongated lower fourth premolar (P_4) with high talonids; reduced molar cingula; elongated lower molars with tall, peripheralized cusps, broad basins, and relatively early dentine penetrance; and reduction in lower third molar (M_3) size. For these and other reasons, the Rudabánya fossils can be attributed to the genus *Dryopithecus* (*12*, *13*).

Comparisons of the cranial anatomy of *Dryopithecus* to other Miocene and more recent hominoids reveal a pattern of similarities with great apes and humans, to the exclusion of earlier Miocene hominoids. *Dryopithecus* shares with great apes and

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humans (including the fossil forms *Sivapithecus*, *Ouranopithecus*, *Lufengpithecus*, and *Australopithecus*) a large number of traits listed under node 2 in Table 1. In all of these features, *Dryopithecus* differs from hylobatids and from early and most middle Miocene forms, including *Proconsul*, *Micropithecus*, *Dendropithecus*, *Afropithecus*, *Turkanapithecus*, and "*Kenyapithecus*" from Maboko, though this last taxon is poorly known cranially. For this reason, *Dryopithecus* is included among the Hominidae, as defined by Groves and others (*14–17*).

The addition of cranial material attributable to *Dryopithecus* increases the number of comparisons that can be made to other taxa and provides a number of new insights into both the relation of *Dryopithecus* to other hominoids and relations among Hominoidea more generally. Among living hominoids, *Dryopithecus* shares with African great apes and *Australopithecus* a continuous, although poorly developed, supraorbital torus, a shallow sulcus supratoralis, a prominent glabella, and an increase in the anteroposterior development of the frontal bone in the temporal fossa (node 2, Table 1). The first three traits have been related to increased ventral flexion of the face relative to the cranial base, or klinorhynchy (*18*). The anteroposterior increase in the frontal contribution to the temporal fossa also appears only in more klinorhynch apes (African apes) and may also be directly related to the anterior and ventral rotation of the klinorhynch face. The presence of these four traits in *Dryopithecus* (RUD 44, RUD 77) (*19*) suggests that *Dryopithecus* may have been klinorhynch as well. *Dryopithecus* also shares with African apes a broad, flat nasal aperture base, a broad, relatively shallow canine fossa, a stepped subnasal floor, a biconvex naso-alveolar clivus, a true incisive canal, a reduced incisive foramen, an ethmoidal frontal sinus, and a broad interorbital distance (node 2, Table 1). A number of these traits (nasal aperture, canine fossa, subnasal floor, naso-alveolar clivus, incisive canal, and incisive foramen) are also found in *Ouranopithecus* and are probably primitive for great apes, with *Pongo* and *Sivapithecus* showing a more derived condition. The ethmoidal frontal sinus may also have been present in more primitive hominoids, such as *Proconsul* (*20*), and secondarily lost in the *Pongo* clade, whereas the broad interorbital distance is clearly primitive. The other traits are absent from all outgroups of the African ape–human clade (*Pongo-Sivapithecus*, early to middle Miocene hominoids, and hylobatids) and are therefore more likely to be shared derived traits. However, other traits shared between *Sivapithecus* and the African ape–human clade suggest that these traits may be homoplasies (see below).

The pattern of similarities shared among *Dryopithecus*, *Gorilla*, *Pan*, and *Australopithecus* provides the basis for testing current hypotheses of the relations among these forms. Among the African ape–human clade, *Dryopithecus* shares a number of features with *Gorilla* not found in other hominids. In contrast to the characters noted above, the traits linking *Dryopithecus* to *Gorilla* are for the most part primitive for the great apes and in some cases primitive for the Hominoidea. They do not, therefore, support a hypothesis of specific evolutionary relations between *Gorilla* and *Dryopithecus*. The characters shared among *Dryopithecus*, *Gorilla*, and other hominoids but not found in *Pan* or *Australopithecus* include (i) relatively large incisive foramen, (ii) comparatively short incisive canal, (iii)

