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Rudabànya: Taphonomic analysis of a fossil hominid site from Hungary

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ABSTRACT

The late Miocene deposits at Rudabànya, Hungary, were laid down in a shallow valley sloping westwards from a range of hills and opening out into the Pannonian Lake. Rise and fall of lake level gave rise to varying conditions, from dry land with soil formation to swamp and lake. The stratigraphic and palaeontological succession has been investigated at one of the sites, Rudabànya 2, where two cycles of deposition and erosion are represented, with soil formation, swamp conditions with lignite formation, and periods of extended high lake level succeeding each other. Both mammal and plant fossils are present at several levels. Taphonomic modifications in the Rudabànya 2 vertebrate faunas include losses of skeletal elements through carnivore selection, fluvial sorting at some levels, and post-depositional destruction by leaching and/or acid soils. The lowest level, the lower lignite, has few fossils. The fossil mammals from the level above, the grey marl, are the least modified but they are mixed with abraded, probably allochthonous, bone fragments and more complete specimens resulting from near-lake deaths. Modifications of bones by carnivores are indicated, but the specimens were too broken post-depositionally for the impact of the carnivores to be assessed. Carnivore action is also indicated for the fauna of the black clay which formed on the surface of the grey marl. The fauna consists of relatively abundant small mammals and the primates *Anapithecus hernyaki* and *Dryopithecus hungaricus*, with the latter much less common. The predator accumulating the smaller species was probably a viverrid. The red marl fauna is a transported assemblage from higher up the valley with the fossils extremely fragmentary and abraded and few identifiable specimens, almost all of which are teeth. The black mud fauna is also probably a transported assemblage, lower energy than the red marl environment, and the bones are much modified subsequently by acid corrosion similar to that seen today in bone preserved in peat bogs. *Dryopithecus* is a major constituent of the fauna, with *Anapithecus* less common. *D. hungaricus* is thus associated more strongly with swamp forest and shallow riverine conditions with low energy movement of water, and *A. hernyaki* is associated with lake shore (probably forest) conditions, accumulating in lake sediments and lake-flat sediments. The palaeoecology of the area as a whole, based on the associated flora and fauna, is a combination of swamp forest, lake shore forest and open mud flats.

1. Introduction

The Rudabànya fossil deposits were first investigated at the end of the 19th century, and in the mid to late 20th century the site was extensively excavated first by Kretzoi (1969, 1975, 1984) and latterly by Kordos (1982, 1987, summarized in Kordos and Begun, 2001). More recently a team led by Bernor and Kordos excavated for three seasons at Rudabànya 2 in 1992–1994 (Bernor et al., 2003b). The two aims of the Bernor excavations were to investigate the taphonomy of the deposits to see if there were faunal differences within the stratigraphic section and to provide for a comprehensive systematic, biogeographic and paleoecologic assessment based on the vertebrate fauna (112 species; 69 species of mammals (Bernor et al., 2003a, 2005). The large mammal fauna known from Rudabànya is unusual in that the mammal fauna includes two primate species, *Dryopithecus hungaricus* and *Anapithecus hernyaki* (Kordos and Begun, 2001), for species of these two genera are rarely found together in one deposit (Andrews et al., 1996). The aim of the taphonomic excavations at Rudabànya was to investigate sources and associations of faunas and floras within the Rudabànya sequence, and in particular to see if the two primate species were present in the same levels and at the same time at Rudabànya.

There are a number of fossiliferous localities within the Rudabànya Basin, and this paper describes the excavations at one of these, Rudabànya 2 (Fig. 1). This is the site from which the majority of primates has come, including much of the material of *Dryopithecus* and *Anapithecus* described by Kretzoi (1975) and the skull described by Kordos (1991). Other sites include one with abundant fossil leaves well preserved (Kretzoi et al., 1974) and several mammal localities, but strict age equivalence cannot be determined for these and no

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Fig. 1. General view of Rudabànya 2 looking due east close to and up the axis of the Miocene valley in which the sediments accumulated. The lower excavation (foreground) has most of the grey marl exposed in section; in the middle is part of the surface of the red marl; and at the back is the upper excavation where the black mud and upper lignite are exposed.

taphonomic work has been done on their floras or faunas. The depositional setting of these sites appears to be broadly equivalent to Rudabànya 2, and they will be mentioned briefly when reconstructing the landscape ecology of the region during the Miocene.

The age of Rudabànya 2 is determined on the basis of its mammalian fauna. The sequence is too short to tie into the geomagnetic timescale, but on the basis of the evolutionary stage of the fauna, Rudabànya 2 fits into the MN9 land mammal stage, similar in age to Can Llobateres (Agusti et al., 1999).

2. Material and methods

Excavation was by stratigraphic level, and as far as possible all squares were excavated at the same level, following bedding planes. The total extent of the excavation was 7 by 4 m, although not every square was excavated to the same level and not every square was fully excavated. Excavation was done by hand trowel and brush, and all residues were collected, dried and washed in 800 µm screens. The marl deposits were soaked for at least 1 h in an 8–10% solution of hydrogen peroxide to facilitate break down of the sediment. This was partially successful, but in many cases the washed residues had to be washed again after drying. After washing, the residues were brought back to the laboratory for hand-picking. Because of limited facilities in the field, only the coarse residues were picked, and the fine residues were re-bagged for further work in Budapest. The fossils from the coarse residues were taken to the Natural History Museum, London, for counting, identification and taphonomic analysis.

Specimens found during the course of excavation were recorded in three dimensions. In addition to the location measurements, the square number of every find was recorded, together with a number of taphonomic observations. Where possible, the angle of dip was measured, and the angle of orientation was measured in the direction of dip. If the specimens were broken and too fragmentary to be conserved, their spatial coordinates were measured and drawings or photographs used to record their undisturbed state. Drawings were made by Eleanor Weston and photographs by Phil Crabb. If not measured in the field, all specimens were subsequently measured in the laboratory by DC, together with taphonomic observations on breakage and preservation of specimens and any evidence of pre-depositional or post-depositional damage or modifications.

Individual fragments of fossil bone from one element (e.g. femur) were not measured when associated with other fragments from the same bone (broken post-depositionally). Rather the full length/breadth of the “complete” element before disturbance by excavation was measured on site. Definitions for Bone Breakage Patterns are as follows:

1. Complete
2. Fragment (splitting–cracking undefined)
3. Shaft of long bone only (ends missing)
4. Proximal or distal end of bone (shaft missing)
5. Splinter spiral break (long bone fragment with angled break i.e., not transverse)
6. Transverse break (clean vertical break not angled)
7. Post-depositional breakage (bone fragments from one element clustering together)
8. Unidentified (unidentifiable).

The type of modification is subdivided into abrasion, trampling, weathering, root marks, insect marks, gnawing by carnivores and digestion by carnivores, and in each case, the degree of modification is divided into three classes, light, medium and heavy (Behrensmeyer, 1975, 1978). The definitions for surface modifications are as follows:

9. Abrasion and rounding (directional scratches with smooth edges)
10. Abrasion and chipping of edges (directional scratches with edges chipped)
11. Abrasion and pitting (directional scratches with pitting exposing cortex)
12. Trampling (very fine striations, usually numerous, often directional)
13. Weathering and pitting (bone shows cracks with pitting)
14. Weathering and splitting (bone shows cracks with finer splitting)
15. Root marks (irregular grooves)

16. Bone table not preserved (unidentifiable)
17. Scoring by insects (irregular fine striations)
18. Gnawing (usually long bone fragments with dental pits and striations)
19. Digestion (localized pitting and surface corrosion)
20. Cranial (numbers of cranial fragments)
21. Mandible (numbers of mandibles)
22. Teeth (numbers of teeth)
23. Postcranial (numbers of postcrania).

The fossil wood found in situ was mapped onto site plans and selectively collected for further analysis. Those samples which were collected were also entered on the site specimen catalogue with information pertaining to three categories: 1) stratigraphic horizon; 2) dip and 3) orientation. These data were analysed in the same way as for the bone specimens. Distribution of taphonomic modifications in individual squares or stratigraphic horizons has been examined and compared to unravel the depositional processes which accumulated fossil materials in the different sedimentary units.

2.1. Correspondence analysis

The four main faunas from Rudabànya 2 have their taphonomic modifications summarized in Appendices 1–4, and all the data on bone modifications and bone breakage have been analysed by correspondence analysis. Correspondence analysis is a form of ordination suitable for individual categorical data, which are unweighted and transformed into binary numbers using Wrights DISJUNCT programme and analysed using MV-NUTSHELL (Wright, 1994). It is used here because it examines complex correlations between objects and variables, in this case excavated units (lithologies) and taphonomic modifications on the fossils. The variables examined in this analysis are based on their presence or absence within each of the four main fossiliferous units. All variables in the analysis were equally weighted.

2.2. Measures of abundance

MNI values were calculated by Miranda Armour-Chelu for the whole assemblage under study so that comparisons could be drawn between the representation of dentitions as opposed to postcranial remains and to assess any variability in element survivorship between individual taxa. Meaningful analyses of MNI values derived from teeth and postcranial elements assume that both data sets are equally identifiable which is unlikely. Teeth are inherently more identifiable to taxon than fragmentary postcranial remains, with the consequence that unidentifiable bone parts become “analytically invisible” (Lyman, 1994). This will be the subject of a future study (Armour-Chelu, pers. comm..) and in this study we have limited our approach to assigning postcranial remains, regardless of whether they can be taxonomically identified, to body size category, element and bone part where possible. The aim here is to better understand the way in which the animal fauna accumulated.

2.3. Material

The fossil material excavated from Rudabànya 2 can be divided into three categories. Most of the fossil bone on which the detailed taphonomic results are based were excavated in 1992–1994, and included with the animal bone was some plant material, mostly fragments of fossil wood. These fossils were excavated with great care, and their state of preservation after excavation is the same as that before excavation. Many of the fossils were found to be broken in the ground, with conjoining fragments maintained in position by the sediment. These were collected as single units and measurements and descriptions are based on their complete state before removal from the sediment. These collections are all in the Geological Institute, Budapest.

Secondly, the sediment from each grid square was screened and the wood and bone extracted from the screened residues either in the coarse fraction, which is analysed here for wood/bone frequency, or in the fine fraction, for which we have only investigated the surface modifications. Degree of breakage of the screened fossils is much greater because fossils that were already broken while still in the sediment inevitably became fragmented during the screening process. The coarse fraction is at present at the Natural History Museum, London, and most of the fine fraction, mostly unsorted, is in Budapest. Some samples of fine fraction are in the Natural History Museum in Vienna.

Thirdly, the vertebrate remains recovered from the previous excavations undertaken by M. Kretzoi (1965–1975) and L. Kordos (1982–current), are housed within the collections at the Geological Survey (Armour-Chelu et al., 2005).

3. Description of the sediments

The Rudabànya sediments rest upon Triassic dolomite which formed a local highland in the late Miocene. This highland extended down to the northern margin of the Pannonian Lake. Since the formation of the Mesozoic carbonates, the dolomites have been altered by base metal mineralization, which has enriched the basement rocks in iron, barium, zinc, copper, silver, gold, lead, sulphur, and other elements. The unusual composition of the parent rock allows evaluation of local source rocks on composition of the sediments (Kordos, 1985).

While iron mining (siderite) in recent decades has removed most of the overlying Miocene sediments in the area, it has served to expose several sedimentary deposits at the margins of the open pit. Hundreds of drill holes placed to evaluate the potential for iron mining have allowed reconstruction of the area's contours, and the pre-Pannonian land surface has been reconstructed in detail by Kordos (1985, 1991) showing the presence of a line of low hills 310–320 m in altitude, with valleys dissected between them. Rudabànya 2 is positioned near the top of a small valley that opened to the west into the Pannonian Lake basin. Rises and falls of lake level gave rise to varying environments around the edge of the Pannonian Lake, including lake, swamp, wetland and palaeosol (Kordos and Begun, 2001). The east–west axis of the Rudabànya 2 depression is approximately 750 m long and the north–south axis about 450 m wide. The sediments at Rudabànya 2 formed on this low angled platform extending from the top of the palaeovalley into the Borsod Basin to the west. Because of the low angle of the sedimentary platform, relatively small changes in lake level caused shifts in the depositional environment at any one position in the valley. The high topographic position of Rudabànya 2 led to the development of an incomplete section due to pinching out of many lower level strata (Kordos, 1985).

