

László Kordos

Geological Institute of Hungary, H-1143 Budapest, Stefánia út 14, Hungary. E-mail: Kordosl@compuserve.com

David R. Begun

*Department of Anthropology, University of Toronto, Toronto, ON, M5S 3G3, Canada. E-mail: Begun@chass.utoronto.ca**Journal of Human Evolution* (2001) **41**, 689–700

doi:10.1006/jhev.2001.0523

Available online at <http://www.idealibrary.com> on 

Introduction

Late Miocene great ape crania are rare, mostly fragmentary, and the focus of much debate on great ape and human origins (Brown & Ward, 1988; Bonis *et al.*, 1990; Moyà-Solà & Köhler, 1993, 1995; Begun, 1994; Kordos & Begun, 1997; Schwartz, 1997). Due to poor preservation, information on important features of cranial anatomy (facial angulation, prognathism, relative and absolute brain size) must be estimated from incomplete or reconstructed specimens. This has led to disagreement on the evolutionary history of hominid cranial morphology and contributes to uncertainty with regard to the origin and composition of the clades of living hominids (pongines and hominines). In this preliminary communication we report on the discovery of a new cranium of *Dryopithecus brancoi* from Rudabánya, Hungary. It is the most complete cranium of this taxon ever recovered. The specimen, RUD 197–200, includes a nearly complete dentition and, for the first time in *Dryopithecus*, a neurocranium with a complete glabella toinion chord with direct bony contact to the maxilla. Standard anatomical landmarks are lacking, preventing unambiguous measurement of facial height, and the neurocranium is not complete

enough to directly measure endocranial volume, but preliminary estimates indicate similarities to African apes in terms of facial angles (klinorhinchy) and small female great apes with regard to brain size. While more comparisons are needed to confirm these features in *Dryopithecus*, preliminary analysis supports previous interpretations that *Dryopithecus* is indeed a great ape, and more specifically of a phylogenetic link between this taxon and the African ape/human clade.

Age, paleoecology and stratigraphy

Rudabánya is a rich, well-known set of late Miocene localities from which two primate taxa are known (*D. brancoi* and *Anapithecus hernyaki*). Details of R. II, by far the richest Rudabánya locality, have most recently been reviewed in Kordos & Begun (2001). To summarize what is currently known about R. II, abundant faunal and botanical remains, and detailed taphonomic, paleoecological, geochemical, sedimentological and biochronological analyses all point to a subtropical, forested, swamp margin environment deposited about 10 Ma in shallow embayment of the northern shore of the Central Paratethys (Kordos & Begun, 2001, submitted; Kordos & Bernor, in prep.). The specimen, including all separately discovered pieces, was recovered from the gray marl, a hard, calcium rich clay from which many of the more complete specimens from Rudabánya have been recovered. The gray

Address correspondence to: David R. Begun, Department of Anthropology, University of Toronto, Toronto, ON, M5S 3G3, Canada. E-mail: Begun@chass.utoronto.ca

marl was deposited under low energy conditions and represents a shallow lake margin facies underlying an unconsolidated lignite and black mud layer from which most of the R. II *Dryopithecus* specimens were recovered. The black mud was deposited under higher energy conditions, leading to higher levels of breakage. While *Dryopithecus* is more common in the black mud and *Anapithecus* is more common in the gray marl, both primates are found in both layers, and there is no evidence of a significant lapse of time between them (Kordos & Begun, 2001).

Preservation and recovery

The specimen consists of five separately discovered and catalogued specimens (Table 1). The partial cranium (RUD 200) was discovered by G. Hernyak on 14 July 1999. Three isolated teeth were recovered within centimeters of each other and the cranium on 15 July. RUD 197, the RI^2 , was found by D.R.B., and RUD 198–199 (LC and RI^1) were found by A. Clinton. A left I^1 (RUD 121) was recovered in 1992 by P. Smolt about 4 m from the cranium in the same sediment and level. It is morphologically identical to the antimere found in direct association with the cranium and is attributed to the same individual (Kordos & Begun, 2001). Although the teeth are nearly perfect in their preservation, the cranium was severely crushed, as are many specimens in the hard gray marl, due to various post-depositional processes (slumping and micro-tectonic movements). Great care was taken to remove the specimen intact from the field, and some of the consolidating material continues to adhere to the specimen (visible in superior view). The specimen was prepared in the laboratory with only undistorted fragments with conjoining surfaces reconnected and aligned based on clearly visible surface details. A large number of fragments (>100), most between 1 and 5 mm in maximum dimension, remained

detached. RTV silicone molding compound was used to make a high-resolution mold of the reconstructed specimen and a number of the larger isolated fragments.

