

A New Reconstruction of RUD 77, a Partial Cranium of *Dryopithecus brancoi* From Rudabánya, Hungary

LÁSZLÓ KORDOS¹ AND DAVID R. BEGUN²*

¹Geological Institute of Hungary, H-1143 Budapest, Hungary

²Department of Anthropology, University of Toronto, Toronto, Ontario M5S 3G3, Canada

KEY WORDS Miocene hominids; great apes; cranial restoration

ABSTRACT A newly reconstructed cranium (RUD 77) of the Miocene fossil hominoid *Dryopithecus*, formerly *Rudapithecus* (Kretzoi [1969] Symp. Biol. Hung. 9:3-11; Begun and Kordos [1993] J. Hum. Evol. 25:271-286) is presented here. This specimen, from the late Miocene locality of Rudabánya, in northeastern Hungary, consists of portions of the neurocranium, face, and postcanine dentition. Newly recovered portions of the parietal, occipital, temporal, zygomatic, and premaxillary bones, which are described here for the first time, in association with previously described portions of this specimen (Kordos [1987] Ann. Hist. Nat. Mus. Natl. Hung. 79:77-88) make RUD 77 among the most complete and well preserved neurocrania of any Miocene hominoid. Detailed anatomical descriptions and measurements are provided here, along with comparisons to other relatively complete Miocene hominoid cranial remains, and to living hominoids. While a more complete phylogenetic analysis is in preparation based on the sample as a whole, it is suggested here that RUD 77 provides some additional evidence in support of a previous hypothesis that *Dryopithecus* is more closely related to the African apes and humans than is *Sivapithecus*. Am J Phys Anthropol 103:277-294, 1997. © 1997 Wiley-Liss, Inc.

Rudabánya is a late Miocene hominoid locality in Hungary dating from zone MN 9 (ca. 10 mya) (Kretzoi, 1975; Mein, 1990, 1986; Bernor et al., 1987; Kordos, 1985, 1991; Steininger, et al., 1990) from which fossil hominoids have been recognized since 1967. A number of fossil primates have been described from Rudabánya (Kretzoi, 1975, 1984). The larger specimens, previously attributed to the hominoids *Rudapithecus hungaricus* and *Bodvapithecus altipalatus* (Kretzoi, 1975), are now attributed to *Dryopithecus brancoi* (Begun and Kordos, 1993). The smaller specimens, previously attributed to *Pliopithecus (Anapithecus) hernyaki* (Kretzoi, 1975) and *Rangwapithecus (Ataxopithecus) serus* (Kretzoi, 1984), are now attributed to *Anapithecus hernyaki* (Kordos, 1988; Begun, 1989; in part contra Begun, 1988).

The geomorphology of the primate localities at Rudabánya provides evidence of a peninsula extending into the Pannonian lake, a regional remnant basin of the earlier greater Paratethys sea system (Kordos, 1982, 1991). The peninsula, composed of Triassic limestones and dolomites, was covered with small, steep karstic valleys and other karst related landforms, most of which probably formed during the early and middle Miocene. These paleovalleys, which include the locality from which most of the Rudabánya pri-

Contract grant sponsor: Natural Sciences and Engineering Research Council, Canada; contract grant sponsor: Hungarian Scientific Research Fund (OTKA); contract grant sponsor L.S. Leakey Foundation; contract grant sponsor: Foundation Fyssen.

*Correspondence to: David Begun, Department of Anthropology, University of Toronto, Toronto, Ontario M5S 3G3 Canada. E-mail: begun@chass.utoronto.ca

Received 21 January 1995; revised 28 November 1996; accepted 17 March 1997.

mates were excavated, locality II, typically consist of alternating sequences of lacustrine sediments, fine grained clastics (clays, marls, silts), lignites, and paleosols, representing cyclic episodes of infilling and flooding of the karst depressions.

In 1985 a partial cranium, RUD 77, was discovered by site geologist G. Hernyák, and later described (Kordos, 1987, 1991). This specimen is more complete and less distorted than the remainder of the collection of *Dryopithecus* because it was protected by a network of roots from a tree found in growth position in the overlying upper lignite layer from locality II. Two cubic meters of sediment around the area from which RUD 77 was recovered were collected by L. Kordos. This material was washed, sieved, and sorted, and produced, with the original find, 101 cranial fragments and eight upper teeth. The bones are very fragile, with only the thicker cranial elements remaining. The specimen is highly fragmented but relatively undistorted. In light of new fossil discoveries and additional information on RUD 77, a new reconstruction was completed recently and is described here.

MATERIALS AND METHODS

Frontal and maxillary fragments, portions of the parietal bones, and much of the postcanine dentition were initially assembled and described (Kordos, 1987). Subsequently, additional material from the frontal, temporal, maxillary, sphenoid, and occipital bones were identified and reconstructed. Conjoining surfaces were identified by fracture contours and surface morphology and verified under a stereomicroscope. Pieces were assembled with Ferrobond, a fast setting, highly stable glue soluble in acetone. Cranial contours were identified by surface morphology and maintained with tooth picks until a mold could be made. The specimen was set in Plasticine and molded with Dow Corning HS II RTV Silastic silicone following removal of the tooth picks. Casts were made in dental stone and high resolution epoxy resin. Measurements were made on the original specimen with digital calipers and recorded to the nearest 0.1 mm. Contours were taken with a carpenter's contour gauge. The specimen was compared to fossil

TABLE 1. Dimensions¹ of RUD 77

Interorbital breadth	17.5
Nasion-glabella	6.7
Glabella-bregma chord	52.8
Bregma-inion chord	65.7
Glabella-inion chord	109.7
Biparietal breadth	78 (min. est.)
Nasion-maxillofrontale	9.8
Lateral orbital pillar breadth	
Tubercle	12.7
Zygomaticofrontale	9.9
Orbital breadth	27.0
Orbital height	30 (est.)
Biorbital breadth (external)	84.3
Biorbital breadth (internal)	73.0
Superciliary arch thickness	4.6
Articular eminence length	13.8
Mandibular fossa-porion	14.1
Supraglenoid gutter breadth	8.8
P3-6.6/10.3	RM1-8.8/10.4
P4-6.4/10.6	LM2-9.8/10.9
	RM3-9.2/10.4
	LM1-9.0/—
	RM2-9.6/—
	LM3-9.5/10.8

¹ In millimeters. Dental dimensions are length/breadth.

catarrhines from Kenya, Uganda, Turkey, Greece, China, India, Pakistan, Hungary, Austria, Germany, France, and Spain. Statistics on these data were calculated using Sigma Plot for Windows. The measurements of the specimen are given in Table 1.

DESCRIPTION

Preservation

Premaxilla and maxilla. Detached portions of the alveolar and palatine process with palatal surface and portions of the alveoli; a portion of the maxillo-premaxillary suture and the incisive foramen; portions of the outer bone table of the maxillary body including the root of the zygomatic process and parts of the infratemporal fossa (Fig. 1).

Sphenoid. Detached portions of the greater wing in the area of the infraorbital fissure and lateral pterygoid plate.

Temporal. Portions of the mandibular fossae and associated structures on both sides, the left side including most of the root of the zygomatic process, the superior half of the external auditory meatus, and a small part of the anterior portion of the mastoid process; parts of the petrous pyramid in the area of the internal auditory meatus (both sides), and most of the tympanic tube (Fig. 2).

Occipital. Detached fragments of the nuchal and occipital planes of the occipital



Fig. 1. Occlusal view of the maxilla and dentition of RUD 77.

squama including parts from asterion on both sides; portions of the nuchal crest including adjoining fragments in the area of inion.

Parietal. Conjoining fragments making up most of the left parietal and a large part of the right; detached fragments from close to the coronal and parietotemporal sutures (Figs. 3–5).

Frontal. Largely complete and attached to the parietals; small parts missing from the orbital plates, the right orbital margin, and the squama superiorly and in the infra-temporal fossa.

Zygomatic. Much of the left zygomatic, joined to the frontal, but lacking most of the temporal process, the infraorbital portion, and small pieces from the maxillary process (Fig. 3–5).

Dentition. Left P³ to M³, right M¹ to M³ (Fig. 1). The specimen is housed in the collections of the Geological Museum of the Hungarian Geological Institute, Budapest.

