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Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II

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Contents of Part II*

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References to pages 289 onwards and to the Plates refer to Part I of the present monograph; see footnote on previous page.

Bovidae from the excavated sites at Olduvai Gorge

In the second part of this paper we deal with the identified bovid material from various sites excavated in the 1950s and 1960s. The accounts of most sites conclude with a table showing the numbers of identified bovid fossils (Tables 1–10). Bracketed numbers in these tables indicate immature bones and milk teeth included in the overall totals immediately to the left. Bones are always counted as adult unless they show some obvious sign of juvenile status, for example a proximal metapodial with strong narrowing of the shaft below the articular surface. No molar teeth have been counted as immature although some would have been in wear contemporaneously with deciduous premolars. Thus the totals for immature fossils and individuals are likely to be underestimates. The limb bone columns embrace only the humerus, radius, ulna and metacarpal of the front leg and the femur, tibia and metatarsal of the back leg. The incidence of identifications for other limb bones was too low for them to be useful, as was also the case for the limb girdles and vertebrae. The minimum numbers of individuals are usually based on mandibular remains coupled with M_3s, but sometimes limb bones, for example distal humeri, have given the higher total. The minimum number of individuals may be a satisfactory concept when applied to particular levels of excavated sites, but where fossils from a considerable depth of deposit have been taken as a unit, as at the MNK Occupation Site, it is less likely to be close to the real number of individuals from which fossils have been drawn. SHK II is probably the site at which the minimum number of individuals is least reliable, since fossil material has come from the Annexe living floor, the stream channel and the tuff above the channel.

M. D. Leakey (1971b : 258–262) summarizes current knowledge about the excavated sites at Olduvai. She also gives the authoritative geological accounts of the sites, and our short introductory remarks for each site draw upon her information.

The most recent workers on the geology of Olduvai have given measurements in imperial units (miles, yards, feet, inches). When quoting such measurements we have also given the metric equivalents, but these are not the units in which the measurements were originally taken.

Sites in Bed I

DK I

Site (22) Geologic locality 13

DK I is on the north bank of the Main Gorge, about 1¾ miles (2·8 km) upstream of the third fault. It is one of the earliest sites in the Gorge, lying above the Basalt Member and overlain by Tuff IB, for which an age of 1·75 million years has been obtained (Evernden & Curtis 1965 : 354). Excavations were carried out at the site in 1962 and 1963, during the course of which parallel trenches were dug as a succession of grids or strips. Parts of the site dug in 1962 were called DK IA, DK IB and DK IC; strips I–III were dug in 1963. The sequence of deposits, from above downwards, was as follows:

4–5 ft (1·2–1·5 m) of ignimbrite (Tuff IB).
Level 1. 1½–2 ft (45–60 cm) of brown bentonitic clay with localized lenses of fine-grained white tuff.

Level 2. 2–2½ ft (60–75 cm) of buff-coloured clayey tuff, merging into level 3.
Level 3. 1–2½ ft (30–75 cm) of grey-buff clayey tuff, less clayey than level 2.
Level 4. Silts, clays and tuffs filling depressions in the basalt.

Cultural and faunal remains were found throughout levels 1, 2 and 3 but especially in the lowest part of level 3. Here the material was concentrated on an old land surface, partly on the eroded surface of the level 4 tuff and partly on the basalt where it rose above the tuff. Levels 1, 2 and 3 amount to a combined depth of only 5–6½ ft (1·5–1·95 m) and there is little evidence of a break in the sequence above the eroded surface at the base of level 3. The period of deposition was probably relatively short and material from the three levels is therefore treated as a single unit. Faunal remains are abundant but very broken (prior to fossilization) and with few associations among the bones. Fossil rhizomes similar to those of papyrus and many crocodile remains found on the hominid occupation surface suggest that standing water was nearby.

Tribe Tragelaphini. This tribe is represented by right mandible 36, left mandible 3001, right M^1–M^3 802 and a number of isolated teeth. These are right upper molars 263, 3051A, 3052A, 067/4123; left upper molars 270, 3041, 3049, 067/4123; left lower molars 161, 803, 4152; right M_3 3049; left M_3 154; two right upper premolars 154; left upper premolar 230; left P_4 166; deciduous left P^3 312; deciduous right upper premolar 067/4085; and deciduous left P_4s 3049 and 4152. These dentitions and teeth are about the size of the living greater kudu and are presumably referable to *Tragelaphus strepsiceros maryanus.*

The distal end of right humerus 79, distal end of right radius 4088, complete left metacarpal 4141, complete left metatarsal 4429 and proximal end of left metatarsal 71 are assigned to this tribe. They belong to a smaller animal than the reduncine at this site and are rather small for satisfactory assignment to *T. s. maryanus*. A complete left femur 5400 represents a larger kudu-sized tragelaphine. A complete left tibia 876 is possibly tragelaphine but is short and has an upturned edge to its proximal lateral facet.

Tribe Bovini. An immature left maxilla 4220, incomplete upper molar 067/3473 and deciduous left P^4 265 probably belong to this tribe. Their occlusal morphology does not differ from that of *Syncerus* teeth in other sites at Olduvai.

Tribe Reduncini. Material of this tribe comprises incomplete left mandible 067/4080, immature left mandible 51 and some isolated teeth (right upper molars 54 and 4026; left upper molars 067/3483 and two without numbers; right lower molars 795, 067/3473, 067/3483 and 067/4085; left lower molars 232, 067/4124 and two without numbers; right M_3s 4060 and 067/4085; left M_3s 233, 801, 3043 and 5002; right P_3 067/3483; left P_4 without number; and deciduous right upper premolar 5007). They are too large to fit *Redunca*, and within *Kobus* are of waterbuck rather than kob or lechwe size. Their most likely assignment is to *K. sigmoidalis.*

A right lower molar 797 is too small for *K. sigmoidalis* and is the size of living *Redunca redunca.*

The distal end of right humerus 3230, complete right radius 788, proximal end of right radius 381, distal end of right tibia 4116, distal end of left tibia 119 and proximal end of right metatarsal 3067 are about waterbuck size, but only 788 and 3067 are definitely not tragelaphine.

Tribe Hippotragini. An immature cranium with complete horn cores 067/5496 of *Hippotragus gigas* comes from this site. The cranium with left horn core was found *in situ* below Tuff IB in 1961, while the right horn core was found eroding out in 1964. The occipital condyles and most of the basioccipital are missing.

An immature right maxilla 37+43 is most probably hippotragine; the sockets for the roots on the inside of the maxilla bone suggest that M^1 was not as large as in the bovine immature left maxilla 4220. This fossil has the same preservation as the immature cranium mentioned above and might be from the same individual. A left maxilla 067/3496 with deciduous P^3 and P^4 could also be hippotragine and possibly also the same individual.

Three single teeth also belong in this tribe. These are right lower molar 168, left lower molar 93 and right M_3 067/3483. A deciduous left P_4 067/4149 may belong to this tribe or to the Reduncini.

A complete right femur 3051 shows the anteroposterior elongation of the great trochanter in side view and the shallow hollow between the great trochanter and the articular head in anterior view which are characteristic of this tribe. The pits on the lateral distal condyle for ligament attachment are not so deep as in alcelaphines. The distal end of right femur 3254 is also hippotragine.

Tribe ALCELAPHINI. *Parmularius altidens* is represented by a complete right horn core with part of the frontal preserved 068/6696, the basal halves of right horn cores 4112 and 4113 and an immature right horn core with part of the frontal and orbit 165.

Incomplete right mandibles 4 and 446, left mandible 161, the associated pair of immature mandibles 578 right and 646 left and immature left maxilla 154 are identified as *P. altidens*. There are also some isolated alcelaphine teeth which are probably this species, as follows; they cannot be seen to have a more primitive morphology than those of *P. altidens* at FLKN I.

Right upper molars 208, 284, 523, 530, 653, 768, 870, 4107, four numbered 4152, 067/3448, 067/3450, 067/3470, 067/3473, 067/3482, 067/4085, 067/4095, 067/4124 and one without number; left upper molars 35, 109, 110, 139, 194, 222, 259, 366, 378, 508, 551, 067/3439, 067/3447, 067/3470, 067/3473, 067/3482 and three without numbers; part of an upper molar 067/3482; right upper premolars 067/3483, 067/4095 and 067/4126; left upper premolars 067/4095 and 067/4126; right lower molars 067/3452, 067/3483 and two without numbers; left lower molars 3353, 4124 and three without numbers; lower molars of indeterminate side 88, 162, 271, 279, 530, 533, 837, 4111, two numbered 067/4085 and four without numbers; right M_3s 106, 185, 196 and damaged 067/3045; left M_3s 449, 811, 4106 and 067/3434; right P_4s 56, 4108, 067/3483 and 067/4149; left P_4 067/3498; and deciduous right P_4 235.

Several isolated teeth are considerably larger than those of *P. altidens*. These are right upper molars 284A, 523, 530, 3305 and 4123; left upper molars 139, 067/3044 and 067/3430; part of an upper molar 067/3431; left upper premolar 067/3483; right lower molar 279; left lower molar and left M_3 161; left lower molars 84, 111, 067/3054 and one without number; parts of lower molars 533 and 067/4091; right M_3s 165 and 227; and left M_3 4395. They are larger than the teeth associated with the *Connochaetes* cranium at FLKN I, and this would suggest that *Megalotragus ? kattwinkeli* was present at DK I.

At least two species of alcelaphine are represented by the identified limb bones. These are a more numerous smaller species which presumably goes with the *P. altidens* horn cores, and a less common very large species. Limb bones assigned to the smaller species are as follows; the tibiae differ from those of later *P. altidens* at FLKN I in having a more strongly upturned edge of the lateral facet at the proximal end. There appear to be no other morphological differences.

Distal ends of right humeri 471 and 531, distal end left humerus 3083; proximal ends left radii 5135 and 067/4092, distal end left radius 15; right ulna 3021 and left ulna 3071; complete left metacarpal 76, proximal ends left metacarpals 504 and 3071; distal end right tibia 45, proximal ends left tibiae 78 and 4422A; proximal ends right metatarsals 105 and 067/4081, proximal end left metatarsal 645, distal end metatarsal 3066, immature right metatarsal 185, immature left metatarsal 159; and the associated set of complete left humerus 141, distal end right humerus 168, complete right radius 58, complete left radius with ulna 145 + 57, complete right metacarpal 143, complete left metacarpal 144, and phalanges 53, 85 and 101.

There is quite a size range among the bones of the smaller species, and possibly a still smaller species is represented by the distal end right humerus 67, distal end left humerus 3182, proximal end left radius 5135, complete left tibia 876 and distal end left tibia 45. These are about the size of the small alcelaphine limb bones from levels 1–3 at FLKN I. In Table 1 (opposite) they have been doubtfully referred to Alcelaphini sp. 4.

The size demarcation between *P. altidens* and the larger species is very clear. The limb bones of the latter are proximal end right radius 5190, distal end right radius 414, distal end left radius 067/4093; right ulna 067/4122; complete left metacarpal 85, proximal ends right metacarpals 5 and 521; complete right tibia 4300; distal epiphysis right femur 188; complete right metatarsal 4138A + B, complete left metatarsal 4097, proximal end right metatarsal 316, proximal end left metatarsal 477, distal ends metatarsals 141 and 3073; and associated distal end left humerus 164 and complete left radius 166. The radius and metatarsals of this larger species are very long, whereas those of *Connochaetes* are relatively short. The coronoid fossa on the distal end of humerus 164 is deep, which is unlike *Connochaetes*. These limb bones belong to a very large and long-limbed alcelaphine, most probably *Megalotragus kattwinkeli* or its immediate ancestor.

Tribe ANTILOPINI. *Antidorcas recki* is represented by a complete left mandible 261, incomplete

Table 1 Numbers of bovid bones at DK I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Tragelaphus s. maryanus	–	1	2	21 (4)	–	24	3	2
Smaller tragelaphine sp.	–	–	–	–	5	5	2*	–
Larger tragelaphine sp.	–	–	–	–	1	1	1*	–
Tragelaphini total	–	1	2	21 (4)	6	30		
Syncerus acoelotus	–	1 (1)	–	2 (1)	–	3	–	1
Kobus sigmoidalis	–	–	2 (1)	22 (1)	2	26	4	1
Redunca sp.	–	–	–	1	–	1	1	–
Hippotragus gigas	1 (1)	1 (1)	–	3	2	7	2	1
Megalotragus ? kattwinkeli	–	–	–	22	17	39	3	–
Parmularius altidens	4 (1)	1 (1)	5 (2)	83 (1)	27 (2)	120	7	2
Alcelaphini sp. 4?	–	–	–	–	5	5	2	–
Alcelaphini total	4 (1)	1 (1)	5 (2)	105 (1)	49 (2)	164	10	2
Antidorcas recki	–	2 (1)	4	22	16	44	5	1
Antilopini sp. 1	2	–	–	–	–	2	2	–

* One of the two tragelaphine species represented by limb bones would be *Tragelaphus strepsiceros maryanus*.

left mandibles 272 and 067/4078, right mandible 231, left maxilla 067/4124 and immature left maxilla 191. P_2 is present on mandibles 261 and 272, but its presence or absence on the other mandibles is uncertain. There are also several isolated teeth. These are right upper molars 067/3046, 067/3477, 067/4091, 067/4123 and 067/4124; left upper molars 1475, 067/3451, 067/4123 and 067/4124; upper premolar 067/4085; right lower molars 067/3050, 067/3498, 067/4085 and two numbered 067/3483; left lower molars 4111, 067/3065 and two numbered 067/4085; and right M_3s 4565 and two numbered 149.

A number of limb bones agree well with those of *A. recki* at other sites. These are distal end right humerus 144, distal end left humerus 4100; complete left radius 4087; proximal ends right metacarpals 194 and 362, distal ends metacarpals 615 and 067/3093; complete left tibia 4366, distal end right tibia 195, distal end left tibia 375; complete left metatarsal 3292, proximal ends left metatarsals 228 and 3129, and distal end metatarsal 639.

Two complete right femora, 3330 and 5385, are about the size of the proximal end of a left femur 1027 at FLKN I and are therefore presumably *A. recki* although rather large. They are smaller than the small alcelaphine limb bones at FLKN I (p. 19).

Two left horn cores, 1962.067/3963 and 3965, from the surface of DK I, could be an antilopine species other than *Antidorcas recki* (see p. 444). This is the species listed as 'Antilopini sp. 1'.

SUMMARY. DK I is interesting for the early records of *Hippotragus gigas* and *Megalotragus ? kattwinkeli*, and for one of the rare reduncine teeth small enough to fit *Redunca*. There is a comparatively high representation of tragelaphines and reduncines, and the normal Bed I partnership of *Antidorcas recki* and *Parmularius altidens* has appeared.

The numbers of bovid bones of each species at DK I is given in Table 1.

FLK Sites

Three adjacent erosion gullies form a recess in the western wall of the Main Gorge just above its junction with the southern branch. The recess measures some 350 yds (320 m) north–south by about 450 yds (410 m) east–west. There are six sites within the area. These are FLKNN I, FLK I, FLKN I, FLKN II, FLK II, FLK II Maiko Gully and FLKN Ostrich site.

FLKNN I

Site (38) Geologic locality 45

FLKNN I is the most northerly site within these gullies. It consists of a low ridge running approximately east–west and is capped by some 10–12 ft (3·0–3·6 m) of fawn-coloured tuff resembling the Naisiusiu Beds and lying unconformably on the Bed I sediments, the whole of Beds II–IV having been eroded away before its deposition. The site was excavated in 1960–61 and four levels were uncovered, from above downwards:

Level 1. A greenish-grey silty clay with scattered bones and artifacts on its surface and in its upper parts. The top was irregular and friable, indicating weathering. The faunal remains are not weathered but are rather fragmentary. This level can be correlated with level 22 (the occupation or '*Zinjanthropus*' level) of FLK I.

Level 2. A fine-grained buff-white tuff containing some faunal remains but no artifacts. The antelope material was noticeably more complete than in levels 1 and 3 and several partial skeletons were recovered. The remains were mostly found in patches of clay within the tuff.

Level 3. A hominid occupation floor on the surface of a grey silty clay, 6 ins–2 ft (15–60 cm) thick, resting on Tuff IB. The bones were found on the clay surface or in its topmost part which was more friable than the lower part.

Level 4. A clay underlying Tuff IB. This is the equivalent of the upper levels of DK I. There were very few antelope remains.

The many root casts and impressions of reed stalks in Tuff IB and the occurrence of fish, amphibians and waterfowl suggest that the site was near a lake or swamp.

Tribe TRAGELAPHINI. A frontlet with nearly complete horn cores, 60, of *Tragelaphus strepsiceros maryanus* (Leakey 1965 : 40; pl. 42) was found in level 1 at this site. Maxillae (right 557 and left 553) and mandibles of both sides (right 62 and left 66+548) and a full set of incisors and canines, 548, were found with this frontlet. The tooth rows are complete and are the same size and morphology as those of Tragelaphini at FLK I and FLKN I. Part of the skeleton of this animal was found beside the skull and dentitions; this consists of most of the pelvic girdle 56, right scapula 549, left patella 544, a crushed radius 541 and several vertebrae (atlas 556, axis 63, three cervicals 63, 64a and 64b, and seven lumbars 539, 540, 550, 551, 552 and 558).

Part of a lower molar 067/1180 from level 2 or 3 is tragelaphine.

Limb bones assigned to this tribe are the associated distal end of right humerus 896, proximal end of right radius 902 and complete right metacarpal 895 from level 2; and the proximal end of left metacarpal 855+883+884 from level 3. They closely resemble limb bones identified as Tragelaphini at FLKN I, a site where reduncines are almost unknown, but here at FLKNN I it is apparent that there is very little difference from contemporary reduncines (Fig. 35), and the

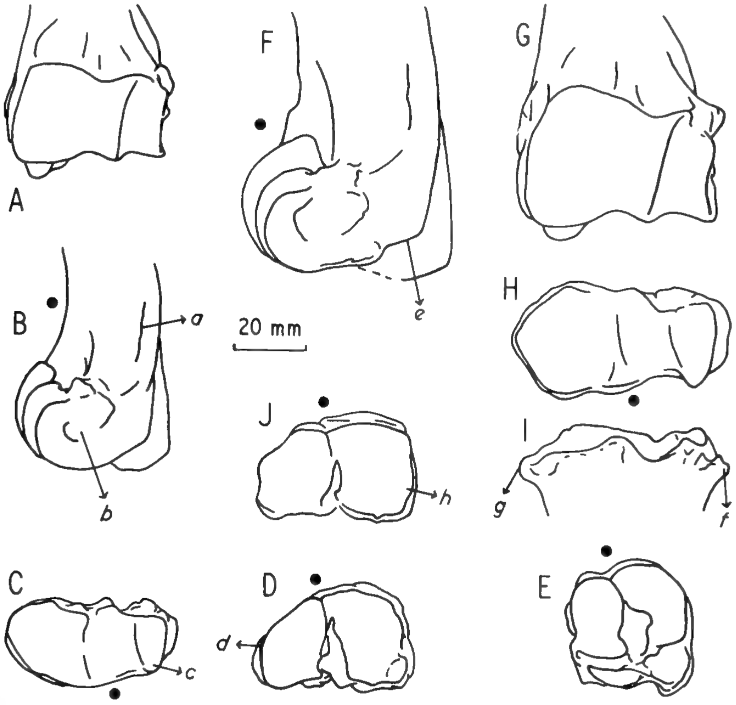

Fig. 35 Limb bones of Olduvai antelopes; A–E Tragelaphini, F–J Reduncini. Figs A–D and G are of the left side; the remainder have been reversed to appear as if from the left side. Solid dots indicate anterior sides.

A, B. Anterior and lateral views of distal humerus FLKN I 8248.
C. Proximal articular surface of radius FLKN I 8275.
D. Proximal articular surface of metacarpal FLKN I 067/1073.
E. Proximal articular surface of metatarsal FLKN I 7333.
F. Lateral view of distal humerus FLKNN I 368.
G. Anterior view of distal humerus FLK I 235.
H. Proximal articular surface of radius FLKNN I 370.
I. Anterior view of proximal end of same radius.
J. Proximal articular surface of metacarpal FLKNN I 369.

a=strong ridge for extensor carpi radialis origin in tragelaphines, *b*=shallow hollow for lateral humeroradial ligament in tragelaphines, *c*=lack of anterior projection in tragelaphines, *d*=unciform facet not angled in tragelaphines, *e*=distal end of lateral side low in reduncines, *f*=small proximal lateral tubercle in reduncines, *g*=pronounced medial rim in reduncines, *h*=an infrequent dorsally-directed protuberance on the magnum-trapezoid facet in reduncines.

identifications are correspondingly insecure. It is also odd that the limb bones are much smaller than one would expect for *T. s. maryanus*. The humeri differ from those of living Tragelaphini by having a strong ridge on the lateral side of the distal end for the origin of the extensor carpi radialis. They differ from Reduncini at this site only in having a shallow hollowing for the lateral humeroradial ligament and being slightly smaller. The radii differ from the contemporaneous reduncines in the lack of anteriorly-directed points on the proximal lateral facets (such points are frequent in living tragelaphines, and occasional in living reduncines). The metacarpals are without an angled unciform facet or the upward protuberance of the magnum-trapezoid facet found in reduncines, but again distinction from reduncines is poor.

The associated distal end of left humerus 730, proximal end of left radius 732 and left ulna 731 from level 2 are more doubtfully tragelaphine.

Tribe REDUNCINI. The pedicel and lower half of a right horn core, 871 from level 2, belongs to *Kobus sigmoidalis*. A small part of the same skull (basioccipital and auditory bullae) and nearly complete maxillae, numbered 872, are also preserved. The crushed right side of an immature skull, 296 from level 3, with the horn core base, complete deciduous premolar row and first two molars, is also of this species.

Many partial dentitions at this site are reduncine. They are comparable with the maxillae associated with the horn cores, and are all about the same size and can probably be referred to *K. sigmoidalis*, though it would be impossible to separate individual jaws from the living waterbuck. These dentitions are as follows.

Right mandibles 64 and 067/1200, left mandible 13 and immature right mandible 067/1196 from level 1; right maxilla 373, left maxilla 535, right mandibles 629 and 965, immature right maxilla 79, immature left maxilla 374, immature right mandible 516, immature left mandible 591, and the associated immature right and left mandibles 910 and partial right maxilla 911 from level 2; right mandible 351, left mandible 131, immature right mandibles 135 and 920, immature left mandibles 73, 770, 934 and 067/1191, associated immature left maxilla and right and left mandibles 769, and associated immature right 268 and left 266 mandibles, immature left maxilla 269, and possibly immature right maxilla 113 from level 3.

There are also a number of isolated reduncine teeth; they can probably all be assigned to *K. sigmoidalis*. These are as follows.

From level 1 three right upper molars, two right upper premolars and three left upper premolars from one individual 067/1197; from level 2 three right upper molars and three left upper molars from one individual 430, a right lower molar and two right lower premolars from one individual 067/1192, a right lower molar, right M_3 and right P_4 from one individual 067/1195 (possibly the same individual as 067/1192), right upper premolar 067/1201 and two deciduous left upper premolars without numbers; from level 3 two left upper molars, two left lower molars, three right deciduous P_4s and a left deciduous P_4 all numbered 067/1199, and right P^3–M^3 523. Parts of three left lower molars are from level 2 or level 3.