The dentition is more complete than any other specimen of the genus, lacking only the left I^2 (CLI 18,000 lacks the LC and both I^2 and RUD 44/45/47/140–144 is missing the LI^2 , RP^4 and LM^1). The left maxilla lacks the palatine process posterior to M^1 . Preserved are most of the left premaxilla with incisor alveoli, the right maxilla to M^1 , the right zygomatic, most of the right frontal squama, the medial half of the left superior orbital margin, most of the right parietal and right temporal, and fragments of left parietals and basicranium (Figure 1). The right frontal process of the zygomatic bone is in contact with the zygomatic process of the frontal bone, which is in turn in contact with the neurocranium posteriorly to inion and slightly beyond. The fragment of the left orbit including a portion of the interorbital space is preserved slightly lateral to the midline. Orbital contours are well preserved on the right side to the zygomatico-maxillary suture, and on the left side medially from nasion to the mid-superior orbital margin. The orbital margins below nasion and medial to the zygomatico-maxillary suture are not preserved. The nasal aperture margin is preserved from the floor of the aperture to about the level of the canine apices. The material is housed in the Geological Institute of Hungary. Measurements appear in Table 1.

Description and comparisons

RUD 200 is small compared to other specimens from Rudabánya (Kordos, 1988; Begun, 1992; Kordos & Begun, 1997, 2001) (Table 2). Like other *Dryopithecus*, it has a relatively short face for a great ape, with a vertically oriented, bi-convex premaxilla and a stepped subnasal fossa. The anterior face is similar to juvenile great apes in that the premaxilla lacks the dramatic

Table 1(a) Dental measurements and indices for RUD 200 and associated specimens where noted

I ¹	6·9/7·0/11·1/10·8 (RUD 121)		6·9/7·0/10·8/10·9 (RUD 199)
I ²	—		4·3/6·1 (RUD 197)
C	8·8/6·9/11·5/8·2 (RUD 198)		9·0/6·8/11·6/8·2
P ³	6·2/10·2		6·4/10·0
P ⁴	6·1/9·7		6·1/9·6
M ¹	9·1/9·9		9·1/9·7
M ²	9·7/10·8		9·9/10·5
M ³	9·7/10·6		9·7/10·9
Min/max ratios (<i>n</i>)			Canine shape ratios
I ¹ mesiodistal MI	1·36 (8)		HT/L RT/CR
I ¹ labiolingual MI	1·14 (8)	Right	1·29 0·91
M ² mesiodistal MI	1·33 (8)	Left	1·31 0·93
M ² buccolingual MI	1·25 (8)		

Measurements from left to right in each tooth type as follows: I¹-mesiodistal, labiolingual, labial height and lingual height; canine-maximum length and perpendicular breadth, labial height, root length up to the cervix; all other dental measurements are mesiodistal and buccolingual. MI=maximum/minimum index. Measurements in mm.

Table 1(b) Cranial measurements for RUD 200

Orbital breadth	28·0
Orbital height	29·0
Interorbital breadth	14·6
Bi-orbital breadth	75·0
Malar depth (along the zygomatico-facial suture)	20·1
Zygomatic root height	16·9
Zygomatic frontal process breadth	7·1
Zygomatic temporal process depth	10·2
Zygomatic temporal process breadth	3·1
Temporal fossa depth	9·5
Palatal breadth @ canine	18·7
Palatal breadth @ P3	19·7
Palatal breadth @ P4	21·7
Palatal breadth @ M1	23·4
Palatal breadth @ M2	25·8
Palatal breadth @ M3	27·3
Palatal breadth @ (I1-M3)	55·8
Maximum external palatal breadth	47·0
Cranial length (glabella-inion)	100·0
Postorbital constriction	56·0
Glabella-bregma	48·5
Facial height (prosthion-nasion)	49·5

Bi-orbital breadth and postorbital constriction are the right side measurements × 2. Measurements in mm.

elongation of many adult great apes [though *Dryopithecus* overlaps *Gorilla* in relative premaxillary length (Begun, 1994)]. It is distinguished from other anthropoids including *Hylobates*, which have a much smaller premaxilla, in both length and breadth, a

narrow or notched nasal aperture, a smooth transition to the nasal fossa, and a large fenestration between the premaxilla and the maxillary palatine process. RUD 200 also preserves a high and broad root of the zygomatic process positioned above the mesial