Anatomy

Palate and dentition (fig. 1). The specimen is an adult with well worn dentition

and completely obliterated cranial sutures. The maxilla is highly fragmented, but several important anatomical features can be discerned. A portion of the maxillary palatine process is preserved attached to a portion of the alveolar process, which is itself attached to the lingual roots of the first and second molars. Near the midline it is thick in cross section. In the region of the molars, the alveolar process is shallow lingually. A small portion of the palatal process of the premaxilla preserves part of the incisive foramen, which was small compared to extant primates with fenestrated palates (prosimians, monkeys, and hylobatids) and very similar in size to that of RUD 12, a *D. brancoi* female hemipalate (see below). A small portion of the right lateral incisor alveolus in the same fragment indicates relatively vertically implanted incisors placed well medial to the molar row. A small portion of canine alveolus from the left side indicates a canine root medial to the most lateral extent of the root of the P³. The root of the zygomatic process of the maxilla, preserved on a separate fragment, was thick anteroposteriorly. It is difficult to position relative to the dentition, but appears to have been high and probably between M¹ and M², judging from a small portion of alveolar process surface bone that fits onto the mesial buccal root of the M¹. No other conjoining or identifiable fragments of maxilla are preserved.

All the teeth are high crowned with long, slender buccal roots and thicker, bilaterally compressed lingual roots. The premolars are oval and very close to the same size. The P³ is slightly longer buccally than lingually, but is not truly triangular, as it is in RUD 44, a large male of the same species identified as such from its canine morphology (see below). The metacone is slightly larger than the protocone, but the cusps cannot be said to be heteromorphic, as they are in early Miocene hominoids. There is a broad, relatively narrow mesial fovea separated from a larger, more elongated distal fovea by a subtle crest, probably a worn medial metacrista. The cusps are placed slightly more mesially than distally on the crown (though this is partly due to wear), resulting in premetacristae and preprotocristae that are somewhat



Fig. 2. The temporomandibular fossa and associated structures in RUD 77 in lateral (left) and inferior (right) views. a, entoglenoid process; b, postglenoid process; c, anterior wall of the auditory canal; d, external auditory meatus.



Fig. 3. Lateral views of RUD 77. Note the well developed ridge in the temporal fossa visible on the left side (bottom photo).



Fig. 4. Superior view of RUD 77.

shorter than the postmetacrista and postprotocrista. The postprotocrista is slightly flared lingually to form the distolingual corner of an expanded talon. The P⁴ is slightly longer

with a larger, more elongated talon, and more centralized cusps (along the buccal and lingual margins). The precrista and postcrista of both cusps are roughly equal in length, as are the buccal and lingual mar-

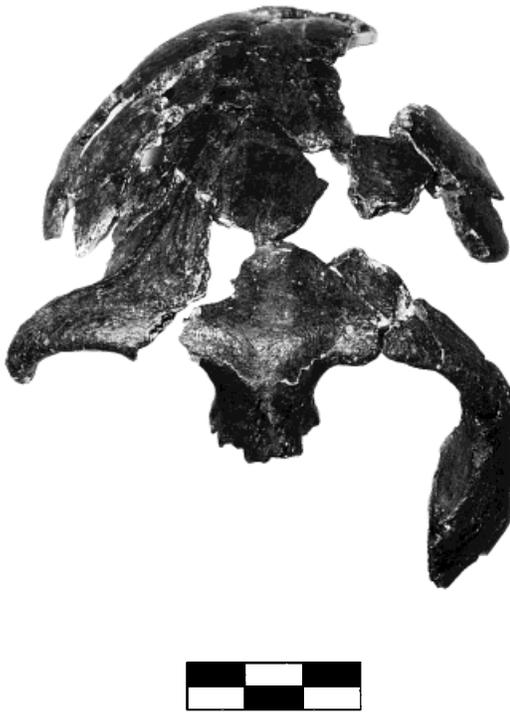


Fig. 5. Frontal view of RUD 77.

gins of the tooth, giving it a more rectangular shape than the P^3 . In other details it is quite similar to the P^3 . Both premolars have three roots (two buccal, one lingual).

The molars have a simple occlusal morphology. The protocones and hypocones of both M^1 's are worn down to the roots, though asymmetrically, with the protocone being more worn on the left side and the hypocone more worn on the right. Only the mesial most portion of the protocone and the preprotocrista remain on the right (nothing remains of the left), while only a part of the posthypocrista near the middle of the distal edge of the left M^1 remains (the hypocone is completely worn away on the right). The buccal cusps are also worn, but quite distinct, with only very small dentine pits at their tips. Among the lingual cusps, the metacone is larger than the paracone, and there is a well formed buccal notch between the two. On both cusps, the mesial crista are shorter than the distal crista, which contributes to the formation of a very short, narrow mesial fovea (bounded buccally by a short

preparacrista and a very small paraconule) and a more elongated, large distal fovea. The trigon basin, though larger than the fovea, is nevertheless short buccally compared to the M^2 . The transverse crista demarcating the mesial and distal edges of the trigon are worn but still well marked.

The M^2 's are also well worn lingually, but more symmetrically than the M^1 's. On both M^2 's the protocone is gone, but slightly more of the hypocone is preserved on the left side than on the right. Buccally, the paracone is noticeably larger than the metacone. The preparacrista ends at a small, lingually displaced paraconule, which is somewhat larger than on M^1 and contributes to the formation of a somewhat more elongated mesial fovea than on the M^1 . The crista proportions are the same as on the M^1 but all are more elongated mesiodistally, resulting in broader fovea and a broader trigon. The transverse cristae are also well marked, though worn.

The M^3 's preserve more occlusal anatomy than the more anterior molars. Dentine pits are exposed on the protocones only, with the right one being more worn than the left. For M^3 's, their occlusal morphology is relatively simple, though somewhat more complicated than the anterior molars. The protocone and paracone are roughly equal in size, followed by the hypocone, with the metacone being the smallest. This gives the teeth a slightly distolingually tapered shape, though less so than in RUD 45 and RUD 140, associated with the male palate RUD 44. Preparaconules and preprotoconules are present, the former roughly the same size as on the M^2 's. Transverse cristae are not distinct on either M^3 , despite less wear than on the anterior molars, resulting in a more or less continuous, flat occlusal surface from the mesial to distal ends of the tooth lingual to the apices of the buccal cusps. This flat surface undulates slightly from the presence of indistinct accessory cristae descending from the buccal cusps. RUD 45 and 140, though less worn, have a similar pattern of a flat occlusal surface, small accessory cusps, and less distinct crista than the more anterior molars associated with the same individual.

In all three molars the cusps are peripheralized, that is, they are buccolingually compressed and their apices occur at the mar-

gins of the crowns. In all details, the dentition of RUD 77 is extremely similar to that of RUD 12 and other isolated teeth from Rudabánya attributed to *D. brancoi*. It is also very similar to RUD 44 and associated teeth (RUD 45 and RUD 140), with minor differences in premolar morphology that are probably related to sexual dimorphism (see below).

The anterior molars of RUD 77 have a distinctive pattern of occlusal wear compared to other fossil hominoid taxa, but one that is reminiscent of other specimens from Rudabánya. As noted above, the M¹ and M² are strongly worn lingually, with wear extending well up the roots. This pattern is similar to that seen in RUD 6, the only other *Dryopithecus* molar from the site exhibiting a similar degree of wear. One possible explanation for this pattern of extreme but localized wear is damage to the crown surface related to caries. This is an intriguing possibility in light of the fact that another individual, RUD 44, has large bilateral crown caries on the P³s and a smaller caries involving the distal margin of the M² and the mesial margin of the M³ (RUD 45). We know of no other Miocene hominoid sample with this frequency of caries or potential caries, nor have caries been identified in any teeth of *Dryopithecus* other than those attributed to *Dryopithecus* from Rudabánya. If these wear features are related to caries formation, this may have interesting implications for reconstructing certain aspects of the diet, ecology, and health of *D. brancoi*. Finally, the pattern of dentine exposure in RUD 77 suggests that the enamel was relatively thin and dentine penetrance (the degree to which the dentine horns penetrate the enamel cap) relatively high, compared to forms with thick enamel and low penetrance (*Sivapithecus*, *Ouranopithecus*, *Australopithecus*).

Neurocranium. The temporal bones are highly fragmented, but large articular portions of both temporal bones, most of the left tympanic plate, and fragments of both petrous pyramids provide a number of important anatomical details (Figs. 2, 6, 7). The mandibular fossa, preserved on the left side, is more strongly concave anteroposteriorly than mediolaterally (Fig. 2). It is anteropos-

teriorly constricted, and bordered anteriorly by a broad, saddle-shaped (transversely concave and anteroposteriorly convex) articular eminence, and posteriorly by a small, posteriorly inclined postarticular eminence (Fig. 2). On the right side, a very large, broad, inferiorly directed entoglenoid process is preserved, missing only the tip. On the left side the entoglenoid process is more seriously damaged, exposing extensive pneumatization of this process. On the right side a broad, well formed articular tubercle projects inferiorly from the base of the root of the zygomatic process (Fig. 2). A separate fragment originally posterior and lateral to the articular fragment includes the large, semi-circular superior portion of the external auditory meatus, posterior to the postglenoid process, and posterior to that the anterior end of the mastoid crest. With these two fragments conjoined, it is possible to reconstruct a broad supraglenoid gutter with a laterally flared lateral margin superior to the mandibular fossa (Fig. 2).