Rudabànya 1, which is the type site of *Rudapithecus hungaricus*, is slightly lower and in a side branch off the valley, while Rudabànya 3 is much lower down the valley (Kordos, 1985). When the Pannonian basin was flooded, this valley formed an embayment of the lake, and as the lake level rose and fell, the valley was alternately dry land, swamp and lake, with the formation of soils, swamp deposits/lignites and lake deposits, but as the three sites are all at different levels, there is no concurrence in the time of formation of lithologically similar sediments. This makes it difficult to correlate the deposits in the three sites, even between 1 and 2 which are only a few hundred metres apart.

The description of the lithology of Rudabànya 2 that follows has been compiled from field notes by PA, Gerd Theobald and Douglas Ekart (Fig. 2).

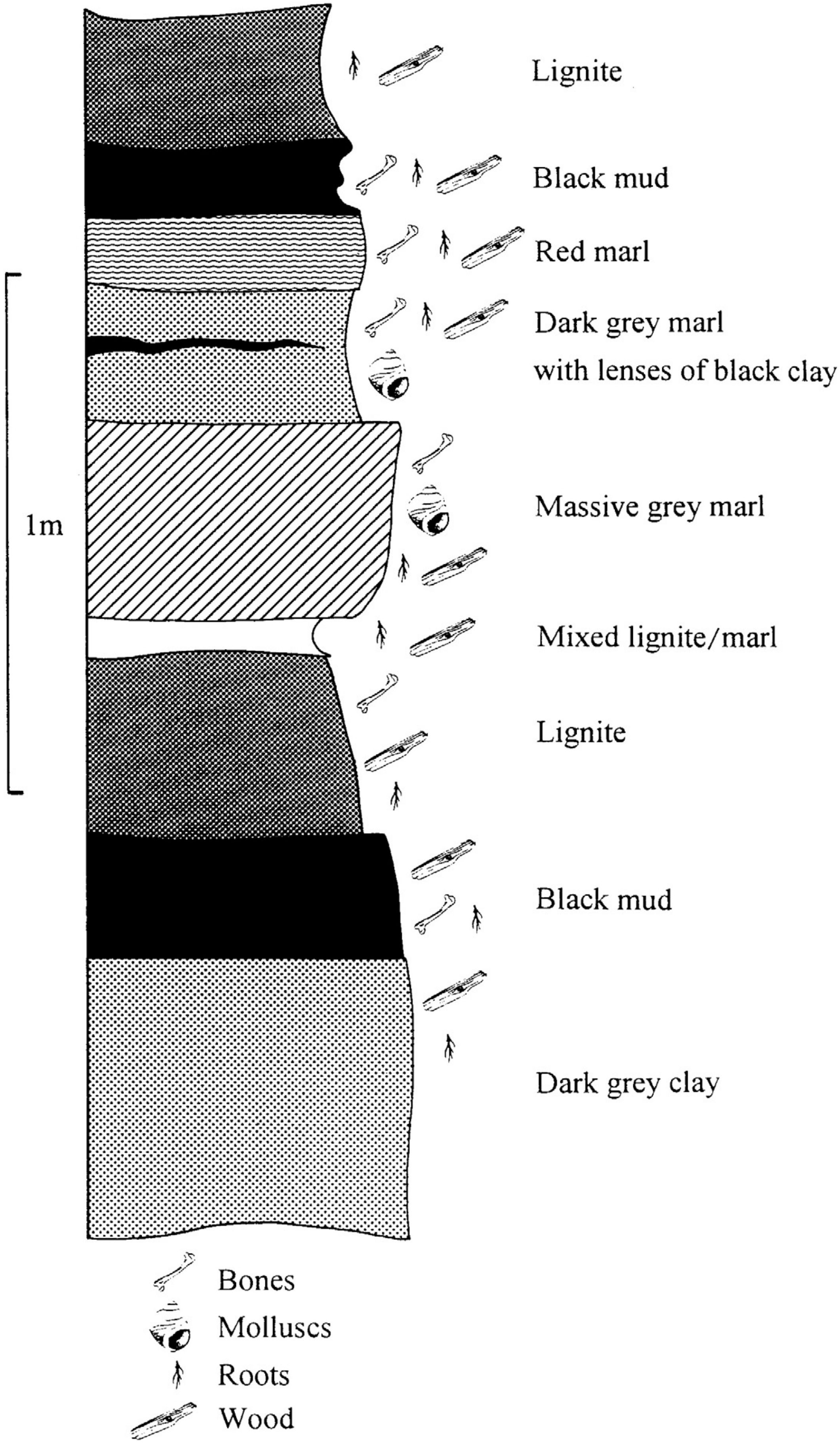

Fig. 2. Stratigraphic section of the Rudabànya 2 deposits (after Theobald 1994).

Fig. 3. The lower lignite–marl transition showing mixing of the deposits or rip-up clasts of lignite in the marl due to wave action or to fluctuating depositional conditions.

3.1. Dark grey clay

The lowest sediments exposed at Rudabànya 2 are predominately a dark grey clay with significant silt, with little sand and rare pebbles. The depositional mode is unclear because of subsequent soil development and because the bottom of the unit was not reached during our excavation. For this reason also the thickness of the dark grey clay is unknown. Possible modes of accumulation of this unit include alluvial/colluvial transport, distal deltaic deposition in the Pannonian Lake, or aeolian origin. Mineral content suggests a local origin of sediments, favouring the alluvial/colluvial depositional model. Palaeosol development is indicated by highly weathered clasts of weathered carbonate from the bedrock valley walls suspended in the fine grained sediments, ferruginous concretions associated with fossil roots, destruction of sedimentary fabrics, and chemical profiles consistent with leaching processes.

The grey clay passes upward into a black clay, 10–15 cm thick, which is described by Gerd Theobald (pers. comm..) as the A horizon of the palaeosol formed on top of the grey clay B horizon. Roots and wood are present in the black clay, with occasional animal bones, but the root traces were the only biotic remains in the grey clay. They are succeeded by a lignite, which is interpreted as the 0 horizon of the palaeosol, indicating slow rise in lake level resulting in water-logged anoxic conditions and a high rate of organic accumulation.

3.2. Lower lignite

An increase in the Pannonian Lake level flooded the terrestrial soil surface at a shallow depth and initiated accumulation of the lower lignite. This approximate water level was maintained for sufficient time for trees and other organic matter to accumulate over an anoxic shallow water body, producing 30–35 cm of lignite. Several marl lenses within the lignite suggests fluctuating conditions with temporary increase in lake level and cessation of lignite formation, but this does not appear to have been of sufficient duration to alter the vegetation structure. There are abundant remains of wood forming the bulk of the lignite deposits, but no bones were found.

3.3. Massive grey marl

At the end of the lignite formation at Rudabànya, rise in lake level flooded the swamp, with the last generation of trees falling into the water and being deposited as logs on the surface of the lower lignite. Marl deposition increased and lignite particles decreased as sedimentation continued until full marl deposition was uninterrupted, resulting in the formation of a light grey massive marl 40–45 cm thick. There was some mixing of the lignite and marl at the base of this unit (Fig. 3). The marl now exposed at the excavation site has been oxidized to a pale yellow in the modern exposures and it has massive structure. It is penetrated by roots throughout its exposure (Fig. 4) from vegetation growing in higher levels, and bones are present throughout, although never abundant. Within the grey marl a number of slippage/fault lines were also observed. These features were stained a dirty reddish-brown due to the accumulation of clay and other sediments. Many of these slippage lines were interrupted or partially broken by tree roots, indicating they were penecontemporaneous with the marl deposition, and they produced some vertical movement within the marl deposit.

The upper part of the grey marl is darker in colour, but there appears to be no break in sediment accumulation. Within this upper marl is a horizon which contains abundant gastropod shells, a thin sandy layer with transported charcoal, and above this is a black clay.

3.4. Black clay

Lowered lake level at one period of deposition of the massive grey marl is indicated by the formation of mud flats exposed to air, with local ponding resulting in the accumulation of black clays in one part of the excavation area. Resting on the surface of the black clay, but

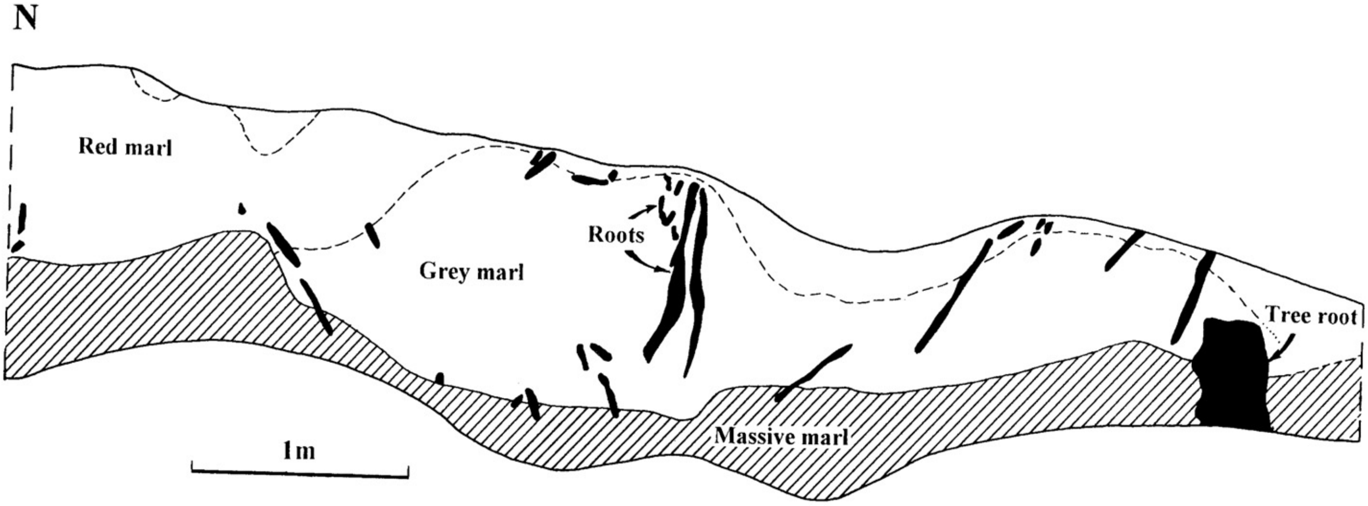

Fig. 4. Section through the grey marl/red marl transition showing the uneven top of the red marl and the penetration of roots from one bed to the other.

covered by further grey marl deposits, was a concentration of rhino, suid and equid fossils, but there is no evidence of any vegetation growing at this time, and the exposure time was very short. The intense black colour indicates high organic content, low oxygen level and the presence of stagnant water. This seems to be related with a period of relative desiccation, and a reconstruction of the sequence at the top of grey marl is as follows:

Stage 6. Deposition of the uppermost grey marl with increase of the lake level.
Stage 5. Thin reworked level. Increased level of the water. Erosion.
Stage 4. Dry surface with ponds, with black clay accumulated in the ponds.
Stage 3. Presence of fire. Charcoal transported to the lake.
Stage 2. Shelly layer. Low level of the lake. Shore vegetation.
Stage 1. Massive grey marl. High level of the lake.

The black clay is generally thicker in the southeast section of the site (where the large mammal bones were collected within the black clay) and pinches out in the northwest. There is evidence that the north-west extension of the black clay was defined by a build up of log-wood material which appears to have acted as a dam and stopped the extension of the clay in this direction. Just east of this "log" jam the underlying grey marl (i.e., below the black clay) is characterised by a high ridge running in a general east–west direction. This ridge and the adjoining log jam obstructed the extension of the black clay in the north-western region of the site, but overall this lens of black clay also follows the general westerly dip of the overlying marl deposit.