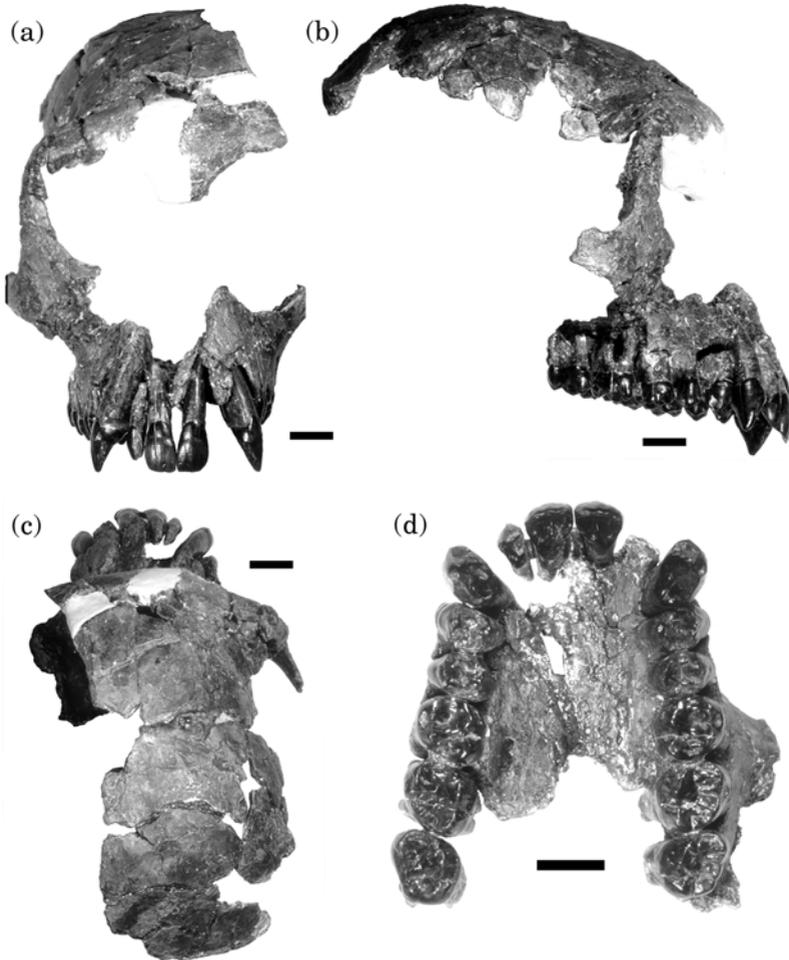


Figure 1. RUD 197–200, showing the main conjoinable parts. (a) Frontal view. Note the relatively high crowned incisors and canines, the high zygomatic process root and the broad interorbital breadth. (b) Lateral view. Note the direct contact from the maxilla through the neurocranium. (c) Superior view. Note the elongated neurocranium, limited postorbital constriction and moderate projection of the nasoalveolar clivus anterior to glabella. (d) Palatal view of RUD 200. Note the closely similar size of the molars and the length of the premolars. Bars = 10 mm.

half of M^2 , a vertically oriented maxillary nasal process preserved from the base of the nasal aperture for about 1.5 cm along the edge of the aperture, and a shallow canine fossa (damaged on right side). The interorbital space is broad and the orbits have sharp lateral margins. The frontal sinus is moderate in size and largest at nasion, continuing from below nasion into frontal squama. Two small zygomatico-facial

foramina occur infero-lateral to the lower lateral corner of the orbit (preserved only on the right side) near the orbital margin. The malar surface of zygomatic is anterolaterally oriented and the frontal process of the zygomatic is comparatively robust given the overall size of the specimen. RUD 200 has a relatively projecting midface compared to *Pan* and *Pongo*, with the distal surface of canine alveolus about 8 mm from the

Table 2(a) Comparative dental measurements

Dimension	RUD 200	RUD 77	RG 29060	RG 29074	<i>P. p. fem</i>	<i>P. t. s. fem</i>	<i>H. synd.</i>
Body mass	?	?	27 kg	31.5 kg	33.2 kg	33.7 kg	11.9 kg
RI1	48.3	—	75.5	98.6	79.0	104.6	31.2
RI2	26.2	—	52.9	68.8	53.9	74.8	24.5
R C (female)	61.2	—	53.7	106.2	61.6	105.3	57.2
RP3	64.0	68.0	63.2	79.0	67.5	81.9	35.3
RP4	58.6	67.8	49.8	66.7	55.7	70.3	37.0
RM1	88.3	91.5	79.9	112.3	88.3	120.9	52.6
RM2	104.0	106.8	85.3	114.0	90.1	119.5	64.0
RM3	96.0	95.7	71.8	113.2	78.0	100.4	56.2

Length × breadth. RG 29060 is a female *Pan paniscus* and RG 29074 is a female *Pan troglodytes schweinfurthii*, both of known body masses. *P. p. fem.*—*P. paniscus* female ($n=10$). *P. t. s. fem.*—*P. troglodytes schweinfurthii* female ($n=10$). *H. synd.*—*Hylobates syndactylus*, sex unknown, (Remane, 1960), ($n=9-39$). All tooth measurements from the right side (except RUD 77 P³⁻⁴ and M²). Measurements of hominid teeth by D.R.B. as described in Table 1, in mm. Extant body masses from museum records and Smith & Jungers (1997).

Table 2(b) Comparative cranial measurements

Dimension	RUD 200	RUD 77	RG 29060	RG 29074	<i>P. p. fem</i>	<i>P. t. s. fem.</i>	<i>H. synd.</i>
Body mass	?	?	27 kg	31.5 kg	33.2 kg	33.7 kg	11.9
Orbital breadth	28	31 (est.)	29.8	33.5	29.9	33.5	25.0
Orbital height	29	31 (est.)	31.0	33.3	30.8	33.9	22.8
Bi-orbital breadth	75	84.3	89.6	101.4	86.3	102.2	68.7
External palatal breadth	47.0	54 (est.)	51.8	57.5	50.0	57.0	40.2
Cranial length	100.0	109.7	126.1	137.2	121.3	133.8	88.2
Postorbital constriction	56	63 (est.)	68.1	67.3	64.7	70.8	48.5

Abbreviations and samples as in Table 2(a). All measurements in mm. RUD 77 orbital measurements corrected from Kordos & Begun (1997). Comparisons with the more complete RUD 200 revealed residual distortion due to crushing in the orbit of RUD 77.

anterior-most extension of the maxillary sinus. The maxillary sinus extends to P³–P⁴ anteriorly and is large, with some extension into zygomatic. The palate becomes deeper and broader posteriorly, and is shallow anterior to P³.