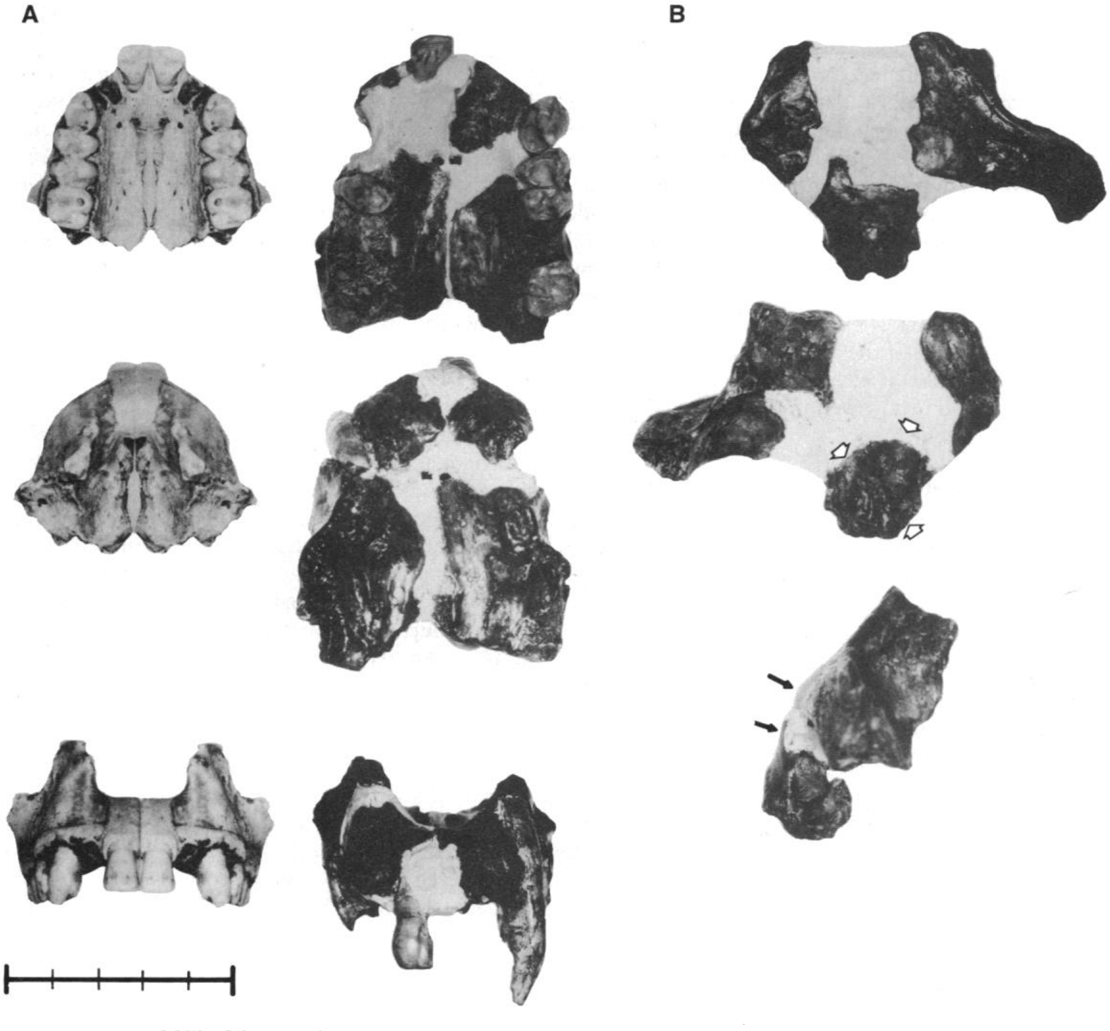

Fig. 1. Reconstructed cranio-dental specimens from Rudabánya. (**A**) Palatal specimens. Left column, RUD 12; hemipalate with photographically reversed mirror image. (Top) palatal, (middle) nasal, and (bottom) anterior. Right column, RUD 44/47. (Top) palatal, (middle) nasal, and (bottom) anterior. Scale applies to both specimens. (**B**) Frontal specimen. RUD 44. (Top) anterior, (middle) posterior (open arrows demarcate frontal sinuses), and (bottom) lateral (arrows demarcate supraorbital torus). Scale in centimeters. All photographs of casts.