3.5. Red marl

Above the grey marl and black clay deposits, a coarse deposit of reworked marls and lignites accumulated. These are dark grey to brownish, and in places the upper part of the dark grey reworked marl has been oxidised to a reddish-brown colour indicating subaerial exposure. It has variable thickness, 10 to 40 cm, being almost absent in places (Fig. 4), and it contains clasts of the massive grey marl and sparse remains of quartz sand grains. It is thought to have formed as a result of further lowering of the lake level, which exposed marl deposits further up the valley which were eroded and redeposited at Rudabànya 2. The variations in thickness appear to be the result of being banked up against large objects such as logs. The accumulation build up on the northeast sides of the logs gives an inferred current direction of 220°. The surface of the red marl was irregular, with a series of troughs and ridges, and it had a slope from east to west of approximately 15 cm per m (Fig. 5), in line with the reconstructed palaeotopography at Rudabànya 2, which is situated in a shallow west-sloping valley. It contains abundant root traces, and some of the roots could be followed from this level, through the underlying black clay and into the massive marl below. These roots have taken on the colour of the sediment in which they were preserved, so that they change from dark grey to black as they pass through the black clay and back to light grey again as they enter the underlying marl.

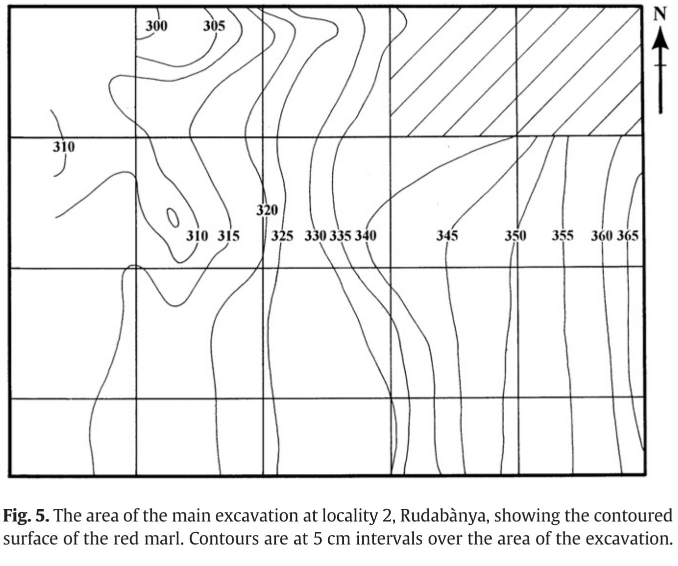

Fig. 5. The area of the main excavation at locality 2, Rudabànya, showing the contoured surface of the red marl. Contours are at 5 cm intervals over the area of the excavation.

3.6. Black mud

The red marl is succeeded by another black clayey mud, referred to as the black mud, which is taken to represent the A horizon of another soil, with further lignite formation above, the so-called upper lignite, forming the O horizon. These sediments are rich in vertebrate remains, with abundant wood remains, some in position of growth and some decayed tree stumps. The black mud is a breccia of mud, marl, bones and plant fragments which indicates it was a quickly deposited and many of the constituents of the breccia were transported in during deposition, including the animal bones. Conditions returned to a water-logged swamp environment, indicated by deposition of the upper lignite. The black mud grades upward into the lignite with increasing organic content. This lignite is the top unit remaining at Rudabànya 2 and was at least 1 m in thickness.

4. Fossil distribution by stratigraphic level

The palaeontology of Rudabànya 2 is described in reverse order, from the top down, because many of the plant remains consist of roots that passed down through the sediments. In other words, specimens that were first encountered at higher levels could be traced down through lower levels as excavation proceeded.

4.1. Upper lignite and black mud

Almost no animal fossils were found in the upper lignite, but there were abundant plant remains. Seeds or endocarps were common throughout the deposits, without any apparent pattern of distribution, but the most abundant biotic remains were in the form of wood, either plant stems or roots. A general plan of wood distributions in the upper lignite, extending downwards into the black mud is shown in Fig. 6, with abundant and large fragments of wood and root, some of

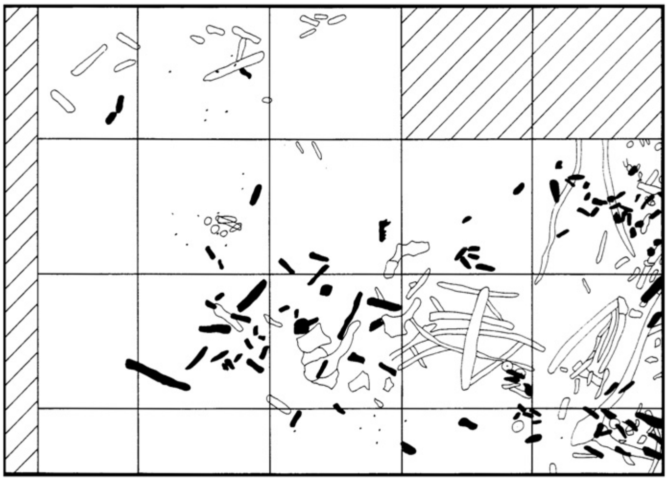

Fig. 6. Excavation plan of the black mud and upper lignite, showing the distribution of fossil wood. These two units are mapped together because in practice it was difficult to separate the fossil wood. The fossil wood is shown in outline, the fossil bone in black, and the tree stumps in growth position shown as circle with dot in the centre. Hatched areas were not excavated.

which is in original growth position but some forming the slightly modified remains of fallen or decaying tree stumps. Measured dips and orientations of the fragments showed no preferred alignment or angle of dip, but a significant feature was the number of vertical fragments apparently still in growth position (Fig. 7). These originated in the black mud below or even lower in the grey marl (see below), thickening downwards, and it is thought that they represent the aerial roots of trees such as Taxodiaceae that were growing in permanently wet or water-logged conditions. Also in Fig. 7, the remains of a fallen tree stump with the roots still interconnected are shown, indicating that this and similar remains represent trees that were in position of growth.

Fossil bone was found to be locally abundant in the underlying black mud (Table 1). There was almost no bone at the top of this unit, which in any case is gradational into the overlying upper lignite, the difference being an increase in silt and clays and decrease in abundance of wood in the black mud. There is no colour change in the transition from lignite to mud, and the contact surface is very irregular.

The fossils were generally fragmentary, with broken postcranial bones being the most abundant type (Appendix 1). Most fragments were small, less than 4 cm, but there were some larger mammal limb bones that had been broken in place (Fig. 8). These specimens consisted of numbers of conjoined fragments which were held in place by the sediment but which would have become separated from each other during screening, and it is probable that the high number of small fragments at this level reflects more advanced post-depositional breakup of the bones. There is some vertical displacement of shaft portions and horizontal displacement in other specimens. Both breakage and displacement were probably the result of differential sediment compaction or bioturbation because the angles of dip of the larger bones are relatively low. There are also partial remains of chelonians, with a number of associated scutes distributed over adjacent areas, and small groups of amphibian bones, some of which may be associated and all of which are abraded (Appendix 1).

Table 1
Sample sizes of sediment and fossil vertebrates.

	N	Volume of sediment	Numbers of mammals	Identifiable amphibians	Specimens reptiles	Gastropods
Black mud	475	7.2	15	53	49	21
Red marl	678	7.2	54	54	23	26
Black clay	1059	1.1	82	82	51	90
Grey marl	1337	10.8	125	125	33	472
Lower lignite	237	12.1	2	2	0	19

Broken edges of the fossil bones are abraded, with over 72% of the specimens showing some degree of abrasion, sometimes heavy

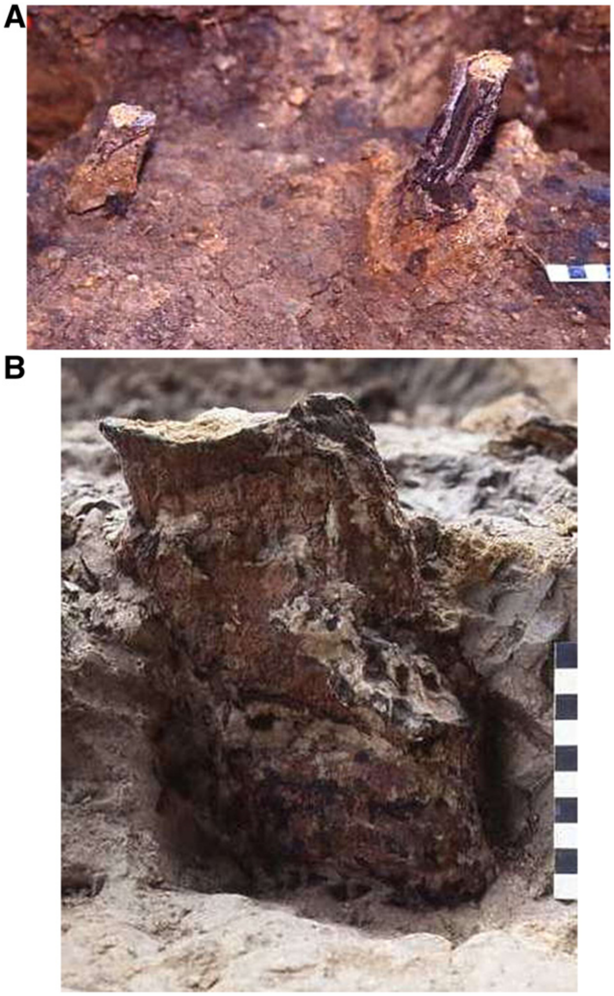

Fig. 7. Two views of the upper lignite with vertical aerial roots in growth position. A, two roots in place, and root on the left could be traced down to the grey marl as shown in Fig. 15; B, a single vertical root partially excavated.

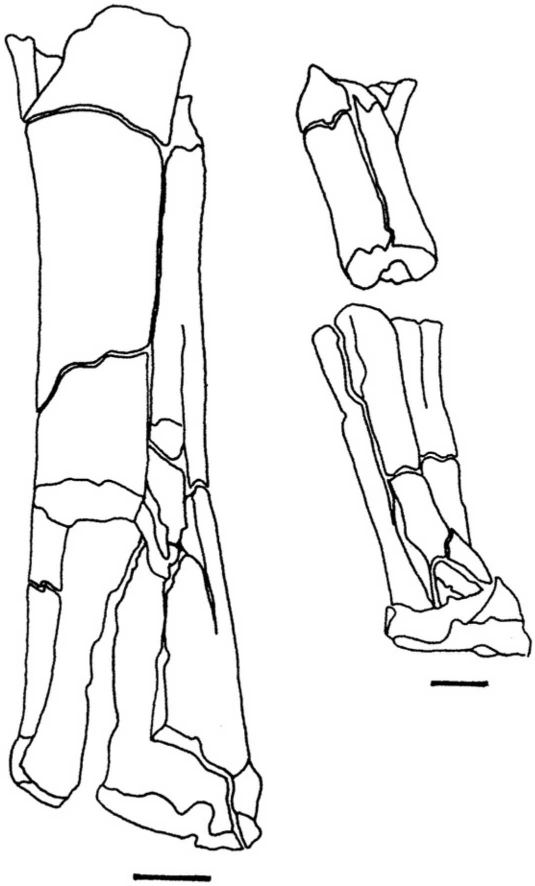

Fig. 8. Right, a fragment of long bone broken in place, with displacement of one portion with respect to the other (right) and differential angulation of the lower portion with respect to the upper. Left, fragment of hipparion tibia with carnivore gnawing distally (bottom); the ends of the bone were destroyed before deposition, but the breakage of the shaft is post-depositional. The scale bars denote 1 cm. Drawings by E. Weston.

Table 2
Surface modifications of fossils by stratigraphic level.

	N	Polishing	Light rounding	Heavy rounding	Corrosion	Abrasion
Black mud	475	20	13	0	16	0
Red marl	678	283	249	10	15	46
Black clay	1059	760	814	49	212	2
Grey marl	1337	221	860	21	5	42
Lower lignite	237	123	80	9	0	0

(Table 2). This may be due in part to soil movement and in part to trampling. Rather fewer of the fossil bones show signs of weathering (14.8%), and degree of weathering is generally low (Appendix 1). Both flaking and pitting has been observed, and most of this appears to be due to subsurface weathering in the fossil soil. Weathering where it occurs was subsequent to the abrasion Andrews (1995). A relatively small number of fossil bones show signs of corrosion and most have relatively fresh surfaces (N = 16 or 3% of the total number in the coarse sieving residues: see Table 2). The corrosion is not localized, and for this reason it is attributed to the general effects of acid soils rather than to digestion by a predator (Andrews, 1990). There may be loss of surface bone, with deep penetration of acid into any weak place on the bone such as at the ends of bones, on epiphyses and alveolar margins. A small number of the animal fossils from the black mud (N = 13) have signs of carnivore damage (see Appendix 1).