Damage in the area posterior and medial to the postglenoid process suggests that there was fusion of the articular and tympanic portions of the temporal. The tympanosquamosal suture, which would be present if these two portions were fused, is not visible, and is replaced by a broken bone surface exposing pneumatization deep to the postglenoid process. The breakage extends some distance medial to the postglenoid process. More medially, between the postglenoid process and the entoglenoid process, the anterior face of the petrotympanic fissure is preserved intact. If the articular and tympanic portions were not fused, the tympanosquamosal suture would likely have been preserved more laterally, to a point distal to the postglenoid process. The tympanosquamosal suture is typically not preserved when the tympanic and articular portions separate in taxa in which the suture fuses, but is typically present in taxa in which the two portions do not fuse, as in *Sivapithecus* and *Pongo* among the great apes (Ward and Brown, 1986). Finally, damage on the endocranial side of the articular and petrous portions of the temporal indicate extensive pneumatization of the articular eminence,

the root of the zygomatic process, and the postglenoid process.

Two small fragments preserve parts of the endocranial and internal surfaces of the petrous pyramids in the region around the internal auditory meatus and the fenestra (Fig. 6), and a third preserves the basicranial surface of the left tympanic plate and a portion of the wall of the tympanic cavity (Fig. 7). The left dorsal surface preserves a large internal auditory meatus, posterior, superior, and lateral to which there is a shallow subarcuate fossa (Fig. 6a). Posterior and lateral to the meatus there is a prominence that probably accommodates the posterior semicircular canal within the bone. Inferior to this prominence there is a small notch corresponding to the aqueduct of the vestibule (Fig. 6a). Posterior and lateral to the prominence and the aqueduct is a concave surface representing a small portion of the cerebellar surface (Fig. 6a). Superior and lateral to the prominence and the cerebellar surface is a shallow groove running posterolaterally that probably represents a portion of the superior petrosal sinus. The dorsal surface on the right side is less completely preserved, and is essentially a mirror image of the homologous anatomical features described for the left side. On both specimens, the distance between the internal auditory meatus and the cerebellar surface is relatively short, suggesting that the complete petrous pyramid was mediolaterally compact (Fig. 6a).

The internal aspects of two pieces of the petrous pyramid just described preserve details of the morphology of a portion of the wall of the tympanic cavity (Fig. 6b). Both specimens preserve the cochlear and vestibular fenestrae, the promontory, the medial half of the canal for the facial nerve, and part of the posterior wall of the carotid canal (Fig. 6b). Posterolaterally, both specimens preserve evidence of mastoid pneumatization. CT scans reveal a typical great ape morphology of the bony labyrinth (Spoor, 1996).

The last temporal fragment preserves a few details of the left tympanic plate (Fig. 7a). Anteromedially a moderate eustachian process is preserved. Lateral and slightly posterior to it is the posterior surface of the

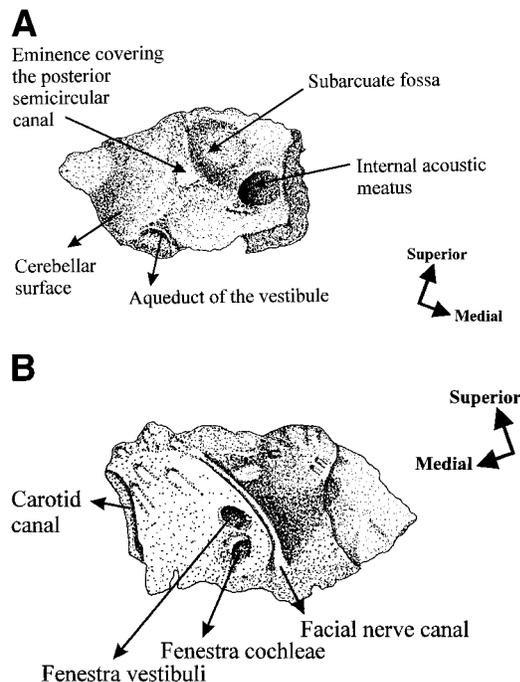


Fig. 6. Drawings of the endocranial (A) and lateral (B) views of the left petrous pyramid of RUD 77. Approximately six times natural size.

petrotympanic fissure. Most laterally is a damaged, pneumatized region that corresponds to the area posterior to the postglenoid process in the vicinity of the tympanosquamosal suture (Fig. 7a). The medial extent of the tympanic plate is preserved mostly intact (Fig. 7a). It is relatively broad and flat, with a concavity more pronounced medially than laterally. The concavity separates the eustachian process from the raised medial end of the tympanic crest, which rises anterior and medial to a well developed styloid pit. The tympanic crest is well developed, and courses posterolaterally (Fig. 7a). Posterior to the lateral most extent of the tympanic crest is the anteromedial half of the stylomastoid foramen. Judging from the orientation of the petrotympanic fissure surface, which normally faces anteriorly to meet the tegmen tympani, the tympanic plate in RUD 77 must have been oriented more vertically than horizontally (Fig. 7a).

A portion of the tympanic wall contribution of the tympanic plate is also preserved

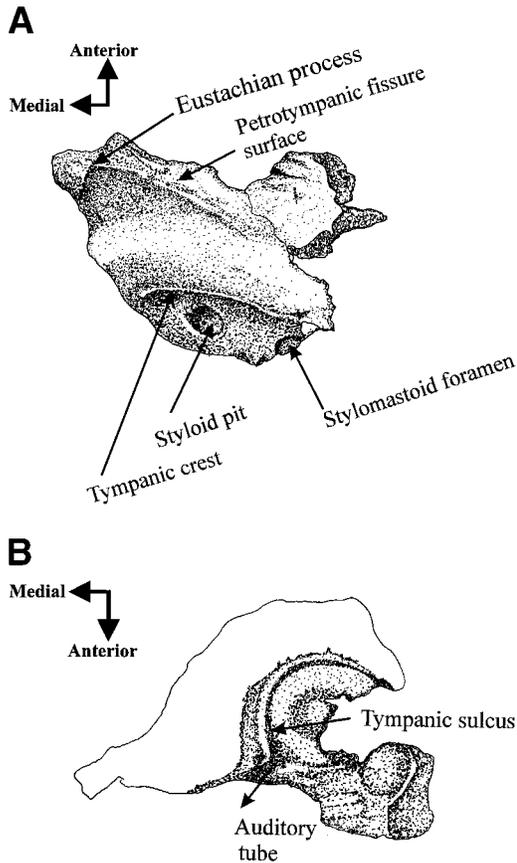


Fig. 7. Drawings of the basicranial (A) and tympanic (B) surfaces of the left tympanic plate of RUD 77. Approximately six times natural size.

on this specimen, deep to the basicranial surface described above (Fig. 7b). The most prominent feature in this view is the tympanic sulcus, which is very well preserved (Fig. 7b). Lateral to it is a broken, pneumatized area that corresponds to the base of the external acoustic meatus. Medially, a small groove marks the probably position of the auditory canal.

The orbital and neurocranial regions are well preserved (Figs. 3–5). The nearly complete supraorbital region is preserved from very close to the frontozygomatic suture on the right to the left frontozygomatic suture, to which is attached most of the left zygomatic bone. The most prominent feature of the supraorbital region is glabella, which is preserved intact at nasion (the nasal bones

are missing). At glabella, the interorbital space is convex transversely and superoinferiorly, contributing to a mild projection of glabella (Figs. 3, 5). Superior to glabella there is a shallow but distinct transverse depression separating the orbital portion of the frontal bone in the midline from the squamous portion (Fig. 3). Continuous from glabella are short, low, rounded ridges, oriented posterolaterally. The left ridge, which is more distinct than the right, is no longer palpable beyond about 25% of the distance across the breadth of the orbit. At this point this ridge is separated from the orbital margin by a shallow groove running parallel to the ridge. The superior orbital margins on both sides are formed from thickened, horizontally oriented ridges. The superior surfaces of these ridges face superoanteriorly, and are separated from the anterior temporal lines by a shallow but distinct groove. Based on comparisons to other primates, we believe that the mild ridges connected to glabella are supraorbital tori, and the thickened ridges above each orbit are supraciliary arches. The groove superior to glabella and the ridges is the supratoral sulcus. Comparisons of these structures to their homologues in other primates are provided in Begun (1994, 1995).