comparatively short premaxilla, (iv) broad (thick) lateral orbital margin along the frontal zygomatic process, (v) smoothly convex anterior surface of the frontal zygomatic process, (vi) sloped mandibular ascending ramus, (vii) narrow upper lateral and lower incisors, (viii) conical, asymmetrical upper lateral incisors with strongly sloped incisive edges distally, (ix) long P_4 relative to M_1, and (x) elongated lower molars relative to breadth (node 2, Table 1). The evidence of *Dryopithecus*, then, suggests that a number of characters previously interpreted as either primitive or homoplastic traits shared between *Australopithecus* and *Pan* are more likely to be derived traits linking the two phylogenetically to the exclusion of other great apes. These traits include spatulate, symmetrical upper lateral incisors; greatly elongated premaxillary alveolar process; elongated incisive canal constricted in caliber (premaxilla and canal more elongated and canal more constricted than in *Dryopithecus* and *Gorilla* but less elongated and constricted and differently oriented than in *Pongo* and *Sivapithecus*); a short subnasal portion to the premaxilla; narrow, flat lateral orbital margin; vertical ascending ramus; broader lower incisors; short P_4; and broader lower molars. *Pan* and *Homo* are also thought to share an acceleration of premaxillary-maxillary fusion (*21–23*), which may be causally related to the similarities in the premaxilla of *Pan* and *Australopithecus* (node 4, Table 1). *Australopithecus* and *Pan* together share with *Gorilla* a number of traits that suggest these hominids belong together in a clade to the exclusion of *Dryopithecus*. These include broader incisors; longer premaxilla; longer, better defined incisive canal; and larger maxillary sinuses (node 3, Table 1). The incisive canal–foramen complex and the associated premaxillary morphology are characterized by a series of character states

Table 1. Characters used in this analysis and their states at nodes 1 to 4, Fig. 2. Character states that differ from the preceding node are synapomorphies at their designated nodes. Node 1 states are primitive for the Hominoidea.

Node 1	Node 2	Node 3	Node 4
Labiolingually narrow upper incisors	Thicker incisors	Broader I^1†	Same as node 3
Narrow lower incisors	Thicker incisors	Same as node 2	Broader lower incisors
I^2 labiolingually compressed	More robust	Same as node 2	Spatulate I^2
I^2 with lingual cingulum	Lacks cingulum	Same as node 2	Same as node 2
I^2 with asymmetrical crown	Same as node 1	Same as node 1	Symmetrical I^2 crown
Large canines/postcanine	Smaller canines	Same as node 2	Same as node 2
Bucco-lingually robust canines	Compressed canines	Same as node 2	Same as node 2
Narrow canine distal cingula	Thick, rounded cingula	Same as node 2	Same as node 2
Premolar cusp heteromorphy	Reduced heteromorphy	Same as node 2	Same as node 2
Narrow P_3	Broad P_3	Same as node 2	Same as node 2
P_3 lacks mesio-lingual beak	P_3 with mesio-lingual beak	Same as node 2	Same as node 2
P_3 lacks metaconid	P_3 with metaconid	Same as node 2	Same as node 2
Short P_4	Longer P_4	Same as node 2	Shorter P_4
Low P_4 talonids	High P_4 talonids	Same as node 2	Same as node 2
Molar cingula	Reduced molar cingula	Same as node 2	Same as node 2
Short lower molars	Longer molars	Same as node 2	Broader lower molars
Large M_3	Reduced M_3	Same as node 2	Same as node 2
Sloped ascending ramus	Same as node 1	Same as node 1	Vertical ascending ramus
Low maxillary alveolar process	High maxillary alveolar process	Same as node 2	Same as node 2
Anteroposteriorly thin zygomatic root	Anteroposteriorly thick zygomatic root	Same as node 2	Same as node 2
Small maxillary sinus	Large maxillary sinus	Larger maxillary sinus†	Same as node 3
Thin maxillary palatine process	Thick maxillary palatine process	Same as node 2	Same as node 2
$\underline{C}$ roots even with nasal aperture	$\underline{C}$ roots anterior to nasal aperture	Same as node 2	Same as node 2
Short premaxillary alveolar process	Long premaxillary alveolar process	More elongated	Still more elongated
Very short nasal premaxilla	Long nasal premaxilla	Same as node 2	Shorter nasal premaxilla
Transversely shallow glenoid fossa	Transversely deep glenoid fossa	Same as node 2	Same as node 2
Indistinct entoglenoid process	Prominent entoglenoid process	Same as node 2	Same as node 2
Small postglenoid process	Prominent postglenoid process	Same as node 2	Same as node 2
Medial, flat postglenoid process	Lateral, vertical postglenoid	Same as node 2	Same as node 2
Anteroposteriorly short frontal in the temporal fossa	Anteroposteriorly long frontal in the temporal fossa*	Same as node 2	Same as node 2
No supraorbital torus	Continuous supraorbital torus*	Same as node 2	Same as node 2
No sulcus supratoralis	Shallow sulcus supratoralis*	Same as node 2	Same as node 2
Indistinct glabella	Prominent glabella*	Same as node 2	Same as node 2
Lateral orbital margins broad	Same as node 1	Same as node 1	Lateral margins narrow
Lateral orbital margin surface convex	Same as node 1	Same as node 1	Lateral orbital margin surface flat
Narrow, convex base of the nasal aperture	Broad, flat base of the nasal aperture*	Same as node 2	Same as node 2
Variable, often deep canine fossa	Broad, shallow canine fossa*	Same as node 2	Same as node 2
Divided subnasal floor	Stepped subnasal floor*	Same as node 2	Same as node 2
Flat naso-alveolar clivus	Biconvex naso-alveolar clivus*	Same as node 2	Same as node 2
No incisive canal	Short incisive canal	More elongated incisive canal†	Same as node 3
No incisive canal	Large caliber incisive canal	Reduced caliber	More reduced caliber†
Large incisive foramen	Reduced incisive foramen	More reduced incisive foramen†	Same as node 3
Anterior edge of incisive fossa anterior to canine	Anterior edge of incisive fossa between $\underline{C}$-P^3	Same as node 2	Anterior edge of incisive fossa posterior to P^3
?Ethmoidal frontal sinus	Ethmoidal frontal sinus*	Same as node 2	Same as node 2
Broad interorbital distance	Same as node 1*	Same as node 1	Same as node 1