There are several associations among the limb bones assigned to this tribe, particularly in level 2: distal end right humerus 368, complete right radius 370 and complete right metacarpal 369; distal end right humerus 892, complete right radius 890, right ulna 891 and complete right metacarpal 889; distal end left humerus 500, complete left radius 499, left ulna 499 and complete left metacarpal 498; proximal end left radius 957 and distal end left metacarpal 956; complete right metatarsal 738 and proximal end left metatarsal 736. The above associations are all from level 2. A complete right metacarpal 616 and distal end right humerus 617 are associated in level 2 (field catalogue) or level 3 (written on bones).

There are some other reduncine limb bones. From level 1 these are distal end right humerus 102, proximal end right metacarpal 45, proximal end right metatarsal 818 and proximal end left metatarsal 20. From level 2, distal end left humerus 998, proximal end left radius 1014, distal ends left tibiae 285 and 343, complete right metatarsal 738 and proximal end right metatarsal 579. From level 3, distal end left humerus 067/1253, proximal end right radius 728, nearly complete left radius 936 and ulna 935, proximal ends left radii 364 and 601 (with ulna 604), complete right metacarpal 349+350, and proximal ends left metacarpals 168 and 210.

The humeri differ from those of living reduncines in that the distal end of the lateral side descends to a low level behind the insertion for the humeroradial ligament, and in this they resemble tragelaphines (Fig. 35, p. 7). The radii have a lower and smaller proximal lateral tubercle and a more pronounced medial rim of the proximal medial facet than in living waterbuck. The metacarpals differ from those of living reduncines in the less frequent medial protuberance on the magnum-trapezoid facet. The size of these limb bones is about that of a waterbuck, but a few are smaller and thus nearer the size of contemporaneous tragelaphines. It seems safe to assume that the majority are of *K. sigmoidalis*.

An immature horn core, 067/1174 found at the junction of levels 2 and 3 in 1960, is little compressed and possibly also of *K. sigmoidalis*.

Tribe HIPPOTRAGINI. A *Hippotragus* cranium with horn cores, both mandibles and parts of the maxillae, numbered 608, was found during 1960 in the clay above level 1 at this site, and was thought to be possibly alcelaphine by Leakey (1965 : 66(c)). The braincase has been damaged and distorted behind the horn cores. Several points concerning the anatomy of this interesting find have already been mentioned in the discussion of *Hippotragus gigas*, p. 346. The mandibles have a much smaller P_2 than in the roan and a short diastema. On P_4 the entostylid is set diagonally to the line of the jaw and not parallel to the entoconid. This condition occurs more frequently in sable than in roan, but the condition on other P_4s from Olduvai cannot be seen. The horizontal ramus of these jaws is deep.

A partial skeleton of a large hippotragine, probably *Hippotragus gigas*, was found at the base of the tripartite level of FLKNN in 1961. This is slightly higher in the sequence than level 1 of FLKNN I and is overlain by Tuff ID (M. D. Leakey 1971b : fig. 19).

Other hippotragine limb bones are a complete left tibia 821 from level 1, and an associated complete right metacarpal 960, right ulna 962 and distal end of right humerus 961 from level 2. The humerus distal end agrees closely with that of the hippotragine skeleton found at the base of the tripartite level. The metacarpal is short and massive and differs from equally-sized reduncines in the absence of a tuberosity on the medial side of the magnum-trapezoid facet, the lack of an angle on the unciform facet, the slightly wider distal condyles, scarcely any hollows at the top of the condyles posteriorly, and from reduncines and living *Hippotragus* in the flatter top articular surface. An associated distal end of right humerus 825, proximal end of right radius 824 and complete right metacarpal 826, all from level 2, are also hippotragine. However, the humerus looks alcelaphine in its deep medial groove and indented top of the medial condyle, and would have been identified as such except for the association with the other bones.

Tribe ALCELAPHINI. A complete right horn core 067/1173 of *Parmularius altidens* was a surface find at this site in 1960. Its backward curvature is very like that of the DK I horn core, or is possibly intermediate between that and the sort of curvature seen in cores from FLK I. The distal half of a *P. altidens* horn core 749 P.P.R.9, referred to as probably Caprini by Leakey (1965 : 68(b)), came from level 3.

An incomplete right mandible, 733 from level 3, with isolated teeth of the same individual (right upper molars 943 and 067/1188; left upper molar 948; left lower molar and left M_3 numbered 067/1188; right M_3 067/1194) agrees in size and morphology with *P. altidens* dentitions at FLKN I. This mandible shows none of the red coloration present in other FLKNN I dentitions including those from level 3. An alcelaphine right M_3 714 is from level 2 and a right upper molar 067/4676 from level 4.

There are no *in situ Parmularius* limb bones at this site; the alcelaphine limb bones are all of one or more species larger than *Parmularius*. As with the reduncines there are associated sets of limb bones in level 2. These are complete right radius 578, right ulna 578 and complete right metacarpal 577; distal end right humerus 344, proximal end right radius 306+341, right ulna 342 and complete right metacarpal 305. There is also a complete right alcelaphine humerus 358 from level 2 with no known association, and a complete right metacarpal 405 from level 1. These bones could be of *Connochaetes* or *Megalotragus*. A damaged and very long right tibia 355 and a crushed right femur 354 from level 2 belong more definitely to *Megalotragus ? kattwinkeli*. Finally, the distal end of an immature left radius, 347 from level 3, is alcelaphine.

Tribe ANTILOPINI. A left upper molar and upper premolar, 067/4676 from level 4, belong to this tribe. Part of a left metacarpal 067/1280 from level 1, and the fragmentary distal end of a left tibia 067/1269 and complete right metacarpal 649, both from level 3, may represent *Antidorcas* or *Gazella*. However, the first and second limb bones could belong to the Alcelaphini.

SUMMARY. The main feature of FLKNN I is its many reduncine remains and unusually few alcelaphines. The reduncine predominance must be connected with proximity to water. The associations among limb bones in level 2 are valuable in showing the difficulty of distinguishing tragelaphines from reduncines at a time level of nearly two million years ago. The best Bed I skull of *Hippotragus gigas* and a rare stratigraphically-placed horn core of *Kobus sigmoidalis* occur here. One or more large alcelaphine species are better represented than *Parmularius altidens*, and Antilopini are very poorly represented, a situation in contrast with other Bed I sites.

The species list for the site is:

Tragelaphus strepsiceros maryanus (may include the rather small limb bones)
Kobus sigmoidalis
Hippotragus gigas
Megalotragus ? kattwinkeli
? *Connochaetes* sp.
Parmularius altidens
Antilopini sp.

The numbers of bovid bones in levels 1, 2 and 3 are shown in Table 2. A large proportion of the reduncines in level 3 are immature.

FLK I

Site (41) Geologic locality 45

FLK I is almost in the centre of the FLK series of erosion gullies. It was excavated in 1959–60 by means of a trial trench and a succession of trenches designated A, B, C, D, E, F and G. Several levels were uncovered, many of which were barren. From the top downwards the levels with artifacts or fossils were:

Level 7. An irregular seam of clay, between two layers of yellow-grey tuff, about 5–6 ft (1·5–1·8 m) below Tuff IF. A few antelope remains were recovered.

Level 10. A fairly coarse reworked tuff some 9–10 ft (2·7–3·0 m) below Tuff IF. A few antelope bones were found.

Level 11. A hard yellow-buff tuff layer between two layers of clay. There were no antelope remains.

Level 12. A hard, massive buff-yellow tuff about 10–11½ ft (3·0–3·45 m) below Tuff IF. It yielded a crushed antelope skull and skeleton which is impossible to identify.

Level 13. A level some 2 ft (60 cm) thick consisting of irregular and discontinuous bands of clays and tuffs. In some areas the tuffs were well defined but in others they merged into one another.

Level 15. A clayey tuff about 1 ft (30 cm) thick and 15 ft (4·5 m) below Tuff IF.

Levels 16, 17 and 21. Thin tuff layers which were not very fossiliferous.

Level 22. A grey-green silty clay about 1 ft (30 cm) thick and 20 ft (6·0 m) below Tuff IF. This is the level at which the '*Zinjanthropus*' skull was found in 1959. The upper surface of the clay was slightly uneven and the topmost part more friable than the lower part, indicating weathering into a palaeosol. The fossil material, concentrated into a central area a short distance from the skull and an irregular outer margin (M. D. Leakey 1971b : 50, fig. 24), was recovered from the surface of the clay or its uppermost part but was not weathered. There was no vertical diffusion of fossils as in other levels.

At this site the field numbers of fossils and artifacts are preceded by the trench letters.

Tribe TRAGELAPHINI. This tribe is represented by a palate C.067/1083, and associated mandibles right G.067/1100 and left G.067/1095, which are adult, and an associated set of upper (right G.067/1088 and left G.067/1089) and lower (right G.067/1086 and left G.067/1085) immature dentitions. They are all from level 13. The adult lower tooth rows are complete and are comparable in size and morphology with those of the greater kudu. All the dentitions can probably be assigned to *Tragelaphus strepsiceros maryanus*.

Table 2 Numbers of bovid bones at FLKNN I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 1								
Tragelaphus s. maryanus	1	2	2	–	1	6	1	–
Kobus sigmoidalis	–	–	4 (1)	8	4	16	2	1
Hippotragus gigas	1	2	2	–	1	6	1	–
? *Connochaetes* sp.	–	–	–	–	1	1	1	–
Level 2								
Smaller tragelaphine sp. ?	–	–	–	–	3	3	1	–
Kobus sigmoidalis	1	7 (3)	6 (4)	15 (2)	21	50	3	2
Hippotragus gigas	–	–	–	–	6	6	2	–
Megalotragus ? kattwinkeli	–	–	–	–	2	2	1	–
? *Connochaetes* sp.	–	–	–	–	8	8	2	–
Parmularius altidens	–	–	–	1	–	1	1	–
Alcelaphini total	–	–	–	1	10	11	4	–
Level 3								
Smaller tragelaphine sp.	–	–	–	–	1	1	1	–
Kobus sigmoidalis	1 (1)	4 (4)	12 (10)	13 (4)	10	40	3	7
Large alcelaphine sp.	–	–	–	–	1 (1)	1	–	1
Parmularius altidens	1	–	1	6	–	8	1	–
Antilopini sp. indet.	–	–	–	–	1	1	1	–

A few isolated teeth also belong in this tribe. These are right upper molar G.067/904, left upper molar C.067/894, right lower molar G.067/896, right M_3 G.067/909 and left M_3 C.067/908 from level 13; left lower molar Balk 067/895 and left M_3 Balk 067/1092 from level 15; P^3 and P^4 in a right maxilla fragment 067/883 of unknown level. These may well also be *T. s. maryanus*.

A number of limb bones are tragelaphine. These are distal end of left humerus G.236 and complete right metatarsal G.067/959 from level 13; complete right metacarpal F.213 from level 21; and complete right metatarsal D.155 from level 22. These are smaller than one would expect limb bones of *T. s. maryanus* to be. The distal half of a left femur G.313 and associated incomplete proximal end of a right metacarpal G.311 from level 22, and a complete left metacarpal G.258 from level 13, are from a larger kudu-sized species, as is the complete femur 5400 from DK I.

Tribe BOVINI. A left mandible with only an unworn M_3 preserved, C.1045+1065+1186, comes from level 22 of this site. It is presumably conspecific with the bovine at other Bed I sites.

Tribe REDUNCINI. A left maxilla B.46, right mandible D.41, left mandibles B.23 and D.122 and associated right and left mandibles G.388 all come from level 22 of this site. Two incomplete right mandibles, 067/1087 and 067/1091, are of unknown level. These dentitions are of a species of *Kobus* which is probably conspecific with that at FLKNN I, that is, *K. sigmoidalis*. As mentioned in the reduncine discussion, the mandible D.41 has a complete tooth row and may well have a shorter premolar row relative to molar row length than in examples of extant *K. ellipsiprymnus*.

Several isolated reduncine teeth are of *Kobus* rather than *Redunca* size and these can probably also be referred to *K. sigmoidalis*. They are right upper molar G.067/905 and right lower molar G.067/913 from level 13; right F.162, and left lower molars F.156 and G.067/915 from level 15; right lower molars B.566, B.661 and B.067/907, left lower molars B.382 and B.067/906, right M_3s B.70 and B.067/1082, left M_3 B.449 and right P_4 Balk 134 from level 22. Right and left upper molars numbered 067/4621, deciduous left P^2–P^4 (separate teeth) 067/879, and two right upper molars, two right lower molars, a left lower molar, four right lower premolars, two left lower premolars, a deciduous right P^3, and two deciduous left P^4s all numbered 067/921 are of unknown level.

There are some reduncine limb bones at this site, which are about the size of those of the living waterbuck and show the same differences from living reduncines as given in the FLKNN I account. It seems likely that they are all *K. sigmoidalis*. They are as follows.

Proximal end right metacarpal G.197 from level 10; distal ends left humeri G.234 and G.235, proximal end left radius F.220, proximal end left metacarpal G.255 and proximal end right metatarsal C.067/949 from level 13; proximal end right radius F.153, proximal end right metacarpal G.067/964, distal ends left tibiae F.140, D.167 and D.067/970 and proximal ends left metatarsals G.067/932 and D.067/935 from level 15; distal ends right humeri Balk 231 and C.835, distal end left humerus C.1043, proximal end right radius B.59 with right ulna B.60, proximal end right radius B.580 with right ulna B.579, proximal end left metacarpal B.274+277, associated distal end left humerus E.95, proximal end left radius E.96 and left ulna E.94, associated complete right humerus C.1092, complete right radius C.1094 and complete right metacarpal C.1095, distal end right tibia B.478, distal end left femur B.20 and proximal ends right metatarsals G.364 and 067/931 from level 22; distal end right tibia K.067/979 from an unknown level above level 22.

The distal end of right humerus B.122, proximal end of right femur B.104 and distal end of right femur A.22, all from level 22, are most probably reduncine and would be of the same species. A complete left metatarsal C.1085 from level 22 is identified as reduncine or hippotragine.

Tribe HIPPOTRAGINI. A species of *Oryx* is represented by a left horn core with part of the frontal and orbital rim, G.390 (Leakey 1965 : 51; pl. 62). The specimen came from level 22 and is only the second record of this genus at Olduvai.

A left mandible G.067/1097 with unworn P_4–M_3 preserved, part of a right lower molar 067/921 and a right M_3 G.067/897 represent a species of *Hippotragus*. The finds are from level 13 and could be from the same individual. The specimens are referred to *H. gigas*.

A deciduous left P_4 067/921 of unknown level is probably hippotragine.

Tribe ALCELAPHINI. *Parmularius altidens* is represented by a right horn core G.233+235 **P.P.R.3**, part of a left horn core G.252 and part of a right horn core C.067/1078 from level 13, part of a horn core G.067/1080 from level 15, a frontlet with nearly complete horn cores Balk 126+199 (Leakey 1965 : 58; pl. 72) and a left horn core with the orbital rim preserved F.206 P.P.F.7 from level 22. The horn cores of the last two fossils are long, with the lower parts straight and backward curvature limited to the upper parts. There is a fairly large medial swelling at the base, above which the divergence increases. The horn core figured by Leakey (1965 : pl. 74) is not F.206 as stated but left horn core FLKN I 1410 of the same species. The base of a right horn core G.232 from level 13 is probably *P. altidens*.

A number of partial mandibles and isolated teeth are assigned to *P. altidens*. These are as follows.

Part of a left M_3 D.543 from level 7; right mandible G.067/1098 from level 12; right upper molar C.067/920, left upper molar C.067/891 and unworn left M_3 G.067/892 from level 13; right mandibles F.157 and D.067/1094, right upper molars F.163 and F.223, left upper molar D.067/910, right lower molar F.067/916, left lower molars F.159, C.160 and G.067/911 and right P_4 F.124 from level 15; right mandibles D.42, G.361 and C.857, partial left mandibles E.129 and B.347, right upper molars Balk 140, Balk 147, MS 067/912 and 067/917, left upper molars C.1046, B.067/898, MS 067/920 and B.067/4551, right lower molar D.111, left lower molars E.52 and B.067/900, two left lower molars and left M_3 numbered F.247, immature left mandible D.85, and deciduous left P_4 C.932 from level 22. An immature left mandible K.067/1099 is from an unknown level above level 22.

Mandible G.361 would have had a P_2 in life, in mandible G.067/1098 this is uncertain, but in mandibles D.42 and E.129 there is no alveolus in the jaw for a P_2 so that P_2 was missing at the time the animals died. The rounding of the lateral lobes of lower molars may be less developed than in *P. altidens* at later FLKN I, but this is not certain.

Several alcelaphine limb bones at this site are assigned to *P. altidens*. These are as follows.

Proximal and distal ends of a left tibia D.540 and D.541 and distal end left femur D.539 from level 7; distal end right humerus C.067/811, proximal end left metacarpal C.067/965, distal end metacarpal C.067/962, distal end left tibia C.067/972, distal end right femur C.067/817, proximal end left metatarsal C.067/934 and distal ends metatarsals C.067/951 and C.067/952 from level 13; distal end right humerus G.067/807, proximal ends right radii F.152 (with right ulna F.166) and G.067/985, proximal end left radius G.067/990, distal end right radius F.155, complete right metacarpal G.520, proximal end left metacarpal F.149, distal ends metacarpals G.519 and D.067/953, complete right tibia F.138+141, distal end left tibia F.139, complete right metatarsal Balk 067/929 and proximal end left metatarsal F.145 from level 15; distal ends left humeri E.92, E.103 and F.216, proximal end left radius Balk 179, distal ends right radii B.674 and immature MS 067/984, associated distal end left humerus K.3 and proximal end left radius K.1, proximal end right tibia F.193, proximal end left femur C.1001, and proximal end right metatarsal C.067/4547 from level 22. Proximal end right metatarsal K.067/945 is from an unknown level above level 22.

A left maxilla B.067/1093 with P^4–M^3 preserved differs from *P. altidens* dentitions in its larger size and more complicated central cavities. Its less rounded medial lobes may be a feature of being in early wear. A left mandible B.17 with P_4–M_3 is also larger than *P. altidens*. Both pieces are from level 22 and may well represent *Connochaetes* at this site.

A few limb bones are larger than those of *P. altidens* and are possibly conspecific with the larger dentitions. These are proximal end left radius C.067/987 from level 13; distal end right radius G.516 and proximal end left metatarsal F.146 from level 15; distal end right humerus C.895 and distal end left tibia D.106 from level 22; and possibly the associated distal end right humerus D.537 and proximal end right radius D.538 from level 7.

A complete left radius K.067/986 from an unknown level above level 22 is larger and longer than the radii FLKNN I 578 and FLKN I 181+926 and could be conspecific with the very large alcelaphine *Megalotragus ? kattwinkeli* at DK I.

Tribe ANTILOPINI. *Antidorcas recki* is represented by an associated pair of horn cores, right G.229 and left G.230, from level 13 (Leakey 1965 : 65(g); Gentry 1966 : 57). Both have the midfrontal suture, part of the orbit and supraorbital pit preserved.

A number of mandibles and isolated teeth are referred to this species. These are left mandible G.067/1090 and fragmentary right mandible G.515 from level 15; right mandibles B.119, G.154, G.294 and G.323, left mandibles D.35, D.65 and B.492, three right upper molars and two left upper molars all D.91, two right lower molars Balk 135, right M_3 B.127, left M_3s B.125 and Balk 180, a right and left upper molar from the Balk without number and an immature left mandible B.188 from level 22. Four right upper molars, a left upper molar and two right lower molars, all numbered 067/899, are from unknown levels. On the M_3s the talonid is very well developed, as in the similar-sized living *Gazella thomsoni*, and in some it approaches the size of the other two lobes. P_2 is present on mandible B.119 and on G.067/1090 there is an alveolus for a P_2, but as Gentry (1966 : 61; pl. 2B) has noted, mandibles D.65 and G.154 have very reduced P_2s and in G.294 P_2 was absent altogether as there is no alveolus in the jaw for it. The presence or absence of P_2 on mandible B.492 is uncertain.

Several limb bones are antilopine and probably all can be assigned to *A. recki*. These are as follows.

Distal end metatarsal D.542 from level 7; proximal end right metacarpal D.545 and proximal end right femur G.188 from level 10; distal end metacarpal C.067/937, proximal end right tibia C.067/971, distal ends right tibiae G.25, C.067/967 and C.067/977 and distal ends metatarsals F.219, G.253 and F.067/944 from level 13; proximal end right radius F.154, right ulna G.523, proximal end right metacarpal G.509, distal ends metacarpals G.517 and G.067/961, distal ends left tibiae G.510 and Balk 067/967, distal end left femur F.150 and proximal end left metatarsal F.147 from level 15; proximal end right humerus D.81, proximal end left humerus D.56, distal ends right humeri B.75 and Balk 120, distal end left humerus 499, associated distal end right humerus B.135 and proximal end right radius (with ulna) B.136, associated distal end left humerus C.1181, proximal end left radius C.1177 and left ulna C.1176, proximal ends left radii D.100 (with ulna) and Balk 119, part of a right ulna B.40, complete left metacarpal D.133, proximal ends left metacarpals B.166 and one without number, distal ends metacarpals B.387 and MS 067/954, complete right tibia K.9, complete left tibia F.161, part of shaft at proximal end right tibia D.104, proximal ends left tibiae D.36, D.69 and E.115, distal ends right tibiae B.364, B.380 and B.067/978, almost complete left femur F.220, distal end right femur MS 067/818, complete right metatarsal K.10, complete left metatarsal F.219, proximal ends right metatarsals B.140, G.358 and C.1054, proximal end left metatarsal C.067/942 and distal end metatarsal D.26+124 from level 22. Proximal end left femur K.067/814, proximal end right metatarsal K.067/930, and distal end metatarsal K.067/950 are from an unknown level above level 22.

A left M_3 C.067/901, proximal end left humerus B.139, distal end metacarpal D.129 and complete right metatarsal D.129, all from level 22, are rather larger than the other antilopine remains.

SUMMARY. At FLK I the association between *Parmularius altidens* and *Antidorcas recki* reappears, but tragelaphine and reduncine fossils are still numerous. The oryx horn core is a notable occurrence. The species list for the site is:

Tragelaphus strepsiceros maryanus
Tragelaphus sp.
Syncerus acoelotus
Kobus sigmoidalis
Oryx sp.
Hippotragus gigas
Megalotragus ? kattwinkeli
? *Connochaetes* sp.
Parmularius altidens
Antidorcas recki
(Also large teeth and limb bones perhaps of a second antilopine species)

The numbers of bovid bones in levels 13, 15 and 22 are shown in Table 3.

