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Received 27 August 1999
Revision received
31 May 2000 and accepted
9 August 2000

Keywords: *Dryopithecus*,
Anapithecus, infants,
juveniles, adults, males,
females, predation.

Primates from Rudabánya: allocation of specimens to individuals, sex and age categories

Fossil primates have been known from the late Miocene locality of Rudabánya since 1965. Numerous campaigns of collecting, sampling and excavation have been carried out since that time by several teams of researchers, but the sample of primates has never been fully catalogued and published. Here we provide a comprehensive list of all primate specimens from Rudabánya with provenience data and allocation to individuals. At the main locality of R II 16 individuals are attributed to *Anapithecus* and nine to *Dryopithecus*, based on dental remains. *Anapithecus* comes mostly from a layer of gray to black marl and *Dryopithecus* is found mostly in a less consolidated overlying black mud. However, both taxa are found in both layers. *Anapithecus* is represented by larger proportions of juveniles and females, and *Dryopithecus* by more adult and subadult males. Both species are represented primarily by dental remains, but those of *Dryopithecus* are more commonly associated with mandibles and maxillae, while in *Anapithecus* most individuals are represented by associated dentitions. *Dryopithecus* is better represented by postcrania other than phalanges. *Anapithecus* age and sex frequency distributions are more typical of those of carnivore and chimpanzee prey assemblages than *Dryopithecus*.

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Journal of Human Evolution (2001) 40, 17–39
doi:10.1006/jhev.2000.0437

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Introduction

Since 1965 fossil catarrhines have been collected and excavated from the slopes of the Vilmos iron ore mine near the village of Rudabánya in northern central Hungary (Table 1). Over the last 35 years, 171 catalogued primate specimens from two species, *Anapithecus hernyaki* and *Dryopithecus brancoi*, have been accessioned into the collections of the Geological Museum of Hungary. These fossils were recovered from four separate but closely spaced localities, the richest being the R II locality (Table 2). The purpose of this paper is to report the full catalogue of primate specimens from Rudabánya following the last field season (1999), describe the allocation of separate specimens to individuals, and discuss basic

comparisons between the assemblages of both primates.

Background

The geology, age and depositional environment at Rudabánya have been described in some detail elsewhere (Kretzoi *et al.*, 1976; Kordos, 1982, 1988, 1991; Begun & Kordos, 1993; Bernor & Kordos, in preparation). Key aspects of the locality are briefly summarized here. R I, II and III are lake shore and shallow lake deposits associated with a large marshy bay of the Central Paratethys sea, known locally as the Pannonian lake. In lower Pannonian times (early late Miocene) the Pannonian lake expanded, filling the Borsod basin, in which the bay at Rudabánya lay, with water and

Table 1 History of fossil discoveries at Rudabánya

Year	Activity
ca. 1900	Fossil mammals recovered by local collectors.
1965	Hominoid mandible collected by Gabor Hernyák, chief geologist of the Vilmos mine.
1967	Mandible (RUD 1) published by Miklos Kretzoi in two newspaper items (Anonymous, 1967; Tasnádi Kubacska, 1967).
1969	RUD 1 selected as the holotype of <i>Rudapithecus hungaricus</i> Kretzoi, 1969.
1970–1978	Kretzoi's work at Rudabánya led to the recovery of more fossils from R I, and the discovery of additional localities along the edge of the mining operations.
1972	RUD 7 is the first primate specimen recovered from R II, the richest locality at Rudabánya, and later selected as the holotype of <i>Bodvapihhecus altipalatus</i> Kretzoi, 1975. RUD 9 from R II collected in the same year selected as the holotype of <i>Pliopithecus (Anapithecus) hernyaki</i> Kretzoi, 1975. All specimens collected by Hernyák.
1977	Primates first discovered at R III.
1979–1984	Small scale excavations and intensive geological survey and analysis carried out by László Kordos. RUD 71 recognized as the holotype of <i>Ataxopithecus serus</i> Kretzoi, 1984.
1985–1992	Systematic excavation resumed under the direction of Kordos.
1991	New primate locality, R VII, discovered.
1993–1994	Excavations directed by Kordos, Peter Andrews and Ray Bernor focused on the taphonomy and paleoecology of the locality.
1997–1999	Last three seasons of excavations directed by Kordos and David Begun. No further excavations are planned for the immediate future.

lake sediments (Figure 1). The hominoid localities at Rudabánya were situated in the valleys of a peninsula, roughly 7 km long by 1–2 km wide, running south-southwest from the highlands to the north of the lake.

All three localities preserve similar sediments, alternating sequences of near shore lignites and clays, representing changing lake water levels along the peninsula. In contrast, R VII is a karst locality with an erosional karst topography of the type associated with subtropical and tropical conditions today. Similar karst relief features have been discovered at R II, which represents the basement below the shallow subtropical soils of the Rudabánya peninsula. Briefly, the majority of fossils at R II come from two distinct layers, an unconsolidated sandy black mud with large wood fragments and large vertebrate fossils indicative of higher energy depositional conditions, and an underlying fine grained carbonate-rich clay (marl) with better preserved specimens, including articulated limbs, suggestive of lower energy conditions. The black mud is thicker towards the east of R II, and thinner

in the area with the greatest preserved thickness of marl, towards the west and north. Karst topography crops out south and east of R II, indicating the original shore line. The disposition of sediments suggests a catchment shore toward the southeast and deepening water levels trending north and west. This is also consistent with the direction of transport of specimens thought to be associated with single individuals (see Figure 2). While black mud and marl sediment are superimposed, the thicker deposit of overlying muds to the southeast and thicker marls to the northwest suggest that these are also lithofacies of a lake shore depositional environment with fluctuating lake levels. Taxa recovered from both sediment types are identical, suggesting a relatively brief period for the accumulation of sediments. Based on biostratigraphic correlations and regional lithostratigraphic correlations to a dated rhyolite, an age of 10 Ma has been estimated for all the localities of Rudabánya (Kordos, 1991). Local geology (karst topography), geochemistry, flora and faunal evidence all

Table 2 Specimens currently or at one time attributed to primates from Rudabánya

RUD no.	Location	Taxon	Anatomy	Individual	DOD
RUD 1 ¹	I	D	Left mandibular corpus with P ₄ -M ₃ . Female.	D1	1965
RUD 2 ²	I	D	Right mandible with C-M ₃ and the symphyseal base. Female.	D2	1969
RUD 3	I	D	Right M ₁ crown	D1	1971
RUD 4	I	A	RC, tip broken	A1	1971
RUD 5	I	D	RP ³ germ	D3	1971
RUD 6	I	D	LM ¹		1972
RUD 7 ³	II	D	Right maxillary fragment with P ⁴ -M ²	D4	1972
RUD 8	II	A	LC. Female.	A11	1972
RUD 9 ⁴	II	A	Left mandibular ramus with roots of dp ₃ , dp ₄ , M ₁ , and unerupted left canine, LP ₄ , LM ₂ , and RM ₁ -M ₃ . Female.	A2	1972
RUD 10	II	D	LP ³ germ	D10	1973
RUD 11	II	D	RM ₃ germ	D4	1974
RUD 12	II	D	Left maxilla with I ¹ , C-M ¹ . Female.	D5	1974
RUD 13	II	D	LM ³ crown		1974
RUD 14	II	D	Mandible corpus fragments with LM ₁ and Rm ₁ -M ₂ , and RI ₁ -P ₄ , LI ₁ -C, P ₄ , LM ₂ . Male.	D4	1974
RUD 15	II	D	Maxilla with LI ² -M ² , RP ³ -M ² , and RI ¹ -I ² , and LI ¹ . Female (contra Wolpoff, 1980).	D6	1974
RUD 16	II	D	RM ₃ germ	D10	1974
RUD 17 ⁵	II	D	Right mandibular corpus with C-M ₃ and LI ₂ -C. Female.	D5	1974
RUD 18	II	D	LM ³ crown	D6	1974
RUD 19 ⁶	II	D	LM ₂ germ		1975
RUD 20	II	A	RC. Female		1975
RUD 21 ⁷	II	?			
RUD 22	II	D	Proximal half right ulna (2 conjoining fragments)		1974/1990
RUD 23	II	NP			1974
RUD 24	II	NP			1973
RUD 25	II	NP			1974
RUD 26	II	NP			1972
RUD 27 ⁸	II	A	Left talar body and neck		1974
RUD 28	II	NP			1974
RUD 29	II	NP			1974
RUD 30	II	NP			1974
RUD 31	II	A	Proximal phalanx lacking the proximal end		1974
RUD 32	II	NP			1974
RUD 33	II	NP			1974
RUD 34	II	A	Distal portion of a proximal phalanx		1974
RUD 35	II	P	Proximal phalangeal shaft fragment		1974
RUD 36	II	NP			1974
RUD 37	II	NP			1974
RUD 38	II	A	Proximal phalanx lacking the proximal end		1974
RUD 39	II	A	Intermediate phalangeal shaft fragment		1974
RUD 40	II	NP			1974
RUD 41/42 ⁹	II	A	Intermediate phalanx lacking the proximal end		1974
RUD 43	II	A	Terminal phalanx lacking the apical tuft		1974
RUD 44/47/144 ¹⁰	II	D	Partial face. Left maxilla with C-P ⁴ , M ² , Right maxilla with P ³ ; premaxillary fragments with RI ¹ -I ² ; right zygomatic bone; three frontal periorbital fragments. Male.	D7	1975
RUD 45	II	D	RM ¹ and RM ³ crowns	D7	1976

