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A New Skull of Early *Homo* from Dmanisi, Georgia

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Another hominid skull has been recovered at Dmanisi (Republic of Georgia) from the same strata in which hominid remains have been reported previously. The Dmanisi site dated to ~1.75 million years ago has now produced craniofacial portions of several hominid individuals, along with many well-preserved animal fossils and quantities of stone artifacts. Although there are certain anatomical differences among the Dmanisi specimens, the hominids do not clearly represent more than one taxon. We assign the new skull provisionally to *Homo erectus* (=*ergaster*). The Dmanisi specimens are the most primitive and small-brained fossils to be grouped with this species or any taxon linked unequivocally with genus *Homo* and also the ones most similar to the presumed *habilis*-like stem. We suggest that the ancestors of the Dmanisi population dispersed from Africa before the emergence of humans identified broadly with the *H. erectus* grade.

The new Dmanisi cranium (D2700) and associated mandible (D2735) were found in squares 60/65 and 60/66 (Fig. 1), embedded in the black to dark-brown tuffaceous sand immediately overlying the 1.85-million-year-old Masavera Basalt. Sedimentary horizons above the basalt also yielded two partial crania in 1999, along with mandibles discovered in 1991 and 2000 (*1*–*7*). The new hominid remains were associated with animal fossils that include an entire skull of *Stephanorhinus etruscus etruscus*, a skull of *Cervus perrieri* with a full rack of antlers, a *Dama nesti* antler, two crania of *Canis etruscus*, a complete mandible of *Equus stenonis*, and the anterior portion of a *Megantereon* cranium. Human occupation at Dmanisi is correlated to the terminal part of the (magnetically normal) Olduvai Subchron and immediately overlying (magnetically reversed) horizons of the Matuyama Chron, and is ~1.75 million years in age (*5*, *6*, *8*). Faunal remains also support the dating of Dmanisi to the end of the Pliocene or earliest Pleistocene (*8*, *9*).

The evidence suggests that much of the Dmanisi fauna was buried rapidly after death, in many cases with ligaments still attached, and that the bones were buried very gently, with minimal transport. The protection afforded the bones in lower layers by the overlying calcareous horizon halted further diagenetic damage and compaction that normally occur. Sedimentological information and the appearance of all the fossils found nearby reinforce the conclusion that the hominid and faunal remains were deposited in a brief interval. Seventy percent of the assemblage is in weathering stage 0 or 1, and none in stages 4 or 5 (*10*). Rapid, low-energy deposition was followed by formation of petrocalcic horizons higher in the section, which arrested further destruction of bone. We estimate that in the sample of over 3000 vertebrate faunal remains recovered thus far, about 30% of the specimens are unbroken, and almost 90% are identifiable to genus if not species.

The diversity and high proportion of carnivores in the assemblage are paralleled by some tooth pits and characteristic carnivore breakage patterns, and also some hyena coprolites, but the general character of the assemblage in many ways does not fit conceptions of carnivore lairs (*11*).

The mammalian fauna includes new rodent species, which confirm that Dmanisi predates the holarctic dispersal of rootless voles (*Allophaiomys-Microtus* group). We also found a large, archaic *Mimomys*, which fits well in the *Mimomys pliocaenicus* group from the late Pliocene (Villanyian biozone) in European sites (Tegelen in the Netherlands, Val d'Arno in Italy, East and West Runton in England), a smaller vole of the *Tcharinomys* (*Pusillomimus*) lineage, abundant gerbils (*Parameriones* sp.), and hamsters (*Cricetus* sp., *Allocricetus bursae*) (*12*).

Stone artifacts were found throughout the sediment section, but, as in the previously

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excavated areas, artifact concentrations are much larger in the upper deposits (Stratum B) than in the deeper sediments. All tools are produced out of local raw materials, and there is clear selection of finer grained stone such as quartzite and basalt for tool manufacture. The Dmanisi lithic assemblage belongs to a Mode 1 industry similar to the Oldowan of East Africa. The Dmanisi finds imply that early humans with primitive stone tool technology were able to expand out of Africa (*5*, *8*, *13*).