FLKN I

Site (40) Geologic number 45

FLKN is situated on the far side of the ridge which lies to the north of FLK. There are more than 20 ft (6·0 m) of deposit in lower and middle Bed II and the upper part of Bed I. As at FLKNN I, erosion has removed Beds III and IV and the upper part of Bed II so that later deposits rest

Table 3 Numbers of bovid bones at FLK I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 13								
Tragelaphus s. maryanus	–	3 (2)	4 (2)	5	–	12	2	1
Smaller tragelaphine sp.	–	–	–	–	2	2	1*	–
Larger tragelaphine sp.	–	–	–	–	1	1	1*	–
Kobus sigmoidalis	–	–	–	2	5	7	2	–
Hippotragus gigas	–	–	1	2	–	3	1	–
? *Connochaetes* sp.	–	–	–	–	1	1	1	–
Parmularius altidens	3	–	–	3	8	14	2	–
Antidorcas recki	2	–	–	–	8	10	3	–
Level 15								
Tragelaphus s. maryanus	–	–	–	2	–	2	1	–
Kobus sigmoidalis	–	–	–	3	7	10	3	–
? *Connochaetes* sp.	–	–	–	–	2	2	1	–
Parmularius altidens	1	–	2	8	14	25	3	–
Antidorcas recki	–	–	2	–	9	11	2	–
Level 22								
Smaller tragelaphine sp.	–	–	–	–	1	1	1*	–
Larger tragelaphine sp.	–	–	–	–	2	2	1*	–
Tragelaphini total	–	–	–	–	3	3		
Syncerus acoelotus	–	–	1	–	–	1	1	–
Kobus sigmoidalis	–	1	5	9	18	29	4	–
Oryx sp.	1	–	–	–	–	1	1	–
? *Connochaetes* sp.	–	1	1	–	2	4	1	–
Parmularius altidens	2	–	6 (1)	15 (1)	11 (1)	34	4	2
Alcelaphini total	2	1	7 (1)	15 (1)	13 (1)	38	5	2
Antidorcas recki	–	–	8 (1)	12	38	58	5	1
Larger antilopine sp.	–	–	–	1	3	4	1	–
Antilopini total	–	–	8 (1)	13	41	62	6	1

* One of the two tragelaphine species represented by limb bones would be *Tragelaphus strepsiceros maryanus*.

unconformably on the eroded surface of Bed II within 13 ft (3·9 m) of the I–II contact. The sequence of deposits, from those of Bed II downwards, is as follows.

Bed II. (a) A grey-brown silty clay of maximum depth of 6½ ft (1·95 m), without remains.

(b) A sandy conglomerate 10 ft (3·0 m) above the base of Bed II. The horizon can be traced through other deposits west to the fourth fault. At HWK East II the deposit (there forming level 4) is 2 ft (60 cm) thick; here at FLKN II it is only 1 ft (30 cm) thick. It yielded a number of artifacts, many of which are made from chert, and some bones.

(c) Six levels of clay and limestone of varying thicknesses down to the underlying Tuff IF. The lowest level from which artifacts and faunal remains were recovered from Bed II at FLKN was a clay horizon which contained many root casts, 4½ ft (1·35 m) thick. Artifacts and bones were sparsely scattered through the deposit. This level can be correlated with level 2 at HWK East II.

Bed I. (a) Tuff IF.

(b) Levels 1+2+3, the top levels of FLKN I. A single horizon, 2–3 ft (60–90 cm) thick, of grey-brown silty clay, arbitrarily subdivided into levels during excavation. Remains were especially concentrated in levels 1 and 3, indicating two periods of hominid occupation. A small amount of material was found in level 2 but was probably derived from level 1. Material from the upper occupation level is therefore given as from levels 1–2, that from the lower as from level 3, and that of unknown origin (excavated before 1961) as levels 1–3.

(c) Level 4. A dark brown silty clay, 3 or 4 ins (7·5 or 10·25 cm) to 1½ ft (45 cm) thick. In some places it lensed out entirely so that level 3 rested directly on level 5.

(d) Level 5. A green-yellow clay with one or more ferruginous bands and several thin horizontal seams of fine-grained white tuff near the base. Artifacts and bones were more plentiful at the top of the deposit than in the lower part, though the surface did not seem so weathered as on the occupation floors of FLKNN I and FLK I.

(e) Level 6. A dark grey-brown silty clay with white streaks, 1½ ft (45 cm) thick. The deposit is mostly overlain by a massive layer of limestone, several feet thick, so only a part has been excavated. An elephant had been butchered at this level.

All the levels of FLKN I were contorted and faulted on a local scale, with displacements of a few inches, and all yielded cultural and faunal remains. The site was excavated by a series of trenches; a trial trench and trenches I and II were dug in 1960, trench III in 1961 and trenches IV and V in 1962. The lowest part of the site was 5 ft (1·5 m) below Tuff IF and thus 15 ft (4·5 m) above level 22 (the occupation or '*Zinjanthropus*' level) of FLK I.

Tribe TRAGELAPHINI. This tribe is represented by a right mandible 7634 from levels 1–2; associated incomplete maxillae right 6061 and left 6060, left upper molar 067/21, right lower molar 6170 and right and left upper premolars 067/368 from level 3; left mandible 882 from levels 1–3; right mandible 1182, right upper molar 067/182 and left upper molar 6225 from level 4; immature left mandible 7846 from level 5. The teeth are close to the size of the greater kudu and these dentitions are presumably *Tragelaphus strepsiceros maryanus*. The mandible 7634 is fairly complete and has a tooth row and horizontal ramus the same size as in mandibles DK I 3001 and FLK I 067/1100. An unworn left P_3 from level 1–3, and an unworn left upper molar 067/170, right upper premolar 067/238, left upper premolar 067/228, right lower premolar 067/237 and deciduous right upper premolar 067/4774, all from level 6, are more doubtfully assigned to this tribe.

The proximal end of right radius with ulna 7686 and proximal end left radius 8379 from levels 1–2; proximal end left metacarpal 825 from levels 1–3; complete left metacarpal 9269 from level 4; distal end left humerus 9292, complete left radius 9290, proximal end left radius with ulna 10199, complete left metacarpal 067/1073 and complete right metatarsal 7333 from level 5; and associated complete left humerus 8248, complete left radius 8275, left ulna 8249 and proximal end left metacarpal 8250 from level 6 are all assigned to the Tragelaphini but are rather small to be *T. s. maryanus*. The proximal ends of radii 7686 and 8379 have projecting anterior points on the lateral facets, unlike the other tragelaphine radii. The distal end of a right femur 10227 from level 5 is relatively smaller than the other bones.

Tribe Bovini. Ten isolated teeth belong in this tribe. These are associated left P_3, P_4, M_1 and four incisors 1567, and left lower molar 171 from levels 1–2; left P^2 067/226 and right P^3 067/227 from level 6. Their occlusal morphology is about as simple as that of *Pelorovis oldowayensis* but they are smaller than *P. oldowayensis* or buffalo species. On the P_4 1567 the paraconid and metaconid are growing towards one another, but there is no actual fusion to form a complete medial wall anteriorly. In this respect the tooth is less advanced than in *P. oldowayensis* or living *Syncerus caffer*.

By its size and low distal condyles the distal end of a metacarpal 437 from levels 1–2 is bovine and probably belongs to the same species as the teeth.

Tribe Reduncini. Deciduous left P^3 and P^4 067/336 from level 3 are reduncine and of a size appropriate for *Kobus sigmoidalis*, although attribution to *K. ellipsiprymnus* is possible for such pieces as noted above (p. 327). A right lower molar 067/185 from level 4 is smaller and probably of *Redunca*.

Tribe Hippotragini. On the evidence of left lower molar 067/4778 from level 6 and complete right metacarpal 5152 from level 4 a member of this tribe is present. A right M_3 and part of another lower molar 7122 from level 4, complete left tibia 7207 from levels 1–2, proximal end left tibia 7797 and proximal end right metatarsal 7097 from level 3, and immature left radius 1800 and complete left tibia 1450 + 1459 from level 5 are possibly also hippotragine. The proximal end of left femur 896 from levels 1–3 is identified as belonging in this tribe or possibly in the Bovini.

Tribe Alcelaphini. This tribe is represented by 39 horn cores and skull pieces, 31 adult and 14 immature partial dentitions and many teeth and limb bones. Thirty four of the horn cores and skull pieces are of *Parmularius altidens* and the majority of the alcelaphine remains can confidently be referred to this species. The cranial pieces of *P. altidens* are as follows.

An associated pair of complete horn cores with most of a crushed cranium and the parietal boss 8065, part of a cranium consisting of the parietals with parietal boss, the occipitals and basioccipital 7465, an immature frontlet with the basal halves of both horn cores 1315 P.P.F.15 (Leakey 1965 : 58; pl. 73), a parietal boss 067/9 and a possibly immature horn core 637 from levels 1–2; the base of a right horn core with the midfrontal suture and part of the orbital rim 1166 P.P.R.8, an incomplete frontlet with partial horn cores 1392, complete left horn core 1410 P.P.R.6 (Leakey 1965 : pl. 74 which is not FLK I 206), complete right horn 5123, parietal boss 6174, frontlet with both horn core bases and the parietal boss 10130, and a frontlet with the parietal boss, complete left horn core and base of the right 10160 from level 3; a partial cranium consisting of the parietal with parietal boss and bases of both horn cores, the occipital, occipital condyles and paraoccipital processes 178 + 979 P.P.R.11 (Leakey 1965 : 59(e)), left horn core 067/267, and parietal bosses 858 and 067/244 from levels 1–3; the basal half of a right horn core with part of the orbital rim 1775, base of a left horn core 1777, a partial frontlet with the right horn core 8129, and parietal bosses 067/245 and 067/247 from level 4; a frontlet with complete horn cores 9401, a frontlet with horn core bases and parietal boss 10220, base of a right horn core 10279, base of a horn core 7814, part of a horn core 067/268, and parietal bosses 7869 and 067/253 from level 5.

The horn cores at this site differ from the complete specimens known from FLK I in having a smaller basal swelling and the tips still less backwardly curved. There is a certain amount of variability among the horn cores; 1410 P.P.R.6 and 9401 are rather long, while 1410 P.P.R.6, 5123 and 10160 show little backward curvature in side view. Parts of horn cores 485 and 9108 from levels 1–2, 7516 from level 3, 695 and 990 from levels 1–3, and 7329 and 9371 from level 5 probably belong to *P. altidens*.

The more complete dentitions assigned to *P. altidens* are as follows.

Left maxillae 1037 and 1604, right mandibles 208, 1109, and 8045 and left mandible 1099 from levels 1–2; left maxilla 1155 and associated right and left maxillae 1136, right mandibles 1406, 1728, 5167, 8115 and 10144 from level 3; right mandibles 208, 211, 340 and 824 + 841, and left mandibles 21, 38 and 265 from levels 1–3; right mandible 5175, left mandibles 1179 and 067/184 and associated right and left mandibles 1198 from level 4; right maxillae 9383 and 067/79 and left maxilla 10209 from level 5. The above dentitions are all adult. There are also a number that are immature. These are right mandible

7685 and left mandible 1589 from levels 1–2; right maxilla 5008, left maxilla 1138, and right mandibles 6111, 7733 and 7775 from level 3; left maxilla 430, right mandible 706 and left mandible 405 from levels 1–3; right mandible 1746 from level 4; right mandibles 6269 and 10212 from level 5; left mandible 9476 from level 6.

These dentitions are all of *P. altidens* size and are slightly smaller than the living hartebeest. Mandible 1109 lacks an alveolus in the jaw for a P_2 so that P_2 was missing in life, and P_2 was probably also missing in mandible 265. The presence or absence of P_2 in mandible 1406 is uncertain, but in mandibles 38, 208, 1198 (right) and probably 1728 P_2 or its alveolus is still present. Deciduous P_2 is present on the immature mandibles 1746, 7775, 9476 and 10212. A number of isolated alcelaphine teeth also belong to *P. altidens.*

Only the complete limb bones of *P. altidens* are listed here although there are many other, more fragmentary, remains at this site.

The limb bones are right humeri 7070 and 067/515, left humerus 260, right radii 2+57, 688 and 067/4741, left radius 1046, right metacarpals 51, 404, 1291 and 8836, left metacarpals 1053 and 8044, left tibiae 7074 and 7084 and right metatarsals 88, 99+100, 1265, 1266 and 1347 from levels 1–2; left radius 7779+7780, right metatarsals 5002+5019 and 6191 and left metatarsals 1120, 6201 and 10168 from level 3; right metacarpal 749, left metacarpals 639, 965 and 973, right metatarsal 067/1076 and left metatarsals 657 and 811 from levels 1–3; right metacarpals 1776 and 5107 and left metatarsals 8128 and 8141 from level 4; right metacarpals 7853 and 8157, left metacarpals 5195 and 8196, right metatarsal 5135 and left metatarsals 7867 and 9342 from level 5; and left radius 8247 and left metacarpal 10440 from level 6.

A cranium of *Connochaetes* sp. with complete horn cores 7154 comes from level 5. The horn cores are dorsoventrally compressed but less so than in living male wildebeests, and there is less tendency for a keel to be developed along the anterior edge. The horn core insertions are wide apart and lie between the orbits and the occipital top instead of at the occipital top. As the horn cores pass outwards they bend less downwards and slightly backwards, and the tips turn upwards but less inwards than in most *C. taurinus.* There are transverse ridges on the middle part of the top surface of the horn cores. The basioccipital is as found in the living species. A few teeth were found in association with the cranium. These are two left upper molars, a right upper molar and right upper premolar, a damaged upper premolar and an incisor or incisiform canine. They correspond in size with the smaller teeth of the Bed II size group (i), which are supposedly of *Connochaetes,* and are smaller than the very large teeth from DK I which are taken to belong to *Megalotragus.*

A partial left maxilla 9382 and immature left maxilla 067/240 from level 5, and an incomplete left mandible 1431 from level 4, are larger than dentitions of *Parmularius altidens* and are possibly of *Connochaetes.*

A right metacarpal 5107 from level 4 is alcelaphine but not of *Parmularius altidens* since it is shorter and the distal condyles are too low and wide in anterior view; its shortness contrasts with the very long radius and metapodials of *Megalotragus ? kattwinkeli* at DK I, and it could well belong to *Connochaetes.*

A complete left horn core, 5123 from level 3, is of *Beatragus antiquus.* It is longer and thicker than horn cores on a Recent skull of *B. hunteri* with a sheath length of 600 mm and a horn core length of 480 mm. It has marks made by the grubs of a moth allied to or identical with *Ceratophaga vastella.* The basal half of a right horn core of *B. antiquus* 7132 comes from the surface of level 5.

A few alcelaphine limb bones are larger than those of *P. altidens.* These are the distal end of immature right radius 393+345, incomplete proximal end left femur 9058, distal end right femur 8704 and proximal end right metatarsal 7042 from levels 1–2; distal end right humerus 5036 and distal ends right tibiae 7101 and 9180 from level 3; associated distal end right humerus 927 and complete right radius 181+926 from levels 1–3; complete left metatarsal 8127 and proximal end right metatarsal 5087 from level 4; proximal end right radius 7844 and proximal end left radius 1225 from level 5. Probably none of these limb bones are from a species so large as the largest alcelaphine at DK I. It seems likely that they belong to *Connochaetes* sp. and *Beatragus antiquus.*

A horn core 7884 from level 6 and a horn core with a crushed braincase 5196 P.P.R.10 from level 5 could be of a small alcelaphine. The horn cores are very compressed, long and spiralled and have not been found at any other site. They are described more fully on p. 418 as Alcelaphini sp. 4. Two mandibles with complete horizontal and vertical rami but both lacking teeth, right 1293 from levels 1–2 and left 137 from levels 1–3, could perhaps be conspecific although there is no association with the horn cores. They agree well with two other Olduvai mandibles, left 1941 F.109 from the surface of Bed I and left 1941 F.102 from the surface of Bed II, which have more complete tooth rows.

Some small limb bones from levels 1–2 are probably small Alcelaphini rather than large Antilopini. These are proximal end right radius with ulna 84, distal end left radius 8778, proximal end right femur 8809 and proximal end left femur 233. Perhaps they are conspecific with the horn cores 7884 and 5196.

Tribe NEOTRAGINI. A pair of horn cores 10229 from level 5, with a small part of the frontal preserved, are tentatively placed in this tribe.

Tribe ANTILOPINI. *Antidorcas recki* is represented by a number of skull pieces. These are a frontlet with the bases of both horn cores 1039 (figured as Reduncini by Leakey 1965 : 47; pl. 53), frontlet with complete right horn core and base of the left 1307 (Leakey 1965 : 65(h)), base of right horn core with the frontal 1650, left horn core 7266 with associated maxillae and mandibles, right horn core with the midfrontal suture and supraorbital pit 8659 and base of a horn core 10008 from levels 1–2; left horn core with the midfrontal suture, top of the orbital rim and an unusually large supraorbital pit 1139 (Leakey 1965 : 65(g); Gentry 1966 : 104(g)) from level 3; the occipital and basioccipital region of a skull 067/257 from levels 1–3; crushed skull with both horn cores and maxillae 6334 (Leakey 1965 : 65(i); Gentry 1966 : 58; pl. 1B), left horn core with the midfrontal suture, top of the orbital rim and supraorbital pit 8194 with several associated limb bones, crushed skull with maxillae 067/466, complete right horn core 067/250 (Gentry 1966 : 78; pl. 7A) and parts of horn cores 6173 and 10284 from level 5.

Several dentitions, mostly incomplete, belong to this species. They are as follows.

Right maxilla 9055, left maxillae 7426 and one without number, right mandibles 7015 and 8532, left mandibles 8711, 067/400, 067/434, 067/453 and 067/462, and associated right 1045 and left 1044 mandibles from levels 1–2; right maxilla 618, left maxilla 1152, and right mandibles 6010 and 6044 from level 3; right maxilla 871, left maxillae 627 and 067/463, right mandibles 681, 935 and 067/26, and left mandibles 503, 914, 976 and 067/465 from levels 1–3; right mandible 5148 and left mandible 8136 from level 4; palate 7555, left maxillae 7564 and 10286, right mandibles 7332, 7554 and 9377, and left mandibles 1211 and 7873 from level 5. A left maxilla 067/464 is known only to be from levels 1–5. These are all adult dentitions. There are also a few immature dentitions. These are right maxilla 1281, left maxillae 1327 and 1511 and an associated pair of mandibles 1310 from levels 1–2; left mandible 9196 from level 3; left mandible 231 from levels 1–3; and left maxilla 6176 and right mandibles 7828 and 067/74 from level 5.

A P_2 is present on mandible 9377, and on 6010, 7015, 7873 and 067/453 there is an alveolus for a P_2 although the tooth itself is now missing. Mandible 976 has a very reduced P_2 (Gentry 1966 : 61). The presence or absence of P_2 on 8532 is uncertain. Deciduous P_2s are present on the immature mandibles 231, 1310 (right and left) and 7828, and there is an alveolus in the jaw for deciduous P_2 on 067/74.

The pair of maxillae 7266, together with right 7284 and left 7266 mandibles of the same individual, which belong with the left horn core 7266 from levels 1–2 listed above, are of interest because the right maxilla provides the first nearly complete facial region of *A. recki* to occur in Bed I. From this specimen it can be seen that the face is larger than in males of living *Gazella thomsoni*. The preorbital fossa has an upper rim and more marked lower rim as in all Antilopini, and is as small in area as in *G. dorcas*. It is, however, less deep, and is also less deep than in the *A. recki* holotype skull. The fossa is probably larger than in the living springbok, but the face larger in size than in gazelles coupled with a small fossa are definitely resemblances to springbok. The mandibles would have had a P_2 in life, but in both cases the tooth is now missing.

There are a number of isolated antilopine teeth which are assigned to *A. recki*, but they will not be listed here.

A complete right maxilla 1662 from levels 1–2 (Pl. 40, fig. 6; Gentry 1966 : 59; pl. 1C) and some isolated teeth are possibly large enough to represent a larger species of Antilopini in Bed I. The isolated teeth are a right upper molar 8594, a left upper molar without number, right lower

Table 4 Numbers of bovid bones at FLKN I

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Levels 1+2+3								
Tragelaphus s. maryanus	–	2	2	4	–	8	2	–
Smaller tragelaphine sp.	–	–	–	–	4	4		
Syncerus acoelotus	–	–	–	8	1	9	1	–
Kobus sigm./ellipsiprymnus	–	–	–	2 (2)	–	2	–	1
Beatragus antiquus	1	–	–	–	–	1	1	–
Larger alcelaphine sp.	–	–	–	–	9 (1)	9	2	1
Parmularius altidens	20 (2)	8 (3)	20 (6)	100 (5)	266 (9)	414	22	5
Alcelaphini sp. 4?	–	–	2	–	4	6	1	–
Alcelaphini total	21 (2)	8 (3)	22 (6)	100 (5)	279 (9)	430	25*	6
Antidorcas recki	8	13 (3)	24 (4)	57 (2)	191 (4)	293	18	5
Larger antilopine sp.	–	1	–	10	–	11	2	–
Antilopini total	8	14 (3)	24 (4)	67 (2)	191 (4)	304	18	5
? Caprinae sp.	–	–	–	–	3	3	1	–
Level 4								
Tragelaphus s. maryanus	–	–	1	2	–	3	1	–
Smaller tragelaphine sp.	–	–	–	–	1	1		
Kobus sigm./ellipsiprymnus	–	–	–	2	–	2	1	–
Redunca sp.	–	–	–	1	–	1	1	–
Hippotragini sp.	–	–	–	–	1	1	1	–
Connochaetes sp.	–	–	1	–	1	2	1	–
Larger alcelaphine sp.	–	–	–	–	2	2	1	–
Parmularius altidens	5	–	6 (1)	17 (3)	37	65	5	1
Alcelaphini total	5	–	7 (1)	17 (3)	40	69	6†	1
Antidorcas recki	–	–	2	19	10 (1)	31	2	1

* One of the two adult individuals represented by the larger alcelaphine limb bones could be the *Beatragus antiquus* and has been omitted.
† The individual represented by the larger alcelaphine limb bones could be the same as the *Connochaetes* sp. and has therefore been omitted.

Table 4 (*cont.*)

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Level 5								
Tragelaphus s. maryanus	–	–	1 (1)	–	–	1	–	1
Smaller tragelaphine sp.	–	–	–	–	7	7	2	–
Connochaetes sp.	1	2 (1)	–	6	–	9	2	1
Beatragus antiquus	1	–	–	–	–	1	1	–
Larger alcelaphine sp.	–	–	–	–	2	2	1	–
Parmularius altidens	9	3	2 (2)	15	27	56	5	1
Alcelaphini sp. 4	1	–	–	–	–	1	1	–
Alcelaphini total	12	5 (1)	2 (2)	21	29	69	7‡	2
? Neotragini sp.	2	–	–	–	–	2	1	–
Antidorcas recki	6	8 (1)	7 (2)	80 (1)	69 (2)	170	14	2
? Caprinae sp.	–	–	–	–	1	1	1	–
Level 6								
Smaller tragelaphine sp.	–	–	–	–	4	4	1	–
Syncerus acoelotus	–	–	–	2	–	2	1	–
Hippotragini sp.	–	–	–	1	–	1	1	–
Parmularius altidens	–	–	1 (1)	10	12 (1)	23	3	1
Alcelaphini sp. 4	1	–	–	–	–	1	1	–
Antidorcas recki	–	–	–	12	11 (1)	23	2	1

‡ The individual represented by the larger alcelaphine limb bones could be the same as the *Connochaetes* sp. or *Beatragus antiquus* and has been omitted from this total.

molar 8712 and right M_3 067/427 from levels 1–2; right upper molars 121 and 067/34, left upper molars 122 and 067/24 and right P^3 and P^4 183 from levels 1–3.

Several small limb bones found in level 5 were associated with the horn core 8194. These are complete left humerus 8191, distal end left humerus 8186A, complete right radius 8179, proximal half left radius with ulna 8188, complete left metacarpal 8192, distal half metacarpal 8193, complete right tibia 8180, head of left femur 8186, complete right metatarsal 8178, complete left metatarsal 8183, right scapula 8181, left scapula 8184, right astragalus 8187 and some other foot bones. Since there are parts of two left humeri more than one individual is represented.

Apart from the associated collection, only the complete antilopine limb bones at this site are listed, as follows.