Table 2 *Continued*

RUD no.	Location	Taxon	Anatomy	Individual	DOD
RUD 46 ¹¹	II	D	RP ₄ fragment		1976
RUD 47	II	D	RI ¹ (see RUD 44/47/144)	D7	1976
RUD 48	II	A	RM ₃	A3	1976
RUD 49	II	A	LM ₂ -M ₃	A3	1976
RUD 50	II	A	LC-M ₁ , RI ₁ , C-M ₁ . Female.	A3	1976
RUD 51	II	NP			
RUD 52	II	A	LI ₁ -I ₂	A3	1976
RUD 53	II	D	Distal end of a left humerus		1976
RUD 54	II	A	Distal portion of a proximal phalanx		1976
RUD 55	II	NP			1976
RUD 56	II	NP			1976
RUD 57	II	D	Distal end of a first metatarsal		1976
RUD 58	III	D	RM ² germ	D13	1977
RUD 59	II	A	Proximal end of a terminal phalanx		?1976
RUD 60	II	A	Proximal end of a terminal phalanx		1976
RUD 61	II	A	LP ₃ -M ₃ , RP ₄ , M ₂ -M ₃	A17	1977
RUD 62	II	NP			1977
RUD 63	II	A	Distal part of an intermediate phalanx		1977
RUD 64	II	NP			1977
RUD 65	II	A	RI ²		1977
RUD 66	II	?A	Proximal radial fragment		1977
RUD 67	II	NP			1977
RUD 68	III	A	Left lower canine, RP ₄ -M ₁ . Female.	A18	1978
RUD 69	III	A	RM ₂	A19	1978
RUD 70	II	D	LP ₃	D4	1978
RUD 71 ¹²	II	A	Palatal fragments with LI ¹ -M ³ , RC-M ¹ . Male	A4	1978
RUD 72	III	NP			1978
RUD 73 ¹³	III	?	p ³		1978
RUD 74	III	A	Distal part of a proximal phalanx		1978
RUD 75	II	A	Intermediate phalanx lacking the distal end		1978
RUD 76	II	A	LM ²		1985
RUD 77	II	D	Cranial fragments. Most of the frontals, left zygomatic, right parietal, fragments of left parietal, occipital, sphenoid, temporals. Maxilla with LP ³ -M ³ , RM ¹ -M ³ . Female	D8	1985
RUD 78	II	D	Proximal phalanx lacking proximal end		1986
RUD 79	III	D	LP ⁴ germ	D13	1987
RUD 80	II	A	Proximal part of an intermediate phalanx		1987
RUD 81	II	A	Intermediate phalanx		1988
RUD 82	II	D	LI ¹	D11	1988
RUD 83	II	A	Cranium. Maxilla with RP ³ -M ² , LP ⁴ -M ² ; Periorbital fronto-zygomatic fragments, parietal fragments, premaxillary fragments. Female	A5	1988
RUD 84	II	A	Intermediate phalanx lacking the proximal end		1988
RUD 85	II	D	LM ³	D11	1988
RUD 86	II	A	Right zygomatic fragment		1989
RUD 87	III	D	Ldc ¹	D13	1989
RUD 88	II	A	Rdp ³ crown	?A6	1989
RUD 89	II	A	LM ₁	A6	1989
RUD 90	II	A	RI ¹ , M ¹ -M ² , dc ¹ , dp ⁴ , LI ¹ , P ⁴ -M ² , dc ¹ -dp ⁴ . Female	A6	1989
RUD 91	II	A	RI ₁ -M ₁ , dc ₁ -dp ₄ , LI ₁ -P ₄ , M ₂ , dc ₁ -dp ₄ . Female	A6	1989

Table 2 *Continued*

RUD no.	Location	Taxon	Anatomy	Individual	DOD
RUD 91	II	A	LM ₃ , LM ³ , RM ₃ , RM ³	A6	1989
RUD 93	II	A	LI ² crown	A6	1989
RUD 94	II	A	RI ² crown	A6	1989
RUD 95	II	A	Distal half of an intermediate phalanx		1989
RUD 96	II	A	LC. Female.		1989
RUD 97	II	A	RP ³ -M ¹ , M ³ , LI ² -C. Female	A7	1989
RUD 98	II	A	RI ₁ -M ₃ , LI ₁ , C-M ₃ . Female	A7	1989
RUD 99	II	A	LP ⁴ crown	A7	1989
RUD 100	II	A	RM ₂ crown		1989
RUD 101	II	A	Rdp ³	A12	1989
RUD 102	II	A	LI ¹		1989
RUD 103/112/119 ¹⁴	II	A	LI ₁ , C-M ₃ , RP ₄ -M ₃ . Female	A9	1989
RUD 104	II	A	Left lower canine. Male	A8	1990
RUD 105	II	A	LP ₄ , RM ₃	A8	1990
RUD 106	II	A	Left mandibular fragment with M ₂ -M ₃	A8	1990
RUD 107	II	A	RI ₁ -I ₂	A8	1990
RUD 108	II	A	LM ₁	A8	1990
RUD 109	VII	D	Right pollical proximal phalanx		1990
RUD 110	II	?A	Distal part of a proximal phalanx		1990
RUD 111	II	A	Cranial fragments and associated teeth. LP ³ , M ¹ , RP ³ -M ¹	A9	1990
RUD 112	II	A	LI ₁ , P ₃ -P ₄ , M ₂ -M ₃ , RP ₄ , M ₂ -M ₃ and three root fragments (see RUD 103/112/119). Female	A9	1990
RUD 113	II	A	LI ₁ -I ₂ , P ₄ -M ₁ , dc ₁ , dp ₄	A10	1990
RUD 114	II	A	Distal part of a right humeral shaft		1991
RUD 115	II	A	Proximal part of an intermediate phalanx		1991
RUD 116	II	?D	Left medial cuneiform		1991
RUD 117	II	A	Associated teeth. LI ¹ , M ¹ , di ¹ , dc ¹ , rI ¹ , M ¹ , di ¹ , dp ³	A10	1991
RUD 118	VII	D	RI ₂ crown	D14	1991
RUD 119	II	A	LM ₁ (see RUD 103/112/119)	A9	1991
RUD 120	II	D	Terminal phalanx		1992
RUD 121	II	D	LI ¹	D12	1992
RUD 122	II	A	RP ₃	A9	1993
RUD 123	II	A	RM ₂ germ		1993
RUD 124	II	D	Ldp ⁴	D9	1993
RUD 125	II	A	LI ²		1993
RUD 126	II	D	Ldp ³	D9	1993
RUD 127	II	A	Ldp ⁴	A10	1993
RUD 128	II	A	RM ₁ germ	A10	1993
RUD 129	II	A	Proximal phalangeal shaft		1993
RUD 130	II	NP			1993
RUD 131	II	NP			1993
RUD 132	II	?A	Proximal phalangeal shaft		1994
RUD 133	II	?D	Terminal phalanx		1994
RUD 134	II	?D	Distal end of an intermediate phalanx		1994
RUD 135	II	D	Left talus lacking the proximal half of the trochlea		1994
RUD 136 ¹⁵	II	P	Left talus		1994
RUD 137	II	D	Right radial shaft fragment		1994
RUD 138	II	D	Right talar neck and head		1994
RUD 139	II	?P	Canine		1994
RUD 140	?II	D	LM ³ crown (see note 10)	D7	1976
RUD 141	?II	D	RM ² crown (see note 10)	D7	1976
RUD 142	?II	D	LI ¹ (see note 10)	D7	1976

Table 2 *Continued*

RUD no.	Location	Taxon	Anatomy	Individual	DOD
RUD 143	?II	D	RC (see note 10). Male	D7	1976
RUD 144	II	D	Premaxillary fragment with RI ² (see RUD 44/47/144)	D7	1976
RUD 145	II	A	LI ¹ germ	A13	1994
RUD 146	II	A	Ldi ¹	A13	1994
RUD 147	II	D	RP ³ germ	D9	1994
RUD 148	II	NP			1994
RUD 149	II	A	RM ¹ germ	A13	1994
RUD 150	II	D	RI ¹	?D9	1994
RUD 151	II	A	LC tip. Female	A13	1994
RUD 152 ¹⁶	II	A	RI ² tip, di ¹ , dc ¹ fragment, ldp ³ , lower canine tip	A13	1994
RUD 153	II	D	Rdc ¹	D9	1994
RUD 154	II	A	Ldp ₃ crown	A15	1994
RUD 155	II	NP			1994
RUD 156	II	A	LI ₁ -I ₂ , P ₃ -P ₄ fragments, M ₁ , dp ₄ , RI ₁ , canine tip, M ₁ -M ₂ , dp ₃ -dp ₄ Female	A13	1994
RUD 157	II	NP			1994
RUD 158	II	NP			1994
RUD 159	II	A	Left lower canine tip. Male	A15	1997
RUD 160	II	A	RM ¹ -M ³	A16	1997
RUD 161	II	A	RP ⁴ crown	A16	1997
RUD 162	II	A	I ₁ crown	A10	1997
RUD 163	II	A	LP ³ crown	A14	1997
RUD 164	II	A	LM ²	A14	1997
RUD 165	VII	A	LM ₁	A20	1997
RUD 166	II	D	Base of a proximal phalanx		1997
RUD 167	II	D	Right capitae		1997
RUD 168	II	D	Terminal phalanx		1994
RUD 169	II	D	Terminal phalanx		1994
RUD 170	II	D	Proximal hallucal phalanx		1994
RUD 171	II	?	Distal end of an intermediate phalanx		1994
RUD 172	II	A	Rdi ¹	A15	1994
RUD 173	II	A	Rdi ²	A15	1994
RUD 174	II	P	Phalangeal shaft		1997
RUD 175	II	A	RI ²	A14	1998
RUD 176	II	A	RI ¹	A14	1998
RUD 177	II	A	RI ¹		1998
RUD 178	II	A	RM ²	A14	1998
RUD 179	II	A	RP ⁴	A14	1998
RUD 180	II	A	LM ³	A14	1998
RUD 181	II	A	LC. Female	A14	1998
RUD 182	II	A	RM ¹	A14	1998
RUD 183	II	A	Left Femur		1998
RUD 184	II	A	Right Femur		1998
RUD 185	II	A	LM ¹	A14	1998
RUD 186	II	A	LC. Female	A16	1998
RUD 187	II	A	RP ⁴ and LM ¹	A16	1998
RUD 188	II	A	LM ²	A16	1998
RUD 189	II	A	RI ¹	A16	1998
RUD 190	II	A	LP ³	A16	1998
RUD 191	II	A	Left distal humeral diaphysis		1998
RUD 192	II	A	LP ⁴	A16	1998
RUD 193	II	A	RI ²	A16	1998
RUD 194	II	A	Right lateral cuneiform		1998
RUD 195	II	A	LI ²	A16	1998

Table 2 Continued

RUD no.	Location	Taxon	Anatomy	Individual	DOD
RUD 196	II	A	Proximal phalanx		1999
RUD 197	II	D	RI ²	D12	1999
RUD 198	II	D	LC. Female	D12	1999
RUD 199	II	D	RI ¹	D12	1999
RUD 200	II	D	Cranium with RC-M ³ ; LP ³ -M ³ , most of maxilla, right zygomatic, frontal, parietal and temporal and fragments from the left side and basicranium. Female.	D12	1999

Isolated teeth are described as crowns if little or no root is preserved. Germs have no or minimal root development and no wear. P=Primate, A=*Anapithecus*, D=*Dryopithecus*, ?A/?D=probably *Anapithecus*/*Dryopithecus*, ?=Unknown. DOD refers to date of discovery. RUD 22b, 132–139, and 166–167 were all collected in the Kretzoi years and rediscovered in the museum collections and recognized as primate by the authors.