The supraciliary arches, which are superoinferiorly compressed and anteriorly projecting, merge bilaterally with the surface of the zygomatic process of the frontal close to the frontozygomatic sutures. In this region on each side the superior surfaces face more superiorly. These surfaces, between the lateral third or so of the orbital margins and the anterior temporal lines, are roughened by transversely oriented grooves, which fade laterally and disappear at the frontozygomatic suture.

The lateral orbital surface continues inferior to the frontozygomatic suture, being preserved on the left side on the zygomatic bone (Fig. 5). The margin is thicker at the frontozygomatic suture than more inferiorly, but it does not form a sharp edge as in many primates. A bend in the margin about 1 cm superior to the level of jugale and just above the level of the most superior zygomaticofacial foramen marks the beginning the medial curvature of the orbit toward the

maxilla. Not enough of the inferior portion of the orbit is preserved, however, to confidently reconstruct the shape of the orbit. The lateral orbital margin is vertical superior to this point, which is more typical of primates with orbits that are broader than tall.

The anterior temporal lines are strongly developed, especially for a hominoid of this size (Fig. 4). From the frontozygomatic tubercle they run a nearly straight course posteromedially toward the midline. About half way across the orbits, they turn sharply posteriorly. At this point, they change from raised, prominent ridges marking the anterior and superior boundaries of the infratemporal fossa, to rounded, more subtly defined ridges on the distal portions of the frontal squama and the parietal bones (Fig. 4). At their closest to each other, which is slightly posterior to midcranial length, the temporal lines are about 9.8 mm apart. The frontal trigone, bounded bilaterally by the anterior temporal lines and anteriorly by the supraorbital ridges, is biconvex, but more curved anteroposteriorly than transversely. The interorbital space is broad with small air sinuses inferior to nasion. In frontal view it is mildly hourglass shaped, being broader at the superior orbital margins and at the most inferiorly preserved end than between the two, suggesting that the orbital space would have become broader distally. Two distinct surfaces are apparent on the nasal processes of the frontal bones. The orbital surfaces face laterally into the orbits. The facial surface, between the rounded orbital margins and the nasal sutures, face anteriorly and laterally. These are slightly concave transversely, and probably mark the superior most portion of the lacrimal grooves.

The frontonasal suture is V shaped and strongly acutely angled. The bone is about 8 mm thick between the surface for the nasal bones on the frontal and the endocranial surface of the frontal, and is not extensively pneumatized. However, bilaterally to the central portion of the nasal suture are well developed sinuses that excavate the interorbital region from the point at which it is preserved to the level of nasion. The plates of bone that remain, on the facial and endocranial sides, are thin. The left side, which is

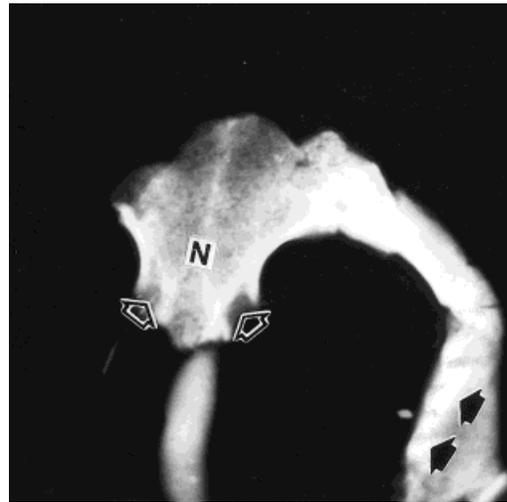


Fig. 8. Radiograph in frontal view of RUD 77. Open arrows indicate the small frontal sinuses placed inferior to nasion (N). Also note the buttressed lateral orbital pillar running inferiorly and slightly medially from the frontozygomatic tubercle (closed arrows). See text.

slightly more complete than the right, preserves two small loculi separated by a ridge. A frontal radiograph of RUD 77 (Fig. 8) reveals the low position and minimal extension of the frontal sinuses.

The frontozygomatic suture, preserved on the left, is oriented nearly vertically. At the frontozygomatic suture the anterior temporal lines are thickened into well defined tubercles. From the frontozygomatic tubercles, in addition to the strongly anterior temporal lines, strongly developed crests run inferiorly and posteriorly (Figs. 3 and 8). On the left side, where more of the infratemporal fossa is preserved, this crest forms a strong buttress, triangular in cross section, with inferolateral and superomedial faces separated by a ridge. This buttress is also visible in the radiograph (Fig. 8). The ridge and the superomedial face are roughened for the attachment of the anterior fibers of temporalis. This prominent buttress separates the infratemporal fossa into two sections. The superomedial portion is relatively broad and shallow. The inferolateral portion is very deep and narrower, forming a large sulcus oriented vertically and slightly medially, and bounded laterally by the temporal process of the zygomatic bone (Figs. 3 and 4).

The lateral orbital pillar (frontal process of the zygomatic bone) is broad and the facial surface convex and oriented anterolaterally. The body of the zygomatic bone is pierced by at least four very small zygomaticofacial foramina. It is convex superiorly but concave inferiorly, indicating the presence of a depression lateral to the zygomaticomaxillary suture. A small portion of the temporal process of the zygomatic is preserved, arching posteriorly with little lateral flare, and enclosing a deep, broad sulcus for anterior and lateral portion of temporalis. Jugale is just below the level of the inferior orbital margin.

The parietals have low, rounded, but clearly marked superior temporal lines separated by a roughened bare area midsagittally (Fig. 4). The coronal contour is broad and the postorbital constriction appears to have been relatively slight. The infratemporal surface was broad anteroposteriorly. The parietals are mostly preserved close to the midline, but enough is preserved laterally and inferiorly to say that the cranium was fairly broad, probably with a biparietal breadth that was greater than the biorbital breadth. In this reconstruction, 20 to 21 mm are missing along the midsagittal chord between the most posterior edge of the main set of conjoined fragments and a smaller set of conjoined fragments with inion and a portion of the nuchal torus. This smaller section can be positioned with confidence, however, using three anatomical features (inion, the nuchal torus, and the superior temporal line), and by aligning the ectocranial contours (Figs. 3 and 4). It is, in fact, fairly clear how this smaller, posterior piece must be placed. The anterior end of the temporal line of the posterior piece can be aligned with the posterior end of the temporal line of the anterior fragment. There is a slightly medialward convexity to this line on both sections, so that in superior view they can be aligned to create a smooth contour to the temporal line. In posterior view, the ends of the temporal lines serve to position the fragments relative to one another, and both the plane of the bare area between the temporal lines and the nuchal crest serve to position the smaller fragment relative to the anteroposterior and transverse axes. In the

final analysis, though the two pieces are not connected, the presence of so many clearly marked anatomical features makes it possible to fit these two pieces of neurocranium with confidence (Figs. 3, 4).

The angle between the occipital and nuchal planes is relatively wide. The nuchal torus is not strongly developed, and is damaged at inion. A small suprainiac fossa indicates the position of inion, and corresponds with the midsagittal contour, reinforcing the placement of anterior and posterior cranial fragments. The torus, which is better preserved on the left side, is slightly raised superior to the occipital surface, and projects more strongly posterior to the nuchal surface. Only about 10 mm of the length is preserved, but the nuchal torus does arch with a mild anterosuperiorly oriented convexity. The bare area is relatively broad posteriorly, and marked by fine pitting and striations that distinguish it from the portions of the parietal bones originally deep to the deep fascia of temporalis (Fig. 4).

Without the inferior orbital margins or a completely secure basis for positioning the temporal fragments on the neurocranial and facial portions of the specimen, it is difficult to orient this specimen in lateral view. However, a few nontraditional characters give some indication of a possible orientation of this specimen. In most catarrhines the orbital margins are vertical, or they are curved symmetrically relative to a vertical axis, in lateral view. The anterior most parts of the superior orbital plates are also usually oriented nearly horizontally. While there is some error in positioning RUD 77 based on these landmarks, an approximation can be made. On this basis, it is unlikely that the frontal squama was as vertically oriented as in humans or orangs, or as horizontally oriented as in African apes or australopithecines. Posteriorly, the neurocranium curved inferiorly toward inion, and the nuchal plane was oriented posterosuperiorly. The neurocranium overall has a long superior cranial contour. Figure 9 presents a comparison of cranial lengths in some hominoids relative to orbital size, a good correlate of overall body size in anthropoids (Aiello and Wood, 1994). RUD 77 is indistinguishable from African apes while *Pongo* and *Hylobates*

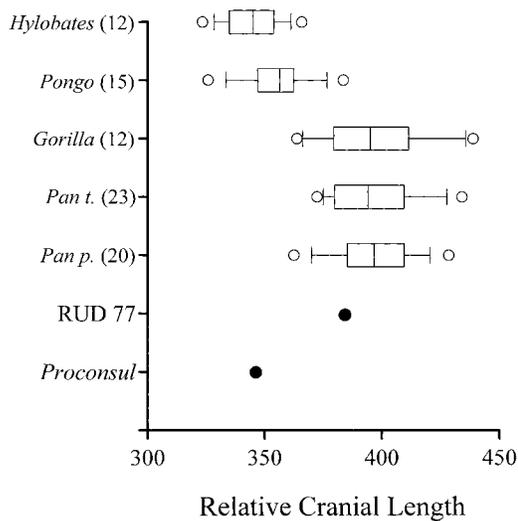


Fig. 9. Box plot of selected hominoid cranial lengths (glabella-inion chord) over orbital size [(orbital breadth + orbital height)/2]. Boxes enclose 25th and 75th percentiles, and vertical lines represent the medians. Horizontal lines represent the 10th and 90th percentiles, and open circles the 5th and 95th percentiles. Note the long cranium of RUD 77 and the short cranium of *Pongo*, *Hylobates* and *Proconsul*. See text for discussion.

have shorter crania, as does *Proconsul*. Endocranially, the frontal poles are well preserved, narrow, and inferiorly projecting. Posteriorly, small portions of the occipital lobe and cerebellar impressions are preserved either side of midline. A sharp frontal crest is preserved, continuous with a well marked superior sagittal sulcus.