Right humerus 7276, left humerus 7213, associated right 1010 + 1041 and left 1300 radii, left radius 1605 with some associated footbones, right metacarpals 7029, 7368, 7448 and 10034, left metacarpals 1273, 1306, 7064, 7406 and 7671, associated right 1246 and left 1284 tibiae, and right metatarsals 7017, 7371 and 8737 from levels 1–2; left radius with ulna 6049, right metacarpals 7781 and 067/1168, left metacarpals 6050, 7782 and 7784, right metatarsal 6198, and left metatarsal 5000 from level 3; associated right 50 and left 70 radii with ulnae, left radii 666 (with ulna), 682 and 730, left metacarpals 655, 762 and 764, left tibia 157, right metatarsal 464 and left metatarsals 3, 179 and 530 from levels 1–3; right humerus 10263, left humerus 8191, right radii 8179 and 067/4787, right metacarpals 1450 and 7540, left metacarpal 8192, right tibia 8180, right metatarsals 1454, 1758, 5194, 8178, 9369, 10230 and 10232, and left metatarsals 8183, 9372, 10288 and 10289A from level 5; right femur 8256, and associated left tibia 8264 and right 8263 and left 8259 metatarsals from level 6.

These bones are presumably all of *A. recki*, and show considerable variation in size (Pl. 39, fig. 3). The largest limb bones referred to the Antilopini, for example the proximal end of left femur 1027 from levels 1–2, are still slightly smaller than the small alcelaphine limb bones (p. 19) found at this site.

The proximal ends of two radii from levels 1–2, right 7725 and left 7066, are of normal antilopine size but possibly belong to a very small alcelaphine because the rear part of the lateral facet is far forwards.

Subfamily ? CAPRINAE. A right metatarsal 067/1009 from level 3, a left metatarsal 068/6665 from levels 1–3, and a left metacarpal 9394 from level 5 are complete and very short. We can only suggest that they may represent some species of caprine. The distal end of a left tibia 7243 from levels 1–2 may belong with the metapodials.

SUMMARY. Site FLKN I is all but overwhelmed by *Parmularius altidens* and *Antidorcas recki*, the first being more abundant in levels 1–4 and the second in levels 5 and 6. There is also evidence of *Connochaetes* sp. and *Beatragus antiquus*, but *Megalotragus* has not been found. A few tragelaphine fossils are present, but reduncines and hippotragines are almost absent. A *Redunca*-sized tooth occurs.

The species list for the site is:

Tragelaphus strepsiceros maryanus (may include the rather small limb bones)
Syncerus acoelotus
Kobus sigmoidalis/*ellipsiprymnus*
Redunca sp.
Hippotragini sp.
Connochaetes sp.
Beatragus antiquus
Parmularius altidens
Alcelaphini sp. 4
? Neotragini sp.
Antidorcas recki
(Also large teeth perhaps of a second antilopine species)
? Caprinae sp.

The numbers of bovid bones in levels 1–6 are shown in Table 4.

HWK I

Site (46) Geologic locality 44

Tribe Alcelaphini. A well-preserved left side of a braincase with almost complete left horn core 068/6650 was found at this site in 1962 (Pl. 20, fig. 1). It is marked '*In situ* top of Bed I near *Deinotherium* skeleton'. It belongs to *Parmularius altidens.* The mid-dorsal part of the braincase is unfortunately not preserved to show the condition of the parietal boss. The horn core is obliquely inserted and bends very slightly backwards as in advanced *P. altidens* and in *P. angusticornis.*

Other HWK sites are discussed below (p. 24).

Other remains from Bed I

Apart from material collected before the Second World War and mostly housed in London, some bovid remains from Bed I have been found later as isolated occurrences or at archaeological sites with little fauna.

Tribe Hippotragini. The female paratype cranium of *Hippotragus gigas*, 1957.56 P.P.T.3, came from VEK at the top of Bed I.

Tribe Alcelaphini. Part of a right horn core of *Beatragus antiquus* was found at MJTK in 1963. The base of a left horn core 1959.129 of *Aepyceros* was found at THC at a horizon equivalent to DK I. The horn core is marked 'MTK I'. Impala horn cores from BK II and the surface of SHK II have been identified as *A. melampus*, and the THC horn core cannot be separated from them at species level. However, it has yet to be established whether the impala at this level is the same as the living species.

Tribe Antilopini. A right horn core THC I 068/6656 of *Antidorcas recki* was a surface find in 1962. The midfrontal suture, supraorbital pit and part of the orbital rim are preserved.

Sites of uncertain stratigraphic position within Beds I and II

FLKN Ostrich Site

Site (39)

This site is of uncertain stratigraphic position. At present it is thought to be a Bed II deposit which has slumped into Bed I, or possibly it was originally Bed I. It has yielded some artifacts, ostrich and crocodile remains and fragmentary bovids.

Tribe Tragelaphini. An immature left mandible with deciduous P_4, M_1 and M_2 342, part of a right upper molar 288, left lower molar 350, part of a lower molar 287, right P_4 312, left P_4 311 and right P_3 346 belong in this tribe.

Tribe Hippotragini. A right upper molar 355 and a right M_3 354 are both hippotragine.

Tribe Reduncini. A right upper molar 290 probably belongs in this tribe and is of the size of the *Kobus sigmoidalis/ellipsiprymnus* lineage.

Tribe Alcelaphini. A mandible 067/243 with M_1 to erupting M_3 and erupting P_3 and P_4 lacks an alveolus in the jaw for a P_2. Some isolated teeth also belong in this tribe. These are right upper molars 291 and 292, left upper molars 356 and 067/175, part of upper molar 289, parts of lower molars 351 and one without number, parts of right M_3s 294 and 298, left M_3s 248 and 297, part of left M_3 290 and right lower premolar 309. They are all of medium, not large, size.

A complete left metacarpal 275 and proximal end of a right radius are the size of *Connochaetes* or *Megalotragus.* The distal end of a left tibia 219 is rather small for *Parmularius altidens.*

Tribe Antilopini. A right lower molar 306 and left lower molars 352 and 369 belong in this tribe. A complete right metacarpal 276, distal end of a metacarpal 365, damaged distal end of a metacarpal 366, distal end of a metatarsal 277 and distal end of a left radius 304 are also antilopine.

KK

Site (49) Geologic locality 42

A number of fossils were recovered from KK in 1959. They came from Beds I and II, but it was difficult to determine the levels in relation to the stratigraphic sequence elsewhere in the Gorge. M. D. Leakey (1971b : 287) concludes that the Bed II fossils originate from middle Bed II.

Tribe TRAGELAPHINI. A cranium 068/5813 of *Tragelaphus strepsiceros maryanus* is the most interesting bovid at KK, supposedly from Bed II. If it were from middle Bed II it would supplement the evidence of a tooth at HWK EE II that *T. s. maryanus* survived the end of lower Bed II. However, Leakey (1965 : 42) stated that it came from Bed I. It has been omitted from Table 12 (pp. 56–7).

Tribe BOVINI. A right astragalus, 211 from Bed II, is large enough to belong to *Pelorovis oldowayensis*.

Tribe ANTILOPINI. A horn core of *Antidorcas recki*, 309 from Bed I, has strong mediolateral compression, and agrees closely with two horn cores from HWK II and HWK EE II. *Gazella* sp. is represented by 310 from Bed I and 224 from Bed II. The former is a female horn core and the latter a horn core tip. Proximal and distal metatarsal pieces 248 and 249 from Bed I belong to a gazelle-sized species, but the proximal end shows some non-antilopine characters (Gentry 1966 : 73).

Sites in Lower Bed II

HWK Sites

The HWK gullies lie to the south of the confluence of the Main and Side Gorges and were first located in 1931. They originate from a saddle connecting two pinnacles capped with Beds III and IV which are known as the 'Castle' and the 'Tower'. HWK Main or Castle is a long, narrow gully running northwards from the saddle down to the floor of the Gorge; excavations in lower Bed II took place in 1959–60. HWK East is a gully beginning at the saddle and running mainly eastwards for ¼ mile (0·4 km), then northwards to drain into the Main Gorge; excavations in lower Bed II and the lower part of middle Bed II were carried out in 1962–63. In the whole of the HWK area the Upper Member of Bed I is represented only by the upper series of deposits since the underlying basalt rises in irregular hummocks to within 20 ft (6·0 m) of Tuff IF. (For HWK I see above, p. 23.)

HWK II

Site (46) Geologic locality 44

Tribe REDUNCINI. An almost complete right mandible 451 and a right M_3 455 are of *Kobus sigmoidalis* size. The distal end of a reduncine left radius 414 is also comparable in size with the Bed I reduncine. Presumably they belong to the *K. sigmoidalis/ellipsiprymnus* lineage.

Tribe ALCELAPHINI. Three horn cores from this site belong to a species which may be related to *Parmularius rugosus*. These are a complete right horn core 067/5523, a complete left horn core 58 and the distal half of a right horn core 54.

A right mandible 477, right upper molar 454, left upper molars 452 and 551, right lower molar 456 and left lower molar 453 are alcelaphine. They are the size of Bed I *Parmularius altidens*.

A few limb bones are alcelaphine. The proximal ends of right radii 413 and 415, distal end right radius 411, distal end left radius 418, proximal end left metacarpal 426 and distal ends left tibiae 402, 403 and 405 are probably all *Parmularius*. The proximal end of right radius 412 and distal ends of right radii 409 and 410 are larger and probably *Megalotragus kattwinkeli* or *Connochaetes*.

Tribe ANTILOPINI. Four horn cores are of *Antidorcas recki*. These are a right horn core without the base 473, a complete left horn core with the frontal suture, orbital rim and supraorbital pit 568, the base of a left horn core with the frontal and supraorbital pit 471 and a complete right horn core 472 which is small, transversely compressed and possibly female (Gentry 1966 : 57, 64). 473 and 568 resemble Bed I *A. recki* horn cores.

A few limb bones are antilopine and probably belong to *A. recki*. These are distal end right humerus 408, proximal end right radius 417, distal end left radius 416 and distal end metatarsal 423.

HWK East II

Site (48) Geologic locality 43

Three parallel trenches were cut into the northern side of the HWK East gully and the sequence of deposits, from above downwards, was as follows.

(a) A thick deposit of red-brown and grey tuffs with some minor clay horizons. The top was some 30 ft (9·0 m) above the base of Bed II.

(b) Level 5. A reworked tuff, 1–2 ft (30–60 cm) thick, with lenses of unconsolidated coarse grey sand in hollows in the surface of the underlying sandy conglomerate. It yielded fragmentary faunal remains, including two teeth of *Pelorovis oldowayensis*.

(c) Level 4. The sandy conglomerate, a chert-bearing horizon about 2 ft (60 cm) thick and its lower surface some 8 ft (2·4 m) above the base of Bed II. The same horizon occurs at FLKN II. It yielded a few rolled animal bones.

(d) Level 3. A buff-grey reworked tuff, 9 ins–2 ft (23–60 cm) thick, with sparse animal remains. Antelope material from levels 3, 4 and 5 is treated as a single unit.

(e) Tuff IIA, the Lemuta Member. The tuff is aeolian and very thin in this area, occurring in depressions on the surface of level 2.

(f) Level 2. About 5½ ft (1·65 m) of light brown clay containing many root casts and a horizontal band of limestone nodules some 2 ft (60 cm) from the base. This level corresponds to the clay with root casts at FLKN II. Artifacts and faunal remains were scattered throughout the clay but were more concentrated near the base and midway. The bones were more plentiful and better preserved than in any other level at this site. The horizon was subdivided at the time of excavation but is now treated as a single unit.

(g) A coarse-grained grey tuff with rootlets sometimes occurred between levels 1 and 2. It occurred also at FLKN I and elsewhere in the HWK gullies.

(h) Level 1. A palaeosol on the surface of an irregular horizon of brown silty clay filling depressions in the surface of Tuff IF. This appeared to be a hominid occupation floor. Faunal remains were scarce and fragmentary. Tuff IF had undergone erosion in this area before the deposition of the clay.

HWK East II Levels 1 and 2

Tribe Tragelaphini. The holotype of *Tragelaphus strepsiceros maryanus* was found in level 2 (M. D. Leakey, personal communication) of this site in 1959 (Leakey 1965 : 40; pls 40–41). This cranium is now in the National Museum of Tanzania in Dar es Salaam. A small piece of horn core, 4038 found in level 1 in 1963, has the keel and open spiral of the kudus and may also be *T. s. maryanus*. The spiral is anticlockwise, so the piece is probably from the right side.

A few teeth and limb bones are identified as tragelaphine. These are right upper molar 990, part of an upper molar 767, left lower molars 251b and 976, a P_3 probably of the right side 067/1792, left P_3 766, deciduous left P_3 3819, deciduous left P_4 3819b, distal end of a metacarpal 230 and distal end of a left femur 3778. These are all from level 2. The metacarpal distal end is of a size appropriate for *T. s. maryanus*, but the femur distal end may be too small.

Tribe Bovini. Half a right upper molar 067/1812 from level 1, and a left upper premolar 067/1855 from level 2, are probably bovine and could belong to *Syncerus acoelotus*. They are too small for *Pelorovis oldowayensis*. The proximal end of a right metatarsal 2083 from level 1 is probably bovine.

Tribe Reduncini. Four isolated teeth from level 1 are reduncine and the size of *Kobus sigmoidalis*. These are left upper molar 4088, right lower molar 79, left lower molar 142 and part of right M_3 136. Similar teeth in level 2 are a left upper molar 703 and a damaged deciduous left P_4 3819. Presumably they are from the *K. sigmoidalis/ellipsiprymnus* lineage.

Tribe Hippotragini. Right upper molar 835, right lower molars 251c and 705 and a well worn left P_4 3819a belong in this tribe and are presumably *Hippotragus gigas*. They are all from level 2.

Tribe Alcelaphini. A horn core, 131 found in level 1 in 1962, is most likely to be a female of *Beatragus antiquus*. It is shown to be of the right side by a small part of the orbit and a shallow postcornual groove. Its upright insertion and course agree closely with other specimens from

Olduvai. A well-preserved frontlet S.217 of the same species was found in 1971 *in situ* in the rootlet clay of level 2.

A horn core tip 891 from level 2 is very like the type A horn cores from BK II tentatively assigned to *Damaliscus niro*, but is less mediolaterally compressed. A horn core tip 980 also from level 2 could possibly be the same undetermined species.

There are a number of alcelaphine dentitions. These are incomplete right maxillae 520, 2193 and 3942, right mandible 128, left mandibles 168 and 3983 and immature left mandible 25 from level 1; left mandible 2895, immature right maxilla 711, immature right mandible 1059 and immature left mandibles 455 and 1050 from level 2. These dentitions have the size and morphology of *Parmularius altidens*. Mandibles 25, 168 and 455 have the horizontal ramus almost entirely preserved, and in 128 and 3938 enough is present for it to be clear that in all five mandibles the ramus is deep under the teeth (Pl. 37, fig. 6), and in this respect they resemble *Connochaetes*. The teeth, however, are too small relative to this jaw size for *Connochaetes*. It is probable that the dentitions belong to some species of *Parmularius*. Somewhat smaller mandibles with deep horizontal rami are known from size group (ii) dentitions at BK II. Mandibles 168 and 3938 have P_3–M_3 preserved and no alveolus in the jaw for a P_2, while enough of the jaw of 128 is preserved to show that there is again no alveolus for a P_2. Immature mandible 25 has no alveolus for a deciduous P_2 and at this early stage P_2 is already missing. Maxilla 3942 has a very reduced P^2.

Several isolated teeth are alcelaphine. These are as follows; the teeth are mostly the same size as those of the more complete dentitions, and no attempt will be made to assign them to species.

Right upper molars 513, 2121, 3914, 4059 and 4072, left upper molars 78, 141, 514, 2154, 4065, 067/1795, 067/1796, 067/1798 and 067/1800, part of an upper molar 4036, right lower molars 4090 and 067/1803, left lower molars 4073, 067/1804 and 067/1806, right M_3 26, parts of two molars numbered 067/1809, left P^4 4089, left P_4s 564 and 067/1799, and deciduous left P^4 067/1802 from level 1; right upper molars 251a, 587, 590, 888, 920a, 920b, 981, 067/1853 and 067/1857, left upper molars 576, 577, 586, 589, 787, 945, 965 and 067/1778, right lower molars 692 and 974, left lower molar 067/1775, two lower molars numbered 920, part of a lower molar 920b, right M_4 251a, left M_3s 251, 579 and 920b, left upper premolar 251a, and left P_4s 712 and 2328 from level 2. A right upper molar 067/1765, left upper molar 067/1781, left lower molar 067/1771, right upper premolar 067/1786, left upper premolar 067/1774, and deciduous left P^4 067/1777 are either from level 1 or level 2.

Nearly all the alcelaphine limb bones are the size of Bed I *Parmularius altidens* or possibly a little larger. They could belong to *P. altidens*, or *P. altidens* at a stage transitional to *P. angusticornis*, or more probably to the species from various levels in the HWK area which has resemblances to *P. rugosus*.

The limb bones from level 1 are complete left humerus 82, distal ends right humeri 17, 63, 1097 and 3894, distal end left humerus 72, complete right radii 14 and 58, proximal ends right radii 124, 214 and 4052, proximal ends left radii 59 and 87, distal end left radius 2201, right ulnae 175 and 3867, left ulna 19, associated complete left humerus 1098, complete left radius 1099 and left ulna 2173, complete right metacarpal 1093, complete left metacarpals 66 and 67, immature right metacarpal 2038, distal end metacarpal 2020, complete right tibia 2002, almost complete left tibia 2162, distal ends right tibiae 2170, 4002 and 4008, distal ends left tibiae 68 and 2208, proximal end right femur 2132, proximal end left femur 532, almost complete right metatarsal 3974, proximal ends right metatarsals 61, 71, 2175, 3969, 4034 and 4110, shaft of right metatarsal 4009, proximal end left metatarsal 2035 and distal ends metatarsals 2096, 3863 and 3966. From level 2 there are distal end left humerus 3782, proximal end right radius 958, proximal end left radius 1054, associated complete right humerus 935 and complete right radius 936, immature left metacarpals 62+83 and 1063+1067, proximal end right metacarpal 930, distal ends metacarpals 452, 1019 and 1045, distal end left tibia 1076, proximal end right metatarsal 1056, proximal end left metatarsal 1088, and distal end metatarsal 1047.

A few limb bones belong to a larger species, perhaps *Megalotragus kattwinkeli*. The bones are less common than at some sites, DK I for instance, and the only pieces are a complete right radius 3886, distal end metacarpal 2081, distal end left tibia 4020, complete left metatarsal 2053 and proximal end right metatarsal 2026 from level 1, and a complete right metatarsal 067/4691 from level 2. The radius is the size of the large radius 166 at DK I, and the complete metatarsals are unlike *Connochaetes* in their great length.

The distal end of a left radius 2100 from level 1 is intermediate in size between the smaller limb bones and those of the larger species. A complete left metacarpal 2176 from level 1 is of a species smaller than *P. altidens*. To it may belong the proximal end of left metacarpal 3910 and distal end of metacarpal 3857 from level 1, and distal end of metacarpal 236 from level 2. These are about the size of the small alcelaphine limb bones at FLKN I, and in Table 5 (p. 28) they have been doubtfully referred to Alcelaphini sp. 4. The distal ends of alcelaphine tibiae at this site are less indented at the back of the articular facets in ventral view than those of the living species.

Tribe ANTILOPINI. *Antidorcas recki* is represented by three horn cores from level 2. These are a complete right horn core 278, a right horn core without the base 979 and part of a horn core 972. The horn cores are short, with a flattened lateral surface, strong transverse ridges and no greatly increased divergence of their distal parts. They agree well with Bed I horn cores. The base of a horn core 1962.068/6653 is of unknown level.

A few dentitions and isolated teeth are assigned to *A. recki*.

These are left maxilla 2041, left mandible 2103, right upper molars 11, 563 and 067/1810, left upper molars 563, 067/1805 and two numbered 562, right lower molar 067/1811, left lower molar 4091, parts of two molars numbered 067/1809, and a right lower molar and right and left lower premolars without numbers from level 1; right maxilla 301, left maxilla 907, left mandible 067/1854, right upper molars 067/1838 and 067/1842, left upper molars 977, 067/1773, 067/1793, 067/1859 and two numbered 920c, two upper molars numbered 920, two right lower molars numbered 920c, left lower molar 920c, right M_3 067/1852 and left M_3 790 from level 2. A right lower molar 067/1785, left lower molar 067/1766, left M_3 067/1768 and deciduous right P^4 067/1787 are either from level 1 or level 2.

Limb bones assigned to *A. recki* are distal end right humerus 37, distal end left humerus 067/1895, distal end right radius 43, complete left tibia 2010, distal end right tibia 3984, distal end right femur 067/1881, complete left metatarsal 4026, proximal end left metatarsal 2003 and distal ends metatarsals 51 and 4049. These are all from level 1. The distal end of right tibia 3790 and distal end of metatarsal 3791 are from level 2.

SUMMARY. Levels 1 and 2 of HWK East II have scanty remains of reduncines and hippotragines, and for almost the last time until Bed III deposits there appear reduncine teeth of a size appropriate for the *Kobus sigmoidalis/ellipsiprymnus* lineage. *Antidorcas recki* is common and is found in association with an alcelaphine as in Bed I sites, but here the alcelaphine is not known to be *Parmularius altidens*; more probably it is *P. rugosus* or its ancestor.

The species list for levels 1 and 2 together is:

Tragelaphus strepsiceros maryanus
Syncerus acoelotus
Kobus sigmoidalis/ellipsiprymnus
Hippotragus gigas
Megalotragus ? kattwinkeli
Beatragus antiquus
? *Parmularius* sp.
Alcelaphini sp. 4 ?
Antidorcas recki

The numbers of bovid bones in levels 1 and 2 are shown in Table 5.

FLKN II (Clay with root casts)

This level can be correlated with level 2 at HWK East II.

Tribe TRAGELAPHINI. The proximal end of a right metatarsal 067/4958 belongs in this tribe, and probably also the distal end of a right tibia 067/4886. These are the size of most of the tragelaphine limb bones in Bed I.

Tribe REDUNCINI. A right upper molar 067/5013 and a left P_4 067/5025 are definitely reduncine, while the proximal end of a right radius 067/4985 and distal end of a right tibia 067/4953 are probably reduncine. They are the size of the *Kobus sigmoidalis/ellipsiprymnus* lineage.

Tribe ALCELAPHINI. The proximal half of a left horn core 067/4998 is of *Beatragus antiquus*.

Table 5 Numbers of bovid bones at HWK East II, levels 1 and 2

							Minimum number of individuals	
	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Adult	Immature
Level 1								
Tragelaphus s. maryanus	1	–	–	–	–	1	1	–
Syncerus acoelotus	–	–	–	1	–	1	1	–
Kobus sigm./ellipsiprymnus	–	–	–	4	–	4	1	–
Megalotragus ? kattwinkeli	–	–	–	–	2	2	1	–
Beatragus antiquus	1	–	–	–	–	1	1	–
Large alcelaphine sp.	–	–	–	–	3	3	1	–
Large/medium alcelaphine	–	–	–	–	1	1	1	–
? *Parmularius* sp.	–	3	4 (1)	27 (1)	46 (1)	80	6	1
Alcelaphini sp. 4?	–	–	–	–	3	3	2	–
Alcelaphini total	1	3	4 (1)	27 (1)	55 (1)	90	10*	1
Antidorcas recki	–	1	1	14	10	26	2	–
Level 2								
Tragelaphus s. maryanus	1	–	–	8 (2)	2	11	1	1
Syncerus acoelotus	–	–	–	1	–	1	1	–
Kobus sigm./ellipsiprymnus	–	–	–	2 (1)	–	2	1	1
Hippotragus gigas	–	–	–	4	–	4	1	–
Megalotragus ? kattwinkeli	–	–	–	–	1	1	1	–
Beatragus antiquus	1	–	–	–	–	1	1	–
? *Parmularius* sp.	–	1 (1)	4 (3)	30	15 (2)	50	3	2
Alcelaphini sp. 4?	–	–	–	–	1	1	1	–
Alcelaphini total	1	1 (1)	4 (3)	30	17 (2)	53	6	2
Antidorcas recki	3	2	1	15	2	23	3	–

* Omitting the individuals represented by the large and large/medium limb bones.