There is a weak indication of preferred alignment of the fossil bone in the black mud (Fig. 9). The angles of orientation have been summarized in Appendix 1, and these show essentially no overall preferred direction of deposition of the bones for the site as a whole. For the west end of the site, however, there is evidence of a pronounced trend in alignment along the 140–160° axis (Fig. 9 bottom), while at the east end of the excavation area, the major axis of alignment is at 300°, with the bones dipping both northwest and southeast in approximately equal numbers (Fig. 9 top), and there is a secondary axis of alignment in the 220–240° direction. Most of the bones were lying across the slope, which was west to north-west, with the secondary component dipping against the slope, and it

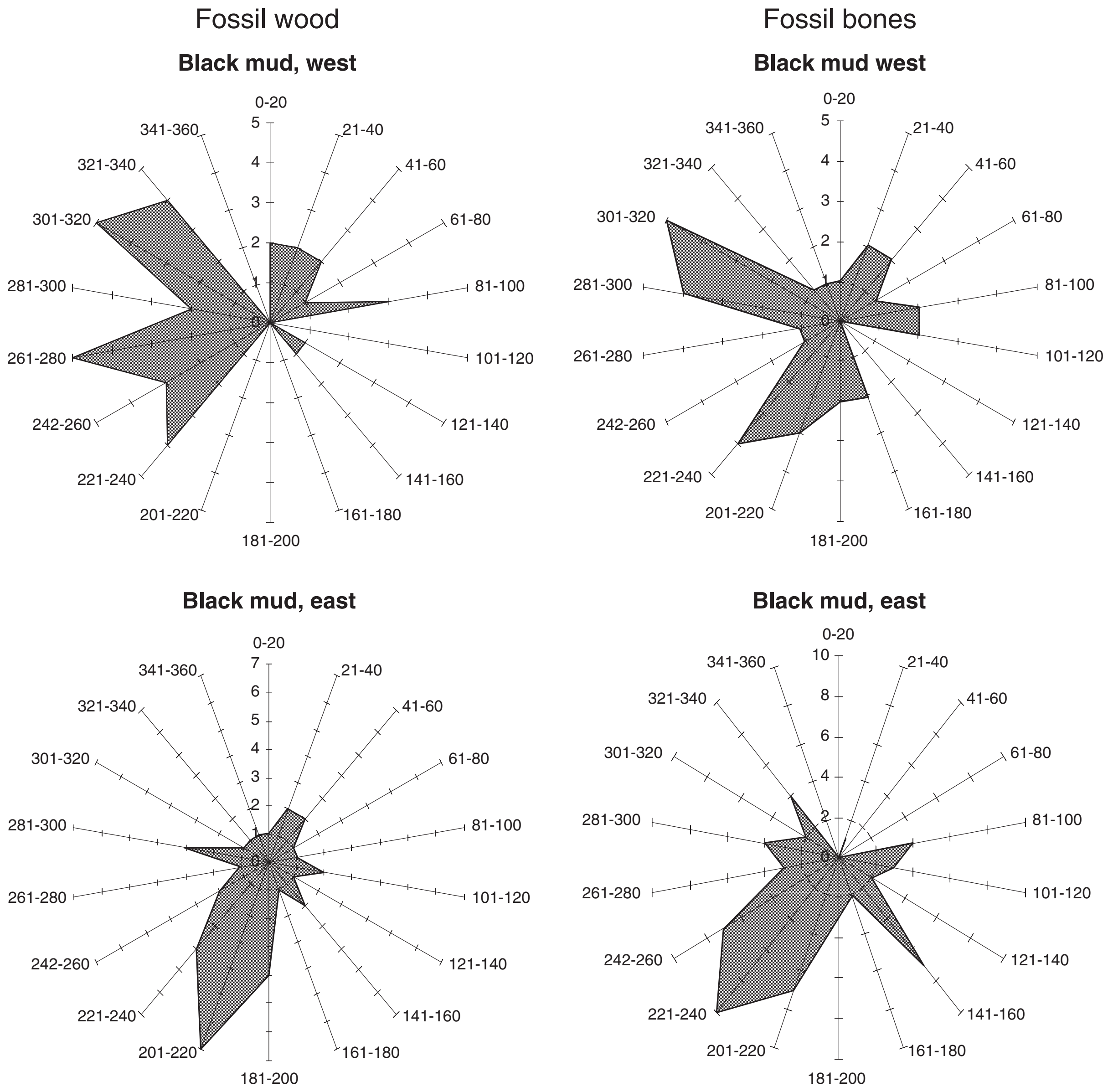

Fig. 9. Fossil bone orientations in the black mud, left fossil wood and right fossil bones. The two upper figures show the directions in the western part of the excavated area (N = 34 for fossil wood, N = 28 for fossil bone); and the two lower figures show the directions in the eastern part of the excavation (N = 30 for fossil wood, N = 59 for fossil bone).

Table 3
Fragmentation of fossils by stratigraphic level.

	N	1–2.5	Size classes	Lengths	In mm	>15.1
			2.6–5.0	5.1–10	10.1–15	
Black mud	475	1	18	52	21	8
Red marl	678	1	18	57	18	6
Black clay	1059	6	27	55	9	4
Grey marl	1337	3	35	51	8	4
Lower lignite	237	1	19	52	14	14

seems, therefore, that the slope of the deposits was not a major component in determining the direction of the bones. It is likely, therefore, that the major factor here is water flow during the initial accumulation of the silts that make up the black mud, supporting the contention that the bones were brought in with the sediment.

Several isolated teeth of *Dryopithecus* were found in the black mud, including both permanent and deciduous teeth, but no specimens of *Anapithecus* were found in this part of the section. In the coarse screening residues several *Dryopithecus* phalanges were found in one sample, and it is likely that these come from one individual. On the evidence of our limited excavation, *Dryopithecus* appears to be relatively common in the black mud, but no information is available on the stratigraphic position of any of the earlier collections.

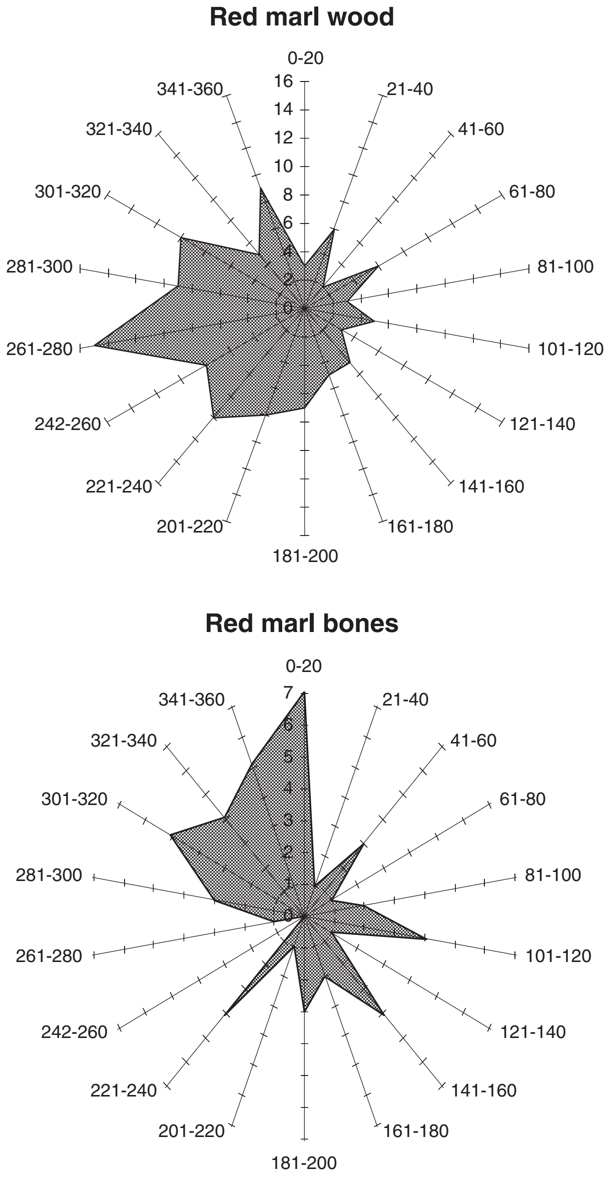

Fig. 10. Bottom, bone orientations in the red marl (N = 49); top, fossil wood orientations in the red marl (N = 120).

In summary, fossil bone is found only in the black mud, whereas fossil wood in the overlying lignite extends down into the black mud, indicating that the mud was soft enough for compression to cause the wood to penetrate far into it. There is some indication that where this occurs, bone is restricted or absent (Fig. 6). Directionality of wood and bone is similar: for the site as a whole, the direction appears random (N = 133), but when different parts of the site are analysed separately, there is a clear difference in direction of both wood and bone for two parts of the site. This pattern would seem to indicate similar depositional conditions for both the fossil wood and the fossil bone.

4.2. Red marl

Fossil bone is moderately common in the red marl (Table 1), with a similar size range to that seen in the black mud, consisting almost entirely of small fragments less than 10 cm long (Table 3, Appendix 2). There are a few complete bones, 9.5% of the total, and these consist almost entirely of isolated teeth and small skeletal elements of amphibians. A few rodents but no primate fossils have been found at this level.

The fossil bones from the red marl are stained a brownish-red, 37–42% abraded with rounded ends of broken fragments, and often with extensive chipping of abraded ends (Table 2). There is little evidence of weathering, again possibly because of the subsequent effects of abrasion, and some bones also show corrosion similar in nature and degree to that seen in the black mud. There are frequent striations on some of the fossil limb bones due to trampling by large mammals.

There is a strong directionality to the fossil bones in the north-west part of the site (Fig. 10). This directionality is particularly evident in the more northerly part of the site, where the surface of the red marl also slopes in a north-westerly direction (Fig. 5), and it seems likely that this is a primary angle of deposition of these sediments, affecting both the red marl and the black mud. Directionality is also evident in the fossil wood (Fig. 10), but in this case there is a more strongly east

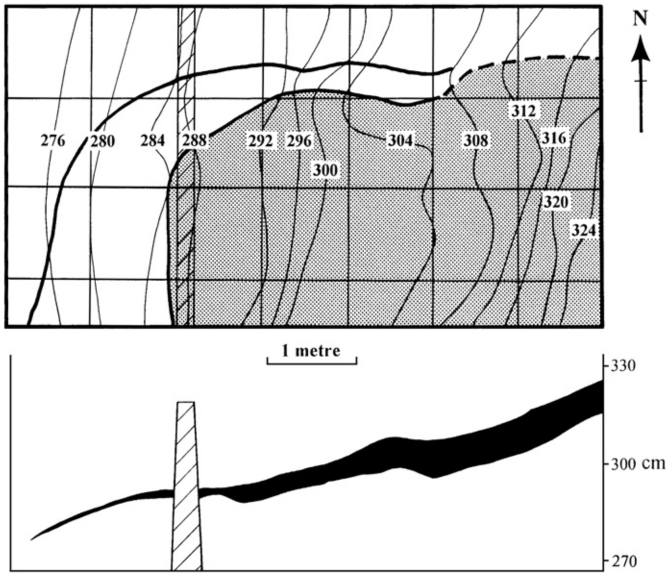

Fig. 11. Surface plan of the black clay/grey marl contact, with contours at 4 cm intervals, showing the northern and western limits of the black clay and the lateral equivalent of the black clay (see text for explanation of names). Below is an east–west profile of the slope and thickness of the black clay.

to west alignment of the wood, probably reflecting the wider distribution of wood over the whole site. Directionality was calculated separately for small fragments (less than 4 cm) and large fragments, for while large fragments were probably in growth position and had completely random orientation, the small fragments of abraded wood derive from post-depositional breakup of the longer pieces and had strong east–west alignment.