COMPARISONS TO OTHER FOSSIL HOMINIDS

A less complete reconstruction of RUD 77 has been compared previously to other fossil and living hominoids (Kordos, 1987, 1991). Here we focus on comparisons based on the newly reconstructed portions of the specimen, and to specimens not previously compared to RUD 77. These comparisons are directed at establishing the sex of RUD 77 and the basis for its attribution to *D. brancoi*. A more comprehensive analysis including details of the functional anatomy and the phylogenetic relations of *D. brancoi* will be based on the entire sample from Rudabánya, and is in preparation.

On the basis of similarities in the dentition of RUD 77 to other specimens from

Rudabánya, this specimen can be attributed to *D. brancoi*, previously identified at Rudabánya on the basis of a large sample of specimens (Begun and Kordos, 1993). The teeth are morphologically very similar to all upper molars and premolars attributed to *Dryopithecus* from Rudabánya. They are very close in size to the postcanine dentition of the female hemipalate RUD 12 attributed to a female on the basis of its unambiguously female canine morphology (Begun, 1987, 1992a; Kelley, 1995) (Table 2). The postcanine dentition of RUD 77 is slightly smaller in most dimensions than that of RUD 15, which is also attributed to a female based on canine morphology (Begun, 1987) (Table 2). RUD 77 is similar to but smaller and more gracile than RUD 44, another partial cranium from Rudabánya attributed to a male of the same species, based on canine morphology (Andrews and Martin, 1987; Begun, 1987; Kordos, 1991). There is no evidence of any other great ape taxon at Rudabánya.

Despite the absence of a canine, there can be little doubt that RUD 77 is a female. As noted above, a small portion of the alveolus of the canine is present indicating a medial position of the canine root relative to the P^3 , as is typical of the small canines of female anthropoids. As noted earlier, the P^3 , in being more rectangular rather than triangular, is morphologically more similar to two known females (based on the associated canines), and unlike either the male from Rudabánya with an associated canine, or other males of *Dryopithecus* with associated canines and P^3 s (*D. laietanus* and *D. crusafonti* [see below]). The small dental size of RUD 77 is also a strong indicator of the sex of this specimen (Table 2). In primates in which evidence of postcanine dimorphism is lacking, size cannot be considered a reliable indicator of sex. However, at Rudabánya the sample consists of a number of males and females that are identifiable as such on the basis of preserved, associated canines. RUD 77 very clearly falls among the females both in morphology and size (Table 2). The dentition of RUD 77 is the same size or smaller than a number of specimens attributed to females (RUD 12 and 15), and much smaller than specimens attributed to males (RUD 7 and 44) (Table 2).

TABLE 2. Dental size¹ comparisons among male and female *Dryopithecus brancoi* and RUD 77

	P ³	P ⁴	M ¹	M ²	M ³
<i>D. brancoi</i> males					
RUD 44	9.7	9.0	10.2	11.7	10.6
RUD 7	—	9.4	11.0	—	—
<i>D. brancoi</i> females					
RUD 12	7.9	8.5	9.9	—	—
RUD 15	9.0	8.6	10.1	10.5	—
RUD 77	8.4	8.5	9.6	10.4	9.4

¹ (Length + breadth)/2, in millimeters.

Compared to other cranial material of *Dryopithecus*, RUD 77 differs from a male *D. laietanus* from Can Llobateres, CLI 18000 (Begun and Moyà-Solà, 1992; Moyà-Solà et al., 1992; Moyà-Solà and Kohler, 1993, 1995; Begun, 1994, 1995) in having a convex frontal trigone and glabella, a narrower, more deeply excavated zygomatic temporal surface, less well developed anterior temporal lines, slightly less extensive frontal sinus, a higher nasion relative to the superior orbital margin, a flat interorbital surface between nasion and glabella, more superiorly facing frontal zygomatic process, a more convex malar surface, a slightly lower zygomatic root, and smaller zygomaticofacial foramina. Dentally the two specimens are very similar, though in RUD 77 the P³ is more symmetrical and closer in size and shape to P⁴, and the M² is largest in RUD 77, while in CLI 18000 the M³ is the largest tooth. More detailed morphological differences in dental morphology between *D. brancoi* and both *D. laietanus* and *D. crusafonti* have been published elsewhere (Begun, 1992b). Both specimens are close in size, dentally and cranially (interorbital breadth, orbital breadth, orbital margin thickness, etc.), despite the fact that the Can Llobateres specimen is a male (based on canine morphology) and RUD 77 a female (see above). The upper dentition of *D. crusafonti* is larger than that of *D. laietanus*, and closer in size to that of male *D. brancoi* (RUD 44) (Begun, 1992b).

A number of the differences noted above between RUD 77 and CLI 18000 are not diagnostic of species differences between *D. brancoi* and *D. laietanus*. There is overlap in morphology when other specimens attributed to *D. laietanus* and *D. brancoi* are included in the comparisons. Premolar het-

eromorphy, which distinguishes CLI 18000 from RUD 77, is also found in the male RUD 44, and is probably associated with sexual dimorphism rather than taxonomy (see above). RUD 44 is also closer to CLI 18000 than to RUD 77 in anterior temporal line development, palatal depth, and probably frontal zygomatic process orientation, suggesting that these differences are also a matter of sexual dimorphism and not of taxonomy. In contrast, in the individual represented by RUD 44, M² was the largest tooth, like RUD 77 but unlike CLI 18000. RUD 44 is associated with an isolated M³, RUD 140, that is smaller than the M² of RUD 44 (Kordos and Begun, submitted, a). The mesial interstitial facet of RUD 140 matches the distal facet on the M² of RUD 44 perfectly (Kordos and Begun, submitted, a). M²/M³ size ratio may in fact be a difference from *D. laietanus* of taxonomic significance.

Other potential species specific differences also include zygomatic root height, malar surface flattening (intermediate in RUD 44), nasion position, glabellar and frontal trigone morphology, and overall size. Zygomatic root height is difficult to assess in *D. brancoi* because most specimens preserve the zygomatic process of the maxilla only very close to the origin. Its position on the maxilla is clearly relatively high, as in modern great apes, and not very close to the alveolar margin, as in most early and middle Miocene forms. As measured on the single specimen on which it is reasonably well preserved, the zygomatic root height is lower than in CLI 18000, but both are well within the ranges of extant great apes (Begun, 1994, Fig. 9). The difference may be species specific, though the small sample size precludes a definitive judgment. Much the same is true for the difference in malar surface morphology. A diversity of malar surface shapes from flat to more convex can be found in *Pan* and *Pongo*, so that the difference between RUD 77 and CLI 18000 may not be significant. As noted above, *D. laietanus* males, identified on the basis of canine morphology, are dentally smaller than *D. brancoi* males. While there are no female canines found in association with other teeth in *D. laietanus*, there are many very small premolars and molars of *D. laietanus*, includ-

ing those of the type specimen, which are smaller than any *D. brancoi* postcanine tooth. There is thus abundant evidence of a small form of *D. laietanus*, significantly smaller than males of that taxon or than males and females of *D. brancoi*, and almost certainly attributable to females.

The morphology of RUD 77 conforms to a pattern of morphological diversity that serves to distinguish among the currently recognized species of *Dryopithecus*. Though the sample sizes are small, this morphological patterning and a corresponding temporal and geographic clustering of *Dryopithecus* localities support the view that *D. brancoi* is distinct from other species of *Dryopithecus* (Begun and Kordos, 1993).