The neurocranium is in anatomical connection with the face via the lateral orbital pillar on the right side. This pillar was found damaged by post-depositional processes but re-alignment was not problematic due to the comparative robusticity of this structure and good preservation of surface details. The neurocranium is elongated relative to cranial height and breadth (estimated), and inion is situated above the superior orbital margin in the approximated Frankfurt horizontal. On

the frontal bone there is a shallow supra-glabellar sulcus and a detectable but poorly developed supraorbital torus. In configuration these are much like those on RUD 77 (Kordos & Begun, 1997). A subtle temporal line (right side) continuous with the lateral edge of the lateral orbital pillar converges toward the sagittal suture posterior to bregma, but remains at least 1 cm lateral to the sagittal plane. RUD 200 has a broad, bi-convex, relatively horizontal frontal squama that broadens posteriorly. Posteriorly the bi-parietal breadth is greatest near asterion, and a strong nuchal crest separates the occipital and nuchal surfaces of the occipital bone. The articular and petrous portions of the right temporal bone are present but

poorly preserved. They are smaller but otherwise essentially identical to those described for a more fragmentary female cranium from Rudabánya, RUD 77, with a shallow but concave glenoid fossa, prominent entoglenoid, vertical postglenoid, fused articular and tympanic aspects of temporal laterally (inferred from the pattern of breakage), shallow subarcuate fossa, and details of the petrous morphology as described for RUD 77 (Kordos & Begun, 1997). The endocranial surface has well preserved sulcal and gyral impressions and an artificial endocranial cast is under analysis. The anterior cranial fossa is narrow but relatively tall. All cranial sutures are closed but not obliterated.

The dentition is similar to Rudabánya *Dryopithecus* as described elsewhere (Begun & Kordos, 1993; Begun, 1994; Kordos & Begun, 1997). Briefly, the incisors are high crowned and relatively narrow with prominent lingual pillars and marginal ridges. The canine is also high crowned but clearly female in morphology, with the crown flared at the cervix and having a large angle between the apex and the mesial and distal edges. Canine indices that have been shown to effectively distinguish male and female hominoids are within the ranges of all female hominoids though they are also at the low end of the ranges of some males (Kelley, 1995) (Table 1). The P³ is ovoid with mild labial crown flare, and minimal cusp heteromorphy, as in other females of the taxon (Kretzoi, 1975; Begun & Kordos, 1993). These observations are consistent with overall dental and cranial size, both of which also suggest that RUD 200 is female. The P⁴ is more rectangular and symmetrical than the P³. Molar size order is M¹ < M² < M³, but all the molars are close in size. All the molars have a typical *Dryopithecus* morphology with cusps positioned toward the edges of the crown, enclosing relatively deep occlusal basins, and crossed by well-marked occlusal crests. The occlusal surfaces are

more complex than many *Dryopithecus* molars due to the relative lack of wear. All three molars lack cingula, though M¹ and M² have small mesiolingual notches. M¹ is nearly square in outline and slightly smaller than M². M² is more elongated with a larger hypocone and a reduced metacone. M³ is somewhat unusual in being elongated and tapered, with a strongly reduced metacone and a number of accessory cusps between the metacone and the hypocone along the distal marginal crista. M³ was in occlusion at the time of death, but with minimal wear. The root apices on the M³ are still open, while all other root apices are closed. All teeth are minimally worn and perikymata are clearly visible on most of the teeth. A linear hypoplastic defect is apparent on the buccal surface of the right P³. The right M² crown has a clean transverse break between the metacone apex and the notch between protocone and hypocone (reassembled in Figure 1), revealing a thinly enameled crown cap with high dentine penetrance. The combined evidence of the dentition and cranium indicates a young adult female individual.

In all dimensions RUD 200 is smaller but morphologically comparable to RUD 77 (Kordos & Begun, 1997) (Table 2). RUD 77 has slightly broader premolars and a less strongly tapered M³, but the same dental proportions. RUD 200 differs more from other females from Rudabánya, such as RUD 12 and RUD 15, which have more robust canines, relatively longer incisors compared to labiolingual breadth, lower crowned molars (at least partly related to differences in wear), shallower palates, more vertically implanted canines in frontal and lateral views, and deeper canine fossae. The males RUD 7 and RUD 44/45/47/140–144 are more similar to RUD 200 in maxillary and dental morphology. Currently we view the diversity in this sample as within the expected range of variation of one species. The I¹ specimens RUD 199 and RUD 121 are the smallest of *Dryopithecus* from

Rudabánya, while another specimen from the gray marl, RUD 82, is the largest I¹. The M² specimens from RUD 200 are also the smallest of *Dryopithecus* from the site, while RUD 85, again also from the gray marl, is the largest M² (this specimen is identified as an M³ in Kordos & Begun (2001), but we now feel it is more probably an M²). At both tooth positions the range of variation as indicated by maxima/minima indices falls within, though at the high end, of the ranges of variation observed within larger samples of living hominoids (Table 1) (Martin & Andrews, 1993). Although the sample sizes are relatively small, this is probably a good indication of high sexual dimorphism in *D. brancoi*. Of course, it is also worth noting that RUD 82 and RUD 85 are the largest specimens in their respective positions for the entire sample of *Dryopithecus*, in which four species are currently recognized (Begun, 2001). Nevertheless, there are no morphological or metric criteria that convincingly justify the recognition of two species of *Dryopithecus* at Rudabánya, though we cannot exclude this possibility.