The D2700 cranium (Fig. 2; figs. S1 and S2) carries four maxillary teeth: right M1 and M2 and left P4 and M2. The D2735 mandible (Fig. 3 and fig. S3) contains eight teeth: P3, P4, M1, and M2 are present on both sides, but the third molars are lacking. Ten isolated hominid teeth were also recovered. Of these, D2732 (upper right canine), D2678 (upper left canine), D2719 (upper right P4), D2710 (upper left M1), D2711 (upper right M3), and D2720 (upper left M3) fit well into the maxilla, but the dentition is still incomplete. When the upper and lower tooth rows are placed in occlusion, there is a good fit of the cranium to the lower jaw. Although the two fossils have separate field numbers, they represent one individual.

The skull is in remarkably fine condition (Fig. 2). The maxillae are slightly damaged anteriorly, the zygomatic arches are broken, and both mastoid processes are heavily abraded. There is damage also to the orbital walls and to the elements of the interorbital region and the nasal cavity. The condyles are missing from the mandible. In other respects, the face, the braincase including the base, and the mandible are largely intact and undistorted. Computerized tomography (CT) scans (figs. S1 and S2) show that internal anatomical structures are well preserved. As the maxillary M3s are only partly erupted (the occlusal surface is level with the base of the crown of M2), D2700/D2735 is a young individual whose age lies between that of the Nariokotome juvenile (KNM-WT 15000) (*14*, *15*) and D2282. The new specimen exhibits generally gracile morphology and may be a female. However, the upper canines carry large crowns and massive roots, and their size counsels caution in assessing sex.

In its principal vault dimensions, D2700 is smaller than D2280 and the specimens attrib-

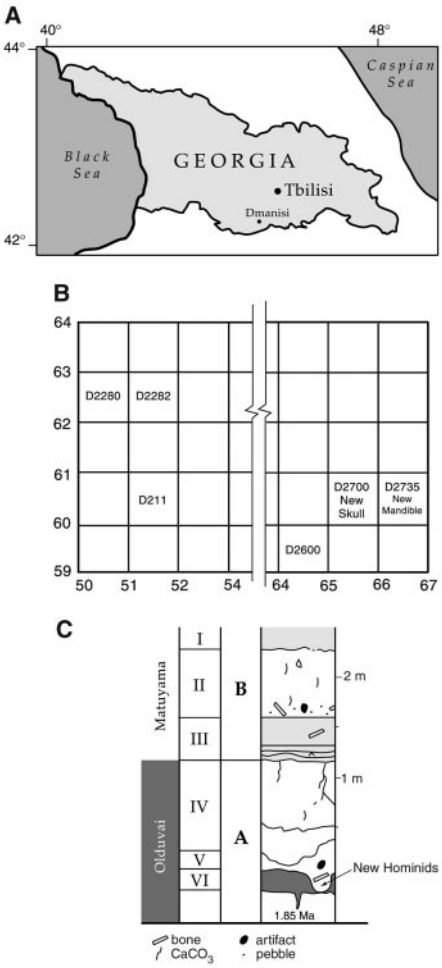

Fig. 1. (**A**) Location map of Dmanisi site. (**B**) The locations of hominid fossils (excavation units are 1-m squares). (**C**) General stratigraphic profile, modified after Gabunia *et al.* (*5*, *6*). The basalt and the immediately overlying volcaniclastics (stratum A) exhibit normal polarity and are correlated with the terminus of the Olduvai Subchron. Slightly higher in the section, above a minor disconformity and below a strongly developed soil, Unit B deposits, which also contain artifacts, faunas and human fossils, all exhibit reversed polarity and are correlated with the Matuyama. Even the least stable minerals, such as olivine, in the basalt and the fossil-bearing sediments show only minor weathering, which is compatible with the incipient pedogenic properties of the sediments.