1. This specimen is the holotype of *Rudapithecus hungaricus* Kretzoi, 1969. This taxon is considered a junior subjective synonym of *Dryopithecus brancoi* (see Begun & Kordos, 1993).

2. This specimen is also said to include a fragmentary left mandibular corpus with C-M₃ and a right condylar process. The authors have not seen the original left mandibular fragment, but a photograph is published (Kretzoi et al., 1976; plate 3, Figures 1–5) confirming the existence of the specimen with M₁-M₃. This plate shows the right side of the mandible, which has been examined by us, as well as a left mandibular fragment with M₁-M₃ and a symphyseal fragment. Figure 2 in this plate is described as the symphyseal fragment, but it is not identifiable as such from the image. It does not resemble the symphyseal specimen known to the authors, which is an edentulous symphyseal base also represented by a good cast. The specimen in Figure 2 appears to have a P₄, and therefore probably belongs with another specimen. For now, we leave this specimen, known only from a poor photographic image, unassigned. The right condyle is not primate.

3. This specimen is the holotype of *Bodvapathecus atipalatus* Kretzoi, 1975, which is considered a junior subjective synonym of *Dryopithecus brancoi* (Begun & Kordos, 1993).

4. This specimen is the holotype of *Pliopithecus (Anapithecus) hemyaki* Kretzoi, 1975. The subgenus *Anapithecus* was elevated to a distinct genus by Kretzoi (1984).

5. This specimen is said to include a left mandibular fragment with I₂-M₃. Only the isolated I₂ and canine from the left side are known to the authors.

6. This specimen is listed as Hominoidea indet. in Kretzoi (1984).

7. Kretzoi (unpublished manuscript) notes that this specimen may be a carnivore. The authors have never seen this specimen.

8. This specimen was previously attributed to *Dryopithecus* (Morbeck, 1983). Revised estimates of body mass in *Anapithecus* and the recovery of additional talar specimens indicate that RUD 27 should be attributed to *Anapithecus*.

9. This specimen was originally catalogued as two separate specimens that were later found to conjoin.

10. RUD 47, originally accessioned separately, was found close to RUD 44 and fits the preserved right I¹ alveolus perfectly. It is considered to belong to the same individual as RUD 44. A premaxillary fragment and associated RI², RUD 144, conjoins with RUD 44. Several other separately catalogued specimens (RUD 140–143) appear to be antimeres or have perfectly fitting interstitial facets and are likely to belong to the same individual. No primary provenience data exist for RUD 140–144 because the specimens were removed from the locality without being recorded. They are currently accessioned in the collections of the Naturhistorisches Museum of Vienna. Data from that institute indicate that the specimens were purchased around the same time RUD 44 and RUD 47 were recovered (see text for discussion).

11. This specimen has never been seen by the authors and has never been figured. Its identification cannot be verified.

12. This specimen is the holotype of *Rangwapithecus (Ataxopithecus) serus* Kretzoi, 1984. Here, as in Kordos (1991), it is assigned to *Anapithecus hemyaki*.

13. This specimen is unknown to the authors.

14. Root fragments allocated to RUD 112 conjoin with RUD 103 and RUD 119.

15. This small primate talus is close to or at adult body size based on the development of the articular surfaces and characteristic talar anatomy. Infant anthropoids have porous articular surfaces and poorly distinguished talar features such as heads, necks and posterior tubercles. Juveniles and subadults are difficult to distinguish from adults, but their tali by this time are adult size, even if they are not (hence the observation that most immature mammals tend to have relatively large feet). Even if RUD 136 comes from a subadult, the sharp edges of the articular surfaces, the lack of porosity, and the distinctiveness of the head, neck and posterior tubercles indicates that this talus had attained near adult or full adult size. This individual would have weighed about 6 kg as an adult, based on regressions from Rafferty et al. (1995). The low ends of the ranges of body weight estimates for *Anapithecus* and *Dryopithecus* are about 15 and 20 kg respectively. This suggests that RUD 136 is a different primate taxon. In our view a talus does not make a suitable type specimen for a fossil primate, so we choose not to name this taxon at this time.

16. The field number assigned to this specimen, 682, includes three additional non primate teeth.

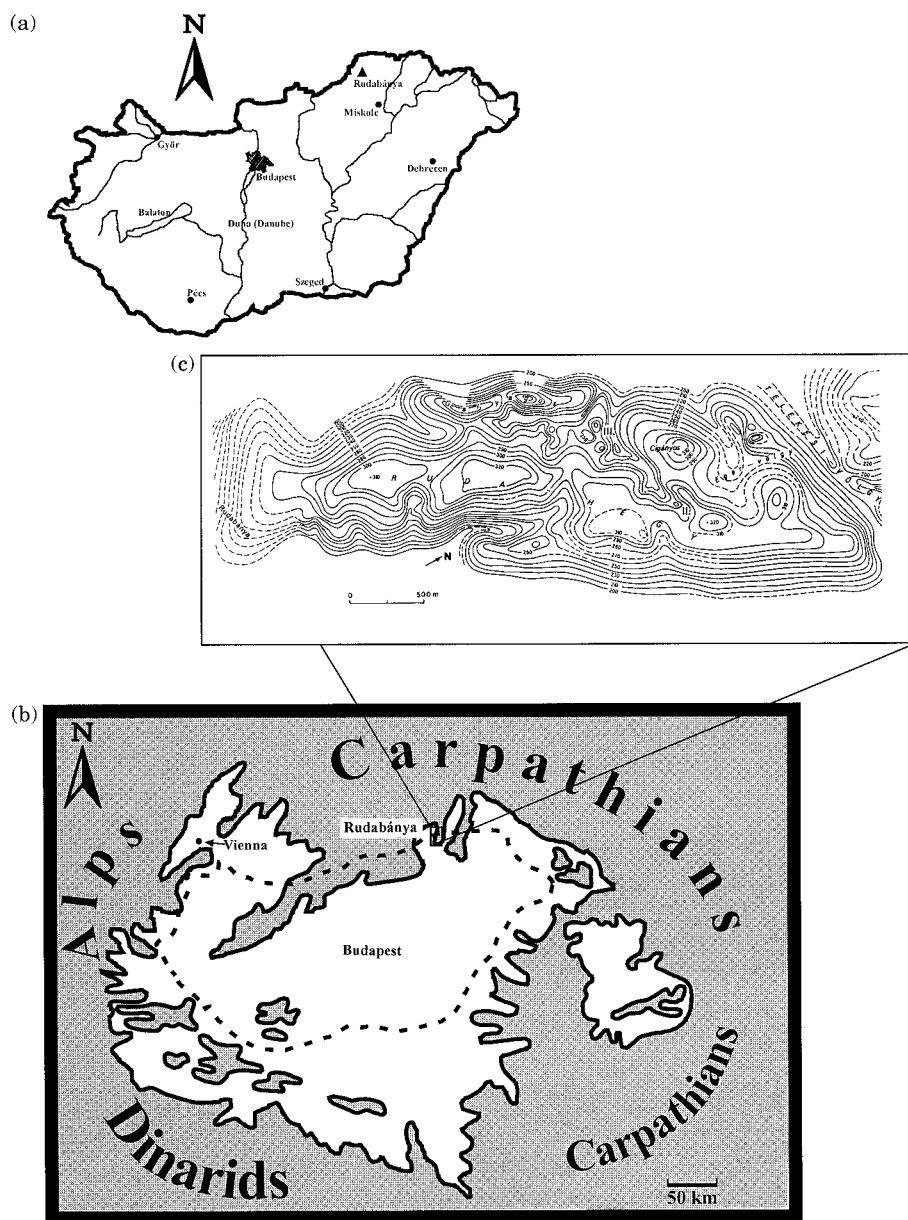


Figure 1. (a) Map of modern Hungary showing the location of major cities, rivers and Rudabánya (north-northwest of Miskolc). (b) Paleogeographic reconstruction of the Pannonian Lake at its peak about 10 Ma. Fossil primate localities from this time period are known from the Vienna Basin in the west and the Borsod Basin in the east. The localities of Rudabánya were located on a peninsula of the Borsod Bay, a small extension of the greater Pannonian Lake. Modified from [Jámbor et al. \(1988\)](#). (c) Topological map reconstruction of the Rudabánya peninsula during the time of deposit of the clays and lignites in which the fossils are found. This reconstruction was made from 3000 bore hole records documenting the depth of the fossiliferous sediments. Modified from [Kordos \(1982\)](#).