RUD 77 has been compared to other hominoids elsewhere (Kordos, 1987, 1988, 1991; Begun, 1994, 1995; Begun and Kordos, 1997). The dental sample of *Dryopithecus* has also been compared extensively to other hominoids. The dentition of RUD 77 is morphologically quite consistent with other *Dryopithecus* from Rudabánya, and, with its heavily worn molars, contributes relatively few new comparative data. Thus, we focus on new comparisons based on the newly identified portions of this specimen described here, mainly from the posterior neurocranial and temporal regions. We focus primarily on comparisons to other taxa known from these anatomical regions, which excludes a large number of otherwise reasonably well known fossil hominoids. The entire sample of *D. brancoi* will be compared to all known fossil hominoids elsewhere (Kordos and Begun, in preparation).

The most complete Miocene hominoid cranial specimen is the female skull of *Proconsul* (KNM-RU 7290) (Le Gros Clark and Leakey, 1951; Walker et al., 1983; Walker and Pickford, 1983). Elsewhere, comparisons have been made between *Dryopithecus* in general and *Proconsul*, and these are consistent with the comparison of RUD 77 and KNM RU 7290 (Kordos, 1987, 1991; Begun, 1994, 1995). For example, the dental, maxillary, and frontal morphology of these two genera have been compared in detail, and it is not necessary to repeat these comparisons here. However, it is now possible to expand these comparisons to include

details of occipital, temporal, and overall neurocranial morphology.

Compared to KNM RU 7290, RUD 77 has a less strongly marked external occipital protuberance, a more posteriorly oriented nuchal plane, and an anteroposteriorly broader temporal fossa. The neurocranium is absolutely longer and broader and more elongated relative to breadth in RUD 77 (Fig. 9). The orbits and the teeth of RUD 77 are slightly larger than in KNM-RU 7290, which indicates that the body size of RUD 77 was very likely to have been somewhat greater than that of KNM-RU 7290. The neurocranial dimensions of RUD 77, however, are considerably larger, indicating that the relative brain size of RUD 77 is larger than that of KNM-RU 7290 (Kordos and Begun, submitted, b).

The articular and petrous portions of the temporal bones of KNM RU 7290 are not preserved as well as those of RUD 77 but some important differences are nevertheless apparent. KNM-RU 7290 has a very large subarcuate fossa (Ward, personal communication), as is the case of most other primates other than great apes and *Dryopithecus* (Moyà-Solà and Kohler, 1995; Begun, 1995). A few interesting exceptions to this pattern exist (Spoor and Leakey, 1996), but these are probably due to the parallel occurrence of a reduction in the size of the subarcuate fossa in these forms and in hominids (Spoor and Leakey, 1996). The glenoid fossa in KNM-RU 7290 is smaller and anteroposteriorly more narrow than in RUD 77, which is consistent overall with its smaller size. The postglenoid and entoglenoid processes are also smaller and less projecting in KNM-RU 7290. These differences, although consistent with the size difference, are also consistent with other differences in cranial robusticity between the two specimens, suggesting functional differences in dietary adaptations as well. RUD 77 has much more strongly developed crests for the temporalis muscle periorbitally and neurocranially than is the case in KNM-RU 7290, in which these crests are poorly developed. All of these differences suggest a more strongly developed masticatory apparatus in RUD 77 compared to KNM-RU 7290. That size may not have

much to do with it is suggested by the presence of strongly developed ectocranial cresting similar to that of RUD 77 in the cranium of *Turkanapithecus* (KNM-WK16950), which is actually somewhat smaller than KNM-RU 7290. KNM-WK 16950 also has an associated mandible with a more robust corpus and an anteroposteriorly larger condyle than KNM-RU 7290, suggestive of a more powerful chewing apparatus. It should be noted, however, that KNM-WK 16950, like RUD 77, has a more strongly worn dentition, which probably indicates older individuals than KNM-RU 7290, in which the M³s appear to have just erupted, and this may explain some but not all of the differences between the KNM-RU 7290 on the one hand and KNM WK 16950 and RUD 77 on the other.

Continuing with *Turkanapithecus*, the new data of RUD 77 reveal a number of additional characteristics to add to a long list of differences between *Turkanapithecus* and *Dryopithecus*. In contrast to the comparisons made between *Dryopithecus* and *Proconsul*, fewer detailed comparisons have been made to *Turkanapithecus*. A comprehensive list of differences between the two taxa is thus provided here. RUD 77 differs from the probably male specimen of *Turkanapithecus*, KNM-WK 16950 (Leakey et al., 1988a) in being larger and in having a longer and relatively larger P⁴ compared to P³, no lingual cingulum, no mesiobuccal cingulum, less P³ cusp heteromorphy, lower P³ paracone in buccal view, with mesial and distal crests of equal length and diverging from the cusp apices at a greater angle, relatively larger M¹ compared to M², reduced metacones relative to paracones on M²⁻³, buccally concave postcanine tooth rows, larger orbits with less anteriorly projecting superior orbital margins, smaller interorbital breadth, better developed supraorbital tori and sulcus, more vertical frontal squama, more projecting glabella, less postorbital constriction, a longer neurocranium relative to breadth, a smaller articular tubercle, and a more anteroposteriorly convex articular eminence. RUD 77 also lacks the distinctive wear pattern of the molars of KNM-WK 16950, which produces a complicated network of crests on the entire occlusal surface

rather than the deep notches confined to the lingual cusps of RUD 77.

RUD 77 differs from an *Afropithecus* male (KNM-WK 16840) (Leakey et al., 1988b) in many of the same dental and cranial features as *Proconsul*. Kordos (1991) and Begun (1994) include some comparisons of frontal morphology between RUD 77 and KNM-WK 16840. Little has been published on comparisons of other aspects of the face or the teeth. RUD 77 has longer premolars and molars, P⁴ longer than P³, relatively larger M¹ compared to M², reduced cingula, less P³ cusp heteromorphy, lower P³ paracone in buccal view, with mesial and distal crests of equal length and diverging from the cusp apex at a greater angle, reduced metacones relative to paracones on M²⁻³, a smaller incisive foramen, shallower palate in the molar region, more superiorly placed zygomatic root, and a thicker lateral orbital pillar than KNM-WK 16840. RUD 77 is further distinguished in lacking the low crowned, low cusped, strongly flared postcanine teeth of KNM-WK 16840, and in being smaller in overall facial dimensions with less mesiodistally compressed molar trigons, relatively larger orbits, narrower interorbital breadth, less strongly developed temporal lines that do not meet to form a sagittal crest, a broad, convex frontal trigone, and relatively and absolutely less postorbital constriction. KNM-WK 16840 is intermediate in cingulum development between *Proconsul* and RUD 77, while another specimen attributed to *Afropithecus* (KNM-WK 17102) lacks cingula on the M²⁻³, as in RUD 77.

RUD 77 differs from male *Sivapithecus* (GSP 15000) (Pilbeam, 1982; Ward and Brown, 1986) in a large number of characters described in several publications (Kordos, 1987, 1988, 1991; Begun, 1994). Despite the substantial differences in cranial and dental morphology, RUD 77 and GSP 15000 are similar in premolar and molar proportions and in lacking molar cingula. Both also share a number of characters of the face found in other hominids (Kordos, 1988, 1991, Begun, 1994).

RUD 77 has also been compared extensively to *Ouranopithecus* male (XIR-1) (de Bonis et al., 1990; Kordos, 1991; Begun, 1994, 1995). As noted in Begun (1995), RUD

77 and XIR-1 differ primarily in characters related to size, but are otherwise similar in dental proportions and facial morphology, as are the samples of *Ouranopithecus* and *Dryopithecus* more generally. These taxa are probably more closely related to each other than they are to other hominids (Begun, 1995; Begun and Kordos, 1997).

RUD 77 has also been compared in detail to a female *Lufengpithecus* (PA 677) (Wu et al., 1986; Kordos, 1988; Schwartz, 1990). As with *Sivapithecus* and *Ouranopithecus*, the differences from RUD 77 overall are less than with early and middle Miocene forms.