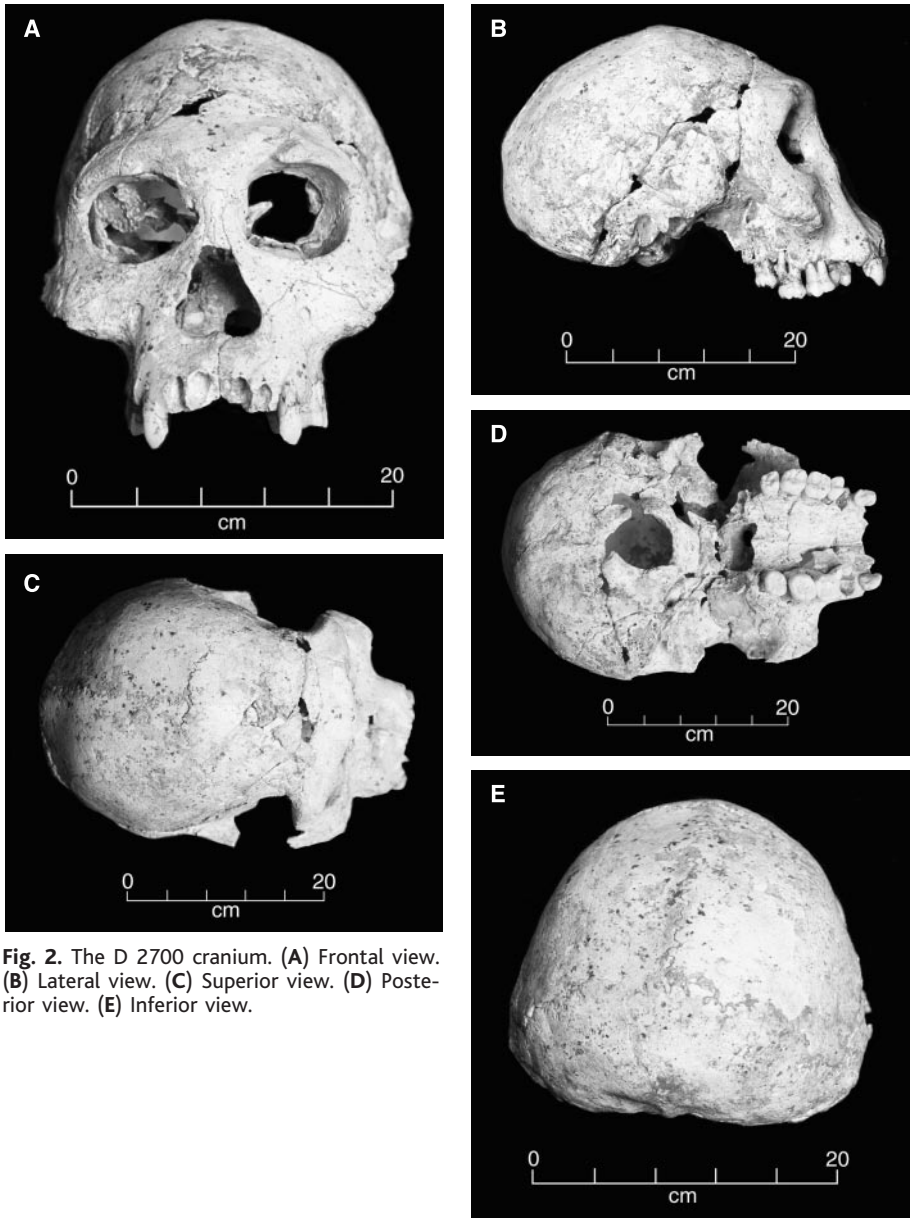

Fig. 2. The D 2700 cranium. (**A**) Frontal view. (**B**) Lateral view. (**C**) Superior view. (**D**) Posterior view. (**E**) Inferior view.

uted to African *H. erectus* (Table 1; figs S1 and S2). The new individual is closer in size to D2282 and equal to the latter in frontal and posterior vault widths. In cranial length and in most breadths, D2700 is larger than KNM-ER 1813 (attributed to *H. habilis*). The face is diminutive in comparison to that of either KNM-ER 3733 or KNM-ER 1470, and it is slightly larger in its transverse width and orbital and nasal measurements than KNM-ER 1813. The new mandible (Fig. 3 and fig. S3) resembles D211 in its dimensions (table S1), and there is no indication of a bony chin. In overall size and anatomical appearance, D2735 closely matches the mandible of the Nariokotome boy (KNM-WT 15000).