Preliminary observations on facial angulation and endocranial capacity

RUD 200 preserves the neurocranium from glabella to inion, and is thus the first specimen preserved to this extent among late Miocene hominids. It is also the only specimen we know of that preserves a direct connection between the face and the neurocranium. While neurocranial contours and contact between the face and neurocranium should provide data useful in estimating such important characters as endocranial volume and cranial angulation (both central to the debate on late Miocene hominid relations to extant hominids), the standard landmarks required to unambiguously measure facial hafting are not preserved on this otherwise fairly complete specimen. Similarly, cranial capacity is not directly

preserved, due to the lack of a basicranium, but previous work on the relationship between cranial capacity and cranial length does suggest a close relationship between these variables, indicating that the latter can be predicted from the former with a known amount of uncertainty. In the interest of reporting results of more general interest for such a well-preserved specimen we present preliminary estimates of both cranial capacity and overall cranial shape in *D. brancoi* based on RUD 200.

Elsewhere it has been shown that cranial length (the glabella–inion chord) or other external dimensions can provide a basis for estimating cranial capacity in hominoids (Kordos & Begun, 1998; Walker *et al.*, 1983). We have estimated the endocranial volume of RUD 77, a slightly larger specimen than RUD 200, at between 305 and 329 cc, mean=320 (Kordos & Begun, 1998). However, RUD 77 is missing a direct connection between the preserved occipital portion and the remainder of the specimen, introducing some uncertainty regarding cranial length. The estimate of cranial capacity in RUD 77 was based on the calculated relationships between measured endocranial volume and several measures of neurocranial length in a small sample of extant great apes ($n=32$). RUD 200, in contrast, has the glabella–inion chord intact. It yields an estimated cranial capacity of 305 cc (95% CI 280–332) based on the regression of cranial capacity and neurocranial length from inion to glabella [$CC=2.5 (CL)+55.3$]. This predicted value is based on the same relatively small sample and must be tested with a larger sample and with other measures of neurocranial size, such as maximum breadth that can be reliably estimated on RUD 200. However, this preliminary estimate is consistent with the overall size of the neurocranium of RUD 200, which is larger, particularly in post-orbital and maximum breadth, than any nonhominoid primate, and close in size to