RUD 77 has not been compared in detail to *Oreopithecus*. The dentition of *Oreopithecus* is well known (Hürzeler, 1951; Harrison, 1986), and quite distinct overall in crown and occlusal morphology from RUD 77. However, there are some similarities. Like RUD 77, *Oreopithecus* has relatively more elongated molars and premolars than early Miocene hominoids, but has more strongly developed molar cingula than RUD 77. M^1/M^2 proportions are similar to RUD 77, but M^3 is the largest molar in *Oreopithecus*, whereas M^2 is largest in RUD 77. The root of the zygomatic process of the maxilla in *Oreopithecus* (IGF 11778) is lower on the alveolar process than it seems to have been in RUD 77 or other specimens from Rudabánya. The interorbital space lacks a frontal sinus, and the glabella is not projecting, as it does, albeit mildly, in RUD 77. In *Oreopithecus* the lateral orbital pillars are narrower and more rounded transversely. There are two small zygomaticofacial foramina superior to the inferior orbital margin, as in RUD 77. The anterior temporal lines, which are more strongly developed than in RUD 77, converge more strongly toward the midline and do so more anteriorly on the frontal in IGF 11778 than on RUD 77. The anterior temporal lines probably met very far anteriorly on this skull, forming a sagittal crest with a very anterior origin. No sagittal crest is present on RUD 77. There are also indications on this specimen of a very deep temporal fossa.

Jugale and the root of the temporal process of the zygomatic bone are also preserved in *Oreopithecus*, and differ from RUD 77. In *Oreopithecus* the temporal process is

deep superoinferiorly, and strongly concave medially, suggesting a relatively more strongly developed masseter muscle than that of RUD 77. The notch at jugale is more acute, and the temporal process runs more posterosuperiorly than on RUD 77. Jugale is also lower on the face in *Oreopithecus*.

The neurocranium is severely crushed on IGF 11778 but a number of comparisons can nevertheless be made with RUD 77. A well developed sagittal crest is apparent, connected posteriorly to a very strongly developed nuchal crest, forming together a compound temporonuchal crest surrounding very deep concavities on the occipital and parietal bones for the temporalis muscle. This extreme ectocranial cresting is very different from RUD 77, and is also much more strongly developed than on male specimens of *Dryopithecus* (CLI 18000, RUD 44). Together with indications of strong postorbital constriction, this morphology implies a relatively much smaller endocranial cavity on IGF 11778 as well.

Portions of the articular and basicranial aspects of the temporal bones are also preserved on IGF 11778. Like RUD 77 there is a broad articular eminence and a strongly developed, projecting entoglenoid process. Although distorted, the mandibular fossa appears to have been somewhat deeper than that of RUD 77, and the articular tubercle more prominent. Unlike RUD 77, the posterior surface of the postglenoid process is preserved intact, indicating that there was no fusion of the articular and tympanic portions of the temporal bone in this region.

The comparison of RUD 77 to IGF 11778 is complicated to some extent by the fact that RUD 77 is a female and IGF 11778 a male. IGF 11778 was probably a bigger individual than RUD 77, judging from the size of the dentition and the associated mandible, but was probably not larger than RUD 44. Where the same comparisons are possible, most of the differences between RUD 77 and IGF 11778 also distinguish RUD 44 from IGF 11778. While size may have played some role in the differences between RUD 77 and IGF 11778, most of the differences are related to fundamental dissimilarities in overall cranial morphology between the *Dryopithecus* and *Oreopithecus*.

Finally, RUD 77 differs from *Australopithecus afarensis* in being smaller with thinner enamel, less molarized premolars, relatively smaller molars, thicker lateral orbital pillars, more convex malar surface, vertical frontozygomatic suture, more strongly developed anterior temporal lines, less strongly developed supraorbital tori and supratoral sulcus, a shorter palate anteriorly with a larger incisive foramen, shorter incisive canal, a shorter and more vertical premaxilla, no groove between the glenoid fossa and the postglenoid tubercle, a more medially placed postglenoid tubercle, a less pneumatized temporal squama in the suprameatal region, more vertical frontal squama, and a higher inion. Detailed occlusal differences in the molar region are similar to those described for *Ouranopithecus* and *Sivapithecus*. The same postcanine morphological differences distinguish *Australopithecus anamensis* from RUD 77 (Leakey et al., 1995). RUD 77 also differs from *Ardipithecus ramidus* (White et al., 1994) in having smaller postcanine teeth with occlusal morphology differences similar to *A. afarensis*, and less temporal pneumatization. Judging from the descriptions in White et al. (1994), *Ardipithecus* may also differ from RUD 77 in having a shallower temporomandibular joint, and a more weakly projecting entoglenoid process. However, RUD 77, like other great apes, is closer to *A. ramidus* than to *A. afarensis* in P³ crown morphology, enamel thickness, and possibly in having a more medially placed postglenoid process (White et al., 1994).

SUMMARY AND CONCLUSIONS

RUD 77 is the most completely preserved cranium of *Dryopithecus*, and one of only two reasonably well preserved and relatively undistorted neurocranial specimens of any Miocene hominoid. New aspects of the anatomy of this specimen, a new reconstruction of RUD 77, and new comparisons to other hominoids have been presented here. A restoration of the female skull of *D. brancoi* based on a number of specimens from Rudabánya has been published in Kordos (1987). Similar composite or hypothetical restorations of *Ouranopithecus* and *Australopithecus* have also been published (de Bo-

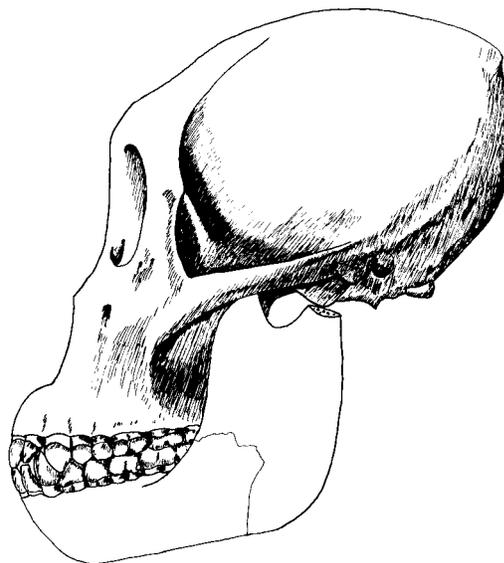


Fig. 10. Restoration of a female *D. brancoi* in lateral view. The mandibular corpus and lower teeth are based on RUD 17, and the ramus on RUD 2. The maxilla and premaxilla are based on RUD 77, RUD 12 and RUD 15. The condylar process has been omitted to expose the TMJ.

nis and Koufos, 1993; Kimbel et al., 1984), as has a restoration of *Proconsul* based on KNM-RU 7290 (Walker et al., 1983). Given the new data presented here, a revised composite restoration of a female *D. brancoi* skull is presented in Figure 10. Like the other restorations noted previously, this should be regarded as somewhat hypothetical, illustrative of general as opposed to detailed aspects of cranial form, and as a starting point for a more refined, more detailed restoration based on future discoveries. A comparison of this restoration with restorations of other fossil hominoids and lateral views of living hominoids is presented in Figure 11.

New characters preserved on RUD 77 tend to reinforce previous suggestions that *Dryopithecus* is more closely related to African apes and humans than is *Sivapithecus* (Kordos, 1987; Dean and Delson, 1992; Begun, 1994, 1995; Begun and Kordos, 1997). These newly identified characters include anteroposteriorly elongated temporal fossae, elongated neurocrania, deeper glenoid fossae, less prominent articular tubercles,

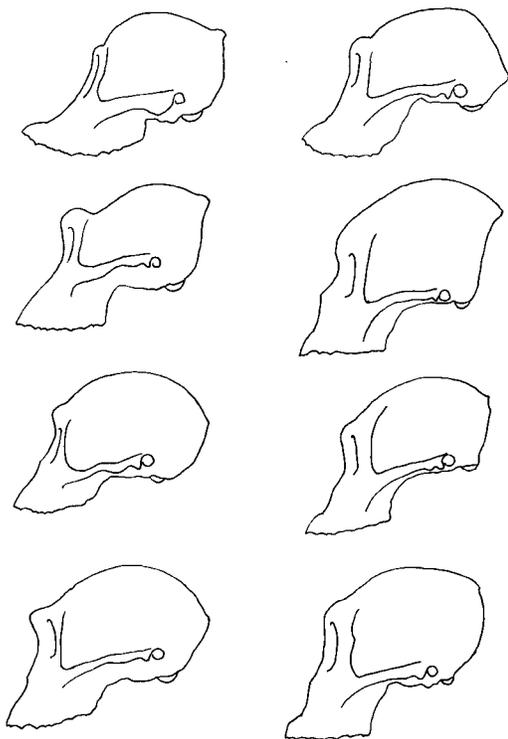


Fig. 11. Lateral views of selected hominoid crania drawn to the same length. From top to bottom: left, *Pongo*, *Gorilla*, *Pan paniscus*, *Pan troglodytes*; right, *Australopithecus afarensis*, *Proconsul*, *Ouranopithecus*, *Dryopithecus brancoi*. *A. afarensis* from Kimbel et al. (1994). *Proconsul* from Walker et al. (1983). *Ouranopithecus* modified from de Bonis and Koufos (1993) based on the authors' personal observations.

more prominent entoglenoid processes, less constricted and elongated postglenoid processes, and possible partial fusion of the articular and tympanic portions of the temporal. RUD 77 also preserves a frontal sinus below nasion, distinct supraorbital tori, an inflated glabella, and supratoral sulci. These characters, previously identified on RUD 44, also serve to distinguish *Dryopithecus* and the African apes and humans from *Sivapithecus* (Begun, 1994).