The face is surmounted by thin but well-defined supraorbital tori, curving gently upward from an inflated glabellar prominence. The nasion itself is set well forward from the orbital margins, as it is in D2280. The narrow nasal bones are waisted as in KNM-ER 1813 but broken inferiorly. The piriform aperture is similar in shape to, but smaller than that of, KNM-ER 3733, and there is a prominent incisive crest. The nasal sill is smooth, but by the criteria of McCollum *et al*. (*16*), the lateral border of the aperture is sharp. In its midfacial profile, D2700 resembles KNM-ER 1813, although the subnasal clivus is relatively flat, lacking vertical corrugations. The canine juga are expanded and reach upward to thicken the margin of the nose. The infraorbital walls are recessed, and a faint

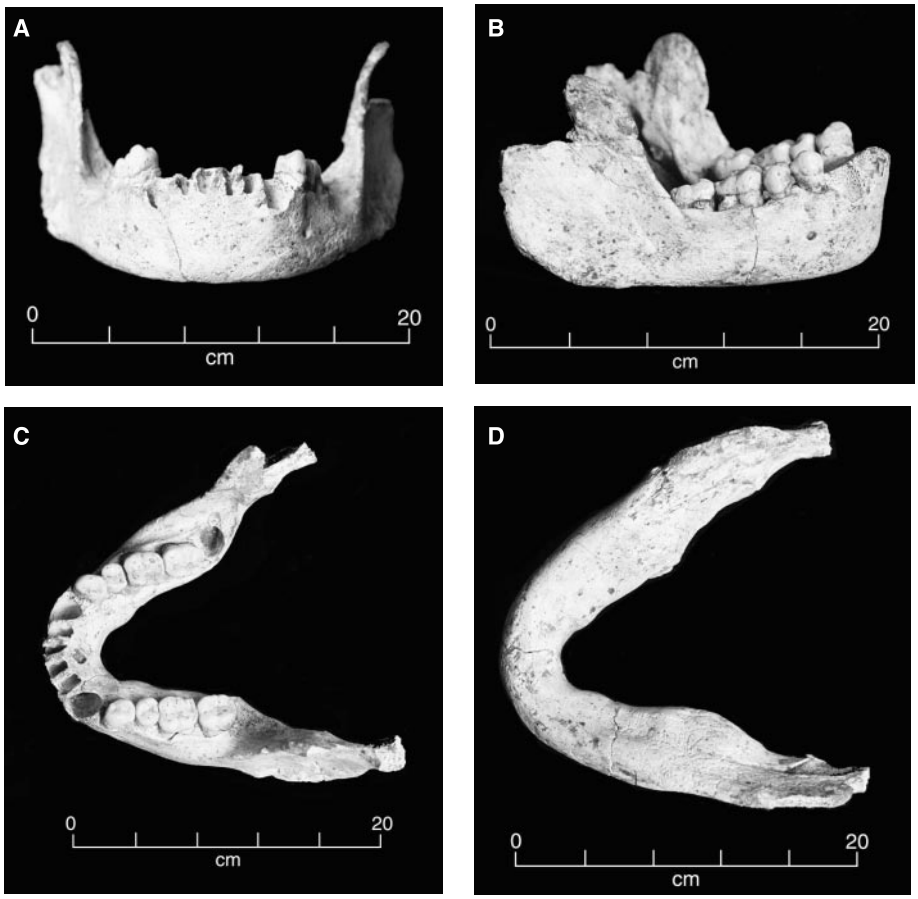

Fig. 3. Views of D 2735 mandible. (**A**) Anterior view. (**B**) Lateral view. (**C**) Superior view. (**D**) Inferior view.

Table 1. Cranial measurements of the Dmanisi hominids and other fossils from East Africa. Numbers in parentheses indicate approximate values; dashes indicate unavailable data. Measurements were made on the original fossils by A. Vekua, D. Lordkipanidze, and G. P. Rightmire, except for those marked "#" which were taken from a cast by A. Walker.