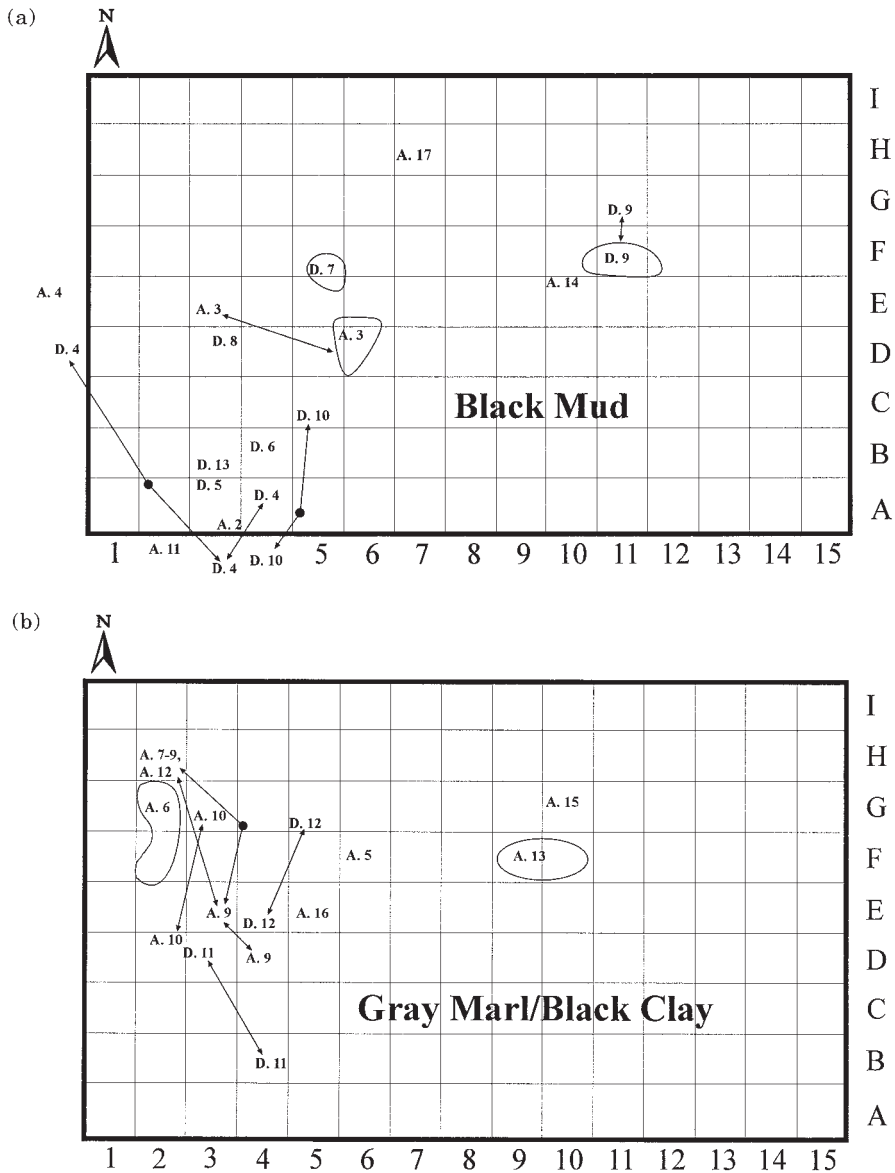


Figure 2. Plan maps of the R II locality. (a) Location of primate individuals in the black mud (upper fossiliferous layer). Most of the *Dryopithecus* specimens were recovered from this layer. Widely separated specimens from the same individual are connected by arrows. Individuals that span more than one adjacent square are enclosed in curves. The direction of these arrows is more varied than in the gray marl [Figure 2(b)], which is consistent with the higher energy depositional environment in the black mud. The earliest specimens recovered from R II, which are outside the grid in this figure, were found before the grid system was put in place. Grids are 2 m², while excavation units are 1 m² (4 units per grid square). Thus, *Anapithecus* individual A14, which is mapped on to grid square E 10, was recovered from excavation unit E 10b, the north-west quadrant of E 10. (b) Location of primate individuals in the gray marl/black clay (lower fossiliferous layer). Most of the *Anapithecus* specimens were recovered from this layer. The black clay is a subunit of the gray marl layer that is laterally discontinuous and characterized by a higher organic content. Most of the specimens are concentrated in this sediment. Specimens within individuals tend to have been moved shorter distances compared to those from the black mud and predominately north to north-northwest. This is the general direction of the dip of this stratum, which was trending towards the deeper parts of the lake.

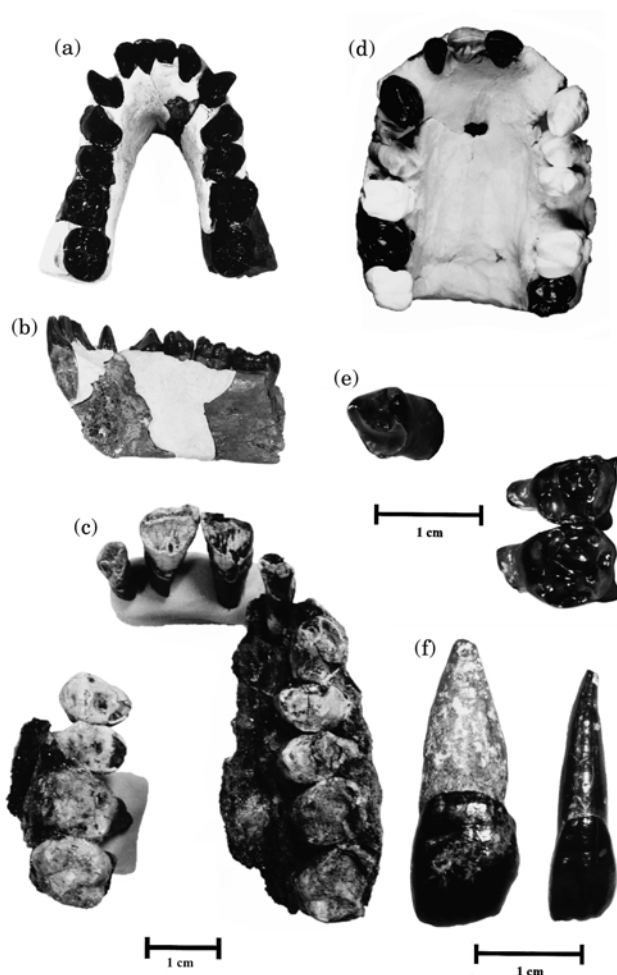


Figure 3. Selected specimens attributed to *Dryopithecus*, illustrating sex and age categories and modes of preservation. (a) Occlusal view of RUD 14/70 (D4). Note the complementary morphology of the left (RUD 70) and right (RUD 14) P₃. An unerupted M₃ also attributed to this individual (RUD 11) is not shown. (b) Lingual view of the right corpus of RUD 14. Note the male morphology of the unerupted canine and the relative lack of occlusal wear on any tooth. Mandibular robusticity of this specimen is partly related to age (Begun & Kordos, 1993). (c) RUD 15 (D6). This poorly preserved specimen is typical of fossils from the interface between the black mud and the upper most portion of the marl (red marl). RUD 18 (not shown), which is associated with this individual, is consistent in morphology and preservation. (d) Casts of specimens attributed to D7 (RUD 44, 45, 47, 140–144) (natural size). Black specimens are accessioned in Vienna while the others are in Budapest (see text and Table 2). (e) Deciduous upper teeth of D9 (Rdc¹, Ldp³⁻⁴). These are the only deciduous teeth of *Dryopithecus* from R II. One additional upper deciduous canine is known from R III. (f) Two upper central incisors of *Dryopithecus* from R II. On the left is RUD 82, probably a male, attributed to individual D11 along with an equally large M³ (RUD 85). On the right is RUD 121, among the smallest of the I¹s from Rudabánya, and from a female with an associated canine (D12). These two individuals are the only *Dryopithecus* so far found in the gray marl. The differences in size between these two teeth is striking. However, ratios of both mesiodistal and buccolingual crown dimensions are within the ranges of variation of living hominoids (Kordos & Begun, submitted). (a), (b) and (d) are half natural size.

point to subtropical seasonal forest conditions (Kretzoi *et al.*, 1976; Kordos, 1982, 1991; Andrews *et al.*, 1997; Bernor & Kordos, in preparation).

Material and methods

The results reported here include the most updated information on the fossil primates from Rudabánya through 1999 (Table 2). These data have been carefully compared to previously published data and verified with reference to the original specimens, casts, photographs, site reports and museum records. All previously published information on preserved anatomy, taxonomic attribution and locality data should be regarded as preliminary and less definitive than the data contained here. Data that remain uncertain are preceded by a question mark. Sex attribution in Table 2 is provided only for those specimens preserving an associated canine, or, in the case of *Dryopithecus*, based on overall size. The primates from Rudabánya are currently housed in three separate repositories. RUD 1–75 are currently unavailable for analysis, and are locked in a safe in the National Museum of Hungary. Among these specimens, RUD 1–43 are actually accessioned into the collections of the Geological Museum, which is independent of the National Museum, and is part of the Geological Institute of Hungary. RUD 76–139 and 145–200 are in the collections of Geological Museum. RUD 140–144 are accessioned in the collections of the Naturhistorisches Museum in Vienna (see note 10, Table 2). The collections of the Geological Museum also include all the site records and original photographs of all the Rudabánya material, so that many of the conclusions presented here could be verified from several sources. With a few exceptions (see below), the authors have examined and analyzed all the original specimens. Exceptions to this are noted in Table 2.

Of the 200 accessioned specimens in the primate catalogue from Rudabánya, 171 are confirmed to be primate. As indicated in the notes to Table 2, five primate genera have been recognized based on fossils from Rudabánya, but only two are currently recognized by the authors.¹ These are *Dryopithecus brancoi* and *Anapithecus hernyaki* (Kordos, 1988; Begun & Kordos, 1993) (Figures 3 and 4). In the case of the dentition, distinguishing between *Anapithecus* and *Dryopithecus* is relatively straightforward given the strong morphological dissimilarity between the two. However, many of the postcranial specimens are less easily distinguished.