ACKNOWLEDGMENTS

We thank Peter Andrews, Louis de Bonis, David Dean, Eric Delson, Clark Howell, Jay Kelley, Tim White, and two anonymous reviewers for comments on an earlier version of this paper.

LITERATURE CITED

- Aiello LC and Wood BA (1994) Cranial variables as predictors of hominine body mass. *Am. J. Phys. Anthropol.* 95:409–426.
- Andrews P and Martin L (1987) Cladistic relationships of extant and fossil hominoids. *J. Hum. Evol.* 16:101–118.
- Begun DR (1987) A review of the genus *Dryopithecus*. Ph.D. thesis, University of Pennsylvania.
- Begun DR (1988) Catarrhine phalanges from the Late Miocene (Vallesian) of Rudabánya, Hungary. *J. Hum. Evol.* 17:413–438.
- Begun DR (1989) A large pliopithecine molar from Germany and some notes on the Pliopithecinae. *Folia Primatol.* 52:156–166.
- Begun DR (1992a) Miocene fossil hominids and the chimp-human clade. *Science* 257:1929–1933.
- Begun DR (1992b) *Dryopithecus crusafonti* sp. nov., a new Miocene hominoid species from Can Ponsic (Northeastern Spain). *Am. J. Phys. Anthropol.* 87:291–310.
- Begun DR (1994) Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yrbk. Phys. Anthropol.* 37:11–63.
- Begun DR (1995) Late Miocene European orang-utans, gorillas, humans, or none of the above? *J. Hum. Evol.* 29:169–180.
- Begun DR and Kordos L (1993) Revision of *Dryopithecus brancoi* SCHLOSSER 1901 based on the fossil hominoid material from Rudabánya. *J. Hum. Evol.* 25:271–286.
- Begun DR and Kordos L (1997) Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids. In DR Begun, CV Ward, and MD Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Origins and Adaptations*. New York: Plenum, pp. 291–316.
- Begun DR and Moyà-Solà S (1992) A new partial cranium of *Dryopithecus laietanus* from Can Llobateres. *Am. J. Phys. Anthropol. Suppl.* 14:47.
- Bernor RL, Brunet M, Ginsburg L, Mein P, Pickford M, Rögl F, Sen S, Steininger F, and Thomas H (1987) A consideration of some major topics concerning old world Miocene mammalian chronology, migrations and paleogeography. *Geobios* 20:431–439.
- de Bonis L, Bouvrain G, Geraad D, and Koufos G (1990) New hominoid skull material from the late Miocene of Macedonia in northern Greece. *Nature* 345:712–714.
- de Bonis L and Koufos G (1993) The face and mandible of *Ouranopithecus macedoniensis*: Description of new specimens and comparisons. *J. Hum. Evol.* 24:469–491.
- Dean D and Delson E (1992) Second gorilla or third chimp? *Nature* 359:676–677.
- Harrison T (1986) A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. *J. Hum. Evol.* 15:541–584.
- Hürzeler J (1951) Contribution à l'étude de la dentition de lait d'*Oreopithecus bambolii* Gervais. *Ecol. Geol. Helv.* 44:404–441.
- Kelley J (1995) Sex determination in Miocene catarrhine primates. *Am. J. Phys. Anthropol.* 96:391–417.
- Kimbel WH, Johanson DC, and Rak Y (1994) The first skull and other discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368:449–451.
- Kimbel WH, White TD, and Johanson DC (1984) Cranial morphology of *Australopithecus afarensis*: A comparative study based on a composite reconstruction of the adult skull. *Am. J. Phys. Anthropol.* 64:337–388.
- Kordos L (1982) The prehomimid locality of Rudabánya (NE Hungary) and its neighbourhood: A palaeoge-

- graphic reconstruction. *M. Áll Földt. Évi. Jel.* 1980-*ROL*.395-406.
- Kordos L (1985) Environmental reconstruction for pre-hominids of Rudabánya, N.-E. Hungary. *Schr. zur Ur-und Frühgeschichte.* 41:82-85.
- Kordos L (1987) Description and reconstruction of the skull of *Rudapithecus hungaricus* KRETZOI (Mammalia). *Ann. Hist. Nat. Mus. Natl. Hung.* 79:77-88.
- Kordos L (1988) Comparison of early primate skulls from Rudabánya and China. *Anthropol. Hung.* 20: 9-22.
- Kordos L (1991) Le *Rudapithecus hungaricus* de Rudabánya (Hongrie). *L'Anthropologie (Paris)* 95:343-362.
- Kordos L and Begun DR (submitted, a) Primates from Rudabánya: Allocation of specimens to individuals, sex and age categories.
- Kordos L and Begun DR (submitted, b) *Dryopithecus* cranial capacity reveals stasis in early hominid encephalization.
- Kretzoi M (1969) Geschichte der Primaten und der Hominization. *Symp. Biol. Hung.* 9:3-11.
- Kretzoi M (1975) New ramapithecines and *Pliopithecus* from the lower Pliocene of Rudabánya in north-eastern Hungary. *Nature* 257:578-581.
- Kretzoi M (1984) New hominoid form from Rudabánya. *Anthropol. Közlem.* 28:91-96.
- Le Gros Clark WE and Leakey LSB (1951) The Miocene Hominoidea of East Africa. *Fossil Mammals of East Africa. British Museum (Natural History)* 1:1-117.
- Leakey RE, Leakey MG, and Walker A (1988a) Morphology of *Turkanapithecus kalakolensis* from Kenya. *Am. J. Phys. Anthropol.* 76:277-288.
- Leakey RE, Leakey MG, and Walker A (1988b) Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. Phys. Anthropol.* 76:289-307.
- Leakey MG, Feibel CS, McDougall I, and Walker A (1995) New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565-571.
- Mein P (1986) Chronological succession of hominoids in the European Neogene. In JG Else and PC Lee (eds.): *Primate Evolution.* Cambridge: Cambridge University Press, pp. 58-70.
- Mein P (1990) Updating of the MN zones. In EH Lindsay, V Fahlbusch, and P Mein (eds.): *European Neogene Mammal Chronology.* New York: Plenum, pp. 73-90.
- Moyà-Solà S, Gibert J, and Begun DR (1992) New specimens of *Dryopithecus laietanus* from the Vallés Penedés Catalonia, Spain. Abstracts of the 24th Congress of the International Primatological Society, pp. 261.
- Moyà-Solà S and Kohler M (1993) Recent discoveries of *Dryopithecus* shed new light on evolution of great apes. *Nature* 365:543-545.
- Moyà-Solà S and Kohler 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.
- Pilbeam DR (1982) New hominoid skull material from the Miocene of Pakistan. *Nature* 295:232-234.
- Schwartz JH (1990) *Lufengpithecus* and its potential relationship to the orang-utan clade. *J. Hum. Evol.* 19:591-605.
- Spoor F (1996) The ancestral morphology of the hominid bony labyrinth: the evidence from *Dryopithecus*. *Am. J. Phys. Anthropol. Suppl.* 22:219.
- Spoor F, and Leakey M (1996) Absence of the subarcuate fossa in cercopithecids. *J. Hum. Evol.* 569-575.
- Steininger FF, Bernor RL, and Fahlbusch V (1990) European Neogene marine/continental chronologic correlations. In EH Lindsay, V Fahlbusch and P Mein (eds.): *European Neogene Mammal Chronology.* New York: Plenum Press, pp. 15-46.
- Walker A and Pickford M (1983) New Postcranial Fossils of *Proconsul africanus* and *Proconsul nyanzae*. In RL Ciochon and RS Corruccini (eds.): *New Interpretations of Ape and Human Ancestry.* New York: Plenum, pp. 325-351.
- Walker, A, Falk D, Smith R, and Pickford M (1983) The skull of *Proconsul africanus*: Reconstruction and cranial capacity. *Nature* 305:525-527.
- Ward SC and Brown B (1986) The facial skeleton of *Sivapithecus*. In DR Swindler and J Erwin (eds.): *Comparative Primate Biology, vol. 1: Systematics, Evolution, and Anatomy.* New York: Alan R. Liss, pp. 413-454.
- White TD, Suwa G, and Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306-312.
- Wu R, Xu Q, and Lu Q (1986) Relationship between Lufeng *Sivapithecus* and *Ramapithecus* and their phylogenetic position. *Acta Anthropol. Sinica* 5:1-30.