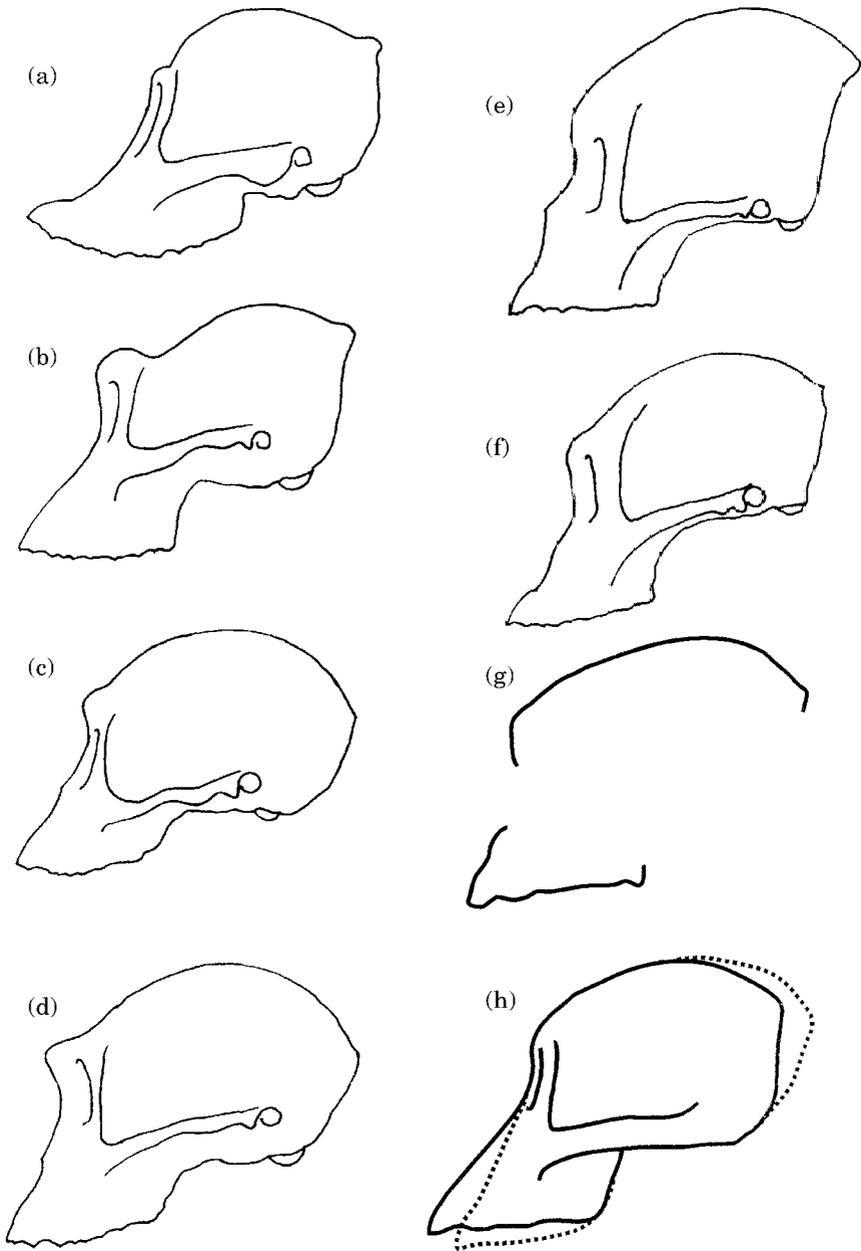


Figure 2. Lateral profiles of female hominoid crania drawn to the same length. (a) *Pongo*, (b) *Gorilla*, (c) *Pan paniscus*, (d) *Pan troglodytes*, (e) *Preconsul*, (f) *Ouranopithecus*, (g) RUD 200 (*Dryopithecus*), (h) composite from Köhler *et al.* (2001) (solid line) with suggested corrected profile based on the data presented here (dashed outline). Based on comparisons to more complete crania from Rudabánya the Köhler *et al.* (2001) composite is unlikely to be correct. Note the ventral inclination of the palate of RUD 200. Modified from Kordos and Begun (1997). See text.

small *Pan*. Estimates of the body mass of RUD 200 would provide a means of calculating relative brain size in *D. brancoi*, but uncertainty about the precise endocranial volume and difficulties in estimating body mass in such a cranially and dentally small hominoid require more detailed analysis. However, it seems fairly clear based on overall dimensions and comparisons to living great apes that the endocranial volume of RUD 200 is within the range of extant female *Pongo* and *Pan troglodytes* (276–494 cc; Tobias, 1971), while in most dimensions it is cranially and dentally smaller than all great apes (Table 2).

The contact among the frontal, zygomatic and maxillary bones in RUD 200 provides the first direct evidence of cranio-facial hafting in *Dryopithecus*. Despite its completeness, the Frankfurt horizontal and the basicranial axis, which are most commonly used to measure facial angulation, are not preserved on RUD 200. Thus it is not possible at present to quantify cranio-facial hafting in RUD 200 in a manner completely comparable to classic measures of facial angulation in anthropoids (e.g., Biegert, 1957; Hofer, 1952; Shea, 1988). However, visual inspection of RUD 200 in lateral view reveals a basic similarity to African apes and a difference from Asian apes. The former are klinorhynch, having a palatal plane that is inclined ventrally relative to the Frankfurt Horizontal, while the latter are airohynch, with their palates inclined dorsally relative to the Frankfurt Horizontal (Shea, 1988). When RUD 200 is figured relative to extant hominoid crania in a manner that approximates the same orientation based on as many comparable landmarks as possible the similarity to African apes is obvious. We are in the process of devising new methods of measuring facial angle based on landmarks preserved on RUD 200. In the meantime, we suggest based on visual comparisons to extant hominoids that RUD 200 is more likely to be klinorhynch than airohynch.

The contact between the face and neurocranium and the shape of the cranium in superior view in RUD 200 also calls into question certain aspects of the composite cranium of *Dryopithecus* recently proposed by Köhler *et al.* (2001). We have to wonder about the usefulness of constructing a composite cranium of *Dryopithecus* based on specimens from males of two different species and a female from a third species. The evidence from Rudabánya suggests that this approach may not be the most fruitful. RUD 200 and RUD 77 have more elongated crania than the composite illustrated by Köhler *et al.* (2001) and lack the expanded nuchal region in superior view. The superior view as illustrated by Köhler *et al.* (2001) is based on an older plaster of Paris cast of a preliminary reconstruction of RUD 77, while their lateral view is based on our more recent reconstruction (Kordos & Begun, 1997). Unfortunately, these differ significantly, illustrating the importance of collecting data on original fossils (the RUD 77 original is available for analysis at the Geological Museum of Hungary and high resolution casts of RUD 77 are available as well). The face of RUD 200 is shorter and more vertical than suggested for *Dryopithecus* in the Köhler *et al.* (2001) composite. A male *D. brancoi* (RUD 44/45/47/140–144) is also described as having a short face, in the range of *Gorilla* rather than *Pan* or *Pongo* (Begun, 1994). In short, the mixing of males and females of three different species, and the actual morphology of one relatively complete cranial specimen of *D. brancoi*, a second relatively complete neurocranium, and a third face all indicate that the composite illustrated by Köhler *et al.* (2001) cannot be considered a reliable reconstruction of *Dryopithecus* cranial morphology.