Within each taxon, many of the separately accessioned specimens can also be allocated to individuals. This was accomplished with reference to a hierarchy of criteria, beginning with locality, followed by conjoining surfaces, matching interstitial facets, anatomy (identification of antimeres), developmental criteria, and wear. In Table 2, individually catalogued specimens have been grouped together into combined specimens only if they have conjoining surfaces. The location of all specimens is precisely documented (with a small number of exceptions, see below, Table 2 and Figure 2). All specimens allocated to the same individual are known to have been separated by less than 20 cm depth, and most by less than 1 m laterally. A few individuals show evidence of intrasite transport. In one case (A9) specimens separated by about 6 m laterally contain conjoining specimens (root fragments that conjoin with dental crowns). However, most individuals identified here consist of specimens that were recovered from the same depth and within a radius of 50 cm laterally. Most individuals thus assembled can be assigned a developmental age and sex. Sex is assigned primarily on the basis of the morphology of the associated

¹Another primate taxon may be present at Rudabánya (see Table 2), but for the moment there is no definitive dental evidence of this form.

canine. Canines were sexed when possible following the methods outlined by Kelley (1995a,b). In some cases canines were too fragmentary to be measured using these techniques, but the preserved morphology of those specimens always allows for a clear comparison to demonstrably male or female canines. In cases in which the canine is not preserved, sex can be reasonably reliably assigned based on size or the morphology of other aspects of craniodental anatomy (Table 3).

Individuals are assigned to infants if there is evidence that the permanent first molars were not yet in occlusion. Juveniles are defined as individuals with mixed deciduous and permanent dentitions. Subadults are defined as individuals that lack deciduous teeth but have not yet fully erupted their adult dentitions. Adults are defined as having an erupting or occluding M3 in the case of *Anapithecus* and erupted or occluding M3s or canines in the case of *Dryopithecus*. The evidence from a number of specimens from Rudabánya suggests that the canine erupted before the M3 in *Anapithecus*, while both teeth have overlapping eruption times in *Dryopithecus*. In a few cases where the M3 or the canine is not preserved, adult status has been inferred from the wear of other teeth, and comparisons with other individuals that preserve the M3 and/or the canine. Individuals are identified on the basis of dental remains only. None of the postcrania can be reliably associated with any specific cranial or dental specimen. In Tables 2 and 3 individuals are identified by taxon. For example, D1 is *Dryopithecus* individual 1 and A1 is *Anapithecus* individual 1. Table 2 lists each specimen by locality, taxon, preserved anatomy, individual and year of discovery. Table 3(a) and (b) list individuals of each taxon by associated specimen numbers, age, sex and preserved anatomy. Tables 4 and 5 summarize the allocation of cranial and postcranial specimens to individuals for both primates at all four localities.

Discussion

Both Rudabánya primates and, in fact, most Rudabánya mammals usually have well preserved teeth, but fragile and often fragmented postcrania and crania. In many cases these are found as crushed specimens or closely associated fragments that are difficult to extract intact from the sediments, particularly the marls. It is likely that this type of preservation is related to post-depositional factors including microtectonics and geochemistry rather than transport. There is no evidence of trampling, for example, as specimens tend to be oriented and inclined along the bedding plane in the gray marl and black clay. Transport over significant distances tends to round specimens, separate teeth from jaws, and spread teeth apart. Rudabánya mammal fossils tend to be fresh, with little evidence of rounding, and the teeth, as demonstrated above, tend to occur as associated dentitions, though in the case of *Anapithecus* without jaws (Figures 4 and 5). The fact that *Anapithecus* individuals occur mainly as clusters of associated teeth without jaws, or with only small fragments of jaws, suggests that the teeth became separated from the skull after arriving in the deposit. Furthermore, the fact that teeth commonly “disperse” in basically the same direction (south–north or southeast–northwest), in the general direction of increasing lake depth, suggests that this movement occurred before the specimens and sediment became consolidated. There is evidence of some slumping of sediments, but not enough to account for the distances separating a number of specimens of single individuals (Figure 2). A gentle current under the low energy conditions of the gray marl may also have contributed to the distribution of these specimens. It is also possible that *Anapithecus* predators preferentially damaged crania, in the process crushing alveolar bone and loosening teeth, though this seems more likely to affect

Table 3(a) Summary of *Dryopithecus* individuals at Rudabánya (based on craniodental remains)

Individual	Specimens	Preserved anatomy	Age/sex*
D1	RUD 1, 3	Left mandibular corpus with P ₄ -M ₃ and RM ₁ crown	A/F
D2	RUD 2	Right mandible with C-M ₃ and the symphyseal base	A/F
D3	RUD 5	RP ³ germ	J?F
D4	RUD 7, 11, 14, 70	Right maxillary fragment with P ⁴ -M ² ; mandible corpus fragments with L M ₁ and R M ₁ -M ₂ ; associated RI ₁ -P ₄₃ , R M ₃ and LI ₁ -C, P ₄₃ , LM ₂ .	SA/M
D5	RUD 12, 17	Left maxilla with I ¹ , C-M ¹ ; right mandibular corpus with C-M ₃ and assoc. LI ₂ -C	A/F
D6	RUD 15, 18	Maxilla with LI ² -M ² , RP ³ -M ² , and RI ¹ -I ² , and LI ¹ ; LM ³ crown	A/F
D7	RUD 44/47/144, 45, 140-3	Male face. Left maxilla with C-P ⁴ , M ² , right maxilla with I ¹ -P ³ ; RM ¹ -RM ³ ; LI ¹ , LM ³ ; right zygomatic; three frontal periorbital fragments	A/M
D8	RUD 77	Major portions of a neurocranium and maxilla with LP ³ -M ³ , RM ¹ -M ³	A/F
D9	RUD 124, 126, 147, 153, ?150	Ldp ³ -dp ⁴ , Rdc ¹ , RI ¹ -P ³	J?F
D10	RUD 10, 16	LP ³ , RM ₃	A?F
D11	RUD 82, 85	LI ¹ and LM ³	A/M
D12	RUD 121, 197-200	Cranium with maxilla, RC-M ³ ; RI ¹ -I ² , LP ³ -M ³ ; LI ¹ , C and right cranium (zygomatic, frontal, parietal, temporal) and fragments from the left and basicranium	A/F
D13	RUD 58, 79, 87	RM ² ; LP ⁴ , Ldc ¹	J?F
D14	RUD 118	RI ₂	J/?

*Notes about allocation to age and sex. *Dryopithecus brancoi* canines are clearly distinguishable by sex, following the typical hominoid pattern (Kelley, 1995a). D2, 4-7 and D12 preserve canines. The well preserved female canines (D5-6, 12) always have low crowns with large angles at the crown apex between the mesial and distal margins, and all have some degree of cervical flare, in which the crown enamel is distinguished from the root at the cervix by a prominent bulge. The less well preserved canine from D2 is indistinguishable from other females and easily distinguished from males in overall size. This is true of the entire dentition of D2. The male canines (D4, 7) both have tall crowns with small angles between the mesial and distal margins at the cervix. In both cases the crown is unflared at the cervix. Those specimens that do not preserve canines can be sexed by canine alveolar size and shape, or by dental size and premolar morphology. D1 has the smallest lower dentition of *Dryopithecus* from Rudabánya, compatible in size with D12, which has the smallest upper dentition (and an associated female morph canine). While there can be overlap in dental metrics, even among strongly sexually dimorphic primates, it is never the case that the smallest specimens in a reasonably large sample are males. It is always the case that they are females. Thus we are confident in attributing D1 to a female. By the same logic we are confident in attributing D11 to a male, since it has by far the largest teeth of any *Dryopithecus* (Table 6). D8 (RUD 77) does not preserve a canine but does preserve major portions of the neurocranium. It is slightly larger but morphologically identical to the cranium of D12 (RUD 200), and easily distinguished from D7 (Kordos & Begun, 1997 and submitted). It is also dentally smaller than D7. It has a P³ that is oval rather than triangular, which distinguishes all female *D. brancoi* from males, and the interstitial facet on the P³ is small though the dentition is strongly worn, unlike the condition in D7, in which the large canine and P³ have larger interstitial facets. Based on all of these criteria D8 can be confidently assigned to a female (Kordos & Begun, 1997). Finally, D9-10 are fragmentary individuals without permanent canines. Both have a P³, which is distinguishable in *D. brancoi* with associated canines (see above), and in both cases the morphology is clearly female. The two teeth attributed to D10 are also in the low end of the range of variation of *D. brancoi*. It would be unlike the pattern in all known sexually dimorphic hominoids if these teeth are male. D9 is really the only individual of *D. brancoi* from Rudabánya that is somewhat problematic for sexing. The P³ is morphologically female (for *D. brancoi*) but the permanent incisor crown is comparatively large. The P³ size and morphology, which is diagnostic of sex at Rudabánya suggests that D9 is a female with a comparatively large I¹ crown, a pattern also consistent with dental variation in living great apes (Table 6). D3, 13 and 14 cannot be sexed with confidence but are most likely to be female based on size or P³ morphology. However, these specimens, which are not from R II, were not used in the analysis of individuals at that locality (see text for discussion). Allocation to age categories as described in the text.