4.3. Black clay

The presently known extent of the black clay is shown in Fig. 11, abutting against a low ridge along the northern edge at the 296–304 cm contour levels which mark the topographic boundary of the black clay. Just to the west of this, at the 292 cm contour, there is a sharp depression at the same boundary, and here there was an accumulation of large pieces of wood which may have acted as a barrier to the further extension of the black clay (Fig. 11). There is no obvious topographic feature marking the western boundary of the black clay, although close to the boundary there were two massive roots which may have altered any original structures that were present.

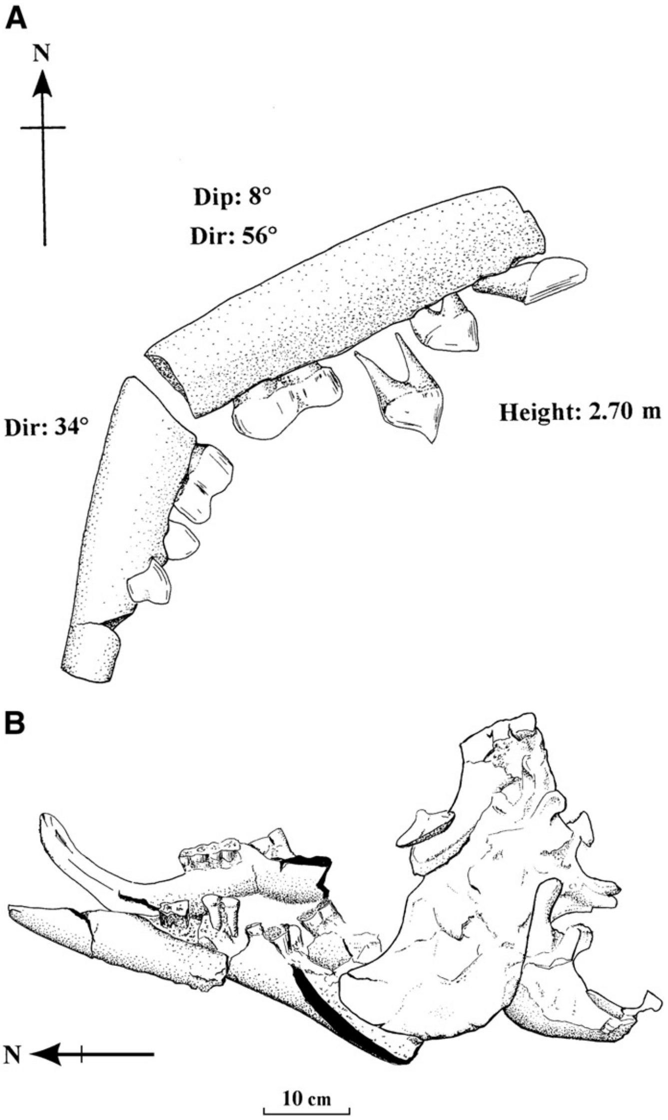

Fig. 12. A, suid mandible drawn in place, with the middle of the mandibular body broken and displaced; B, *Aceratherium* mandible recovered from the black clay showing the breakage and displacement of bone.

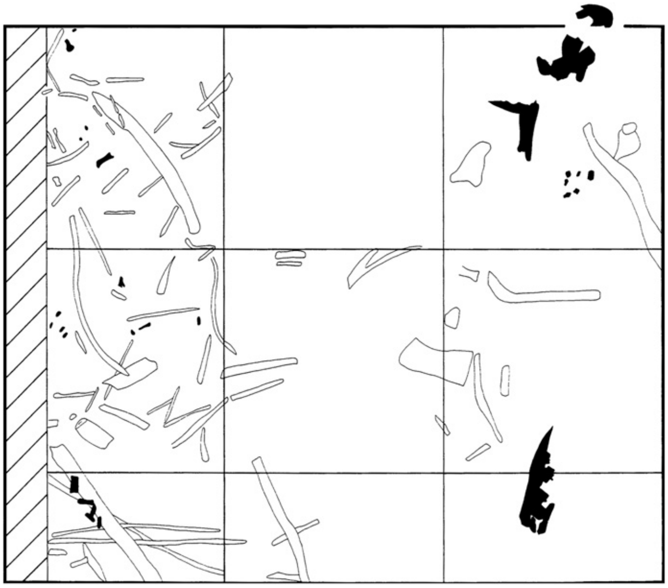

Fig. 13. Excavation plan of the black clay showing the positions of the rhino and suid mandibles and other fossil bones in black. Fossil wood is shown in outline.

The black clay is extremely rich in fossils, particularly when the low volume of sediment excavated is considered (Table 1), and some fossils are relatively complete. For example, complete *Aceratherium* and suid mandibles (Fig. 12) were found, both with the mandibular bodies more or less intact, although part of the rhino mandibular body was displaced downwards, the result of soft sediment compression. The skull of the same individual was also present in the excavation, but it could not be removed as it is embedded in the south face of the excavation with over one metre of sediment overlying it. Lying just south of the suid bones within the south grid was a collection of turtle carapace fragments and amphibian long bones (Fig. 13). Several *Anapithecus* dentitions were recovered from the black clay during excavation and screening representing two immature and two adult individuals.

Most of the fossil bone recovered from the excavation of the black clay consisted of postcranial remains (Appendix 3), which is similar to the specimens from the higher levels. Small mammals, amphibians and chelonians are all more abundant at this level (Table 4). The degree of completeness is only marginally greater than in the transported assemblages higher in the section (Appendices 1–3), and the size distribution of fragments is little different from other levels (Table 3). More than 64% of the excavated fossil bone shows evidence of rounding (see also Appendix 3), with the number rising to over 80% for the sieving residues (N = 863) with 5% of these fossils being heavily rounded (Table 2). For the most part, however, the degree of abrasion is lower than elsewhere. Some carnivore damage is seen, comparable to that seen in other levels, and a low to moderate degree of corrosion (Appendix 3). Three of the rodent incisors from the screening residues had moderate to heavy digestion (out of a sample of 13, giving 23% digested), indicating that a category 3 or 4 predator had killed these individuals (Andrews, 1990). The

Table 4
Numbers of vertebrate fossils (N) with MNI calculated on the basis of most abundant element.

	Rodents					Insectivores	Lagomorphs	Totals
	N	MNI	M	Cranial	Postcranial			
Black mud	475	8	1	1	4	2	0	16
Red marl	678	9	12	4	4	8	0	37
Black clay	1059	13	7	9	5	6	3	43
Grey marl	1337	18	11	5	21	3	0	58

Anapithecus remains and some of the small mammal dentitions form clusters of associated teeth in place in the sediment, and the loss of most of the bone making up the jaws of these individuals indicates selective loss of bone compared with teeth.

There is no evidence of any preferred distribution or orientation of the fossil bone preserved in the black clay (Fig. 14). The fossil bones are scattered through the deposit, with just a suggestion of directionality at the west end of the main excavation where several of the bones have orientations in the 200–220° direction, but the numbers of specimens are too low to come to any conclusion on this. Unlike the fossil bone, the fossil wood has a northerly preferred orientation, with a smaller transverse component (Fig. 14). Much of the wood in this level is roots in growth position, and where the roots pass through the black clay from the levels above there is a conspicuous change in preservation and colour of the roots: above and below the black clay: where the root passes into the black clay the roots are flattened into a wafer-like shape and they change from greyish colour to black.

4.4. Grey marl

In the level immediately below the black clay, there were some very large tree roots in growth position, and concentrated on the east side of these rich accumulations of gastropods were found. The association of gastropods with the roots was very clear, but the nature of the association is not so obvious. The gastropods may have been living near the roots because of locally favourable microenvironments, or they may have been simply preserved there because of locally improved conditions for survival (as fossils).

Wood is generally uncommon in the grey marl except for the remains of in situ roots, which vary in size from thick tree roots to root traces (see Fig. 4). Some of these roots can be traced down from the black mud, where they first appear, and one in particular is interesting in that it first appeared as a vertical root in the black mud (seen on the far left in Fig. 7), passing down vertically through the upper marls and black clay. At the level of the grey marl this root changes both its direction, from vertical to near horizontal, and its size, becoming greatly expanded (Fig. 15). An excavated portion of this root expanding horizontally in the grey marl is shown in Fig. 16. This illustrates that the vertical roots are in growth position and also that they are probably aerial roots or 'knees" of swamp-living tree species like the swamp cypress (Taxodiaceae). This identification could not be confirmed, as there is no internal structure remaining in the specimens preserved, but the gross morphology of the aerial roots is very similar to that of the swamp cypress.

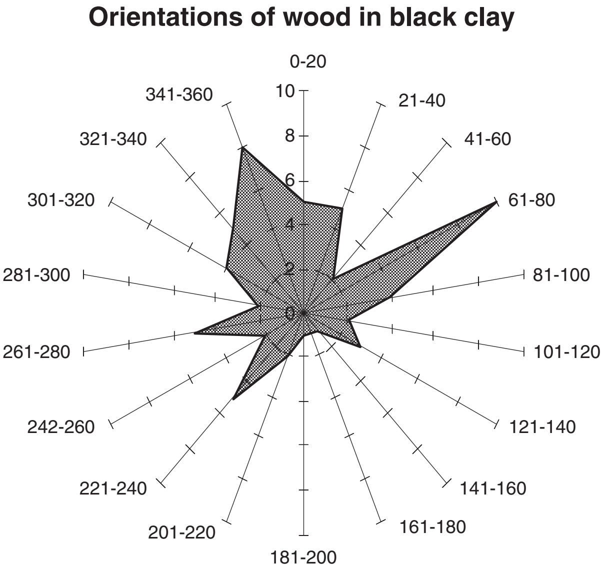

Fig. 14. Orientations of fossil wood fragments in the black clay.

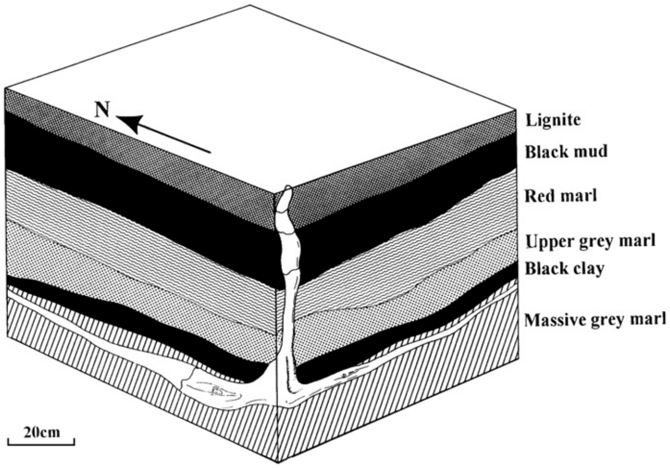

Fig. 15. Section of one of the vertical roots exposed in the black mud (shown in Fig. 7A on the left of the figure). The top of the root is in the upper lignite, and it passes down into the grey marl where it spreads out horizontally.

Numerous fragments of the same *Hippotherium* individual were recovered from the grey marl over a vertical distance of nearly 40 cm. The two parts of the pelvis were found almost in contact and yet vertically oriented and distributed over at least 14 cm. This distribution is likely to have been caused by trampling. Other parts of the same individual consisted of numerous isolated teeth scattered over 100 cm, and in one case there were several teeth apparently in association close together but facing opposite directions. Small mammal bones from the coarse screening residues of the grey marl, such as rodent and mole postcrania (Fig. 17) had light acid etching, as did the few amphibian remains, but other specimens were not modified; other fragments were both rounded and etched, and a small number of rodent incisors had digestion at the tip.

Other large and small mammals have been found scattered in the grey marl, often with some degree of association of elements, so that it would appear on first analysis that the remains come from single individuals that were drowned/washed in/died near the Pannonian Lake. At this stage we cannot distinguish between these possibilities. Some relatively fragile specimens have survived, such as slender cervid antlers, and since these fossils generally lack evidence of abrasion or weathering it is likely that they were washed into the lake from close by. The more fragmentary fossils that do show signs of abrasion were probably washed in from a land surface further away, where they were also subjected to weathering.