*Not present in *Pongo*. †Present in *Pongo*.

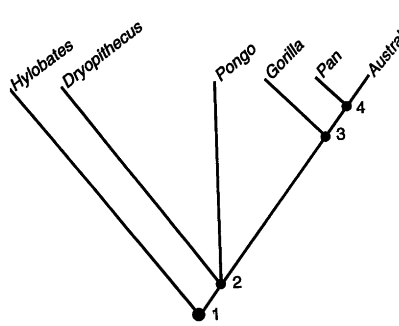

Fig. 2. Cladogram depicting the relations among hominids proposed here. The outgroup is represented by *Hylobates.* Other outgroups include *Proconsul, Kenyapithecus*, and Old World monkeys. Nodes are characterized by character states listed in Table 1.

(morphocline) from *Dryopithecus* to *Pan* and *Australopithecus*. In *Dryopithecus* this area of the face is the least elongated, though it is more elongated than in early Miocene forms and living hylobatids, and is to a degree similar to that in *Ouranopithecus* (*24, 25*). In *Gorilla* the premaxillary alveolar process is somewhat longer on average, though in *Dryopithecus* it is within the range of relative length found in *Gorilla. Australopithecus* and *Pan* have this region most elongated among these forms. Most of the characters shared between *Dryopithecus* and *Gorilla* are also present in *Ouranopithecus* (which may be the sister clade of *Dryopithecus*), lending support from another Miocene taxon to the conclusions presented here.