Table 3(b) Summary of *Anapithecus* individuals at Rudabánya (based on craniodental remains)

Individual	Material	Preserved anatomy	Age/sex*
A1	RUD 4	RC, tip broken	A/M
A2	RUD 9	Left mandibular ramus with roots of dp ₃ , dp ₄ , M ₁ , and left canine germ, LP ₄ , LM ₂ Right M ₁ -M ₃	J/F
A3	RUD 48-50, 52	LI ₁ -M ₁ , RI ₁ , C-M ₁ , M ₃	A/F
A4	RUD 71	Palatal fragments with LI ¹ -M ³ , RC-M ¹	A/M
A5	RUD 83	Cranium with maxilla, RP ³ -M ² , LP ⁴ -M ² . Periorbital fronto-zygomatic fragments, parietal fragments, premaxillary fragments	A/F
A6	RUD 88-94	RI ¹⁻² , M ¹ -M ³ , dc ¹ -dp ⁴ , LI ¹⁻² , P ⁴ -M ³ , dc ¹ -dp ⁴ , RI ₁ -M ₁ , M ₃ , dc ₁ -dp ₄ , LI ₁ -M ₃ , dc ₁ -dp ₄	J/F
A7	RUD 97-99	RP ³ -M ¹ , M ³ , LI ² -C, P ⁴ ; RI ₁ -M ₃ ; LI ₁ , C-M ₃	SA/F
A8	RUD 104-8	Left mandibular fragment with M ₂ -M ₃ , left lower canine, LP ₄ -M ₁ , RI ₁ -I ₂ , M ₃	A/M
A9	RUD 103/112/119, 111, 122	LI ₁ , C-M ₃ , RP ₃ -M ₃ ; LP ³ , M ¹ , RP ³ -M ¹	A/F
A10	RUD 113, 117, 127, 128, 162	LI ₁ -I ₂ , P ₄ -M ₁ , dc ₁ , dp ₄ ; RM ₁ ; LI ¹ , M ¹ , di ¹ , dc ¹ , dp ³ ; RI ¹ , M ¹ , di ¹ , dp ³	J?/M
A11	RUD 8	LC	A/F
A12	RUD 101	Rdp ³	I-J?
A13	RUD 145-6, 149, 151-2	LI ¹ , C, di ¹ , dp ³ ; RI ² , M ¹ , di ¹ , dc ¹	I-J/F
A14	RUD 163-4, 175-6, 178-182	LC-P ³ , M ²⁻³ ; R I ¹⁻² , P ⁴ -M ²	A/F
A15	RUD 154, 159, 172-3	Left lower canine, dp ₃ , Rdi ¹⁻²	I-J/M
A16	RUD 160-1, 186-190, 192-3, 195	RI ¹⁻² , P ³ -M ³ ; LI ² -M ²	A/F
A17	RUD 61	LP ₃ -M ₃ , RP ₄ , M ₂ -M ₃	A?/F
A18	RUD 68	Left lower C, RP ₄ -M ₁	A/F
A19	RUD 69	RM ₂	J?/F
A20	RUD 165	LM ₁	A?/F

*Notes about allocation to age and sex. *Anapithecus hernyaki* canines are clearly distinguishable by sex, following the typical catarrhine pattern (Kelley, 1995a). A1 has a long, curved, robust root and an unflared cervix. A2 has a canine germ with a low crown, flared cervix and large angle at the apex between the mesial and distal marginal ridges. A3 has a lower canine with a low crown, flared cervix and large apical marginal angle. A4 has a canine with a root similar to A1 and a tall crown with an unflared cervix and a low apical marginal angle. A5 lacks a canine but has an upper canine alveolus that is small. Several female upper canines with roots are of appropriate size for this alveolus (RUD 8, 20, 96) while the male canine roots (e.g. RUD 4) are much too large. A6-7, 9 and 18 have lower canines indistinguishable from those of the female A3. A8 has the only fully formed adult male lower canines, with a tall crown, unflared cervix and smaller apical marginal angle. The canine crown fragment from A15 is identical in its preserved morphology. A9, 11, 13, 14 and 16 have upper canine crowns indistinguishable from those of the female A7. A10 is tentatively identified as male based on its lower incisor and molar morphology. It shares uniquely with the male A8 strongly elongated lower molars and tall crowned lower incisors. A17 lacks these characters and is indistinguishable from female lower dentitions, and is thus tentatively identified as female. A19-20 are also tentatively identified as female, but come from R III and R VII, and are not included in the analyses of age and sex distributions at R II.

maxilla more severely than mandibles. Whatever the precise cause, peridepositional processes appear to have been more effective in destroying crania of *Anapithecus* than *Dryopithecus*, leaving mostly clusters of teeth.

Few mammals from Rudabánya show evidence of long-term effects of weathering, and most have been buried soon after

death. Adult large mammals (rhinos, equids, cervids, suids) have been found with articulated distal appendages or associated antlers suggestive of burial relatively soon after death, before decomposition could lead to disarticulation. This is not the case for the primates or the carnivores, which are almost never found with associated postcrania (the only exception being the femora RUD 183

Table 4 Summary of primate individuals at Rudabánya (based on craniodental remains)

Locality	<i>Dryopithecus</i>	<i>Anapithecus</i>
I	N=3: 2 adult females, 1 juvenile/subadult ?female	N=1: adult male
II	N=9: 5 adult females, 2 adult males, 1 subadult male, 1 juvenile ?female	N=16: 7 adult females, 2 adult males, 1 subadult female, 2 juvenile females, 1 juvenile male, 1 infant/juvenile female, 1 infant/juvenile male, 1 infant/juvenile?
III	N=1: juvenile ?female	N=2: adult female, juvenile ?female
VII	N=1: juvenile ?	N=1: adult ?female

Table 5 Summary of primate postcranial remains from Rudabánya

Locality	<i>Dryopithecus</i>	<i>Anapithecus</i>
II*	1 ulna, 1 humerus, 1 capitate, 1 talus, 1 medial cuneiform, 1 first metatarsal, 9 phalanges	1 talus, 1 lateral cuneiform, 2 femora?, 2 humeri, 2 radii, 19 phalanges
III	1 phalanx	2 phalanges

*Four postcranial specimens from R II (1 talus and 3 phalanges) cannot be attributed definitively to either primate taxon.

and 184). It is possible that the primates and small carnivores (mustelids, small felids), which are generally the smallest large mammals at Rudabánya, were more thoroughly processed by carnivores, scavengers, invertebrates and bacteria, leading to disarticulation before burial (Kahlke, 1999).

D. brancoi from R II is known mostly from the black mud, but two individuals (D11 and 12) come from the gray marl [Figure 2(b)]. *A. hernyaki* is known mostly from the gray marl and black clay, but six individuals come from the black mud (A2–4, 11, 14, 17) [Figure 2(a)]. In addition, both primates are found in exactly the same horizon within the gray marl/black clay level, suggesting little time between the arrival of each in the deposit. This finding updates the conclusions presented in Köhler *et al.* (1999) who state that the primates are separated by level at Rudabánya. There are important differences in the taphonomy of these two levels, with the black mud being a

higher energy depositional environment, based on sediment size, fossil orientation and preservation (Kordos & Begun, personal observations, Andrews *et al.*, in preparation). It is possible that smaller bones of *Anapithecus* did not survive as well in a higher depositional regime, but this would not account for the associated dentitions, especially those of infants or young juveniles. It is more probable that each facies at Rudabánya is sampling somewhat different though probably overlapping (in time and space) faunal communities. *Dryopithecus* may have been more common in one and *Anapithecus* in the other, or there may have been other circumstances that made it more likely for *Dryopithecus* bones to accumulate in the black mud and *Anapithecus* bones in the black clay.

There are other interesting taphonomic differences between the two Rudabánya catarrhines. A larger percentage of males of *Dryopithecus* are preserved (Figure 6). A larger percentage of young individuals

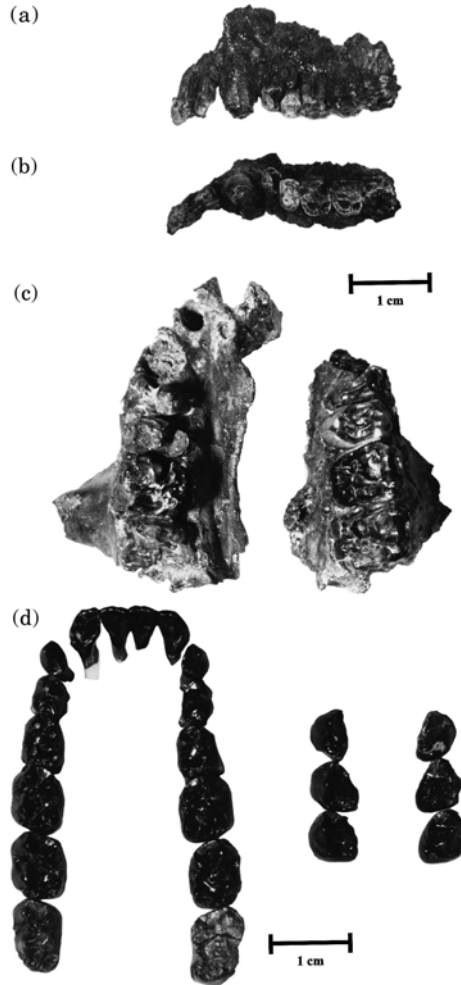


Figure 4. (a)–(d).

(infants, juveniles and subadults) of *Anapithecus* are preserved (Figure 6). Many of the primate remains from Rudabánya show evidence of gnawing, both rodent and carnivore, as well as carnivore puncture marks. However, the age and sex structure of the *Anapithecus* assemblage is more typical of carnivore and chimpanzee prey assemblages (preponderance of young and female individuals). It is possible that the effect of predation acted differently on each primate from Rudabánya. The *Anapithecus* sample may have been accumulated by a

predator or predators that were closer in body mass to *Anapithecus*, placing a premium on selecting relatively small and/or weak individuals (young and old) in preference to prime adult males. Intriguingly, the frequency distributions of age and sex categories of *Anapithecus* from R II are close to those of red colobus monkeys killed by chimpanzees at Gombe and the Tai Forest (Boesch & Boesch, 1989; Stanford *et al.*, 1994; Stanford, 1996, 1998), and different from *Dryopithecus* (Figure 7). The relatively lower percentages of infants and juveniles in

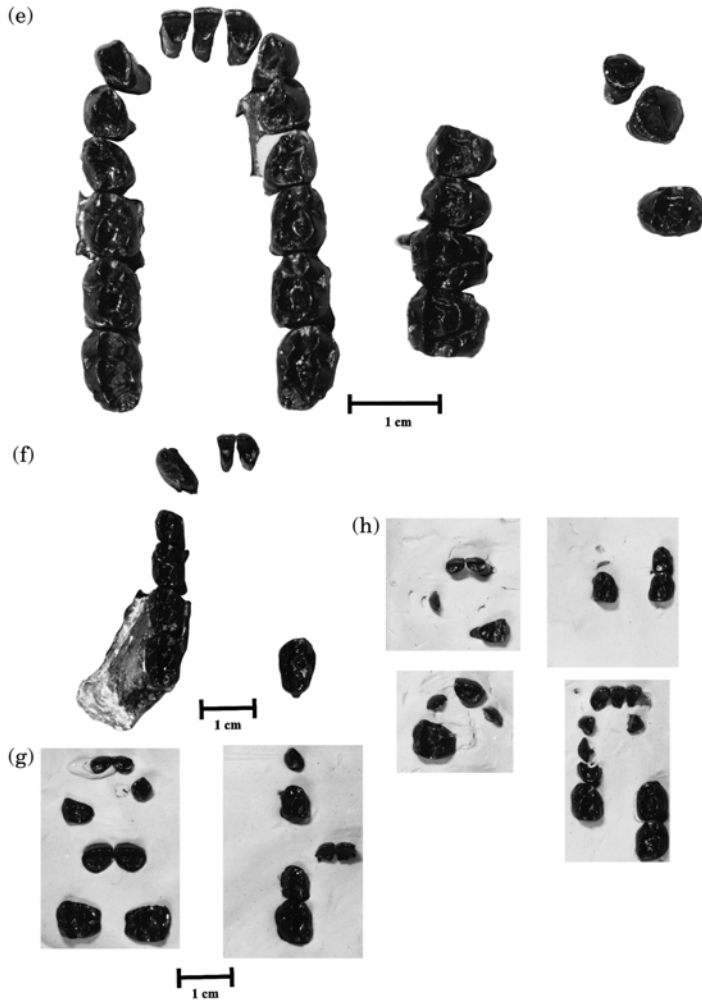


Figure 4. (e)–(h).