Similar patterns of fossil bone preservation are present in the grey marl as at higher levels. Most of the specimens consist of fragments of postcrania, with teeth making up the main elements that are complete (Appendix 4). On the other hand, and what cannot be reflected in Table 3, is that some of the specimens are *relatively* more complete in that more of them is preserved than at other levels (except the black clay). For example large parts of a cervid antler were recovered more or less intact, and the *Hippotherium* mentioned above must have entered the deposit in one piece and become broken post-depositionally. These more complete specimens lack the abrasion present on the bone fragments, for which the proportions of abrasion and polishing (Table 2, Appendix 4) indicate similar preservational processes to the higher levels. Some of the fossil bones also show evidence of weathering (fragments only) and carnivore damage. The weathering is not extreme and has been modified by subsequent abrasion, so that it is difficult to obtain a weathering profile for the

Fig. 16. Photograph of the root seen in Fig. 15 as it spreads out in the grey marl.

assemblage. Similarly, much of the carnivore damage has probably been lost through post-depositional breakage, weathering and abrasion, and only the large tooth marks have survived these later processes. In addition, a number of fossil bones have been corroded through immersion in water.

There is no preferred angle of orientation of the fossil bones, but only 18 bones were measurable in this regard, which would not be enough to give a reliable result. Similarly, there does not appear to be any relationship between fossil bone distribution and that of the fossil wood, since most of the woody fossils are roots and root traces

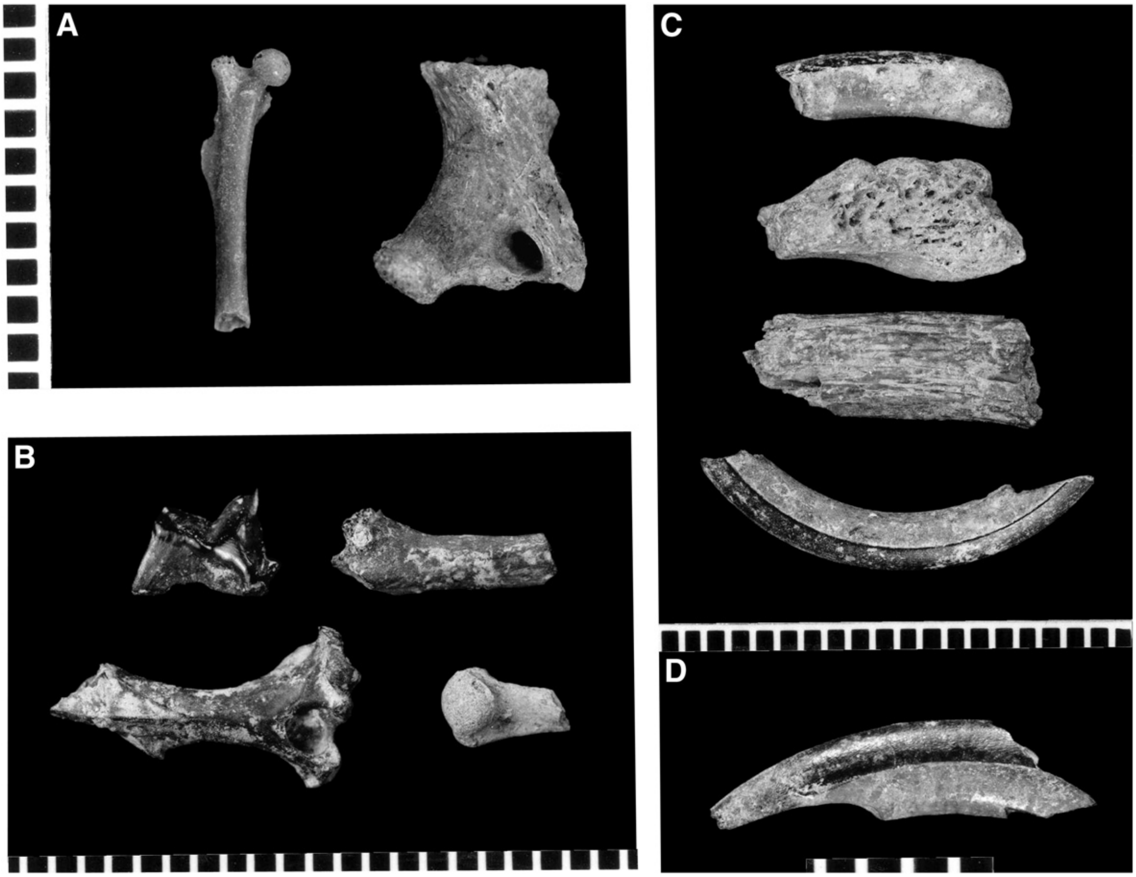

Fig. 17. Fossil bones from the coarse screening residues of the grey marl. A, rodent femur and mole humerus with light acid etching; B, two mammal specimens on the left not modified, two amphibian bones on the right with light acid etching; C, from the top, rodent incisor abraded and etched, but *not* digested, bone fragment rounded and etched, bone fragment with light etching, rodent incisor with light etching; D, rodent incisor with digestion at the tip.

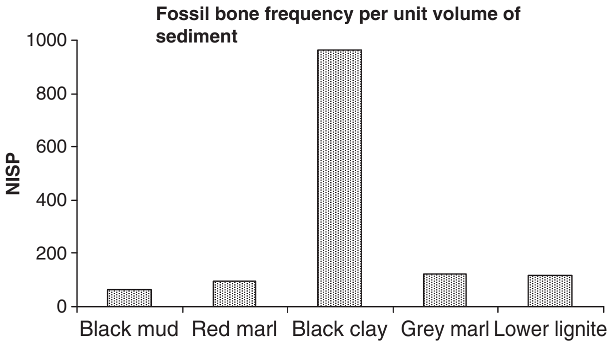

Fig. 18. Fossil bone frequency per unit volume of sediment: NISP—numbers of specimens.

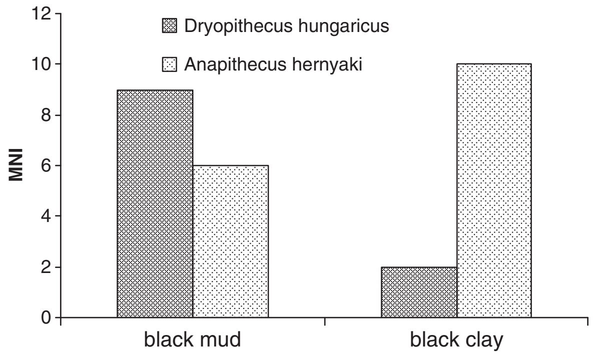

Fig. 19. Numbers of individuals (MNI) of *Dryopithecus hungaricus* and *Anapithecus hernyaki* at Rudabànya by stratigraphic level.

(N = 204) in growth position, passing down through the grey marl from higher levels.

4.5. Lower lignite and lower black clay

The junction of the grey marl with the underlying lower lignite is irregular, with patches of lignite dragged up into the marl (Fig. 3). Rotten wood fragments and many massive logs had been depressed downwards into the top of the lignite. It appears likely that trees growing on the lignite were overwhelmed by a sudden flood, and the dead trees have been preserved as a log pile on the surface of the lignite. No fossil bones were found in this transitional zone, or in the lignite itself, and none have yet been found in either the grey clay or black mud underlying the lignite.

5. Taxonomic composition

The known taxonomic composition of Rudabànya is documented by Bernor et al. (2003a, 2005). We have few data on the variations in composition of the Rudabànya fauna by stratigraphic level. Our collections were too small to provide large enough samples for this purpose (Fig. 18), but they are more than adequate for taphonomic purposes. Only the black clay yielded a high frequency of fossils per unit volume of sediment, but even these were mainly unidentifiable specimens. A detailed faunal list encompassing all levels for all sites at Rudabànya is provided by Bernor et al. (2003b), who also demonstrate the taxonomic similarities of this fauna with the Spanish MN 9 faunas at Can Llobateres and Can Ponsic. Faunas of equivalent age in Greece and Turkey were strikingly different, and for instance the MN 9 fauna from Sinap, Turkey, shares no mammal species in common with Rudabànya. This is interpreted as evidence of strong provinciality of mammal faunas at this time.

The primate fauna shows differences in stratigraphic distribution (Armour-Chelu et al., 2005, but see Kordos and Begun, 2001). The relative abundances of *Dryopithecus hungaricus* and *Anapithecus hernyaki* were recalculated by Armour-Chelu et al. (2005), as shown in Fig. 19. Our collections show that while *D. hungaricus* and *A. hernyaki* occur together in the black mud and the black clay, they do so in different proportions (Fig. 19), with the former being more abundant in the uppermost black mud and the latter more abundant in the black clay.

6. Taphonomic analysis

A detailed breakdown of the taphonomic modifications of the Rudabànya assemblage is shown in the four appendices, which include both excavated fossils and the screening residues. The taphonomic data have been analysed by correspondence analysis (Fig. 20), which examines complex correlations between objects and

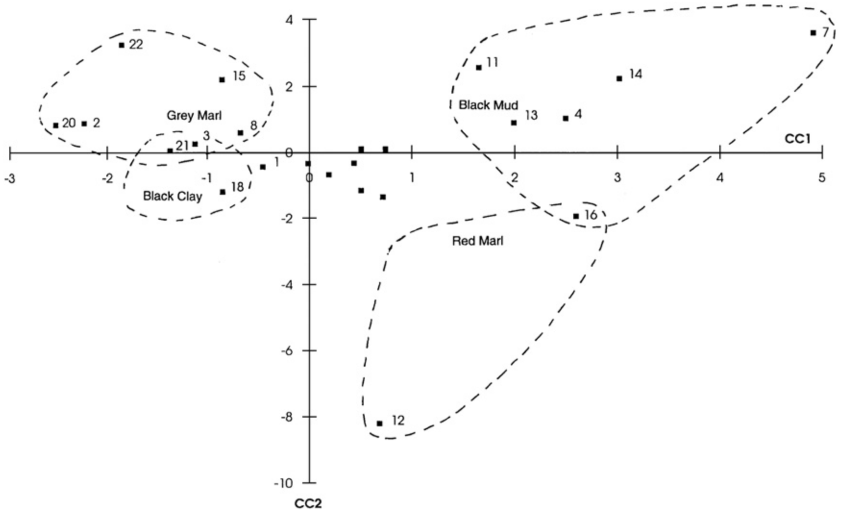

Fig. 20. Correspondence analysis of Rudabànya 2 taphonomic modifications. The values for the variables are given in the appendices and the variables are defined in Table 5. In this analysis, grey marl includes just that part of the unit below the black clay; the black clay includes the lateral equivalent to the black clay; the red marl includes all of the reworked marl above the black clay. See Fig. 2. The associations of closest variables to the unit are shown with dotted lines. The points around the origin lack numbers because they are irrelevant characters to the analysis.

variables, in this case excavated units (lithologies) and taphonomic modifications on the fossils. The variables examined in this analysis are based on their presence or absence within each of the four main fossiliferous units (grey marl, red marl, black clay and black mud). There is a clear division between the four units based on the degrees of modification (Fig. 20). Weathering (variables 13 and 14), loss of outer surface of the bone (variable 16), loss of articular ends and preservation only of long bone shafts (variable 7), abrasion (variable 11) and post-depositional breakage (variable 4) all have high positive values on the horizontal axis (Table 5), and they characterize fossils from the black mud and red marl. These fossils have been shown earlier to have been transported to a greater extent than those of the lower units. In the case of the red marl, the sediments are made up in part by reworked grey marl, and it is likely that the fossils now preserved in the red marl were exposed for a time on the surface before transport, as were the sediments. The black mud has been interpreted as a bone and wood breccia transported to the site, and again it is likely that the bones were exposed to weathering before transport. The lower unit fossils (grey marl and black clay) have negative values on axis 1 characterized by lack of modification (variable 8) and in particular lack of weathering and breakage, resulting in relatively complete bones (variable 3) and even more strongly by the presence of skull (variable 20) and mandibular/dental specimens (variables 21,22): see Table 5 and Appendices. Fossils from the reworked red marl differ from other levels in their negative values on the vertical axis, and this is largely the result of the presence of numerous fine scratches, that because they had strong directionality were identified as trampling marks (variable 12, Table 5) (Andrews and Cook, 1985). It is also possible that some of these modifications may have been the result of sediment movement during reworking of these deposits. The effects of digestion (variable 19) are not so apparent in the CA analysis because so few rodents were found by excavation as opposed to the screening.