The elongation of the naso-alveolar process in *Pongo* is interpreted here as having evolved in parallel with the *Pan-Australopithecus* clade. It is absent in *Gorilla*, which is widely believed to be more closely related to *Pan* than is *Pongo* (*26–28*), and it is morphologically different in *Pongo* and *Pan-Australopithecus*. In the former, the premaxillary alveolar and subnasal portions are both extremely elongated and more horizontally oriented, such that the transition from alveolar to subnasal regions is smoothly continuous. The subnasal elongation of the premaxilla in *Pongo* obliterates the incisive fossa and the stepped subnasal floor, both of which are found in the other great apes and *Australopithecus*, and it reduces the incisive canal to a bony tube of minuscule caliber (*26–29*). These character states in *Pongo* are in fact diagnostic of the clade that includes *Pongo* and *Sivapithecus* and cannot be considered primitive for the Hominoidea, being characteristic only of that clade (*26–29*). *Pongo* is also known to differ from the African great apes and humans in the timing of the fusion of the premaxilla. The premaxilla fuses with the maxilla relatively later in the Asian great ape (*21*), suggesting that the premaxilla may accomplish its elongation in *Pongo* and *Pan* by different mechanisms or processes. The similarity of the elongated naso-alveolar clivus of African and Asian great apes, according to this interpretation, is superficial and not homologous. The characters shared by *Dryopithecus* and African apes, to the exclusion of *Pongo*, are related to klinorhynchy and contrast with those shared by great apes, to the exclusion of *Dryopithecus*, including stronger reduction of the incisive foramina, longer incisive canals, generally longer naso-alveolar clivus, and larger maxillary sinuses. Though the specific similarities between *Pan* and *Pongo* are interpreted here as convergent, some elongation of the premaxilla and enlargement of the maxillary sinuses beyond that seen in *Dryopithecus* may have characterized a hypothetical common ancestor of living great apes and humans, excluding *Dryopithecus*. For this reason, the relation between these forms remains unresolved (Fig. 2 and Table 1).

This reinterpretation of the polarity of the traits shared among living great apes and humans, *Australopithecus*, and *Sivapithecus* is suggested by the introduction of a new outgroup, *Dryopithecus*, into the analysis. The identification of the sample from Rudabánya as *Dryopithecus* allows for the testing of hypotheses of phylogenetic relations among great apes and humans developed from other fossil evidence. From the analysis of *Dryopithecus*, it can be shown that a number of characters shared by *Pan* and *Australopithecus* and previously considered to be primitive for the great apes (*30*) are more likely to be derived for *Pan* and *Australopithecus*, whereas characters previously considered to be derived or autapomorphous in *Gorilla* (*28, 30*) are most probably primitive, being shared with *Dryopithecus* and other Miocene hominoids. A *Pan-Australopithecus* clade, excluding *Gorilla*, implies that characters shared between African apes alone are either primitive or have evolved in parallel. In addition to the characters discussed above, these include characters related to enamel ultrastructure and knuckle-walking (*8, 14, 31, 32*). Details of enamel ultrastructure have yet to be fully described for fossil and living hominoids, and the conclusions presented thus far have been interpreted in a number of ways (*32–34*). More work, especially on early Miocene and *Dryopithecus* specimens, is required to understand the evolutionary significance of the diversity of patterns of enamel ultrastructure in fossil hominoids (*35*). On the other hand, the interpretation of knuckle-walking is more straightforward. There is no evidence for knuckle-walking before node 3 in Fig. 2. Carpal bones from fossil hominoids such as *Proconsul, Sivapithecus*, and *Dryopithecus* indicate that knuckle-walking was not part of the positional repertoire of these taxa (*36–38*), nor did it characterize the locomotion of *Australopithecus* (*39–41*). If *Pan* and *Gorilla* belong to different clades, as suggested here, then knuckle-walking must either be convergent in the two or primitive for the African apes and humans. Knuckle-walking is associated with a number of carpal, metacarpal, and phalangeal specializations that are shared by both African ape genera (*31*). These, however, are all functionally correlated, always occurring together, and may be more legitimately considered as a single complex trait. It is therefore unclear to what extent it would be "unparsimonious" to consider knuckle-walking to have evolved in parallel. However, there is no evidence to rule out the possibility that knuckle-walking is primitive for the great apes and humans and has been lost in *Homo* and in the australopithecines. *Homo, Pan*, and *Gorilla* do share a number of derived wrist characters, including the unique one among catarrhines of lacking postnatally a distinct os centrale (*42*). Because *Pan, Gorilla*, and *Homo* share a more recent common ancestor with each other than with *Pongo*, they must share a most recent common ancestral pattern of positional behavior as well. The loss of the os centrale and other traits shared among African apes and humans (*31*) related to increased stability in the wrist may be indicative of a common ancestry of proto–knuckle-walking, from which the living African apes have diverged minimally.