Figure 4. Selected specimens attributed to *Anapithecus*, illustrating sex and age categories and modes of preservation. (a) Lateral view of RUD 71 (A4), a poorly preserved male from the black mud, showing the effects of contact with the overlying lignites. (b) Occlusal view. a and b are half natural size. (c) Occlusal view of RUD 83 (A5). This female is associated with major portions of the facial skeleton and neurocranium (Kordos, 1990). (d) Individual A6 (RUD 88–94). Lower teeth of a juvenile female. Deciduous canines and premolars were in occlusion and are positioned with the permanent molars and permanent anterior teeth on the left. The M_1 has just come into occlusion, while the M_2 lacks roots and the M_3 crown is incompletely formed. The permanent canines and the P_{3-4} are on the right. (e) Individual A7 (RUD 97–99). A subadult female with the canine and M_3 not yet in occlusion. Lower teeth on the left, upper teeth on the right. (f) Individual A8. An adult male with a portion of the mandible preserved. Note the greatly elongated molars compared to breadth, particularly the M_3 . (g) Individual A10, a young juvenile or infant. To the left are the upper teeth, with deciduous teeth on the top and unerupted permanent tooth germs below. To the right are two deciduous teeth on top and four permanent tooth germs on the bottom. The elongated morphology of the M_1 and the high crowned lower incisors are similar to the male A8. (h) A13, an infant/juvenile female. Upper dentition to the left, with the deciduous teeth on top and permanent germs below. These include fragments of the Rdi^2 and the Ldc^1 . Lower dentition of the right, with deciduous premolars on top and permanent tooth germs, including fragments of both canines, on the bottom.

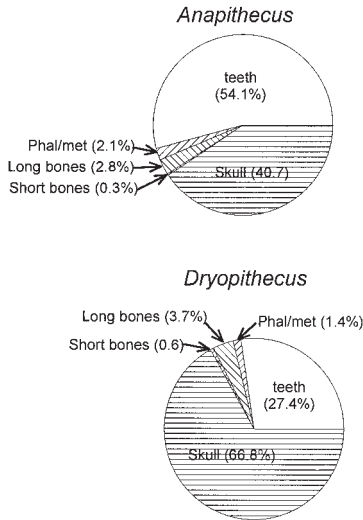


Figure 5. Skeletal part representation in *Anapithecus* and *Dryopithecus*. Samples include all teeth and identifiable tooth fragments in jaws and in isolation, and all individual cranial and postcranial specimens that cannot be conjoined or definitively associated. Short bones are carpals and tarsals. In raw numbers, both taxa are represented primarily by teeth, and both have roughly equal larger representation of phalanges compared to all other postcranial specimens. However, when adjusted based on the number of elements within a category in a living individual and the number of individuals known from the locality (e.g., for *Anapithecus*, $2123 \text{ teeth} \div (32 \text{ teeth/individual} \times 16 \text{ individuals})$), a different picture emerges. *Dryopithecus* is represented by more skull material than *Anapithecus*, which has a much higher percentage of teeth. This adjustment actually minimizes the relative representation of *Anapithecus* teeth because many individuals died with more than 32 teeth (AXII/II probably had 48 teeth erupted, erupting or in crypts).

the R II *Anapithecus* sample compared with those of the chimpanzee hunting assemblages may be related to preservational bias in the fossil record against immature individuals. The high frequencies of females in the *Anapithecus* samples, like the colobus samples, may reflect the fact that females are more likely to be in close proximity to immatures and are taken along with their infants (Stanford, 1998). There is no consistent pattern to the processing of red colobus by chimpanzees (Wrangham, personal communication; Stanford, personal communication). In some cases much of the

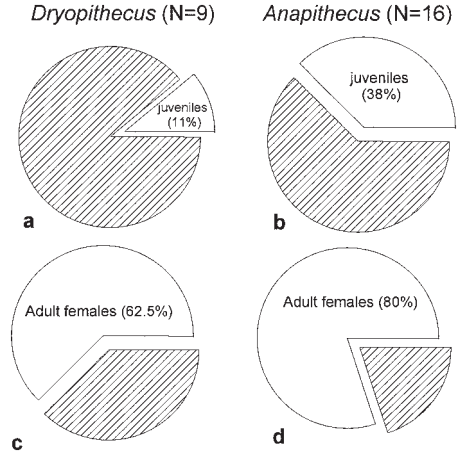


Figure 6. Age and sex categories of *Dryopithecus* and *Anapithecus* individuals at R II. In (a) and (b) juveniles include possible infants and adults include subadults. In (c) and (d) only adults are counted. Note the larger percentages of juvenile and females of *Anapithecus* [(b) and (d)], and smaller percentage of adult male *Anapithecus* (d). Note also the larger number of *Anapithecus* individuals overall compared to *Dryopithecus*.

skeleton is left intact, while in other cases nothing but a few strands of hair found in faeces remains (neither researcher knows what happens to the teeth, though both have looked for them). Gombe chimpanzee males (*Pan troglodytes schweinfurthii*) are larger compared with their typical red colobus monkey prey than are *Dryopithecus* males compared with *Anapithecus* females and infants and Tai forest chimpanzees (*Pan troglodytes verus*) are larger still (Boesch & Boesch, 1989; Boesch, 1994; Stanford *et al.*, 1994, Stanford, 1998) (Table 6 and below). Nevertheless it is tempting to suggest that *Dryopithecus* may have been directly involved in the accumulation of *Anapithecus* at R II through predator pressure (Begun & Kordos, 1996). This is obviously speculative but potentially interesting in terms of the behavioral ecology of both taxa. Nothing in the microwear of *Dryopithecus* molars, which is similar to that of chimpanzees (Kay & Ungar, 1997) precludes this possibility, nor are the bite marks on *Anapithecus* fossils diagnostic of predator or scavenger

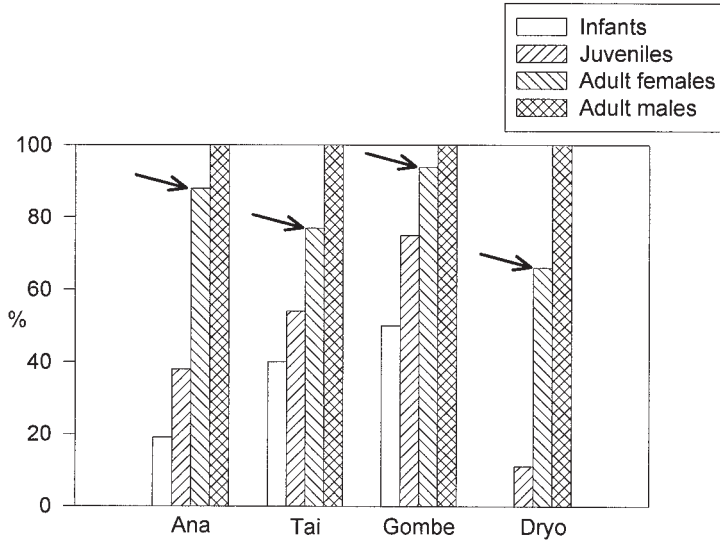


Figure 7. Cumulative frequency histograms of age and sex categories from four primate death assemblages (*Anapithecus*, *Dryopithecus*, and red colobus killed by Tai and Gombe chimpanzees). Note the relatively high frequency of *Dryopithecus* adult males, the absence of infants, and the low frequency of juveniles. In contrast, *Anapithecus* and colobus samples are overwhelmingly dominated by immatures and adult females (arrows). The higher frequencies of immatures in the modern samples compared to the fossil samples may reflect preservation bias against young individuals in the fossil assemblage. Data from modern assemblages from Boesch & Boesch (1989) and Stanford (1996, 1998). See text for discussion.

taxon. The *Dryopithecus* assemblage is more varied in age category, with infants and old adults in roughly equal percentages, and a larger number of young adults (Figure 8). It may have accumulated more catastrophically.

In addition to these preservational differences there are other aspects of the samples of both primate taxa at Rudabánya that indicate biological differences between the two. A large percentage of the *Anapithecus* individuals are relatively complete mixed dentitions, that is, with a large number of deciduous and permanent teeth from the same individuals. Only one *Dryopithecus* specimen preserves a mixed dentition, and it is relatively incomplete (D9). It seems likely that *Anapithecus* developed and erupted its permanent teeth rapidly, such that the M3 crowns were well formed even while the deciduous dentition was still in place. *Anapithecus* permanent molars in associated

dentitions are always at similar stages of wear, with the first molars only slightly more worn than the last molars.