Table 5

Correspondence analysis of taphonomic data. The bone breakage and bone modification categories as listed in Appendices 1–4 are shown here with their relative contributions to the two principal axes shown in Fig. 20.

	C AX 1	C AX 2
1. Fragment	0.45104	0.44295
2. Splinter	2.22686	0.88574
3. Complete	1.11895	0.24806
4. Post deposition	2.49658	1.01263
5. Transverse break	0.43586	0.33523
6. Long bone shaft	0.50381	−1.1638
7. Proximal/distal end	4.91967	3.59166
8. Unmodified	0.67194	0.59188
9. Abrasion-rounding	0.00908	0.34416
10. Abrasion-chipping	0.50596	0.09173
11. Abrasion-pitting	1.65234	2.55489
12. Trampling	0.68387	8.21412
13. Weathering flaking	1.99376	0.88117
14. Weathering splitting	3.02022	2.22307
15. Root marks	0.85537	2.19514
16. Bone table not preserved	2.59415	1.95184
17. Insect scoring	0.74242	0.09446
18. Gnawing	0.84977	1.20148
19. Digestion	0.71522	1.36491
20. Cranial	2.52236	0.83271
21. Mandible	1.36899	0.04826
22. Teeth	1.85112	3.23971
23. Postcranial	0.19351	0.68321

1. Fragment (splitting–cracking undefined); 2. Splinter spiral break (usually long bone fragment with angled break i.e., not transverse); 3. Complete; 4. Post-depositional breakage (bone fragments from one element clustering together); 5. Transverse break (clean vertical break not angled); 6. Shaft of long bone only (ends missing); 7. Proximal or distal end of bone (shaft missing); 8. Unmodified (no sign of surface modification, very good condition); 9. Abrasion and rounding (directional scratches with smooth edges); 10. Abrasion and chipping of edges (directional scratches with edges chipped); 11. Abrasion and pitting (directional scratches with pitting exposing cortex); 12. Trampling (very fine striations, usually numerous, often directional); 13. Weathering and pitting (bone shows cracks with pitting); 14. Weathering and splitting (bone shows cracks with finer splitting); 15 Root marks (irregular grooves); 16. Bone table not preserved (unidentifiable); 17. Scoring by insects (irregular fine striations); 18. Gnawing (usually long bone fragments with dental pits and striations); 19. Digestion (localized pitting and surface corrosion); 20. Number of cranial fragments; 21. Number of mandibles; 22. Number of teeth; 23. Number of postcrania.

7. Discussion

7.1. Depositional setting

The fossil sites at Rudabànya are situated close to the northern edge of the Pannonian basin, which in the late Miocene was a large lake. The Rudabànya 2 deposits were laid down in a shallow valley sloping northwards from a range of hills and opening out into the Pannonian Lake. Rise and fall of lake level gave rise to varying conditions, from dry land with soil formation to swamp and lake. We have attempted to make an initial reconstruction of the series of events leading to the accumulation of the Rudabànya 2 sediments and fossil remains. This reconstruction is shown in Fig. 21.

Stage 1 The lowest known unit, the palaeosol, was apparently deposited as estuarine muds in fresh water, and it may be inferred that the lake level was moderately high at this stage.

Stage 2 During formation of the palaeosol, lake level fell and dry/swampy conditions prevailed for a considerable period of time and the abundance of fossil wood and micro-roots confirms the presence of vegetation.

Stage 3 Water level rose again to produce the swamp conditions necessary for lignite formation to occur, but not so high as to kill the vegetation that contributed to the lignite. The lower of the two cyclic soils was therefore a compound event, with the highly developed soil at the bottom exposed on dry land for a considerable period before being further modified by rise in the water table and the formation of lignite and black mud on its surface.

Stage 4 A further rise in the water table led to the drowning of the lignite and the killing of the trees growing on it. The remains of the trees form a layer of logs on the upper surface of the lignite. Lake conditions led to the formation of the grey marl, which has massive structure and formed under deep water conditions. The whole area of the site must have been inundated by the lake for the time as this unit accumulated. No ground vegetation would have been possible at this time.

Stage 5 Shallowing of the lake led first to the accumulation of the shelly layer within the massive marls, and charcoal accumulations also occur at this level, both indicating near shore conditions. Subsequent formation of the black clay represents local ponding on mud flats exposed on the surface of the marl after the receding of the Pannonian Lake. The margins of the pond were formed by a combination of slight topographic relief and accumulations of logs. Both before and after the formation of this pond there were intermediate conditions in which marl formation continued but with locally increased organic accumulation above the level of the black clay. The ponding was associated with preservation of both large and small mammals, but there is no direct evidence of vegetation growing on the site at this stage.

Stage 6 Deepening of the lake resulted in the formation of the dark grey marl, probably a near shore unit formed in shallower water than the massive marl below.

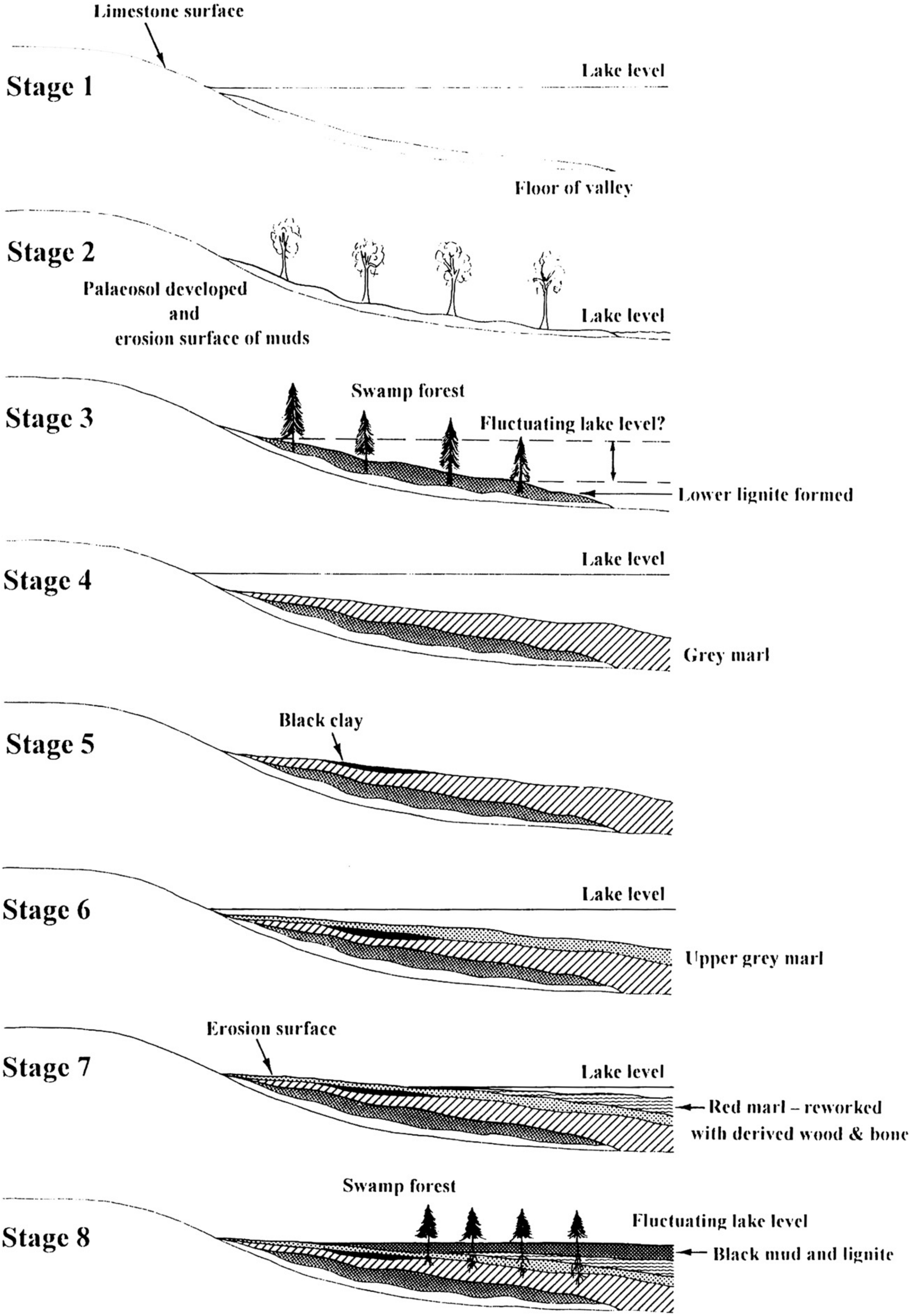

Fig. 21. The stages of Rudabànya 2's sediment accumulation from top to bottom, with indications of probable lake levels, vegetation types and topography. See text for explanation of stages.

Stage 7 On top of the grey marl sequence is the reworked marl, derived from the erosion of deposits of grey marl upstream of the present fossil locality. Much of this unit has been reddened by oxidation of iron compounds which indicates aerial exposure. At this time or later, terrestrial vegetation must have also been present, as indicated by the sparse root traces present in the grey marl and the abundant root traces and plants in growth position within the red marl.

Stage 8 Swamp conditions returned with the raising of the water level, and this brought about the accumulation of the black muds and upper lignite associated with swamp vegetation. Tree stumps are present in this unit, and roots in growth position emanating from this unit have been traced down into underlying deposits.

7.2. Taphonomic modifications and modes of accumulation

Several modes of accumulation and taphonomic modification have been seen in the Rudabànya faunas:

a) Losses of postcrania through carnivore selection, especially in the grey marl and black clay;
b) Some evidence of fluvial sorting, particularly in the red marl but also in the black mud;
c) Evidence of trampling in most units, especially the black mud and black clay but also some in the grey marl;
d) Post-depositional destruction by leaching and/or acid soils, particularly in the black mud. The grey marl fauna is the least modified but is clearly mixed, with abraded bone fragments transported in and more complete specimens resulting from near-lake deaths. Carnivore action is indicated, and was probably important for the latter specimens, but all specimens are now too broken post-depositionally for the impact of the carnivores to be assessed.
e) Methods of accumulation: the black clay fauna consists of relatively abundant small mammals and it was probably accumulated by a small mammalian carnivore such as viverrids. These may be partly arboreal, and they take a broad spectrum of prey, with the larger species taking prey the size of *Anapithecus*. Some relatively complete large mammal specimens were also present. The red marl fauna fossils are abraded and fragmentary, and they differ from fossils at other levels in having many fine striations with strong directionality. This set of modifications is interpreted as showing this was a transported assemblage from further up the valley, and the fine striations indicating trampling. The black mud fauna is abraded and disarticulated, and it was also a transported assemblage, lower energy transport than the red marl environment, and the bones much modified subsequently by acid corrosion similar to that seen today in bone preserved in peat bogs (Andrews, 1990).

7.3. Palaeoecology

The evidence on palaeoecology based on flora and fauna at Rudabànya comes from different sites and from mixed levels, and it is not possible at this stage to correlate these sites or to reconstruct regional environments more precisely. The local environment at Rudabànya 2 is interpreted based on the stratigraphy, taphonomy, palaeontology and the relative abundance of fossil wood in the section, and it is related to the distribution of the two primate species in the fauna.

The Rudabànya deposits were laid down in a shallow valley sloping northwards from a range of hills and opening out into the Pannonian Lake. Rise and fall of lake level gave rise to varying conditions, from dry land with soil formation to swamp and lake. The two cyclical events (Fig. 21) present at Rudabànya locality 2 can each be described as formation of a palaeosol and lignite on top of alluvial deposits. In both cases, three soil horizons can be distinguished: thick lignite horizon grading sharply down into black clay, changing into a light to dark grey clay at the base. Roots from the vegetation growing on and contributing to the lignite formation penetrate down into the underlying inorganic horizons.