It is rather robust and has the usual transverse ridges. A cranium 1960.067/4951 with pieces of both horn cores 067/4946+4948 and 4949 is a possible intermediate stage between *Parmularius altidens* and *P. angusticornis*.

Four single teeth belong in this tribe. These are part of a right upper molar 067/5012, right lower molar 067/5018, right M_3 8820 and deciduous right P^3 067/4942. They are all medium-sized.

There are no very large limb bones at this site and those present are all of smaller size (size group (ii) of later Bed II sites). These are distal end left humerus 067/4952, proximal end right radius 067/4947, proximal end left radius 067/4986, left ulna 067/4880, proximal end left metacarpal 067/4990+067/5002, distal end metacarpal 067/4914, proximal end left metatarsal 067/4963 and distal end metatarsal 8817. The proximal lateral tubercle on the radius 067/4947 is high as in alcelaphines, but the lateral facet is not very indented posteriorly.

Tribe ANTILOPINI. Five teeth belong in this tribe. These are right upper molar 067/4937 and left upper molars 067/4909, 067/4910, 067/4928 and 067/4969.

The proximal end of left tibia 067/4869, distal end metatarsal 067/4925 and distal end metacarpal 067/4855 are the size of *Antidorcas recki* limb bones, but a right femur (proximal end 067/4859, distal end 067/4885, part of the shaft missing) is larger than femora of *A. recki* though smaller than the proximal ends of femora 233 and 8809 of very small Alcelaphini at FLKN I.

Other remains from Lower Bed II

Tribe ALCELAPHINI. A crushed cranium and parts of a skeleton, apparently of *Damaliscus agelaius*, FLK West 1969.82a, were found above Tuff IF in greenish clays below the sandy conglomerate. Some antilopine limb bones were found with the skeleton.

An alcelaphine cranium S.208 was collected in 1970 from the Lemuta Tuff Member. It has some resemblance to *Rabaticeras arambourgi*, but in this paper we have referred it to Alcelaphini species 2.

Sites in Middle Bed II

HWK EE II

In 1972 Mrs M. D. Leakey excavated at this site near the base of middle Bed II at a level equivalent to level 4 of HWK East II. An account is to be published later. Meanwhile we have seen some bovid material from the site.

Tribe TRAGELAPHINI. Part of a right maxilla 3916 with M^2 and M^3 would best fit *Tragelaphus strepsiceros maryanus* by the size of the teeth. A right deciduous P^2 from I/12 is also probably tragelaphine.

Tribe REDUNCINI. A left M_3 1123 is large enough to belong to the *Kobus sigmoidalis/ellipsiprymnus* lineage. It is too large to belong to a kob.

Tribe ALCELAPHINI. A right horn core 2315 from the sandy conglomerate belongs to the primitive *Connochaetes* sp. likely to be ancestral to *C. taurinus* and otherwise confined to Beds I and lower II. We saw a cast of the horn core.

Three pieces of *Parmularius angusticornis* are a frontlet with complete horn cores 172, a frontlet with complete right horn core and virtually complete left horn core 635 and a complete right horn core 2180.

Three more fossils belong to a smaller alcelaphine tentatively associated with the *Parmularius rugosus* lineage. These are frontlets 2061 and 2181 and right horn core 954. The last-mentioned piece may be of a female. We have also seen a cast of frontlet 285 belonging to this species.

A very small alcelaphine is also present, represented by two left mandibles, 1156 with P_3 to erupting M_3 and 4302 with P_3 to M_2. Neither has an alveolus for P_2, nor are paraconid and metaconid fused on P_4. A complete right metatarsal 1168 is likely to be conspecific. It has a strong longitudinal groove on its anterior side and is therefore unlike Antilopini despite its small size. Its length and least thickness are 161 and 11·4 mm.

There are other dentitions and isolated teeth from this site belonging to the Alcelaphini.

Tribe ANTILOPINI. Two horn cores of *Antidorcas recki*, 2780 and 3108, agree with HWK II

1959.472, KK I 1959.309 and BM(NH) M 14512 from Bed I in being very strongly compressed mediolaterally. Part of a left mandible with deciduous P_3–M_1 and erupting M_2 and M_3 and with an alveolus for deciduous P_2 is probably *A. recki* by the great ramus depth below M_2.

Gazella sp. is represented by a complete right horn core 2396.

There are also a few antilopine teeth at this site.

SUMMARY. HWK EE II will be a very interesting site when a complete account can be given. It has three categories of bovids:

(i) The last survivors of species otherwise known only from Beds I and lower II: *Tragelaphus strepsiceros maryanus* (provisional), *Kobus sigmoidalis/ellipsiprymnus* and *Connochaetes* sp.

(ii) Species which appear temporarily in the Olduvai region at this period: *Parmularius* ? *rugosus* and the narrow-horned variety of *Antidorcas recki.*

(iii) One species confined to middle and upper Bed II: *Parmularius angusticornis.*

HWK East II Levels 3–5

Tribe BOVINI. A right upper molar 2687 and a right M_3 2688, both slightly worn, are large with a simple occlusal pattern and are definitely *Pelorovis oldowayensis.* This is the earliest record of known horizon at Olduvai.

Tribe HIPPOTRAGINI. A left lower molar 067/1839 is the only possible evidence of this tribe in these levels. It may be *Hippotragus gigas* by the signs of a well-developed goat fold anteriorly.

Tribe ALCELAPHINI. An immature frontlet 068/6649 with complete right horn core and basal half of the left was found in clay above the sandy conglomerate above these levels. The specimen is smaller than three adult horn cores of a species like *Parmularius rugosus* from HWK II and the midfrontal suture is still open. It is best taken as belonging to this species.

An immature left mandible 2917 is alcelaphine. It has a very small deciduous P_2. A number of single teeth also belong to this tribe; they agree with *Parmularius altidens* but could belong to the species like *P. rugosus.*

These are right upper molars 2890, 3482, 3487, 067/1813, 067/1820, 067/1822, 067/1847, 067/1848 and 067/1850, left upper molars 2918 and 067/1844, right lower molars 690, 068/1815, 067/1824, 067/1860 and damaged 067/1828, left lower molars 2220 and 067/1860, parts of lower molars 067/1824, 067/1834 and 067/1849, right M_3 695, right upper premolar 067/1836, left upper premolars 3485 and 067/1824, right P_4s 2223, 2225 and 067/1829, left P_2 067/1824, left P_4 067/1831, deciduous right P^3 067/1817, deciduous left P^3 067/1823, deciduous right P^4 067/1845, and deciduous right P_4s 3495, 067/1830 and damaged 067/1835.

A number of alcelaphine limb bones are the size of *P. altidens* or possibly a little larger. These are distal ends left humeri 3218 and 067/1899, proximal ends left metacarpals 3337 and 067/1908, distal end metacarpal 2948, proximal end right femur 067/1955, distal left femur 067/1917, complete left tibia 067/1906, distal end right tibia 693, proximal end left metatarsal 067/1904 and distal end metatarsal 067/1907.

The proximal ends of right metacarpals 2976A and incomplete 3154 are larger and perhaps belong to *Megalotragus kattwinkeli.* The proximal end of right radius 067/1900 is the size of the distal end of left radius 2100 from level 1 of this site and is intermediate between the larger and smaller limb bones.

Tribe ANTILOPINI. A few antilopine remains were found in these levels and are presumably *Antidorcas recki.* These are partial right maxilla 067/1788, right upper molar 067/1816, left upper molars 2221, 067/1769 and 067/1818, right lower molars 067/1814 and 067/1819, left lower molars 067/1826 and 067/1827, right M_3s 2219, 067/1782, 067/1843 and 067/1846, left M_3 067/1833, right lower premolar 067/1824, left P_3 067/1789 and proximal end right radius 067/1903.

SUMMARY. The numbers of bovid bones of each species at HWK East II levels 3–5 are given in Table 6, p. 33.

MNK II

Site (71) Geologic locality 88

The MNK gully is on the south bank of the Side Gorge, opposite FC, and about 0·8 mile (1·3 km) upstream from the confluence with the Main Gorge. Much of Beds II, III and IV is visible, the exposures extending down to Tuff IF at the top of Bed I. MNK Skull Site is in the lower half of the gully in the lower part of middle Bed II, 24 ft (7·2 m) above the base of Bed II, while the Main Occupation Site is some 17 ft (5·1 m) higher, in the upper part of middle Bed II, the two sites being about 60 ft (18·0 m) from one another. The sequence of deposits, from above downwards, is as follows:

(a) A fine-grained reworked tuff, exposed to a depth of 10 ft (3·0 m), with patches of clay and grey sand at the base and often reddened in the upper part. The Main Occupation Site occurs within the lower 4½ ft (1·35 m) of this tuff.
(b) About 3 ft (90 cm) of hard grey tuff with pumice particles in the lower part and an irregular, eroded upper surface.
(c) 3 ft (90 cm) of clay.
(d) 4 ft (1·2 m) of reworked tuffs containing thin gravel seams, usually partly reddened.
(e) An irregular layer of limestone, 9 ins (23 cm) thick.
(f) About 13 ft (3·9 m) of reworked tuffs and clays. The Skull Site occurs in the upper part of these deposits.
(g) Several levels of tuffs and clays with layers of chert down to Tuff IF.

MNK II Skull Site

Artifacts and a few faunal remains were scattered throughout the 4½ ft (1·35 m) of grey, sandy reworked tuff in which three hominid teeth were found, and in the underlying 6 ft (1·8 m) of clay in which two fragments of a hominid skull occurred.

Tribe TRAGELAPHINI. Part of a lower molar 067/1460 belongs in this tribe.

Tribe ALCELAPHINI. A right maxilla with M^1–M^3 preserved 89, right upper molars 47, 067/1436 and 067/1445, left upper molar 067/1406, part of upper molar 067/1431, right lower molar 067/1453, part of lower molar 067/1397, part of right M_3 067/1389, right P^3 or P^4 067/1429, deciduous right P^3 067/1458 and deciduous right P^4 067/1391 are alcelaphine. They belong in size group (ii) of later Bed II sites, although the maxilla is clearly small even for this size group.

Tribe ANTILOPINI. Part of a right upper molar 067/1448 represents this tribe.

MNK II Main Occupation Site

The Occupation Site was excavated in 1963 by means of four trenches. Remains were found scattered throughout the 4½ ft (1·35 m) of deposit. Except for material on the eroded surface of the underlying hard grey tuff, the remains were not on any recognizable 'surfaces', so the site may have been reoccupied on successive occasions, at sufficient intervals for soil and vegetation to have accumulated over previous occupation surfaces. At the time of excavation the deposit was subdivided into six levels, and the fossils marked accordingly, but the material is now treated as a single unit.

Tribe TRAGELAPHINI. An incomplete pair of horn cores and four associated skull pieces (the occipital, basioccipital, part of the roof and side of the braincase, and an unidentified fragment), 067/2054, are of a large tragelaphine. The horn cores have the open spiral and prominent keel of kudu species. The spiralling is anticlockwise in one horn core which is therefore from the right side, and clockwise in the other, left, horn core. Both pieces are the upper halves of horn cores and are comparable in size with those of the living greater kudu. On the basis of its very large size as indicated by the occipital fragment and its horn cores having a definite triangular cross-section, the specimen is referred to *Tragelaphus strepsiceros grandis*. There is more of an approach to a posterolateral keel than in living greater kudus. The fragment of skull roof and side of the braincase has a deep groove at the top of the braincase side, below the back of the horn core insertion, as is present on the holotype skull of *T. s. grandis* and to a lesser extent in living greater and lesser kudus; this is a feature connected with horn core size, angle of insertion and shape of the braincase.

A left upper molar 067/1407 of greater kudu size is referred to *T. s. grandis* and two unworn left lower premolars 067/1417 are possibly also of this species.

Tribe BOVINI. *Pelorovis oldowayensis* is now known to be present at this site and this, together with the HWK East II record, extends its temporal range back from SHK II to much earlier in middle Bed II. There are eight single teeth. These are right upper molar 3264, left upper molar 3269, right lower molar 2321, left lower molars 480 and 067/1410, right M_3 2380, right P_3 2336 and right P_4 3113. They agree in size and morphology with later *P. oldowayensis* teeth.

A right upper molar 1130 and possibly a deciduous right upper premolar 1338 belong in this tribe and would be from a bovine smaller than *P. oldowayensis*. These teeth could be of *Syncerus acoelotus* as at other Bed II sites.

A number of limb bones are bovine. These are complete right radius 2411, proximal end left radius 2861, left ulna 067/1372, distal end metacarpal 2825, distal ends right tibiae 1277 and 1591 and distal end left tibia 3423. The complete radius can be seen to be rather small for *P. oldowayensis* but it is not certain to which species any of the limb bones would belong.

Tribe REDUNCINI. The skull, dentitions and partial skeleton of a small kob-sized reduncine were found at this site. The skull 104+106 is crushed and incomplete. The mandibles, right 107 and left 108, and the right maxilla 103 retain only their molars and the P4s. The postcranial skeleton consists of the atlas vertebra 110, right metacarpal 105, right ulna 109, right femur 101, right tibia 102 and right metatarsal 100.

The proximal end of a right metatarsal 715 is damaged and doubtfully reduncine. It is of waterbuck size and is certainly not alcelaphine. A deciduous right P_4 067/1435 is definitely reduncine and is of kob size.

Tribe HIPPOTRAGINI. A single right lower molar 1087 is the only evidence for this tribe.

Tribe ALCELAPHINI. A complete left horn core with the frontal and part of the orbital rim 3258 is of *Megalotragus kattwinkeli*. It is rather shorter than the horn core on the neotype skull BM(NH) M 21447. The horn core insertions would be close together and the horn cores backwardly directed with little divergence at the base and not very downwardly directed (the frontal between the horn cores being regarded as dorsal and not anterior so that the tooth rows would be horizontal if present). The horn core is close to the orbit and there is no temporal fossa. A large, moderately deep but not greatly elongated postcornual fossa is present, and there is transverse ribbing across the front surface of the horn core.

A left horn core 2716 is of *Connochaetes*. It is either *Connochaetes* sp. or *C. taurinus olduvaiensis*, being too incomplete basally for certain assignment. The very little dorsoventral flattening at the base suggests that it is a female.

There are two sizes among the alcelaphine dentitions at this site, corresponding with the size groups at SHK II and BK II.

(i) A left mandible 2070 has a molar row of the same large size and simple occlusal pattern as teeth of *Megalotragus kattwinkeli* as seen on the neotype skull (Leakey 1965 : pl. 82). Eight upper and nine lower isolated alcelaphine teeth of large size are also assigned to this group.

(ii) A partial maxilla 2259 and left mandibles 136, 976 and 2403 belong in this size group. 136 and 976 are the only mandibles at this site which would be complete enough for any presence of P_2 to be seen, and in both cases it is seen to be absent. A rather small right mandible 1725 also belongs in this size group but is likely to be a different species from the other specimens, perhaps *Damaliscus agelaius*. There are 28 upper and 35 lower alcelaphine teeth in this size category.

The alcelaphine limb bones are also divisible into two sizes, which again correspond with the size groups at SHK II and BK II. The group of 'large' limb bones consists of part of the distal end of left humerus 1870, proximal ends left radii 718 and 3050, distal end right radius 3472, distal end left radius 2190, complete left metacarpal 2704, proximal end right femur 1831, complete right tibia 167, complete left metatarsals 169 and 2718 and proximal end left metatarsal 067/1365. The metapodials are relatively longer than in living *Connochaetes* and some pieces, radius 3050 for instance, reach the size of the very large DK I and HWK East II alcelaphine limb bones. They belong with the size group (i) alcelaphine dentitions and most of them are probably of *Megalotragus kattwinkeli*. A complete left metatarsal 752 is of a large-sized alcelaphine, and has proportions and length appropriate for *Connochaetes* rather than *M. kattwinkeli*.

Limb bones of the 'small' category are the distal end of right humerus 3177, distal end left

Table 6 Numbers of bovid bones at HWK East II, levels 3–5

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals: Adult	Minimum number of individuals: Immature
Pelorovis oldowayensis	–	–	–	2	–	2	1	–
Hippotragus gigas ?	–	–	–	1	–	1	1	–
Large alcelaphine sp.	–	–	–	–	2	2	2	–
Large/medium alcelaphine	–	–	–	–	1	1	1	–
Parmularius aff. *rugosus*	1 (1)	–	1 (1)	36 (6)	11	49	3	3
Alcelaphini total	1 (1)		1 (1)	36 (6)	14	52	6	3
Antidorcas recki	–	1	–	15	1	17	4	–

Table 7 Numbers of bovid bones at MNK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals: Adult	Minimum number of individuals: Immature
Tragelaphus s. grandis	1	–	–	3	–	4	1	–
Pelorovis oldowayensis	–	–	–	8	–	8	1	–
Syncerus acoelotus	–	–	–	2 (1)	–	2	1	1
Bovini	–	–	–	–	7	7	2	–
Bovini total	–	–	–	10 (1)	7	17	2*	1
Kobus kob	1	1	2	1 (1)	5	10	1	1
Hippotragus gigas	–	–	–	1	–	1	1	–
Megalotragus kattwinkeli	1	–	1	–	–	2	1	–
Connochaetes ? *taurinus*	1	–	–	–	1	2	1	–
Alcelaphini size group (i)	–	–	–	17	11	28		
Alcelaphini size group (ii)	–	1	3	63 (5)	11	78		
Smaller Alcelaphini, group (ii)	–	–	1	–	1	2		
Alcelaphini total	2	1	5	80 (5)	24	112		
Antilopini sp. indet.	–	–	–	1	–	1		
Antilopini sp. 1	1	–	–	–	–	1	1	–

* Omitting the two individuals represented by limb bones.

humerus 1495, part of proximal end right radius 067/1486, proximal end left radius 1296, distal end right radius 1286, distal end left radius 2953, right ulna 1391, proximal ends left metacarpals 2670 and 3320 and proximal ends right metatarsals 775 and 067/1484. These limb bones are rather larger than those of *Parmularius altidens* of Bed I. They would belong with the alcelaphine dentitions of size group (ii). The proximal end of a rather small right metatarsal 3385 is of similar size to the very small alcelaphine limb bones from FLKN I. It could perhaps be conspecific with the mandible 1725 rather than with the FLKN species.

Tribe ANTILOPINI. A single left upper molar 067/1426 belongs in this tribe. It is not possible to say whether it is *Antidorcas recki* or *Gazella*.

The base of a left horn core 2818 appears to be of an unknown antilopine species with some resemblances to *Gazella*. The specimen is small but adult and has the supraorbital pit preserved. Similar horn cores have been found at BK II and from the surface of DK I, and have been listed as 'Antilopini sp. 1'.

SUMMARY. At MNK II *Tragelaphus strepsiceros maryanus* has been replaced by *T. s. grandis*, and the *Kobus sigmoidalis/ellipsiprymnus* lineage by *K. kob*. The middle and upper Bed II co-existence of *Pelorovis oldowayensis* with *Syncerus acoelotus* has emerged. MNK II is also the first site at which bovines are clearly commoner than tragelaphines, and this is a pattern which continues into Bed III. Another feature in common with other middle and upper Bed II sites is the heavy representation of alcelaphines and a drop in the proportion of antilopines. Except at the highly unusual site of FLKNN I the antilopines have hitherto been present in numbers equal to at least a third of the alcelaphines.

The numbers of bovid bones of each species at the site are shown in Table 7, p. 33. Here the alcelaphine size group (i) includes material likely to belong to *Megalotragus kattwinkeli* and *Connochaetes*, while size group (ii) would contain *Parmularius angusticornis* and *Damaliscus niro* if those species are found here as at later Bed II sites.

FC West II

Site (62) Geologic locality 89

The site lies on the north bank of the Side Gorge, 1 mile (1·6 km) above the confluence with the Main Gorge. A trench was cut into the deposits of Bed II in 1963 and the following sequence, from above downwards, was exposed:

(a) Tuff IID.
(b) About 25 ft (7·5 m) of a buff-white tuff, a clayey tuff, a sandy tuff and a consolidated fine sand. A few implements and bones occurred in these levels.
(c) 1½–3 ft (45–90 cm) of a reworked tuff with scattered cultural and faunal material.
(d) A rich hominid occupation floor on the surface of a clay.
(e) 14 ft (4·2 m) of barren tuffs and clays, starting with Tuff IIB at the top.
(f) The chert-containing bed, as at other Bed II sites.

Tribe REDUNCINI. A complete right metatarsal 1 is possibly reduncine and is *Kobus*-sized with a length and least thickness of 209 and 25·4 mm.

Tribe ALCELAPHINI. A number of single teeth are alcelaphine. These are right upper molars 64, 317 and 067/5252, left upper molars 067/5416 and 067/5265, right lower molars 69, 254 and 067/5265, left lower molars 253, 722 and 067/5265, lower molars 067/5416 and two numbered 067/5252, parts of lower molars 204, 067/5252 and 067/5253, part of a molar 067/5265, right P_4 067/5265, left P_4 067/5277 and deciduous left P^4 067/5252. An unworn right upper molar 1206 is larger than the other teeth.

The distal end of a left radius 452 is alcelaphine and large-sized. It would belong to *Megalotragus kattwinkeli* or *Connochaetes*. The distal end of a left humerus 387 is medium-sized. The distal end of a metacarpal 287 and the distal end of a metatarsal 268 probably belong in this tribe and are medium-sized.

Tribe NEOTRAGINI. An incomplete right mandible 167 with deciduous P_2–P_4 is extremely small and probably belongs in this tribe.

Tribe ANTILOPINI. An incomplete right horn core 201, with the top of the orbital rim, supraorbital pit and postcornual fossa, is *Gazella* (p. 438). It appears to be somewhat more transversely compressed than *Gazella* horn cores from SHK II and BK II, and has a less deep postcornual fossa, but it is probably the same species.

A left M_3 067/5252 and the distal end of a right tibia 85 are antilopine. They could be *Gazella* sp. or *Antidorcas recki.*

SHK II

Site (68) Geologic locality 92

SHK is situated in a long, narrow gully cutting into the south bank of the Side Gorge, about 1½ miles (2·4 km) from the confluence of the Main and Side Gorges. The site is on the west side of the gully where the exposures are from the upper part of middle Bed II to Bed III. On the east side of the gully the exposures extend from the top of Bed II down to Tuff IF at the top of Bed I, including a horizon with chert nodules as at other Bed II sites. Tuff IID is visible at about 62 ft (18·6 m) above the base of Bed II. Excavations in Bed II were carried out in 1953, 1955 and 1957. The sequence of exposures, from above downwards, was as follows.

(a) 8 ft (2·4 m) of tuffs and clayey tuffs, some coarse and others fine-grained. The fossil remains were not concentrated at a particular level. There was some evidence of water rolling. The herd of *Antidorcas recki* now in the British Museum (Natural History) was found in these deposits in 1935.

(b) A conglomerate filling a channel 2½ ft (75 cm) deep and 5–6 ft (1·5–1·8 m) wide, cutting through the lower part of (a) down to the surface of the underlying brown clay, and containing artifacts and bones. The material recovered was mainly fresh but some large artifacts were water-rolled.