Dryopithecus is larger on average than *Anapithecus*, but it is not clear if their body mass ranges overlapped. Cranially and dentally there is almost no overlap in linear measurements between the two taxa, the only exceptions being in M^1 breadths and M_1 and M_3 lengths between the smallest *Dryopithecus* and the largest *Anapithecus* specimens (Table 6). Many postcrania can be attributed to one taxon or the other, but there are a number of specimens (phalanges, tarsals, and the femora RUD 183 and 184) that could conceivably be associated with either one (Begun, 1988, 1993; Kordos & Begun, 1999) (Table 5). Dentally however, *Anapithecus* is interesting in having comparatively relatively little postcanine size sexual dimorphism, though *Anapithecus* does show canine and possibly other dental

Table 6(a) Summary statistics of upper molar dimensions of Rudabánya primates and selected living hominoids

Tooth	<i>Dryopithecus</i>	<i>Anapithecus</i>	<i>H. symphalangus</i>	<i>P. paniscus</i>	<i>P. troglodytes</i>
Female M ¹ LN	9.2 (8.8-9.5); 6	7.6 (7.2-8.1); 12	7.2 (6.2-8.9); 38	8.6 (8.1-9.0); 9	9.5 (8.3-11.3); 103
Male M ¹ LN	9.8 (9.3-10.4); 2	7.5 (7.4-7.6); 2		8.9 (8.0-10.4); 11	10.3 (9.3-12); 80
Female M ¹ BD	9.8 (8.8-11.0); 6	9.2 (8.6-9.8); 12	7.3 (6.4-8.3); 38	9.6 (9.1-10.2); 9	11.1 (9.5-12.9); 102
Male M ¹ BD	11.4 (11.2-11.6); 2	9.0 (8.9-9.1); 2		10.1 (9.2-12.0); 10	11.3 (9.8-13); 78
Female M ² LN	9.8 (9.1-10.4); 6	8.0 (7.5-8.5); 8	8.0 (6.8-9.4); 39	8.6 (8.1-9.0); 9	9.7 (8.1-11.4); 103
Male M ² LN	11.2 (11.1-11.4); 2	—		9.1 (8.0-11.2); 10	10.3 (8-12.5); 82
Female M ² BD	11.0 (10.5-11.9); 6	9.4 (8.8-10.1); 8	8.0 (6.9-9.3); 39	9.8 (9.0-10.3); 9	11.2 (10.0-12.8); 102
Male M ² BD	11.9 (11.5-12.3); 2	—		10.4 (9.0-12.7); 10	11.8 (10.5-13.8); 82
Female M ³ LN	9.7 (9.2-10.6); 5	7.7 (7.4-8.1); 4	7.2 (5.1-8.0); 37	7.8 (7.3-8.5); 6	9.0 (7.2-12); 85
Male M ³ LN	10.9 (9.8-13.1); 3	—		7.9 (7.1-8.8); 8	9.6 (6.0-12.0); 78
Female M ³ BD	10.8 (10.4-11.5); 5	8.9 (8.7-9.1); 3	7.8 (7.2-8.7); 39	9.1 (8.8-9.6); 6	10.7 (9-12.5); 86
Male M ³ BD	11.9 (11.0-13.3); 3	—		9.4 (8.5-11.2); 7	11.4 (9.6-14.3); 77

Means (range); N. Living hominoid data from Remane (1960). *H. symphalangus* mixed sex samples.

Table 6(b) Summary statistics of lower molar dimensions of Rudabánya primates and selected living hominoids

Tooth	<i>Dryopithecus</i>	<i>Anapithecus</i>	<i>H. symphalangus</i>	<i>P. paniscus</i>	<i>P. troglodytes</i>
Female M ₁ LN	9.3 (8.9-9.7); 4	8.0 (7.7-8.6); 11	7.8 (6.7-8.9); 41	9.2 (8.8-9.7); 9	10.4 (9.1-12.2); 97
Male M ₁ LN	11.4 (11.3-11.4); 2	8.5 (7.9-8.9); 4		9.7 (8.9-10.6); 11	10.8 (9.7-12.3); 48
Female M ₁ BD	8.2 (7.9-8.4); 4	6.5 (5.9-6.9); 11	6.3 (5.3-7); 34	8.4 (8.0-8.8); 9	9.5 (7.7-11.4); 91
Male M ₁ BD	10.2 (10.1-10.2); 2	6.6 (6.4-6.8); 4		8.8 (7.9-9.7); 11	9.8 (8.3-11.2); 51
Female M ₂ LN	10.2 (9.8-10.8); 4	8.4 (7.9-8.9); 13	8.4 (7.2-9.7); 22	9.8 (9.2-10.8); 9	10.7 (9.1-12.1); 92
Male M ₂ LN	13.2 (13.2-13.3); 2	8.5		10.1 (8.3-11.8); 9	11.3 (9.6-12.9); 53
Female M ₂ BD	9.2 (8.4-9.9); 4	6.8 (6.2-7.3); 13	6.8 (6.2-7.3); 20	8.8 (8.3-9.3); 10	10.0 (8.6-11.5); 87
Male M ₂ BD	11.0 (11.0-11.1); 2	6.5		9.2 (8.2-10.7); 9	10.7 (9.1-12.1); 92
Female M ₃ LN	10.8 (10.5-11.0); 4	9.6 (8.9-10.1); 11	8.0 (6.7-9.1); 20	8.8 (7.9-9.5); 6	10.0 (8.4-11.4); 80
Male M ₃ LN	12.4	10.8 (10.7-10.9); 2		8.8 (8.0-9.4); 7	10.7 (9.4-13.3); 48
Female M ₃ BD	8.9 (8.4-9.5); 4	6.7 (6.3-7.1); 11	6.5 (6.0-7.1); 19	8.0 (7.7-8.5); 6	9.5 (7.9-10.9); 80
Male M ₃ BD	9.8	6.8 (6.8-6.9); 2		8.8 (8.0-9.4); 7	10.3 (8.8-11.6); 52

Mean (range); N. Living hominoid data from Remane (1960). *H. symphalangus* mixed sex samples.

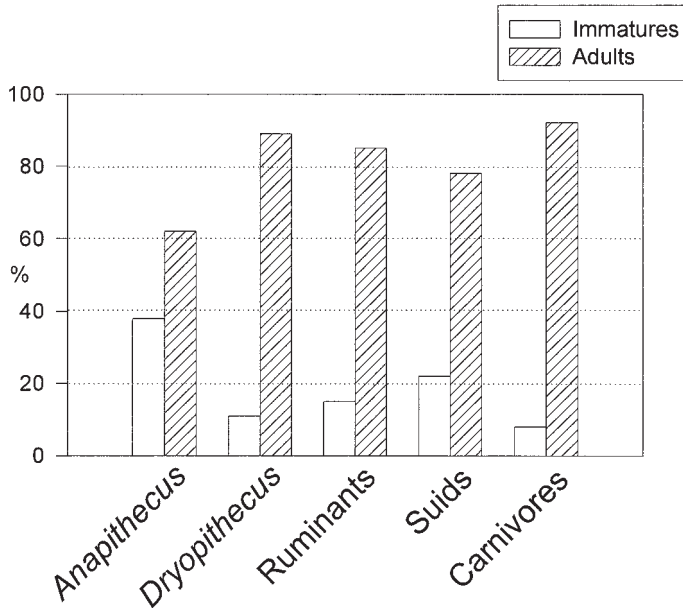


Figure 8. Comparative age distributions. Preliminary assessment of age distributions in catarrhines and other mammals from Rudabánya. Note the high percentage of immatures of *Anapithecus* compared to *Dryopithecus*. Note also the low percentage of immatures of *Dryopithecus*, comparable to that of carnivores and ruminants at Rudabánya. Adults include adults and subadults. Immatures include infants and juveniles.

morphological sexual dimorphism (see [Tables 2 and 6](#)). *D. brancoi* is more sexually dimorphic in dental dimensions and in canine and premolar morphology ([Table 6](#)). Using the equation from [Aiello & Wood \(1994\)](#) for predicting body mass from orbital area, the female A5 individual (RUD 83) has an estimated body mass of 16.9 kg (95% CI 15.3–18.7). The same regression predicts a body mass of 29 kg (95% CI 26–32) and 23 kg (95% CI 20–26) for two reasonably complete female *Dryopithecus* specimens (D8 and 12, respectively). [McHenry \(1992\)](#) provides a regression of distal humeral breadth on body mass that yields a predicted body mass of about 45 kg for the largest postcranial specimen from Rudabánya, RUD 53. This is consistent with the size of the teeth of male *D. brancoi* generally and the face of D7 in particular, the teeth of which are in the range of male *Pan troglodytes* ([Table 6](#)).

Conclusions

The goal of this paper is to provide evidence for the number of primate individuals from Rudabánya and their developmental status and sex. Rudabánya is a set of localities among which one, R II, is rich in fossil primate individuals, many represented by large percentages of their dentitions. Work is in preparation on a detailed morphological analysis of the entire primate sample from Rudabánya, now that the first phase of work identifying and categorizing individuals has been completed. Given the relatively large samples and comparatively complete specimens of both *Dryopithecus* and *Anapithecus*, much additional work is now possible on the functional anatomy, life history and phylogeny of each. Associating the teeth into relatively complete dentitions will allow researchers to describe dental proportions, eruption rates and sequences, and

functional and morphological relationships among upper and lower teeth. For now it is possible to say that *Dryopithecus* and *Anapithecus* were two different kinds of primates, in terms of body mass, functional anatomy and, probably, developmental biology and behavioral ecology. It is our hope that more information on the developmental biology of *Dryopithecus* will emerge, and that it will be possible to associate dental and postcranial remains from both primate taxa. In the meantime, this update and catalogue of the primate sample from Rudabánya should serve as a baseline for future research on these fossil catarrhines.

Acknowledgements

The authors are grateful to Terry Harrison, Jay Kelley and two anonymous referees for useful comments that improved the manuscript. DB is also grateful to Richard Wrangham and Craig Stanford for stimulating discussions about chimpanzee hunting, though the speculation about hunting in *Dryopithecus* cannot be blamed on these two researchers. This research was supported by grants from OTA, Leakey Foundation, Wenner-Gren Foundation and NSERC. Finally, we would like to thank the students of the 1997–1999 Rudabánya field school seasons.

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