Measurements (mm)	D2700	D2280	D2282	ER 1813	ER 1470	ER 3733	ER 3883	WT 15000
Cranial length	153	177	(167)	145	168	182	182	(175)
Max. cranial breadth	125	(136)	(125)	113	138	142	140	–
Max. biparietal breadth	115	118.5	116	100	120	131	134	–
Biauricular Breadth	119	(132)	–	112	135	132	129	–
Supraorbital torus thickness	9	11	10	9	8	8.5	11	–
Min. frontal breadth	66	74.5	65	65	71	83	80	73#
Biorbital chord	90	105	96	91	109	109	110	96#
Postorbital constriction index*	73.3	71.4	68.7	71.4	65.1	76.1	72.7	76#
Frontal arc	95	108	(81)	90	104	119	118	–
Frontal angle	147	149	–	139	140	139	140	–
Parietal arc	91	96	85	77	89	85	95	107#
Lambda-asterion arc	70	75	72	69	88	88	79	76#
Biasterionic breadth	104	104	103	93	108	119	115	106
Occipital arc	82	97	–	96	105	118	101	93#
Occipital angle	115	108	–	114	–	103	101	–
Occipital scale index†	81.8	102.1	–	72.7	75	92.9	106.2	131.5#
Nasion-prosthion length	63	–	–	64	90	81	–	77
Malar height	27	–	(30)	27	40	34	–	30
Nasion angle‡	136	139	–	153	151	155	151	138
Bimaxillary chord	96	–	–	86	98	101	–	100
Subspinale angle§	143	–	154	144	161	143	–	133
Orbit breadth	35	–	–	34	41	44	45	39
Orbit height	31	–	–	30	36	35	36	42
Nasal breadth	27	–	28	24	27	36	–	36
Nasal height	50	–	–	44	58	53	–	57

*Calculated as the ratio of minimum frontal breadth to the biorbital chord. †Calculated as the ratio of the inion-opisthion chord to the lambda-inion chord. ‡Calculated from the nasion subtense and one-half of the biorbital chord. §Calculated from the subspinale subtense and one-half of the bimaxillary chord.

furrowlike sulcus is associated with the infraorbital foramen. A deeper sulcus is common in *H. erectus*. Laterally, the surfaces of the cheeks are hollowed, but these concavities are not comparable to the "canine fossa" of later humans. There is no malar tubercle. The zygomatic process is rooted above M1 and is substantially thickened—more so than in KNM-ER 1813 but resembling the condition in D2282. There is clear expression of a zygomaxillary incisure. A feature not seen in the other skulls occurs just anterior to the zygomatic pillar, in the wall of the alveolar process. Here on both sides, there is a distinct pit behind the canine jugum. The palate is shallow and like that of KNM-ER 1813 in its proportions.

There is no supratoral hollowing behind the brows. Postorbital constriction of the frontal bone is comparable to that in *H. habilis*, *H. erectus*, and the other Dmanisi individuals. There is faint midline keeling on the frontal, and this is more pronounced near bregma. Along the coronal suture, the frontal bone is raised relative to the parietal vault. Where they cross this suture, the temporal lines are 64 mm apart. The parietals themselves are long sagittally, and here there is definite midline keeling extending all the way to lambda. Indeed, the parietal surfaces are slightly depressed in relation to both the frontal and the occiput. This morphology, together with the inward sloping cranial walls above the supramastoid crests, gives the rear of the D2700 braincase a low and transversely flattened appearance, characteristic of both African and Asian *H. erectus*. No angular torus is present, but the supramastoid crests are moderately strong. The temporal squama is shaped like that of *H. erectus*, with a long, straight superior border passing downward toward asterion. In profile the upper scale of the occipital slopes slightly forward. The lambda-inion distance is longer than the inion-opisthion chord as in *H. habilis* and KNM-ER 3733. The occiput is not strongly flexed, and its surface is smooth, with only light sculpting of the superior nuchal lines and a low linear tubercle. There is no transverse torus. This feature is also absent in D2282 and only slightly developed in D2280.