The four fossiliferous units were all in the upper palaeosol, and the taphonomy of the vertebrate faunas can be summarized as follows:

- Black mud: bone and wood assemblage with extensive abrasion and breakage; many stumps of trees and aerial roots of swamp trees in growth position, and relatively abundant *Dryopithecus hungaricus*;
- Red marl: transported sediment consisting of reworked marl and transported fossils, mainly teeth, with extensive abrasion, trampling marks and strong directionality of alignment of bones and wood;
- Black clay: lake flats on the surface of the grey marl, large and small mammals present, some carnivore damage, probably by a species of viverrid, and relatively abundant immature specimens of *Anapithecus hernyaki*;
- Grey marl: deep lake conditions, some fossils relatively complete and with little abrasion, others fragmented and isolated.

The Rudabànya fauna has 112 species so far recorded (Bernor et al., 2003b) including 17 species of amphibian and 69 species of mammal. This is a composite fauna, lacking stratigraphic information except for our 1992–1994 collection, but from evidence currently available there appears to be little difference either in species composition or in evolutionary development of species throughout the Rudabànya section (Kordos and Begun, 2002). The mammal fauna has the appearance of a forest fauna, with two primate species, six glirids, five sciurids, and a number of other taxa that could indicate a forested environment such as the four species of flying squirrels (Kordos and Begun, 2003). Both primate species have long curved phalanges similar to those of *Dryopithecus* from Can Llobateres, Spain (Moyá-Solá and Köhler, 1996). The most common ungulate at Rudabànya is *Miotragocerus*, which has brachydont teeth and it has also been shown to wear patterns on it teeth indicative of browsing diet (Merceron et al., 2007). Other bovids and the equid *Hippotherium* were also shown to have mesowear patterns indicating browsing habits, with 88% of ungulate species having brachydont teeth, but some mixed feeders are also indicated, which suggests that the environment was not totally closed forest (Merceron et al., 2007). The 12% of ungulates with hypsodont teeth is similar to values from Can Llobateres (Agusti et al., 1999), but the latter site has in addition a number of ungulates with intermediate mesodont teeth, so that the proportion of brachydont teeth is lower than in the Rudabànya fauna. The Spanish sites also have more herbivorous and terrestrial species and fewer frugivorous and arboreal species than Rudabànya (Andrews et al., 1997), and so it is likely that the environment at the Spanish sites was less densely forested than at Rudabànya. Both faunas contrast with the Greek and Turkish sites, where the faunal composition of the similar aged sites in the Sinap Formation is totally different, with no species in common (Kappelman et al., 1996). More than half the Sinap ungulates have hypsodont or mesodont teeth and there are few arboreal or frugivorous species (Andrews et al., 1997; Fortelius et al., 2003). Bernor et al. (2003b) have documented the high endemicity of Central and Western European faunas (with specific reference to Rudabànya and Can Llobateres) compared to other Eurasian and African faunas at an international scale.

The flora from other sites at Rudabànya have been described by Kretzoi et al. (1974). There is a great abundance of tree species, both temperate and subtropical, conifers and angiosperms. No information is given on relative abundances, and so it is difficult to assess the nature of the environment just from the list of species, but Taxodiaceae pollen is ubiquitous and thermophyllous taxa such as *Zelkova*, *Celtis*, *Diospyros* and *Engelhardtia* are present at two or more levels, and *Pterocarya* pollen is also common. It may be concluded from this list that a rich and varied form of forest was present in the Rudabànya area during the middle to late Miocene, and it would have been warm temperate to subtropical in nature, but without more data on frequencies it is difficult to say more.

The two primate species from Rudabànya are usually grouped together in composite faunal lists such as that published by Bernor et al., 2003b, but there is some evidence of environmental separation (Armour-Chelu et al., 2005). *Dryopithecus hungaricus* is most abundant in the black mud near the top of the sequence, where nine individuals are now recognized, and this compares with only two individuals in the grey marl and black clay. *Anapithecus hernyaki* also occurs in the black mud, with six individuals known, but it is more common in the grey marl and black clay, where ten individuals are known (Fig. 19). There is also a difference in the age structure of the two primates, with the black mud individuals of both species consisting of 77% adults, with two immature *Dryopithecus* and one immature *Anapithecus* individuals. In the black clay, 50% of individuals are immature, all *Anapithecus* (N = 6), and both species are also represented as adults. The numbers are small, but they provide a possible indication of environmental preference: elevated numbers of young animals in fossil assemblages can indicate that the core territory of a species is being sampled as this is where most juvenile deaths would occur (Armour-Chelu et al., 2005). This is seen for female chimpanzees with dependent young, which usually select the best habitat available to them when the area of their home range is reduced during the period of provisioning juveniles (Reynolds and Reynolds, 1965; Goodall, 1986). The high proportion of juvenile *Anapithecus* in the black clay indicates that this area may have formed optimum habitat or contained favoured resources such as a mineral lick or a spatially delimited food plant that attracted concentrations of animals. *Dryopithecus* is less common in this level, with only two individuals, and no immature animals of this taxon were present. The contrast between the abundance and age distribution of the two primate taxa in the grey marl/black clay suggests that local conditions were favourable for *Anapithecus* but less so for *Dryopithecus*.

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Appendix 1. Taphonomic modifications of the black mud

		(n)	%
Body part	Cranial	1	0.4
	Mandible	4	1.7
	Teeth	20	8.6
	Postcranial	187	81.7
	Unidentified	20	8.6
Size class	<0.99	13	6.0
	1.00–1.99	54	24.9
	2.00–3.99	105	48.3
	4.00–7.99	34	15.7
	8.00–15.9	6	2.8
	>16.0	5	2.3
Dip	0–5°	26	15.8
	6–10°	38	23.4
	11–15°	21	12.8
	16–20°	18	11.0
	21–30°	25	15.2
	31–40°	14	8.5
	41–50°	11	6.7
	51–60°	7	4.2
	>60°	4	2.4
Direction	1–20°	9	5.8
	21–40°	21	13.5
	41–60°	21	13.5
	61–80°	17	11.0
	81–100°	18	11.6
	101–120°	18	11.6
	121–140°	15	9.7
	141–160°	19	12.3
	161–180°	17	11.0
Bone breakage	Fragment	120	51.0
	Splinter	17	7.2
	Complete	20	8.5
	Post-depositional	26	11.1
	Transverse break	39	16.6
	Long bone shaft	4	1.7
	Proximal-distal end	7	3.0
	Unidentified	2	0.9
Surface modification	Unmodified	44	10.5
	Abrasion and rounding	130	31.1
	Abrasion and chipping	100	23.9
	Abrasion and pitting	32	7.7
	Trampling	0	–
	Weathering and flaking	36	8.6
	Weathering and splitting	26	6.2
	Root marks	9	2.2
	Bone table unpreserved	7	1.7
	Insect gnawing	10	2.4
	Mammal gnawing	13	3.1
	Digestion	11	2.6

Appendix 2. Taphonomic modifications of the red marl

		(n)	%
Body part	Cranial	4	1.0
	Mandible	5	1.3
	Teeth	30	7.7
	Postcranial	311	80.2
	Unidentified	38	9.8
Size class	<0.99	16	4.4
	1.00–1.99	89	24.5
	2.00–3.99	159	43.6
	4.00–7.99	85	23.4
	8.00–15.9	13	3.6
	>16.0	2	0.5
Dip	0–5°	68	21.1
	6–10°	82	25.5

(continued on next page)

Appendix 2 (*continued*)

		(n)	%
Dip	11–15°	47	14.6
	16–20°	37	11.5
	21–30°	38	11.8
	31–40°	25	7.8
	41–50°	16	5.0
	51–60°	4	1.1
	>60°	5	1.6
Direction	1–20°	48	15.0
	21–40°	23	7.2
	41–60°	41	12.8
	61–80°	30	9.3
	81–100°	34	10.6
	101–120°	36	11.2
	121–140°	37	11.5
	141–160°	34	10.6
	161–180°	38	11.8
Bone breakage	Fragment	260	61.5
	Splinter	33	7.8
	Complete	40	9.5
	Post depositional	23	5.5
	Transverse break	57	13.5
	Long bone shaft	4	0.9
	Proximal-distal end	1	0.2
	Unidentified	5	1.2
Surface modification	Unmodified	69	11.3
	Abrasion and rounding	242	39.8
	Abrasion and chipping	127	20.9
	Abrasion and pitting	26	4.3
	Trampling	2	0.2
	Weathering and flaking	34	5.6
	Weathering and splitting	18	3.0
	Root marks	13	2.1
	Bone table unpreserved	12	2.0
	Insect gnawing	12	2.0
	Mammal gnawing	35	5.7
	Digestion	19	3.1

Appendix 3. Taphonomic modifications of the black clay

		(n)	%
Body part	Cranial	2	1.5
	Mandible	5	3.7
	Teeth	13	9.7
	Postcranial	102	76.2
	Unidentified	12	8.9
Size class	<0.99	7	5.8
	1.00–1.99	39	32.2
	2.00–3.99	38	31.4
	4.00–7.99	31	25.6
	8.00–15.9	3	2.5
	>16.0	3	2.5
Dip	0–5°	34	27.2
	6–10°	34	27.2
	11–15°	17	13.6
	16–20°	14	11.2
	21–30°	9	7.2
	31–40°	10	8.0
	41–50°	2	1.6
	51–60°	2	1.6
	>60°	3	2.4
Direction	1–20°	13	10.7
	21–40°	20	16.4
	41–60°	10	8.2
	61–80°	18	14.8
	81–100°	17	13.9
	101–120°	7	5.7
	121–140°	9	7.4
	141–160°	17	13.9
	161–180°	11	9.0
Bone breakage	Fragment	77	52.7
	Splinter	27	18.5
	Complete	18	12.3
	Post-depositional	2	1.4
	Transverse break	18	12.3
	Long bone shaft	3	2.1
	Proximal-distal end	1	0.7
	Unidentified	–	–
Surface modification	Unmodified	30	17.5
	Abrasion and rounding	64	37.4
	Abrasion and chipping	44	25.7
	Abrasion and pitting	2	1.2
	Trampling	–	–
	Weathering and flaking	5	2.9
	Weathering and splitting	–	–
	Root marks	4	2.3
	Bone table unpreserved	–	–
	Insect gnawing	4	2.3
	Mammal gnawing	13	7.8
	Digestion	5	2.9

Appendix 4. Taphonomic modifications of the lower grey marl

		(n)	%
Body part	Cranial	4	1.9
	Mandible	4	1.9
	Teeth	45	21.1
	Postcranial	122	57.3
	Unidentified	38	17.8
Size class	<0.99	13	6.9
	1.00–1.99	36	19.1
	2.00–3.99	67	35.6
	4.00–7.99	55	29.3
	8.00–15.9	12	6.4
	>16.0	5	2.7
Dip	0–5°	34	17.0
	6–10°	48	24.0
	11–15°	30	15.0
	16–20°	32	16.0
	21–30°	22	11.0
	31–40°	13	6.5
	41–50°	9	4.5
	51–60°	7	3.5
	>60°	5	2.5
Direction	1–20°	31	15.8
	21–40°	21	10.7
	41–60°	16	8.2
	61–80°	20	10.2
	81–100°	25	12.8
	101–120°	21	10.7
	121–140°	23	11.7
	141–160°	21	10.7
	161–180°	18	9.2
Bone breakage	Fragment	130	57.4
	Splinter	36	15.9
	Complete	28	12.4
	Post-depositional	7	3.1
	Transverse break	23	10.2
	Long bone shaft	1	0.5
	Proximal-distal end	–	–
	Unidentified	1	0.5
Surface modification	Unmodified	48	16.4
	Abrasion and rounding	111	38.0
	Abrasion and chipping	57	19.5
	Abrasion and pitting	17	5.8
	Trampling	–	–
	Weathering and flaking	12	4.1
	Weathering and splitting	7	2.4
	Root marks	13	4.5
	Bone table unpreserved	1	0.3
	Insect gnawing	5	1.7
	Mammal gnawing	16	5.6
	Digestion	5	1.7

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