Despite suggestions to the contrary (*3, 8*), there is evidence of a *Pan-Homo* clade in the craniodental morphology and fossil record of the great apes. However, this evidence was not apparent, in part because of the confusion surrounding the taxonomic affinities of important samples such as that from Rudabánya. The conclusions presented here, based on the analysis of newly identified *Dryopithecus* specimens, are derived from fossil evidence. They complement the increasing volume of evidence from molecular systematics (*4–7*) supporting the view that the closest living relative of the chimpanzee is *Homo sapiens*, and that these species are more closely related to each other than either is to any other living primate.

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DNA Sequences from a Fossil Termite in Oligo-Miocene Amber and Their Phylogenetic Implications

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DNA was extracted from the fossil termite *Mastotermes electrodominicus* preserved in Oligo-Miocene amber (25 million to 30 million years old). Fragments of mitochondrial [16*S* ribosomal DNA (rDNA)] and nuclear (18*S* rDNA) genes were amplified by polymerase chain reaction. Phylogenetic analysis of fossil and extant 18*S* rDNA confirmed morphological cladistic analyses of living dictyopterans (termites, cockroaches, and mantids). The fossil termite shares several sequence attributes with *Mastotermes darwiniensis*. Addition of this fossil to living-species phylogeny is required to substantiate *Mastotermes* monophyly and affects molecular phylogenetic hypotheses of termites in this, the oldest DNA yet characterized.

The tropical northern half of Australia is home to *Mastotermes darwiniensis*, one of the most intriguing of the 2000 or so described species of termites (Isoptera). This species has been a popular candidate for the most primitive isopteran and an apparent "missing link" between cockroaches and termites (*1*, *2*). It is the sole living species in the family Mastotermitidae, classified as such to reflect its primitive phylogenetic position. The features on which this classification is based are (i) an egg mass or pod resembling a rudimentary form of the ootheca in cockroaches, (ii) presence of gut symbionts in certain cockroaches such as the apterous colonial *Cryptocercus*, and (iii) a host of primitive morphological features (*3*). A cladogram of this traditional view of termite phylogeny appears in Fig. 1A.

Established views on the primitive nature of *Mastotermes* have been challenged by a cladistic analysis of dictyopteran insects, based on a review of morphological, behavioral, chromosomal, and cell ultrastructural characters (*4*) (see Fig. 1B). In the scheme of Thorne and Carpenter (*4*) *Mastotermes* is the sister group to the family Kalotermitidae, with Termopsidae as the primitive sister group of the remaining termites. The Isoptera's unquestionable monophyly is based on eusociality (with its associated behavioral and morphological caste polytypism), deciduous wings, and other morphological features. In the relationships proposed by Thorne and Carpenter, termites are the sister group to the mantids and cockroaches (the latter also includes *Cryptocercus*). Thorne and Carpenter do not address what appear to be pleisomorphic features that define *Mastotermes* and its family. Although they cite many derived features, it is unclear whether these attributes pertain to the Mastotermitidae as a whole. The plesiomorphies include, for example, a large anal lobe on the wings seen in mantids, cockroaches, and many orthopteroids (*2*). Thus, the monophyly of the one living species and of fossil mastotermitids is questionable and has implications for the interpretation of other evolutionary aspects of this "group."

Thorne and Carpenter dismiss *Mastotermes* as a "living fossil" because it possesses a large number of derived features and, in their scheme, is not the most primitive of termites. The fossil record of the Mastotermitidae indicates that, if the group is monophyletic, the present distribution is narrowly restricted and relict. Rock fossils indicate that there were extinct genera from the Mio-Pliocene of Brazil, the Eocene of Tennessee, and the early Cretaceous of England; the genus *Mastotermes* occurs from the Eocene to the Miocene (20 million to 40 million years ago) of Europe (*5*). The genus has been found only recently in amber as the extinct and closely related species *M. electromexicus* from Chiapas, southern Mexico (*6*), and *M. electrodominicus* from the Dominican Republic (*7*). Oddly, the genus has been unknown from huge, diverse collections of Baltic amber fossils (*8*). Clearly, a great deal of mastotermitid evolution has been obscured by extinction, glimpses of which are seen in the fossil record.

It is not surprising that *M. electromexicus* and *M. electrodominicus* are closely related, given the paleontology of the ambers in which they are preserved. Both Mexican and Dominican deposits have the same botanical source, the tropical canopy legume *Hymenaea* (*9*). Stratigraphy indi-

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