Summary and conclusions

RUD 200 is the first fossil great ape specimen with direct evidence of overall cranial

Table 3 Great ape and African ape cranio-dental character states of *Dryopithecus*

Great ape character states	African ape character states
Labiolingually thick incisors	Bi-convex premaxilla
Compressed canines	Stepped subnasal fossa
Elongated premolars and molars	Patent incisive canals
M1 ≤ M2	Broad, flat nasal aperture base
No molar cingula	Shallow canine fossa
Reduced premolar cusp heteromorphy	Supraorbital torus
High root of the zygomatic	Inflated glabella
Elongated midface	Frontal sinus above and below nasion
Broad nasal aperture below the orbits	Deep glenoid fossa
Reduced midfacial prognathism	Projecting entoglenoid process
Elongated, robust premaxilla	Fused articular and tympanic temporal
Premaxilla-palatine overlap	Broad temporal fossa
Shallow subarcuate fossa	Elongated neurocranium
Large brain	Klinorhynchy
High cranial base	Moderate alveolar prognathism

morphology. The only other similarly preserved fossil hominoid specimen is KNM-RU 7290, attributed to the basal hominoid *Proconsul* from the early Miocene of Rusinga Island, Kenya (Walker *et al.*, 1983). *Dryopithecus* is thought by some to be more closely related to Asian great apes (Moyà-Solà & Köhler, 1993, 1995, 1996) and by others to African apes and humans (Kordos, 1987; Begun, 1994; Begun & Kordos, 1997; Kordos & Begun, 1997). Until now the cranial remains of *Dryopithecus* have been fairly fragmentary, allowing substantial differences in interpretation of morphological details such as the development of the supraorbital structures, the frontal sinus or the morphology of the premaxilla (Kordos, 1987; Moyà-Solà & Köhler, 1993, 1995; Begun, 1994; Begun & Kordos, 1997; Cameron, 1997; Kordos & Begun, 1997). However, RUD 200 preserves many of these regions intact and undistorted, and it does tend to confirm the impression gleaned from less complete specimens of an affinity to African apes, particularly juvenile African apes that have less well formed supraorbital structures and smaller faces than do adults. Our preliminary assessment of cranio-facial hafting in

RUD 200 also points to an African ape-like orientation of the face relative to the neurocranium in *Dryopithecus*, though the results presented here must be considered preliminary in advance of the development of methods to quantify these features in fragmentary fossils (Figure 2). Asian great apes and *Proconsul* have airorhynchous, or dorsally deflected faces and short neurocrania (Walker *et al.*, 1983; Brown & Ward, 1988) (Figure 2). Asian great apes also have numerous synapomorphies of the midface and orbits not found in *Dryopithecus* from Rudabánya (Andrews & Cronin, 1982; Pilbeam, 1982; Brown & Ward, 1988; Ward, 1997). Early and middle Miocene hominoids lack the alveolar prognathism and premaxillary development of *Dryopithecus*, *Sivapithecus*, *Ouranopithecus*, living great apes and fossil humans (Begun, 1994; Ward & Kimbel, 1983).

These morphological patterns are most consistent with the view that *Dryopithecus* is a hominine (most closely related to African apes and humans), and is neither a member of the Ponginae (Moyà-Solà & Köhler, 1995) nor the “*Dryopithecinae*” (a subfamily designation that we do not recognize) as defined by Andrews (1992) (Table 3).

RUD 200 also provides the best fossil evidence to date to estimate brain size in a fossil great ape. While the conclusions must be regarded as preliminary, indications are that *Dryopithecus* had a great ape-sized brain relative to body size. If this turns out to be verified, it would suggest that great ape brain size has changed little since the origin of the hominids (great apes and humans), except in the human lineage.

Acknowledgements

This research is supported by grants from The Wenner-Gren Foundation, the Natural Sciences and Engineering Research Council of Canada and the Alexander von Humboldt Stiftung. We are grateful to Jay Kelley, Fred Spoor and three anonymous reviewers for helpful comments.

References

Andrews, P. (1992). Evolution and environment in the Hominoidea. *Nature* **360**, 641–646.

Andrews, P. & Cronin, J. (1982). The relationship of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. *Nature* **297**, 541–546.

Begun, D. R. (1992). Miocene fossil hominids and the chimp-human clade. *Science* **257**, 1929–1933.

Begun, D. R. (1994). Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yearb. phys. Anthropol.* **37**, 11–63.

Begun, D. R. (2001). European hominoids. In (W. Hartwig, Ed.) *The Primate Fossil Record*. Cambridge: Cambridge University Press (in press).

Begun, D. R. & Kordos, L. (1993). Revision of *Dryopithecus brancoi*. Schlosser 1901 based on the fossil hominoid material from Rudabánya. *J. hum. Evol.* **25**, 271–286.

Begun, D. R. & Kordos, L. (1997). Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids. In (D. R. Begun, C. V. Ward & M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 291–316. New York: Plenum Press.