(c) A chestnut brown clay whose top was 32 ft (9·6 m) above the base of Bed II, its base not exposed.

Faunal remains from the three horizons have been treated as a single unit. At a subsidiary site, SHK Annexe, about 100 yds (91·4 m) from the Main Site, an occupation level on the surface of the underlying brown clay occurred at the level of the channel conglomerate.

Tribe TRAGELAPHINI. The base of a horn core with an open spiral 1953.286 is of greater kudu size, or still larger, and is presumably of *Tragelaphus strepsiceros grandis.* The spiralling is clockwise so the piece is from the left side, and the sharp keel is anteriorly inserted at the base.

An immature partial right mandible 1953.270 and right M_3s 1957.125 and 1957.227 are tragelaphines of large size and are assigned to this species.

The distal end of a left tibia 1957.474 is from a bushbuck-sized tragelaphine and this must represent another, much smaller, species.

Tribe BOVINI. Three teeth of *Pelorovis oldowayensis* can now be added to the crushed horn core and dental material already known from this site (Gentry 1967 : 253, 257). These are right upper molar 1957.1181, left lower molar 1957.422 and a lower molar 1957.1130.

Four teeth appear to be of *Syncerus acoelotus*, and have a more complicated occlusal pattern than is found in most *P. oldowayensis*. These are right upper molars 1953.259, 1957.148 and 1957.290 and left upper molar from the surface 1953.197.

Tribe REDUNCINI. The basal half of a horn core 1957.579 with a small part of the braincase preserved was a surface find at this site. It is of *Kobus* rather than *Redunca* size (Leakey 1965 : 47, *Kobus* species B, said to be a right horn core but in fact a left), and looks more like a rather large kob than a waterbuck in its small divergence and lack of a flattened lateral surface.

A left M_3 1957.396 is reduncine and the size of a kob.

Tribe HIPPOTRAGINI. The base of a left horn core with the frontal suture, orbital rim and a small part of the braincase 1953.281 is of *Hippotragus gigas* (Leakey 1965 : 50).

An immature right mandible 1957.618, right lower molar 1957.506 and left lower molar 1957.219 are assigned to *H. gigas.* 1957.618 has two molars in place behind the deciduous P_4 and both have goat folds passing down the entire exposed height of the tooth; the M_2 in particular is too small for the jaw to belong to a bovine.

The distal end of a left tibia 1955.32 is probably hippotragine.

Tribe ALCELAPHINI. A number of horn cores of *Parmularius angusticornis* are known from this site, the best preserved being the left one with part of the braincase 1957.1284 assigned by Leakey to *Damaliscus antiquus* (1965 : 56). It shows a massive cross-section near the base followed by a gradual thinning, a slight backwards curvature, no transverse ridges on the front and a rather weak alcelaphine groove without a marked anterior edge. More of the horn core is preserved than in specimens illustrated by Leakey, and its divergence in anterior view exceeds that seen in illustrated specimens. Other horn cores of this species from SHK II are a left 1952.598, base of a right 1955.424 and left 1957.945.

A horn core without number found at this site in 1952 is a *Parmularius* doubtfully referred to the *P. rugosus* lineage.

Damaliscus niro is represented by two fairly large horn cores, right 1953.282 and left 1957.1184 (Leakey 1965 : pl. 55 centre and right specimens), both showing such good identifying features as the overall mediolateral compression, flattened lateral surface towards the distal end, pronounced transverse ridges on the front surface, backwards curvature in side view and the front part of any section of the horn core being wider than the back. 1953.282 has parts of the frontal and braincase preserved and in side view shows the oblique insertion of the horn cores of this species, which is none the less more upright than in the living topi *Damaliscus lunatus*. Enough of the frontal is preserved to show the sharp descent of the braincase roof behind the horn core.

Connochaetes is represented by part of a left horn core 1953.283. The distal part of a horn core 1957.946 (Pl. 16, fig. 2) is probably also of wildebeest, although the curvature is less developed than in other horn cores; the alternative of considering it a *Beatragus* with more curvature than normal is less satisfactory because of the absence of transverse ridges and a cross-section which is too little compressed.

A left horn core with part of the frontals 1953.280, and parts of two other horn cores 1957.92 (a surface specimen) and 1953.234, are thought to be possibly related to *Rabaticeras arambourgi* or to the north African Villafranchian *Numidocapra crassicornis* (p. 418).

The alcelaphine dentitions and isolated teeth at this site can be divided into two size groups as at other Bed II sites.

(i) A left mandible 1957.256 belongs in this size group. In its large size and the simple occlusal morphology of its molar row it is probably *Megalotragus kattwinkeli*. Fifteen upper and five lower isolated alcelaphine teeth are assigned to this category.

(ii) An immature left maxilla 1957.760 and left mandibles 1953.272, 1957.268 and 1957.455 have teeth of smaller size and are probably the dentitions of *Parmularius angusticornis* and *Damaliscus niro*. Twenty upper and 35 lower isolated teeth are assigned to this size group. Left upper molars 1957.457 and 1957.617, right lower molars 1955.15 and 1957.116, left lower molar 1957.309, right M_3 1957.392 and left M_3 1957.228 are rather smaller than other teeth included here.

There are two size categories among the alcelaphine limb bones. Limb bones of the 'large' group are about the size of the MNK II bones, although the metapodials seem a little smaller. They are presumably of *Megalotragus* or possibly some are *Connochaetes*. They are the associated complete right radius 1957.282 and complete left radius 1957.283, proximal ends right radii 1953.270 and 1957.929, right ulna 1957.352, complete right metacarpals 1957.558 and 1957.1350, proximal end right metacarpal 1957.89 (surface), distal ends metacarpals 1957.578 (surface) and 1957.469, proximal end right tibia 1957.729, immature left tibia 1957.762+764, distal end right femur 1957.328, complete right metatarsal 1957.839, complete left metatarsal 1957.231 and immature complete left metatarsal 1957.731. These limb bones would belong with the size group (i) teeth.

The limb bones of the 'small' category, as follows, are more numerous and are an appropriate size to go with the size group (ii) teeth.

Distal end right humerus 1957.1181, distal ends left humeri 1957.23, 1957.581 (surface), 1957.761 and 1957.944, complete right radius with ulna 1957.209, proximal ends right radii 1955.41, 1957.88 (surface), 1957.130 and 1957.1307, distal end right radius 1957.1423, distal ends left radii 1957.470 and 1957.732, part of left ulna 1957.825, complete right metacarpal 1957.330, immature complete right metacarpal 1957.208, immature complete left metacarpal 1957.285, proximal end right metacarpal 1953.274, proximal ends left metacarpals 1955.40, 1957.204, 1957.237 and 1957.805, distal ends metacarpals 1953.271, 1953.272a, 1957.273a, 1957.423 (surface) and 1957.725, distal ends right tibiae 1953.271a, 1957.86 (surface), 1957.87 (surface) and 1957.824, distal end left tibia 1957.556, distal ends left femora 1957.415 and 1957.1180, complete left metatarsal 1957.933, and distal end metatarsal 1957.90 (surface).

There are also a few rather smaller limb bones. These are distal end left humerus 1957.765, proximal end left metacarpal 1955.213 and proximal end right metatarsal 1957.763. These are about the size of the very small alcelaphine limb bones from FLKN I but are not necessarily conspecific with them.

Tribe Antilopini. The herd of *Antidorcas recki*, consisting of some nine or ten mostly immature individuals, was found at this site in 1935. This material is in the British Museum (Natural History) and has already been described (Gentry 1966 : 77). Included in the herd is the young adult cranium M 21464 and older frontlet M 21462 (Gentry 1966 : pl. 5) which both have complete horn cores (see p. 429). A right mandible M 22379 was found with the herd but differs in some morphological details from other mandibles in *A. recki* (Gentry 1966 : 66; pl. 3A).

An incomplete immature right mandible in Nairobi, 1957.75 from the surface of SHK II, is assigned to *A. recki*.

A complete right horn core 1953.285, with the top of the orbital rim, supraorbital pit and the frontal suture preserved, differs from horn cores of *A. recki* in lacking the sharp bending back near the base, the transverse ridges and the outward divergence in the upper part. This horn core curves only slightly back at the base and slightly forwards near the tip. It has a flattened lateral side, a rounded medial side and almost no transverse compression. The level of the frontals between the horn core bases would be about the same as that of the orbital rims. The supraorbital pit is large, and there is a rather large and deep postcornual fossa. This specimen is *Gazella* (Gentry 1966 : 65; pl. 2C).

A left mandible 1957.793, lacking only P_2 which has broken off, has a shallower ramus under the teeth and a relatively longer premolar row than in *A. recki*, the total tooth row length being about the same. This is probably also *Gazella* (Gentry 1966 : 66; pl. 3A) and the same species as the horn core.

A lower molar 1957.756 and the distal end of a left radius 1957.99 (surface) are both antilopine but it is not possible to assign them to *A. recki* or to *Gazella*.

Summary. At SHK II the coexistence of *Pelorovis oldowayensis* and *Syncerus acoelotus* continues as at MNK II. The numbers of bovid bones of each species at SHK II are shown in Table 8. The alcelaphine teeth and limb bones of size group (i) are likely to be *Megalotragus kattwinkeli* and *Connochaetes*, and those of size group (ii) to include mostly *Parmularius angusticornis* and *Damaliscus niro*. Apart from the 1935 herd of *Antidorcas recki*, included in Table 8, only one juvenile mandible of *A. recki* and four other antilopine bones are known from SHK II. Gentry (1966 : 84) gave the minimum number of individuals in the herd as 9 or 10, based on metatarsals. However, it has proved possible to make use of an almost adult individual for which there was an association between mandible and metatarsal, and this produces the new minimum numbers shown here.

Other remains from Middle Bed II

Tribe Bovini. A bovine distal metacarpal of the size of *Pelorovis oldowayensis* 1957.367 was a surface find at FC II.

A frontlet of a small *Syncerus acoelotus* with very short horn cores was found in 1973 in Elephant K in a conglomerate 5 ft (1·5 m) above the Lemuta Member.

Tribe Hippotragini. A complete left horn core with part of the braincase 068/6663 of *Hippotragus gigas* was found at FLK II in 1961.

Tribe Alcelaphini. A damaged frontlet 1962.068/6648 of *Parmularius angusticornis* was found in aeolian grey ash at Long K East II. The basal halves of both horn cores and part of the braincase with a flat-topped parietal boss are preserved. The horn cores taper abruptly just above the base and are inclined slightly backwards.

A large alcelaphine basioccipital 068/6651 was also found at Long K East in 1962.

Table 8 Numbers of bovid bones at SHK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Tragelaphus strepsiceros grandis	1	–	1 (1)	2	–	4	2	1
Tragelaphus cf. *scriptus*	–	–	–	–	1	1	1	–
Pelorovis oldowayensis	1	1	–	7	2 (1)	11	2	1
Syncerus acoelotus	–	–	–	4	–	4	1	–
Bovini total	1	1	–	11	2	15	3	1
Kobus kob	1	–	–	1	–	2	1	–
Hippotragus gigas	1	–	1 (1)	2	1	5	1	1
Megalotragus kattwinkeli	–	–	1	–	–	1	1	–
Connochaetes ? *taurinus*	1	–	–	–	–	1	1	–
Parmularius angusticornis	4	–	–	–	–	4	3	–
Parmularius ? *rugosus*	1	–	–	–	–	1	1	–
Damaliscus niro	2	–	–	–	–	2	1	–
Alcelaphini sp. 3	3	–	–	–	–	3	2	–
Alcelaphini size group (i)	–	–	–	20	16 (2)	36		
Alcelaphini size group (ii)	–	1 (1)	3	48	37 (2)	89		
Smaller Alcelaphini, group (ii)	–	–	–	7	3	10		
Alcelaphini total	11	1 (1)	4	75	56 (2)	146		
Antidorcas recki	4 (2)	4 (4)	14 (7)	15	82 (60)	119 (73)	4	7
Gazella sp.	1	–	1	–	–	2	1	–
Antilopini sp. indet.	–	–	–	1	1	2		
Antilopini total	5 (2)	4 (4)	15 (7)	16	83 (60)	123 (73)	5	7

Two complete horn cores of *Damaliscus niro* were found at Elephant K II in 1963. Right horn core 068/5919 came from *in situ* gravel, while left horn core 068/5920 was a surface find. 068/5920 is rather longer and more robust than 068/5919, and somewhat larger than the two SHK II examples and BK II 1955.159. Both horn cores have slight transverse ridges on the anterior surfaces, and have part of the braincase and orbital region attached.

An incomplete cranium with horn cores 068/5975 came from black sand above the sandy conglomerate at HWK EE II in 1965. It has been tentatively linked with the *Parmularius rugosus* lineage.

A male cranium with incomplete horn cores, S.38 found in 1968 at geologic locality 54, probably came from middle or upper Bed II. It belongs to *Damaliscus agelaius.*

Tribe ANTILOPINI. A complete right horn core of *Antidorcas recki* was found at Long K West II in 1962 (Pl. 39, fig. 1). It is numbered 068/6657 and is marked 'Grey ash *in situ*'. It has preserved the frontal, top of the orbital rim and midfrontal suture. It bends backwards and has transverse ridges on the anterior surface. It is a little more upright at the base and a little more deflected outwards than Bed I horn cores, but the divergence in its upper parts is less than in later SHK II horn cores.

The base of a right *Gazella* horn core 199 with the frontal, supraorbital pit, midfrontal suture and damaged orbital rim came from EF-HR in 1963. It lacks the internally hollowed frontals of *Antidorcas recki* so that the level of the frontal medial to the horn core base is no higher than the orbital rim.

An almost complete right horn core 068/6695 belongs to *Gazella* and probably came from middle or upper Bed II or possibly from Bed I.

Sites in Upper Bed II

TK II

Site (19) Geologic locality 16

TK is a large gully on the north side of the Main Gorge. Beds II, III and IV are exposed over considerable areas. Excavations in the upper part of Bed II were carried out in 1963. Two trenches were cut and the following sequence, from above downwards, was exposed:

(a) The basal part of Bed III.
(b) 4 ft (1·2 m) of tuffs and clays interbedded with limestone, as normally occurs below the base of Bed III.
(c) 2½ ft (75 cm) of tuff with scattered artifacts and a few fragments of bone.
(d) A hominid occupation floor on the weathered surface of a clay at the line of contact with the overlying tuff. There were many artifacts and a number of mammalian remains.
(e) A tuff, 1–2 ft (30–60 cm) thick, with scattered artifacts.
(f) A second hominid occupation floor, also on a weathered clay surface, about 10 ft (3·0 m) below the base of Bed III. The horizon was excavated in one trench only and artifacts and faunal remains were concentrated at one end of this trench.
(g) A channel 3 ft (90 cm) deep cut into the underlying Tuff IID. Artifacts and bone fragments occurred in the lower part of the filling.

The site appears to have been a camping ground which was occupied on two occasions and perhaps visited temporarily at the times when the tuffs between the lower and upper occupation floors and above the upper occupation floor were being deposited. The antelope material from this site has been considered as a single unit.

Tribe BOVINI. Left upper molars 1647, 1684a and two numbered 067/5331a, and right lower molar 1268 are smaller than molars of *Pelorovis oldowayensis* and probably belong to *Syncerus acoelotus.*

The distal end of a right humerus 067/5333 is probably *P. oldowayensis*, but the distal end of a right radius 2627 may well be the *Syncerus*. Part of the proximal end of a left radius 2623 is probably bovine.

Tribe HIPPOTRAGINI. The back of a large skull 067/5310 consisting of the occipital surface, occipital condyles, bases of the paraoccipital processes, basioccipital and the right auditory bulla, is of *Hippotragus gigas*. The lack of a central longitudinal groove in the basioccipital, the small bulla, the short basioccipital and the outline of the occipital surface are typically hippotragine. The nuchal crest is strong, as on the *H. gigas* holotype, but the shallow hollowings on either side of the median vertical line at the top of the occipital surface, which are present on the holotype and DK I skulls, are here absent. The basioccipital of this specimen is shorter than in the living roan or sable. Left M_3 537 is identified as *H. gigas*.

Tribe ALCELAPHINI. There are a number of alcelaphine dentitions and single teeth and these can be divided into the same size groups as at other Bed II sites.

(i) A partial right mandible 067/5329, right upper molar 61 and left lower molar 2269 are of large size and belong in this size group.

(ii) Right upper molars 2192 and 067/5306, left upper molars 918, 1285, 1598, 067/5308, 067/5318 and 067/5332, left lower molars 1164, 1261 and 067/5308, right M_3 067/5332, part of an unworn right M_3 1786 and two right upper premolars numbered 067/5308 belong in this size group. An incomplete right mandible 2395, left upper molars 067/5314 and 067/5331b and left M_3 2519 are smaller than the other teeth. Mandible 2395 has an alveolus in the jaw for a P_2.

The distal end of a left radius 1870 and part of the proximal end of a right ulna 067/5299 are alcelaphine and large-sized, and would belong with the size group (i) teeth.

Tribe ANTILOPINI. A left upper molar 067/5308, right lower molar 067/5332 and left lower molar 067/5307 belong in this tribe. It is not possible to say whether they are *Antidorcas recki* or *Gazella*.

BK II

Site (66) Geologic locality 94

BK lies on the south bank of the Side Gorge about 2 miles (3·2 km) above the confluence with the Main Gorge. Discovered in 1935, the site consists of two erosion gullies, west and east, linked by a short cliff which runs parallel to the river course. Beds II, III and IV are exposed in the gullies and the cliff, although Bed IV has been largely denuded. Excavations in Bed II were carried out from 1952 to 1957 and in 1963, at a level approximately 25 ft (7·6 m) above SHK II. A series of clays, tuffs, silts, sands and gravels in which artifacts and bones occurred represents the filling of an old river channel which cuts out Tuff IID in places. Cross-bedding suggests the river flowed in a north-east or south-west direction, with a maximum depth in the excavated area of 8½ ft (2·6 m). A sequence of deposits within the channel could not be established because of the cross-bedding, so the whole deposit is considered as a unit. A few of the remains from the coarser horizons of sand and gravel are rolled, but most of the material has not been transported far enough for it to become abraded. Much material of *Pelorovis oldowayensis* was found at this site and the more complete remains were found in a clay which seems to represent a swamp or quiet backwater adjoining the main river.

Former subdivisions of the site into a main area, BK II East and BK II Extension have been disregarded, except for the recording of these designations when they occur as parts of specimen field-numbers.

Tribe TRAGELAPHINI. Four isolated teeth belong in this tribe. These are right upper molar 1963.157, left upper molar 1963.3015, right lower molar 1957.695 and unworn right lower molar 1963.1615. These are of greater kudu size and are presumably of *Tragelaphus strepsiceros grandis*.

A large left tragelaphine femur 1963.802 is presumably also *T. s. grandis*.

Tribe BOVINI. A herd of *Pelorovis oldowayensis* was found at BK II and discussed by Gentry (1967). Additional material is now known. A nearly complete left horn core 1957.1509 is from a young individual. A horn core base 1952.356 and a damaged and weathered horn core piece 1963.067/1648 are also of *P. oldowayensis*. Additional isolated teeth are the right upper molars 1963.3251 and two numbered 068/5865, left upper molars 1955.37 and 1963.2127, parts of upper molars 1963.485, 1963.491, 1963,662, 1963.664 and 1963.2552, right lower molar 1963.1972, left lower molars 1955.38 and 1963.1609, right M_3 1963.2486, right upper premolars 298, 067/5201 and 1963.2058, left upper premolars 1963.1447 and 1963.067/2449, upper premolar 1963.2228, right P_2 1953 BK II Ext 150, left P_2 1957.067/2457, left P_3 1955.286 and right P_4 1957.1500.

A few limb bones of *P. oldowayensis* have also subsequently been found in the National Museum of Kenya, Nairobi. These are distal end right humerus 1953 BK II Ext 8, complete left radius

1963.2201, proximal ends right metacarpals 1963.1940 and 1963.3069, proximal end right tibia 1963.2763, and distal ends right tibiae 1953 BK II Ext 178 and 1953 BK II Ext 318.

There is a considerable amount of material of *Syncerus acoelotus* at this site, as at MNK II and SHK II, the teeth being smaller than those of *P. oldowayensis* while the occlusal morphology is more complicated than in many *P. oldowayensis*. The specimens are incomplete left maxilla 1963.2757, incomplete right mandibles 1953.067/5229, 1953.067/5230, 1963.2717, 1963.2765 and 1963.2818, incomplete left mandible 1955.76, immature right mandible 1953 BK II Ext 77 (Pl. 11, fig. 2), immature left mandible 1963.3182, right upper molars 1952.133, 1953 BK II Ext 354, 1955.59, 1955.126 and 1957.858, left upper molars 1953 BK II Ext 83, 1953 BK II Ext 181 and 068/8787, right lower molar 1952.161, part of lower molar 1955.308, right M_3s 1952.128, 1953.85, 1953 BK II Ext 357 and 1957.512, left M_3 1955.31, left upper premolar 1952.135, left P_3s 1963.710 and 1963.067/2479 and right lower premolar 1955.326.

There can be little doubt that nearly all the upper teeth are bovine, matching the large number of definitely identified lower jaws and single teeth. The immature mandible 1953.77 was thought to be bovine rather than hippotragine. Its M_1 has a goat fold, a situation often paralleled in living *Syncerus*. The goat fold does not persist lower down, and does not appear at all on M_2 or M_3. The upward curvature of the lower edge of the horizontal ramus posteriorly also suggests Bovini rather than Hippotragini. The other immature mandible 1963.3182 appears to be bovine by the large size of M_1. The occlusal morphology of these teeth is about as advanced as in the living buffalo *Syncerus caffer*. They are generally smaller than bovine teeth from the Beds III–IV junction.

Two left upper molars, 1953 BK II Ext 84 and 1957.532, are larger than the other teeth of *S. acoelotus*. However, they differ from *P. oldowayensis* by their small size, localized ribs on their lateral walls and complicated outlines of their central cavities (Gentry 1967 : 295). A left upper molar 1963.3362 is either *S. acoelotus* or *P. oldowayensis*, and a left lower molar 1952.163 and deciduous right P_4 1963.1454 are either *S. acoelotus* or a hippotragine.

Some bovine limb bones smaller than *P. oldowayensis* are presumably conspecific with the smaller bovine teeth. They are proximal end right radius 1963.1628, complete right metacarpal 1952.218, distal end metacarpal 1963.824, proximal end left metatarsal 1952.226, distal ends metatarsals 1955.212, 1963.2547 and doubtfully 1952.221.

The distal end of a right humerus 1953.067/5217 from BK II East is probably bovine. The well-marked distal condyles suggest Alcelaphini, but the low level of the distal lateral end behind the hollow, the shallowness of the distal lateral hollow and the prominent extensor carpi radialis ridge on the distal lateral side are unlike alcelaphine humeri. The coronoid fossa is markedly deep and therefore unlike *Connochaetes*. The size eliminates Reduncini, and the presence of a coronoid fossa rules out Hippotragini.

Tribe Reduncini. A frontlet with incomplete horn cores 1953 P.P.R.1 from BK II East (Leakey 1965 : 47, *Kobus* species A) is assigned to *Kobus kob*. The distal end of a *Kobus* horn core 1953.9 was a surface find at BK II. A reduncine left M_3 1957.1362 is the size of a living kob and agrees well with the M_3 1957.396 from SHK II. A nearly complete left humerus BK II East 1953.442 and the distal end of a left humerus 1957.42 are very likely to be of kob by their combination of slanted distal condyles and a deep hollow on the distal end of the lateral side.