The glenoid cavity is largely intact on both sides. Although relatively shallow and smaller in width, the temporomandibular joint surface resembles that of D2280 and KNM-ER 3733 in a number of details, including the forward curvature of the anterior wall, the lack of any barlike articular tubercle, the presence of a flattened preglenoid planum, and the extension of the cavity onto the underside of the zygomatic root. As in *H. erectus*, only the inner portion of the fossa lies below the braincase, while the outer part is lateral to the cranial wall above. However, the postglenoid process is large, as in some *H. habilis*. The inferior margin of the tympanic plate is not appreciably thickened but does exhibit a prominent petrosal spine. On the left, the petrous temporal is preserved. The long axis of the pyramid is angled so as to lie more nearly in the sagittal plane, relative to the transverse orientation of the tympanic plate. Such bending of the temporal axis was noted by Weidenreich (*17*) for the Zhoukoudian crania, and it is present also in the African representatives of *H. erectus*.

A comparison of the new skull to other specimens from Dmanisi, Koobi Fora, and West Turkana suggests that it has a number of similarities to early *H. erectus* (or *H. ergaster*) (Table 1). The cranium is exceptionally small, with a rounded occiput, and its face is like that of KNM-ER 1813, especially in profile. The canine juga of D2700, however, are well defined, and the zygomatic root (zygomaticoalveolar pillar) is very thick. Keeling along the sagittal midline, the generally depressed appearance of the parietal surfaces, the shape of the temporal squama, and the transverse expansion of the base relative to the low vault all make the skull look more like a small *H. erectus* than *H. habilis*. There are other *erectus*-like traits of the glenoid cavity, tympanic plate, and petrous bone. In overall shape, D2700 is similar to D2280 and D2282, and D2735 resembles D211. Despite certain differences among these Dmanisi individuals, we do not see sufficient grounds for assigning them to more than one hominid taxon (*18*). We view the new specimen as a member of the same population as the other fossils, and we here assign the new skull provisionally to *Homo erectus* (=*ergaster*) (*19*–*21*).

Although the 1999 crania have been referred to *Homo ex gr. ergaster*, they exhibit some features indicating a degree of isolation from groups in Africa and the Far East (*5*, *22*). The mandible (D2600) (fig. S4 and table S1) discovered in 2000 underscores the fact that some Dmanisi fossils depart from the morphology characteristic of *H. erectus* (*7*, *23*). Nevertheless, the new skull may be regarded as an extremely small-brained representative of this species. Its endocranial volume of ~600 cm^3 is substantially smaller than expected for *H. erectus* but near the mean for *H. habilis* (*sensu stricto*) (*24*). Although this individual is lightly built, it cannot be identified unequivocally as female. The extent of differences in size and other aspects of morphology within the Dmanisi population implies that reassessment of both the sex and the existing taxonomic assignments of the earliest *Homo* fossils from other localities (particularly in Africa) may be appropriate.

The Dmanisi hominids are among the most primitive individuals so far attributed to *H. erectus* or to any species that is indisputably *Homo* (*25*), and it can be argued that this population is closely related to *Homo habilis* (*sensu stricto*) as known from Olduvai Gorge in Tanzania, Koobi Fora in northern Kenya, and possibly Hadar in Ethiopia (*26*–*28*). The presence at Dmanisi of individuals like D2700 calls into question the view that only hominids with brains equivalent in size to those of mid-Pleistocene *H. erectus* were able to migrate from Africa northward through the Levantine corridor into Asia. It now seems more likely that the first humans to disperse from the African homeland were similar in grade to *H. habilis* (*sensu stricto*).

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and the molars are larger, increasing slightly in size from M1 to M3 (see Table S1) (*32*).
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Supporting Online Material
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Table S1
Figs. S1 and S2

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Rooting the Eukaryote Tree by Using a Derived Gene Fusion

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Single-gene trees have failed to locate the root of the eukaryote tree because of systematic biases in sequence evolution. Structural genetic data should yield more reliable insights into deep phylogenetic relationships. We searched major protist groups for the presence or absence of a gene fusion in order to locate the root of the eukaryote tree. In striking contrast to previous molecular studies, we show that all eukaryote groups ancestrally with two cilia (bikonts) are evolutionarily derived. The root lies between bikonts and opisthokonts (animals, Fungi, Choanozoa). Amoebozoa either diverged even earlier or are sister of bikonts or (less likely) opisthokonts.