Biegert, J. (1957). Der Formwandel des Primatenschädels und seine Beziehungen zur ontogenetischen Entwicklung und den phylogenetischen Specialisationen der Kopforgane. *Gegenbaurs Morphologische Jahrbuch* **98**, 77–199.

Bonis, L. de, Bouvrain, G., Geraads, D. & Koufos, G. (1990). New hominid skull material from the late

Miocene of Macedonia in Northern Greece. *Nature* **345**, 712–714.

Brown, B. & Ward, S. (1988). Basicranial and facial topography in *Pongo* and *Sivapithecus*. In (J. H. Schwartz, Ed.) *Orang-utan Biology*, pp. 247–260. New York: Oxford University Press.

Cameron, D. W. (1997). A revised systematic scheme for the Eurasian Miocene fossil Hominidae. *J. hum. Evol.* **33**, 449–477.

Hofer, H. O. (1952). Der Gestaltwandel des Schädels der Säugetiere und Vögel mit besonderer Berücksichtigung der Knickungstypen der Schädelbasis. *Verhandlungen Anatomischen Gesellschaft* **50**, 102–113.

Kelley, J. (1995). Sexual dimorphism in canine shape among extant great apes. *Am. J. phys. Anthropol.* **96**, 365–389.

Köhler, M., Moyà-Solà, S. & Alba, D. M. (2001). Cranial reconstruction of *Dryopithecus*. *Am. J. phys. Anthropol.* **115**, 284–288.

Kordos, L. (1987). Description and reconstruction of the skull of *Rudapithecus hungaricus* Kretzoi (mammalia). *Annl. Hist. nat. Mus. natn. Hung.* **79**, 77–88.

Kordos, L. (1988). Comparison of early primate skulls from Rudabánya and China. *Anthropologia Hungarica* **20**, 9–22.

Kordos, L. & Begun, D. R. (1997). A new reconstruction of RUD 77, a partial cranium of *Dryopithecus brancoi* from Rudabánya, Hungary. *Am. J. phys. Anthropol.* **103**, 277–294.

Kordos, L. & Begun, D. R. (1998). Encephalization and endocranial morphology in *Dryopithecus brancoi*: implications for brain evolution in early hominids. *Am. J. phys. Anthropol.* (Suppl.), **26**, 141–142.

Kordos, L. & Begun, D. R. (2001). Fossil catarrhines from the late Miocene of Rudabánya. *J. hum. Evol.* **40**, 17–39.

Kretzoi, M. (1975). New ramapithecines and *Pliopithecus* from the lower Pliocene of Rudabánya in north-eastern Hungary. *Nature* **257**, 578–581.

Martin, L. B. & Andrews, P. (1993). Species recognition in middle Miocene hominoids. In (W. H. Kimbel & L. B. Martin, Eds) *Species, Species Concepts and Primate Evolution*, pp. 393–427. New York: Plenum Press.

Moyà-Solà, S. & Köhler, M. (1993). Recent discoveries of *Dryopithecus* shed new light on evolution of great apes. *Nature* **365**, 543–545.

Moyà-Solà, S. & Köhler, M. (1995). New partial cranium of *Dryopithecus* Lartet, 1863 (Hominoidea, Primates) from the upper Miocene of Can Llobateres, Barcelona, Spain. *J. hum. Evol.* **29**, 101–139.

Moyà-Solà, S. & Köhler, M. (1996). A *Dryopithecus* skeleton and the origins of great ape locomotion. *Nature* **379**, 156–159.

Pilbeam, D. R. (1982). New hominoid skull material from the Miocene of Pakistan. *Nature* **295**, 232–234.

Remane, A. (1960). Zähne und Gebiss. *Primatologia* **3**, 637–846.

Schwartz, J. H. (1997). *Lufengpithecus* and hominoid phylogeny. Problems in delineating and evaluating

- phylogenetically relevant characters. In (D. R. Begun, C. V. Ward & M. D. Rose, Eds) *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations*, pp. 363–388. New York: Plenum Press.
- Shea, B. T. (1988). Phylogeny and skull form in the hominoid primates. In (J. H. Schwartz, Ed.) *Orang-utan Biology*, pp. 233–245. New York: Oxford University Press.
- Smith, R. J. & Jungers, W. L. (1997). Body mass in comparative primatology. *J. hum. Evol.* **32**, 523–559.
- Tobias, P. V. (1971). *The Brain in Hominid Evolution*. New York: Columbia University Press.
- Walker, A. C., Falk, D., Smith, R. & Pickford, M. F. (1983). The skull of *Proconsul africanus*: Reconstruction and cranial capacity. *Nature* **305**, 525–527.
- Ward, S. (1997). The taxonomy and phylogenetic relationships of *Sivapithecus* revisited. In (D. R. Begun, C. V. Ward & M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominid Origins and Adaptations*, pp. 269–290. New York: Plenum Press.
- Ward, S. C. & Kimbel, W. H. (1983). Subnasal alveolar morphology and the systemic position of *Sivapithecus*. *Am. J. phys. Anthrop.* **61**, 157–171.