Tribe Hippotragini. *Hippotragus gigas* is represented by a left horn core, possibly female, with the orbital rim and a small part of the braincase 1953 P.P.R.5 from BK II East (Leakey 1965 : 50); a complete horn core 1963.3042 unattached to any skull part but which, by comparison with the horn cores on the *H. gigas* holotype, is from the left side; and a frontal with part of the parietal 067/5345. The horn core 1963.3042 resembles the FLK II horn core of *H. gigas* in being curved back as much as horn cores of the living roan and sable.

A partial left maxilla 1963.2226 and a right mandible with worn P_3–M_1 1952.149 are hippotragine. The short premolar row evident on the mandible resembles that of the *H. gigas* mandible FLKNN I 608. A few single teeth are hippotragine. These are right lower molars 1963.2713 and 1963.067/2437, left lower molar 1955.172, right M_3 1953.067/5224 and deciduous right P^4 1952.167. The last tooth shows an advanced complicated occlusal morphology. The proximal end of a right metatarsal 1953 BK II Ext 137 is probably hippotragine.

Tribe ALCELAPHINI. *Megalotragus kattwinkeli* is represented by the base of a right horn core 1963.2718, labelled '*Alcelaphus howardi*', and differing from the MNK II horn core of *M. kattwinkeli* only in its greater dorsoventral compression. It shows the insertion close to the midline, little divergence at the base and indications of horizontal ribbing on the anterior surface. The pronounced and irregular longitudinal grooving at the base of a complete right horn core 1963.3383 matches that on the holotype of *A. howardi* and suggests that this horn core is not *Connochaetes*. The specimen is narrower transversely at the base than other conspecific horn cores in Nairobi. The base of a left horn core with the frontal 1963.459 is also *M. kattwinkeli*.

Connochaetes taurinus olduvaiensis is represented by a complete right horn core 1963.1353, an incomplete right horn core 1957.18 and a complete left horn core 1955 P.P.F.1. The first shows quite extensive rugosity of the frontals at the horn core base, but less than in the *Connochaetes* specimens from Elandsfontein. 1955 P.P.F.1 was figured by Leakey (1965 : pl. 52 lower picture, which is not BM(NH) M 21452 as stated in the caption), shown in rear view which does not display the full extent of the curvature. The distal half of a left horn core 1963.1278, and the tip of a left horn core 1963.176 showing damage by larvae of *Ceratophaga vastella* or an allied moth, are also of this species. The distal part of a horn core 1957.1505 is extremely similar to 1957.946 from SHK II and may also be from *Connochaetes*.

Parmularius angusticornis is represented by a cranium with the proximal halves of both horn cores 1955 P.P.T.1 which was the holotype of *Damaliscus antiquus* Leakey (1965 : 55; pl. 67), a partial horn core 1963.14, the basal half of a left horn core 1963.2813, a partial frontlet with complete right horn core 1963.2499, a frontlet with both horn cores preserved nearly to the tips 1963.2499, a left horn core 1963.067/1650 and a complete right horn core 1961.068/6660 from BK II East.

A right horn core of *Damaliscus niro*, 1955.159, is very similar to the horn cores already described from SHK II and figured by Leakey (1965 : pl. 55). Its large basal mediolateral diameter diminishes rather rapidly. Other BK II horn cores tentatively assigned to *D. niro* have a different morphology, and have already been listed as types A and B in the species account of *D. niro*; one of them, right 1957.365, had been identified by Leakey (1965 : 51) as *Hippotragus* cf. *equinus*. A fragment of a larger horn core 1953.067/5235 P.P.R.2 (assigned to *Hippotragus* cf. *niger* by Leakey 1965 : 50) has extensive grooving from the activities of a moth larva allied to or the same as the living *Ceratophaga vastella*. A partial skull roof showing the positions of the horn core bases 1963.478 is most likely to be of *D. niro*.

A frontlet without horn cores 1953.067/5460 from BK II East can be assigned to the same species as the horn cores 1941 F.3000 and SHK II 1953.280 by its braincase (see p. 417). The braincase roof bends quite strongly downwards a little way behind the level of the horn core bases. The right frontal is preserved and an internal frontal sinus is present. It is a smaller individual than the other specimens and is the only record of the species at this site.

An incomplete left horn core with the midfrontal suture 1957.662 is of *Aepyceros melampus* (Leakey 1965 : 65; Gentry 1966 : 104); it is one of the few records of the genus at Olduvai.

There is a more complete series of alcelaphine dentitions at BK II than at other Bed II sites, consisting of some 30 partial mandibles and six incomplete maxillae which can be divided into two size groups. None of the dentitions in either size group shows an occlusal morphology as complicated (advanced) as teeth of living *Alcelaphus* or *Damaliscus*.

(i) According to the size and morphology of the teeth on the neotype skull of *Megalotragus kattwinkeli*, the largest dentitions belong to this species. These are left maxilla 1963.2980, immature left maxilla 1963.458, right mandibles 1952.120, 1953 BK II Ext 78, 1955.75, 1957.15, 1957.713 and 1963.2255 and left mandibles 1952.122, 1957.699, 1957.712, 1957.979 and 1957.39 from BK II East. A right mandible 068/5536 is either from this site or SHK II. The mandible 1957.979 has M_1–M_3 preserved and the remains of P_3 and P_4 which have broken off, but no alveolus in the jaw for a P_2. The mandible 1952.122 has a basal pillar on the M_3. A number of dentitions are slightly smaller, but still large, and these presumably belong to *Connochaetes*. They are left maxilla 1963.670, and left mandibles 1952.148, 1952.622 and 1963.3177. The mandible 1952.148 has P_4–M_2 preserved and the remains of P_3, while 1952.622 has P_3–M_1 preserved; neither of these jaws has an alveolus for a P_2. To this size group are assigned 47 upper and 15 lower isolated teeth of large size. The group would have limb bones in the alcelaphine category 'large'.

(ii) Several smaller dentitions are about the size of the living hartebeest and slightly larger than Bed I *Parmularius altidens*. These presumably belong to *P. angusticornis* and *Damaliscus niro*. They are associated right and left maxillae 1952.067/6647 and 067/6646, immature maxilla 1953.067/5219, right mandibles 1957.34, 1963.24, 1963.1065 and 1963.1442, left mandibles 1952.150, 1952.151, 1953 BK II Ext 76, 1957.21, 1963.935, 1963.941, 1963.2444 and 1963.3139, immature right mandibles 1963.291 and 1963.067/1625, and immature left mandible 1963.2550. The adult mandibles 1953 BK II Ext 76, 1963.24, 1963.935, 1963.1065 and 1963.3139 all lack an alveolus in the jaw for a P_2. In the immature mandibles 1963.291 and 1963.2550 deciduous P_2 or its alveolus is present, but in 1963.067/1635 there is no alveolus for a deciduous P_2 and at this early stage P_2 is already missing. Some of the mandibles in this size group, 1963.1065 and 1963.2444 for example, have enough of the mandibular ramus preserved to show that this is deeper under the teeth than in the living hartebeest, and in this respect they resemble the wildebeest. However, the size of the tooth row relative to this depth is too small for *Connochaetes*. These mandibles resemble those with deep rami at HWK East II but are slightly smaller. A left mandible 1957.1452 with P_3–M_3 is smaller than the living hartebeest and is probably a different species from the other specimens, perhaps *Damaliscus agelaius*. It lacks an alveolus for a P_2. In this size group are included 60 upper and 55 lower isolated teeth, although some may belong in size group (i); the difficulty is because we do not know whether an isolated molar is M1, M2 or M3, coupled with the size variations occurring within any one species.

As at other Bed II sites, the alcelaphine limb bones can be divided into two sizes but, among specimens from the 1963 excavation at least, the large size grouping has become more variable. This is unlike SHK II but recalls the earlier sites DK I, FLKNN I, HWK East II and MNK II. The proportion of large limb bones is greater here than at SHK II. The 'large' limb bones are as follows.

Distal ends right humeri 1953 BK II Ext 126 and 1963.378, distal ends left humeri 1957.519, 1963.2440 and 1963.2762, complete left radii 1953 BK II Ext 426+428 and 1963.854+863, proximal ends right radii 1953 BK II Ext 189 and incomplete 1963.644, proximal ends left radii 1953 BK II Ext 50 and incomplete 1963.195, distal ends right radii 1953 BK II Ext 427 and immature 1953 BK II Ext 430, distal ends left radii 1953.067/5234 and 1957.717, complete right metacarpals 1952.219 and 1963.2609, proximal ends right metacarpals 1952.227 and 1963.3378, proximal ends left metacarpals 1953.067/5474 and 1957.541, distal ends metacarpals 1953 BK II Ext 412, 1957.1038, 1963.401 and 1963.3231, incomplete proximal end right femur 1963.403, proximal ends left femora 1953 BK II Ext 8, 1953 BK II Ext 119 and 1955.7, distal ends right femora 1952.83 and 1963.2626, distal ends left femora 1952.81, 1952.82, 1952.211, 1953 BK II Ext 068/6697, 1955.067/5395, 1963.3039 and immature 1952.346, complete right tibiae 1953 BK II Ext 417, 1957.1379, 1963.3036 and immature 1963.801, complete left tibia 1963.2680, proximal ends left tibiae 1952.212 and 1955.316, distal ends right tibiae 1952.215, 1952.229, 1953 BK II Ext 420, 1957.067/5393, 1963.16, 1963.769, 1963.934 and 1963.1934A, distal ends left tibiae 1953 BK II Ext 419, 1955.107B, 1955.283, 1963.1276 and 1963.3232, complete left metatarsals 1953 BK II Ext 416, 1953.067/5508 and 1953.067/5509, proximal ends right metatarsals 1953 BK II Ext 137, 1955.175 and 1963.2434, and distal ends metatarsals 1952.222, 1952.223 and 1953 BK II Ext 411.

The distal ends of tibiae 1955.107B and 1963.769 have some characters resembling Tragelaphini, such as the rear of the back fibula facet being forward from the edge of the bone and the short medial malleolus, but the fairly marked tuberosity on the anterior surface suggests that they are alcelaphine. The metatarsal 1953.067/5509 is short and has an anterior groove, a deep foramen at the top of the posterior surface and deep hollows on the lateral and medial sides of the distal condyles. It has poor flanges on the anterior surface distally and lacks deep hollows above the distal condyles posteriorly. It most probably belongs to *Connochaetes*.

Limb bones of the 'small' category are as follows.

Proximal end right humerus 1953.067/5215, distal ends right humeri 1963.2492 and 1963.2716, distal ends left humeri 1955.263 and 1963.2639, complete left radii 1957.26 and 1957.1466, proximal ends right radii 1953 BK II Ext 173 and immature 1957.1193, proximal ends left radii 1953 BK II Ext 429, 1953.067/5386, 1957.882, 1957.1185 and 1963.2599, distal ends right radii 1952.067/5388, 1953 BK II Ext 067/5209 and 1957.517, distal ends left radii 1953.067/5214, 1955.215 and 1957.1194, right ulna

1963.449, left ulnae 1963.30, 1963.2624 and incomplete 1963.1941, complete right metacarpal 1957.1381, complete left metacarpals 1963.2311 and 1963.3229, proximal ends right metacarpals 1957.15 and 1963.860, proximal end left metacarpal 1957.1469, distal end metacarpal 1957.919, proximal ends left femora 1952.308, 1963.2245 and damaged 1963.2516, distal ends right femora 1953 BK II Ext 30, 1953 BK II Ext 067/5390 and 1955.068/6698, distal ends left femora 1953 BK II Ext 322 and 1953.068/6701, proximal end right tibia 1953 BK II Ext 422, proximal ends left tibiae 1952.217, 1952.632 and 1955.068/6700, distal ends right tibiae 1953 BK II Ext 320, 1953 BK II Ext 321, 1955.36, 1955.107A, 1955.253 and 1957.40 from BK II East, distal ends left tibiae 1952.216, 1953 BK II Ext 177, 1955.319, 1957.57 and immature 1963.067/1633, immature right metatarsal 1957.1192, proximal ends right metatarsals 1955.067/5467 and 1963.2445, distal end metatarsal 1953.207 from BK II East, and the associated complete right femur 1953 BK II Ext 067/5364, complete right tibia 1953 BK II Ext 067/5363 and complete right metatarsal 1953 BK II Ext 067/5506.

A few limb bones are smaller than the others of this category. These are distal ends right humeri 1963.397 and 1963.1642, complete right metacarpal 1953 BK II Ext 337, complete right tibia 1957.1261, proximal end left metatarsal 1953.068/6699 and distal ends metatarsals 1952.224 and 1957.1265.

Tribe ANTILOPINI. An almost complete right horn core 1955.71 is of *Antidorcas recki* (Gentry 1966 : 79).

A nearly complete left horn core 1955.218 + 226 is most probably *Gazella* (Gentry 1966 : 65). Although a little longer and set slightly further from the midfrontal suture, it would be conspecific with the right horn core 1953.285 from SHK II. Despite the very deep postcornual fossa, these horn cores could not be considered as reduncine as they lack forward curvature in their upper parts and are not inserted sufficiently obliquely in side view. An incomplete mandible 1952.152 would probably have a ramus too shallow under the tooth row for *A. recki* and, like the mandible SHK II 1957.793, may well belong to *Gazella* (Gentry 1966 : 66).

A few single teeth and parts of limb bones belong in this tribe. These are right upper molar 1963.2740, left upper molars 1957.1084 and 1963.067/2466, distal end right humerus 1963.3253, distal end left humerus 1957.1039, complete right radius 1963.3037, distal end right radius 1953 BK II Ext 42, proximal end left metacarpal 1957.1264 and distal end left tibia 1963.1365. It is not possible to say whether these would belong to *A. recki* or *Gazella*.

Two horn core bases from this site, right 1957.991 and left 1955.63, appear to be of an antilopine like *Gazella* but with no flattened lateral surface and with considerable divergence (see p. 445). Both specimens have the frontal suture, supraorbital pit and part of the braincase preserved. The same species occurs at MNK II and two horn cores were found on the surface of DK I. It has been listed as 'Antilopini sp. 1'.

SUMMARY. The large size of later Bed II bovids is well shown at BK II by the herd of *Pelorovis oldowayensis*, a number of large *Hippotragus gigas* and the dentitions of *Megalotragus kattwinkeli*. *M. kattwinkeli* and *Connochaetes taurinus*, the largest alcelaphines, are relatively commoner than at earlier Bed II sites. *Damaliscus niro* is common. Antilopini are poorly represented by only one *Antidorcas* horn core and one horn core of *Gazella*. The numbers of bovid bones of each species are shown in Table 9.

Other remains from Upper Bed II

Tribe TRAGELAPHINI. A right upper molar 720 and left upper molar 1220 are from GRC II and are assigned to *Tragelaphus strepsiceros grandis*.

Tribe BOVINI. A right lower molar 640 of *Pelorovis oldowayensis* was found at GRC II in 1952. A left mandibular fragment and a distal metatarsal of *P. oldowayensis*, both unnumbered, are known from MRC II.

The holotype cranium of *Syncerus acoelotus* 068/5811 was recovered from basal gravels at Kar K in 1962. Other pieces of the same species are a cranium collected from FK West in 1962 (National Museum of Tanzania OF 67.48), part of a right mandible 068/5795 which may be associated with the last cranium, a right maxilla 068/6655 from the surface of Rhino K in 1962 and a left metatarsal 068/6662 from SC in 1962.

Table 9 Numbers of bovid bones at BK II

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Tragelaphus strepsiceros grandis	–	–	–	4	1	5	1	–
Pelorovis oldowayensis	28 (1)	–	11	71	76	186	13	1
Syncerus acoelotus	–	1	8 (2)	19	8	36	6	1
Bovini total	28	1	19 (2)	90	84	222	19	2
Kobus kob	2	–	–	1	2	5	2	–
Hippotragus gigas	3	1	1	5 (1)	–	10	2	1
Megalotragus kattwinkeli	3	2 (1)	11	–	–	16	5	1
Connochaetes t. olduvaiensis	5	1	3	–	1	10	3	–
Parmularius angusticornis	7	–	–	–	–	7	5	–
Damaliscus niro	26	–	–	–	–	26	10	–
Alcelaphini sp. 3	1	–	–	–	–	1	1	–
Alcelaphini size group (i)	–	–	–	62 (1)	67 (3)	129		
Alcelaphini size group (ii)	–	3 (1)	15 (3)	115 (3)	61 (3)	194		
Smaller Alcelaphini, group (ii)	–	–	1	–	7	8		
Aepyceros melampus	1	–	–	–	–	1	1	–
Alcelaphini total	43	6 (2)	30 (3)	177 (4)	136 (6)	392		
Antidorcas recki	1	–	–	–	–	1	1	–
Gazella sp.	1	–	1	–	–	2	1	–
Antilopini sp. 1	2	–	–	–	–	2	1	–
Antilopini sp. indet.	–	–	–	–	3	6	9	
Antilopini total	4	–	1	3	6	14	3	–

Tribe Reduncini. A kob frontlet with complete horn cores 068/6659 was found at ? MRC II in 1962, and is smaller than the large kob frontlet and horn core from JK2 GP8 III.

Tribe Alcelaphini. A horn core of *Damaliscus niro* 068/5692 and a few alcelaphine teeth were recovered from GRC II in 1963.

A complete right horn core 068/6654 of *Beatragus antiquus* came from Kit K II at the first fault in 1962.

A left horn core F.3001 P.P.F.5 is probably a male of *Parmularius angusticornis* (p. 388). The fossil is marked 'Bed II *in situ*' and came from upper Bed II in 1941 (Leakey 1965 : 60).

Sites in Bed III and above

JK2 sites

Sites (20, 21) Geologic locality 14

The JK2 sites lie on the north side of the Main Gorge between the third and fourth faults. Beds II–IV are present, except that in this area the separate Beds III and IV give way in a westward direction to Beds III–IV as an indivisible unit. However, the excavated occupation sites are known to be in Bed III.

From the base of Bed IV downwards the following levels are found (R. L. Hay, personal communication, September 1973):

(a) A grey clay.
(b) A prominent horizon of markedly red clay.
(c) A grey clay, this being the level for the occupation site of trench 8, referred to below as the GP8 excavation.
(d) A siltstone, the so-called pit bed.
(e) A sandstone horizon which in its lower parts becomes a conglomeratic sand. The artifacts and fossils excavated in trenches A and B (=JK2 A and JK2 B in the following pages) came from this level, about 1·5 m below trench 8 and 2·7 m above the base of Bed III. These two trenches were formerly believed to have been dug in a channel cutting and therefore to be higher in the section than trench 8, but it is now known that this is not so.
(f) Clay horizons, again giving way below to a conglomeratic sand.
(g) A clay horizon, the base of which rests on Bed II 39 ft (11·8 m) below the top of Bed III.

JK2 III

Tribe Tragelaphini. Four single teeth belong in this tribe. These are right upper molar A.3220 J3, part of a lower molar A.325, right upper premolar JK2 b and deciduous right upper premolar A.1530 J.

The proximal end of a left femur, labelled 'JK2 Top', is tragelaphine. It is rather small compared with the femur 1963.802 from BK II assigned to *Tragelaphus strepsiceros grandis*.

Tribe Bovini. A number of partial dentitions and isolated teeth are bovine. These are right maxilla A.1021, right mandible A.2833, left mandible JK2 b, right upper molars A.975, A.2859, B.FL2, B.FL2-19, B.FL3-16, B.FO3-40 and one from the scree in trench B, left upper molars A.188, A.1091, incomplete A.2101 and one from the scree in trench B, part of an upper molar JK2 b, right lower molars A.1913 I and A.3210, left M_3 B.FFM5-6, parts of lower molars A.370, A.2533, A.N30, B.FO8-5, B.S/F II 43 and two found in 1961, left P_2 A.3270 F3a, and left lower premolars A.3270 G3, B.FL3-79 and JK2 Top. These are presumably of *Syncerus acoelotus* although the larger ones, mandible JK2 b and upper molar A.188 for example, might be of sufficient size for *Pelorovis antiquus*, were this species to occur at so early an horizon.

A few limb bones belong in this tribe. They are distal end right humerus JK2 B, distal end left humerus B.FFL5-6, proximal ends left radii A.1951 and B.FIF N4-14, distal epiphysis of right radius JK2 b, distal end metacarpal A.1830, part of the distal end of left tibia A.1515 and part of the proximal end of right metatarsal A.2879. The bones are of large size and proximal end radius A.1951, distal end metacarpal A.1830 and distal end tibia A.1515 are as large as Bed II *P. oldowayensis*. The medial malleolus on distal end tibia A.1515 is short as in the *Syncerus* and *Pelorovis* group of African bovines (see Gentry 1967 : 282).

Tribe REDUNCINI. A left upper molar A.1438 N is only just larger than upper molars of living *R. redunca* and is probably *Redunca*. A right lower molar JK2 b and deciduous left P_4 A.3271 M8 are probably of a kob-sized reduncine, as at JK2 GP8 III. A larger reduncine left lower molar B.FFM4-9 is from a waterbuck-sized reduncine.

The distal end of a right tibia JK2 b is reduncine and of *Kobus* rather than *Redunca* size.

Tribe HIPPOTRAGINI. The base of a large left horn core A.2677 is probably *Hippotragus gigas*. Three single teeth are of *Hippotragus* and presumably *H. gigas*. They are right lower molar A.3028, left lower molar A.2838 and part of a right lower molar found in 1961.

Tribe ALCELAPHINI. *Megalotragus kattwinkeli* is represented by a complete right horn core, A.72 found in 1961, with the frontal, orbital rim and a series of supraorbital pits preserved. It agrees well with other specimens in the close, posterior horn core insertions, divergence at the base decreasing higher up and strong transverse ridges. The base of the horn core is swollen anteriorly. The horn core is smaller than some other specimens of the species, MNK II 3258 for example, and is therefore possibly a female. It is not dorsoventrally compressed. Part of the right side of the braincase of this fossil is preserved, numbered A.78, but is separated from the horn core. The basal half of a left horn core with the frontal preserved, A.2426, is also *M. kattwinkeli* and demonstrates the extreme bending down of the braincase on the facial axis in this species. It too has a swollen base anteriorly.

Damaliscus niro is represented by a horn core complete to the tip but without a base, marked '1963 JK2 Bed IV basal gravel *in situ*', and the proximal half of a horn core also marked '1963 JK2 Bed IV *in situ*'. They show the characteristic features of this species, being very compressed, with a flattened lateral surface, transverse ridges on the front surface, wider at the front than behind and backwardly curved in side view. They are as large as the horn cores from SHK II and BK II 1955.159. The basal part of a left horn core of *D. niro* A.1130 has the orbital rim and part of the frontal preserved; it lacks transverse ridges, but there is a postcornual groove and the frontal behind the horn core descends too steeply for *Hippotragus*. The base of a right horn core A.118 is also of *D. niro*. Parts of a horn core A.976 and a right horn core A.2348 are like the type A horn cores from BK II tentatively assigned to *D. niro*.

A fairly small right horn core, A.03 220 recovered in 1961, is referred to *Parmularius rugosus* (p. 392). It is clearly alcelaphine by its internal frontal sinuses, postcornual groove and fairly complex curvature.

A frontlet A.1129 with the proximal half of the right horn core and both orbital rims, and an almost complete left horn core B.E/S K7-1 with the frontal, parietal, complete orbital rim and the supraorbital pit, are of *Rabaticeras arambourgi* (p. 408). Both specimens were recovered in 1962. A fragmentary left horn core A.346 found in 1961 is also of this species.