One of the most challenging evolutionary problems is locating the root of the eukaryote tree. The widespread view that early eukaryotes were amitochondrial has recently been dramatically overturned (*1*). Multigene trees, though more reliable than single-gene trees, leave many possibilities open (*2*). We use a derived gene fusion between dihydrofolate reductase (DHFR) and thymidylate synthase (TS), previously known from a few eukaryotes (*3*), to greatly narrow down the position of the root. In eubacteria, both genes are separately translated, often in one operon, TS preceding DHFR (Fig. 1). Animals and fungi also have separately translated DHFR and TS genes (not in an operon), presumably the original eukaryotic condition (*3*). Plants, alveolates, and Euglenozoa instead have a bifunctional fusion gene with both enzyme activities in one protein (*3*). As this fusion is clearly derived compared with separate genes, it suggests that the eukaryote tree's root must be below the common ancestor of plants, alveolates and Euglenozoa (*3*). The root cannot lie among groups all having the fusion gene, because they share this derived character that arose in their common ancestor. As those with separate genes have the primitive condition, the root must lie adjacent to or within one of them.

This reasoning is valid only if the genes fused just once and were never secondarily split or laterally transferred within eukaryotes. Although evolutionary gene splitting is known for a few bacterial genes, it is a priori many orders of magnitude less likely for eukaryotic protein-coding genes, requiring simultaneous evolution at four separate, correctly ordered positions, not just two as in bacteria: we know no examples. Secondary splitting might also theoretically occur by gene duplication and differential deletions within each copy; even this would involve three independent mutations, two positionally precise, so is very improbable.

We amplified and sequenced DHFR-TS fusion genes from four previously unstudied groups: the heterokont chromist '*Cafeteria*' *marsupialis* and three protozoan phyla (centrohelid Heliozoa, Apusozoa, Cercozoa); plus, as positive controls, additional Euglenozoa and Ciliophora (*4*). Multiple alignment shows that all are authentic DHFR-TS fusion genes with one open reading frame. A further control was the choanozoan *Corallochytrium limacisporum*; as expected, because Choanozoa are probably sisters to animals (*5*), we found no fusion gene. Only in one other protist phylum (Amoebozoa, represented by *Phreatamoeba*, *Phalansterium solitarium*) could we similarly detect no fusion gene. In *Phreatamoeba* and *Corallochytrium*, we successfully amplified TS genes alone (*4*).

The presently known phylogenetic distribution of DHFR-TS fusion genes is shown in Fig. 1; strikingly, their origin coincides with that of the biciliate condition. All organisms above the apparent point of origin of the fusion protein in Fig. 1 are ancestrally biciliate and collectively called bikonts (*5*). Bikont monophyly is also shown by trees for 123 genes with ~25,000 amino acid positions (*6*), if rooted as in Fig. 1. In plants, chromalveolates, and excavates, biciliate cells, differentiate their cilia and roots over two successive cell cycles; this developmental complexity strongly indicates that bikont ciliary transformation is derived (*5*). The distribution of the DHFR-TS fusion supports this interpretation. We cannot exclude the possibility that the fusion occurred not at the very origin of bikonts, but after some small and obscure unstudied bikont lineage diverged from the rest. Our conclusion strongly contradicts recent assumptions that the root is among the excavate bikonts [e.g., beside Parabasalia (*7*) or jakobid Loukozoa (*8*)]; the two single amino-acid enolase deletions suggesting early divergence of Parabasalia (*7*) are much more easily reversible than the DHFR-TS fusion.

Archezoa (Parabasalia and metamonads) were formerly considered possible primitive eukaryotes because of absence of mitochondria and deep branching in sequence trees (*7*, *9*), but several lines of evidence now indicate that they are a relatively advanced group within excavates. Neither DHFR nor TS enzymatic activity is detectable in *Giardia intestinalis* (Metamonada), *Trichomonas vaginalis* and *Tritrichomonas foetus* (Para-

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