Two horn cores agree well with those of the herd of *Damaliscus agelaius* excavated from Fifth Fault Korongo (site VFK) III–IV. These are a left horn core A.1446 found in 1962 and a partial horn core marked '1961 B.T.T.F. Floor'. The distal part of a horn core A.345 is probably *D. agelaius*.

The alcelaphine dentitions and single teeth can be divided into two size groups as at the Bed II sites.

(i) An incomplete right mandible A.2828 and left mandible A.3261 are of *Connochaetes* or a rather small *Megalotragus kattwinkeli*. The molars have a somewhat simple occlusal pattern as in *M. kattwinkeli*. A number of large isolated teeth belong in this size group. These are right upper molars A.594 KG, A.1213, A.1914, A.2011, A.2271, A.2334 H, A.2257, A.2573, A.2808, B.FL3, B.F3-29, B.FO4-25, B.FP4-21, one from the scree in trench B, two labelled JK2 b and two labelled JK2 Top, left upper molars A.2931, A.3273, B.FP6-42, one from the scree in trench B, and one labelled JK2 Top, right lower molars A.1424, A.2810, B.FP7-1, JK2 b and one from the scree in trench B, left lower molar A.2000, right M_3s A.1739, A.1955, A.2584 M8, A.2718 and B.FP4-2, and left M_3s A.1099, A.1821, A.2078 and A.3020. A left upper molar A.990 is larger than the others.

(ii) Two partial right maxillae labelled JK2 and a right maxilla labelled JK2 Top belong in this size group. There are also the right mandibles A.1444, A.2060, A.2091, A.2780, A.2934, A.3012, B.FQB-1 and B.FQ4-10, left mandible B.FL2-21 and immature right mandible A.2157. The mandibles A.2060, A.2091, B.FQB-1 and B.FQ4-10 all lack an alveolus in the jaw for a P_2. Both upper and lower molars have more complicated central cavities, with a greater development of indentation, than teeth of this size group in Bed II. A few mandibles are smaller and agree in size and morphology with dentitions of the VFK III–IV herd of *Damaliscus agelaius* with which they are presumably conspecific. They are the left mandibles A.384, A.1372, B.FFM3-14 and 1963.068/6692. Both A.384 and 1963.068/6692 lack an alveolus in the jaw for a P_2. 149 upper and 187 lower isolated alcelaphine teeth belong in this size group.

The alcelaphine limb bones can also be divided into two size groups as at the Bed II sites. The category of 'large' limb bones consists of distal ends right humeri A.556, A.2444 and B.S/F II 39, distal end left humerus A.817, proximal end left radius A.1322, distal end right radius JK2 IV gravel, distal end left radius A.758, complete left metacarpal A.1272, distal ends metacarpals A.719, A.1201, A.1455, A.1859 and B.FQ2-2, distal end left tibia JK2 Top and distal end metatarsal B.FFN5-12. These would belong with the teeth of size group (i). The bones are presumably at least partly of *Megalotragus kattwinkeli.*

Most of the limb bones are 'small' sized. They would belong with the teeth of size group (ii). They are distal end right humerus B.II 10, complete right radius A.1305 + 1491, proximal end left radius B.II, distal ends right radii A.3218, B.FFM3-2 and JK2 b, distal ends left radii A.1454 and B.S/F II 33, left ulna A.1048, complete right metacarpal A.1592, proximal end right metacarpal B.FM5-8, proximal end left metacarpal A.1402, distal ends metacarpals A.646, A.1517 and B.II 36, proximal end right tibia A.1565, proximal end left tibia A.1627, distal ends left tibiae A.L6 135 and JK2 b, proximal ends right femora A.708 and A.926, proximal ends left femora A.142 and A.2198, distal end left femur A.343, complete left metatarsal A.1671, proximal end immature left metatarsal A.2122 and distal ends metatarsals A.376, A.871, A.1872 and B.3. Some of the bones are transitional to the 'large' category. A few limb bones are smaller than the others in this category. These are distal end right humerus A.1219, proximal end right radius A.2077, proximal ends left radii A.1701, JK2 and JK2 Top, right ulna A.1882, proximal end left tibia A.433, distal end right tibia B.34, distal end left tibia B.FFM11-5 and distal end metatarsal A.1478.

Tribe Antilopini. This tribe is represented by two mandibles, a right B.FM4-7 and a left from the scree in trench B. On the left one it can be seen that there is an alveolus for a P_2. There are also a number of isolated teeth. These are right upper molars A.1595 M9, A.1696 J, A.4524 J and JK2 B, left upper molars A.725, A.1696 L and JK2 b, right lower molars A.1643 and A.3271 MO, left lower molars A.963 and one from the scree in trench B, left M_3s A.1696 L and one from the scree in trench B, left P_3 and P_4 JK2 b and a lower premolar A.1643. They are likely to be of *Antidorcas recki.*

Summary. By JK2 III times a different representation of bovids from that at the Bed II sites has appeared. There is no definite *Pelorovis*, and the bovine remains are of *Syncerus acoelotus. Megalotragus kattwinkeli* and *Damaliscus niro* are still present, as in Bed II, but the sparsely represented *Parmularius* is *P. rugosus* and not the common Bed II *P. angusticornis. Rabaticeras arambourgi* is a new arrival among the fossils. Antilopine remains are few.

The numbers of bovid bones of each species at JK2 III are shown in Table 10. Alcelaphine teeth and limb bones of size group (i) are likely to be of *Megalotragus kattwinkeli*, and those of size group (ii) would include *Damaliscus niro* and *Rabaticeras arambourgi.* The most likely identity for the smaller alcelaphines of size group (ii) is *Damaliscus agelaius.*

JK2 GP8 III

Tribe Bovini. Right mandibles GN 24 and Sec 6, right upper molars GN 5 and GN 21, parts of two lower molars Sec 4 1334 and 1335 and a left P^4 labelled 'GP8 Sec 8' are likely to be of *Syncerus acoelotus.* The teeth are smaller than in *Pelorovis oldowayensis* and have a more complicated occlusal pattern. The P_4 on mandible GN 24 has a closed metaconid–paraconid wall which is unlike *S. acoelotus* teeth, but this could be because the tooth is very worn.

Tribe Reduncini. A complete right horn core 1247 and a frontlet with complete left and nearly

Table 10 Numbers of bovid bones from JK2 III

	Skull parts	Maxillae	Mandibles	Isolated teeth	Limb bones	Total	Minimum number of individuals	
							Adult	Immature
Tragelaphus sp.	–	–	–	4 (1)	1	5	1	1
Syncerus acoelotus	–	1	2	26	8	37	3	–
Kobus spp.	–	–	–	3 (1)	1	4		
Redunca sp.	–	–	–	1	–	1	1	–
Hippotragus gigas	1	–	–	3	–	4	1	–
Megalotragus kattwinkeli	2	–	–	–	–	2	2	–
Damaliscus niro	6	–	–	–	–	6	3	–
D. agelaius	3	–	–	–	–	3	1	–
Rabaticeras arambourgi	2	–	–	–	–	2	2	–
Parmularius rugosus	1	–	–	–	–	1	1	–
Alcelaphini size group (i)	–	–	2	39	15	56		
Alcelaphini size group (ii)	–	3	10 (1)	336	30 (1)	379		
Smaller Alcelaphini, group (ii)	–	–	4	–	10	14		
Alcelaphini total	14	3	16 (1)	375	55 (1)	463		
Antidorcas recki	–	–	2	16	–	18	2	–

complete right horn cores 068/6694, both excavated in 1962, are of *Kobus kob* but with some differences from the living representatives of this species. The postcornual fossae are not preserved. A reduncine left M_3 GN 47 can probably be regarded as conspecific with the horn cores. It is larger than the teeth of the MNK II kob and the left M_3 from SHK II attributed to a kob.

The lower part of a damaged left horn core 1654 found in 1961 is probably of *Kobus ellipsiprymnus.* It has almost no mediolateral compression.

Tribe ALCELAPHINI. Two complete right horn cores, 674 and S.6 1627a both excavated in 1962, are of *Damaliscus niro.* They are compressed with flattened lateral surfaces, wider at the front than behind, and backwardly curved in side view, as is typical of the species. 674 lacks transverse ridges on the front surface. It is fairly thick at the base, as in SHK II 1953.282, with the cross-section widest anteriorly. It has a postcornual fossa and the braincase is strongly angled on the face. Both specimens are as large as the SHK II horn cores 1953.282 and 1957.1184. A partial horn core GN 44 also belongs to this species.

Left mandibles GN 16 and Sec 5 1614+1615 are the size of group (ii) dentitions in Bed II. GN 16 can be seen to have an alveolus in the jaw for P_2. A right mandible from Sec 6 is smaller than the others and is the size of dentitions of the VFK III–IV herd of *Damaliscus agelaius.* A left upper molar GN 53, right M_3 286, left M_3s 1501 and Sec 6, and right lower premolar GN 54 are alcelaphine. A left upper molar GN 36 is larger than the others.

A complete right metacarpal GN –, proximal end left metacarpal GN 54, complete left tibia GN 22 and proximal end right tibia GN 38 are 'small' sized alcelaphines and would go with the size group (ii) dentitions.

Tribe ANTILOPINI. A left mandible with P_4 and M_1 preserved, and a left lower molar, both labelled 'GP8 Sec 6', belong in this tribe. It is not possible to determine whether they are *Antidorcas recki* or *Gazella* sp.

Other remains from Bed III

Tribe TRAGELAPHINI. Part of a large tragelaphine horn core was found at JK1 in 1961 and is said to be from Bed III. The piece is from the left side and agrees with *Tragelaphus strepsiceros grandis* in its clearly triangular cross-section.

Remains from Beds III–IV (undivided)

Tribe BOVINI. A left maxilla with M^1 and M^2 which was a surface find from BK III–IV in 1955 could be either *Syncerus acoelotus* or *Pelorovis antiquus.*

A partial juvenile skull of *Syncerus acoelotus* came from the Bos K III–IV surface in 1962, and a frontlet from VFK high in the Beds III–IV unit in 1961. These pieces are both in Dar-es-Salaam with the numbers OF 68.274 and OF 68.196 respectively.

Tribe ALCELAPHINI. Several skulls, mandibles and associated skeletons of a herd of *Damaliscus* were excavated from VFK III–IV in 1962 and have been diagnosed as a new species, *D. agelaius,* in the preceding pages. The herd consists of a male cranium 214; skulls 133, 134, 140, 143, 150, 176, 235, 298, 350, 357, 359, 363 and one without number which are probably all females, most with complete horn cores and maxillae, and 134, 350 and 363 with associated mandibles; partial skull 172; back of a skull without number; three horn cores presumably of females; a palate; right mandibles 154 and 171 and left mandible 156; and a large number of limb bones and vertebrae, mostly rather crushed and embedded in matrix. A right horn core 068/6661 from the surface of Hoopoe Gully was found in 1962, and a frontlet 068/5730 labelled XDK was found in 1961. Both are males of this species. The first probably came from Beds III–IV (undivided) or perhaps Bed II, while the second could have come from the same units or even from Beds III or IV.

Remains from Bed IV

Tribe TRAGELAPHINI. The cranium of *Taurotragus arkelli* F.3665 P.P.T.4 (Leakey 1965 : 43; pls 43–44) came from the surface of Bed IV between LK and RK in 1941.

Tribe BOVINI. A right upper molar 689 from GC IV is either *Syncerus acoelotus* or *Pelorovis antiquus.*

Tribe REDUNCINI. A left horn core 068/6658 of *Kobus ellipsiprymnus* was found at the junction of Beds III and IV at EF-HR in 1962. It was a surface find.

Tribe ALCELAPHINI. A frontlet of *Megalotragus kattwinkeli* 068/6664 was found *in situ* at GTC IV in 1962. It is rather small, but agrees with other specimens in the close insertions, divergence and curvature of the horn cores, and is possibly a female. The horn cores are not dorsoventrally compressed. Part of a braincase found with the frontlet appears to belong to a small tragelaphine. The base of a right horn core with the frontal 596 from GC IV is also *M. kattwinkeli*. It is very anteroposteriorly compressed.

A partial skull 068/5976 came from east of the second fault in upper Bed IV or the Masek Beds in 1963. It is well-preserved and not crushed but lacks horn cores and teeth. It has been rather doubtfully linked with *Rabaticeras* or *Alcelaphus* (p. 417).

The distal part of a horn core from the surface of Bed IV, F.971 found in 1941, is *Damaliscus niro*.

Recent excavations in Beds III and IV and the Masek Beds

Since 1969 Mrs M. D. Leakey has undertaken further excavations in Bed IV, and we have been able to see some of the bovid material during a visit to Africa in autumn 1973.

JK FERRUGINOUS SAND, BED III, 1969. Part of a right mandible 356 with M_1 and M_2 is an alcelaphine of size group (ii). The M_2 has an occlusal length of 21·4 mm. There are also six other alcelaphine teeth of size group (i) and nine of size group (ii).

JK GREY SAND, BED III, 1969. Apart from two left lower molars of *Syncerus*, 623 and 657, the other remains from this site are of Alcelaphini. Part of a left mandible 475 has P_4 and the molar row, an alveolus for P_3 but no alveolus for P_2. Part of a left mandible 472 has M_1 to M_3, and part of a right mandible 697 has M_2 and M_3. All three mandibles belong to size group (ii). In addition there are three teeth of size group (i) and nine of size group (ii).

JK SANDSTONE ABOVE PITS, BED III, 1969. There were found in two trial trenches a fragment of a left mandible with M_2 and M_3, two left P_4s and an atlas vertebra, all alcelaphine.

JK, BED III, 1969. A right upper molar, III/4 607, belongs to *Pelorovis oldowayensis*, and the distal end of a right humerus, III/7 1042, is alcelaphine.

JK2, BED III, 1969. A cranium with horn cores is marked TT 1 and belongs to *Parmularius rugosus*.

HEB IV, 1969. A right lower molar is bovine and a right upper molar alcelaphine.

HEB EAST IV, 1969. A frontlet with horn cores 814 is of *Antidorcas* and may be *A. recki* or an early example of *A. marsupialis*.

HEB WEST IV, 1969. A right mandible IV/3 1540 with P_4 to M_3 is an alcelaphine of size group (ii) and the P_4 and M_3 are erupting. Another alcelaphine right mandible has deciduous P_4 and M_1 with an erupting P_3, but is of size group (i). Three other alcelaphine teeth are all of size group (i).

A tragelaphine and a bovine left upper molars also come from this site.

PDK IV, 1969–70. The base of a right and a left horn core, 969 and 970, belong to *Tragelaphus strepsiceros*. The anteroposterior and mediolateral diameters at the base of 969 were 56·5 and *c.* 47·6 mm.

The base of a left horn core 1498 from trench IV appears to be of *Rabaticeras arambourgi*. We also saw seven alcelaphine teeth of size group (i).

A left and a right upper molar belonged to the Antilopini.

WK IV, 1970. This site is discussed by M. D. Leakey (1971a).

A nearly complete left horn core 3641 belongs to *Taurotragus*.

A left P_3 5353 belongs to the Bovini.

Part of a right mandible with P_2 and P_3 is from a large reduncine.

Part of a right mandible 2196 with deciduous P_4, M_1 and M_2 is an alcelaphine of size group (i). There are seven other alcelaphine teeth of size group (i) and two of size group (ii).

Part of a left mandible 716 with M_2 and M_3 belongs to the Antilopini and there are five other teeth of this tribe. 1580 is a complete right radius of an antilopine with a length and least thickness of 164 and 17·1 mm.

WK East IV A, 1970. A right lower molar 3354 is tragelaphine.

A nearly complete right horn core 2305(5) belongs to *Pelorovis antiquus*.

A left M_3 1922 with occlusal length 45·3 and height 45·1 mm and a left lower molar 1698 are both *Syncerus*. A left upper molar 3287 is also bovine.

A right lower molar 814 is reduncine.

2866 is part of a left alcelaphine mandible with M_2 and M_3 which can be put into size group (i). 3029 is part of an alcelaphine right mandible of size group (ii) preserving P_4 and M_1. There are also eleven other alcelaphine teeth of size group (i).

A right mandible with damaged molars, 486, is antilopine.

WK East IV C, 1970. Two left lower molars, 190 and 660, are bovine, the second being probably an M_3 and probably *Syncerus*.

A left upper molar 355 is reduncine.

Six alcelaphine teeth belong to size group (i).

Two right upper molars are of Antilopini.

FLK, Masek Beds, 1969. We saw from this site a reduncine right upper molar, three alcelaphine teeth and a right upper and left lower molar and a left M_3 of an antilopine.

Conclusions

The evolution of antelope species

The array of fossil bovids at Olduvai, other east African sites and the South African sites can be seen in various ways. In one interpretation, that found in traditional palaeontological work, they represent a great many extinct species, among which one is very unlikely to find any actual ancestors of later or living species. This approach pays attention to the differences between fossils and heightens the degree of faunal endemism at different sites. It implies the contemporaneous existence of very large numbers of evolutionary lineages. In a second interpretation, which we support, the fossils are thought to represent a smaller number of evolving lineages, some or most of which have survived to the present day. The range of variation of horn core characters and even of some tooth characters changes within any lineage from one temporal level to another, and one can imagine that the geographical ranges of infraspecific varieties have fluctuated from time to time. This interpretation has to be fully stretched to account for some anomalies. If, for example, *Damaliscus agelaius* gave rise to either or both the living *Damaliscus* species, how does one account for the ancestral lack of P_2? The shorter premolar row of *Kobus sigmoidalis* than of living waterbuck is a less acute version of the same problem. If the Olduvai kudus are a single lineage leading to living *Tragelaphus strepsiceros*, how is it that a higher proportion of P_4s lack paraconid–metaconid fusion at the present day than in Olduvai times?

While new species may occasionally have arisen from unsuccessful antelope species occupying restricted ranges, they seem more often to have arisen from within successful species or species groups. Successful species are likely to be widespread and to show morphological differences in various parts of their ranges. Some of the anomalies of dental evolution could be explained by postulating origins of new species from fringe populations in which some characters are atypical, or from the less advanced species among pairs or groups of species. Again, the less advanced tooth characters of some living antelopes may indicate that they have less narrow adaptive ranges than their extinct relatives. Perhaps the greater number of contemporaneous species in the past, of pigs as well as antelopes, necessitated a closer adaptive relationship between each species and its environment. Guthrie (1968) faced similar problems with early Tertiary North American artiodactyls, among which the limb bones of later forms were less advanced than earlier forms. He concluded that some Oligocene genera with four fully functional toes in the hind foot had descended from Eocene ancestors with smaller lateral toes. There had been a degree of evolutionary reversal in a character apparently of fundamental importance.

When sufficient numbers of new characters spread through a species, an adequate fossil record will show a smooth transition of one species (= a chronospecies) or subspecies to another. However, R. D. Martin (1972 : 316), in a discussion of lemur evolution, has proposed that a lineage might consist of sequentially-replacing species. Newly-evolved species compete with their immediate predecessors, and the competition favours increasing refinement of features which provide incremental increase in survival value. This is a development of the concept of iteration (see Simpson 1953 : 248), and is a different evolutionary process from that of gradual infra-specific change. We have interpreted most of the changes in bovid lineages as examples of the first process, for example the transition from *Kobus sigmoidalis* to *K. ellipsiprymnus*. One could also imagine, following Simpson (1953 : 198), that there have been bursts of accelerated evolution during a transition, as in the postulated changes from *Pelorovis oldowayensis* to *P. antiquus* and from *Parmularius altidens* to *P. angusticornis*. An example of the second process, sequential replacement, might have been *Tragelaphus strepsiceros* competing successfully against the Shungura *T. gaudryi*, but in this case it is possible that *T. gaudryi* was not exterminated but turned into *T. imberbis* instead. We still do not know enough about the evolution of species. When young male antelopes, perhaps with new characters of survival value, disperse or are chased from the territories of their birth, do they wander far, are they acceptable mates to females living further away and what success do they have in leaving descendants? Perhaps no generalizations are possible about this.

Distribution of bovid species at Olduvai

The species list given in Table 11 summarizes the general account of the Olduvai bovids given in the first part of the paper and shows simply the presence or absence of the species in the various beds. Table 12 (pp. 56–7) shows the distributions in greater detail; it summarizes the account of the various sites given in the second part of the paper and also includes material collected before the Second World War. In both tables we have distinguished between secure records and those for which there is doubt about either the species identification or stratigraphical level. In using the tables one should remember that the collections made until the 1950s included a high proportion of surface finds, and that recent changes of geological interpretation are particularly liable to affect the placing of pre-war material from Beds III and IV. For example, the occurrence of *Pelorovis oldowayensis* in Bed IV is based only on the holotype collected in 1913, and it would be good now to have further substantiation. Fortunately M. D. Leakey (1971b : 282–289) has recorded the horizons of most of the more important specimens collected in earlier decades.

Ecology of the Olduvai bovids

The ecology of the Olduvai bovids may be compared with that of their close living relatives as deduced from Ansell (1960, 1971), Child & Wilson (1964), Hofmann & Stewart (1972), Jarman (1974), Pienaar (1974) and other sources. As a whole, they indicate a rather dry and open environment. The only tragelaphine which is even moderately common is the greater kudu which today has a widespread distribution in diverse habitats which have some degree of cover. It is commoner in Bed I than in later beds. The eland, a gregarious and mainly browsing antelope, is very rare at Olduvai. Like the greater kudu and unlike other tragelaphines it occurs in a variety of habitats, even in fairly dry areas. The buffalo of today is an unselective grazer often found among denser, ideally riverine, vegetation, and it would not have occurred away from areas in which it could find places to wallow. It is not uncommon later in Bed II. The waterbuck lineage is reasonably common only in the lower parts of Bed I, as at the sites DK and FLKNN. Its presence conforms with other evidence at these sites pointing to nearby standing water at this time. Hirst (1975 : 32) observes that waterbuck may depend on habitats which are found only near water, rather than directly on water. Another reduncine, the kob, occurs rather sparsely in the later parts of the Olduvai sequence. While the waterbuck browses less infrequently than other reduncines and sometimes enters lightly wooded country, the kob rarely enters cover. The oryx lives in very arid country, is always rare as a fossil and only one, or perhaps two, horn cores have been found in Bed I. Presumably its normal habitat lay at some distance from the area of the present Gorge, and it came only rarely to water or was hunted only rarely by the hominids. *Hippotragus gigas* could be pictured as grazing in non-arid areas of long grass adjacent to woodland, if it was at all like modern *H. equinus*. It is present but not common in Olduvai Beds I–III. The Alcelaphini are the most characteristic antelopes of Olduvai, especially in middle Bed II and later horizons.

They would have grazed on short grass in open country or in clearings with good visibility, and could have tolerated greater aridity than reduncines or *Hippotragus*. *Antidorcas* is the commonest antilopine, notably in Bed I. As with the living springbok, an important component of its diet may have been arid-country dicotyledonous plants. The rarer Olduvai *Gazella* would have been

Table 11 Bovid species list for Olduvai Gorge

			Bed II					
		Bed I	Lower		Mid. + Up.	Bed III		Bed IV
TRAGELAPHINI								
Tragelaphus strepsiceros maryanus	} L	X	X		O			
Tragelaphus strepsiceros grandis	}				X	X		X
Tragelaphus aff. *spekei* or *scriptus*	L ?	O			X			X
Taurotragus arkelli	A			O				X
BOVINI								
Pelorovis oldowayensis	} E				X	X		O
Pelorovis antiquus	}							X
Syncerus acoelotus	A	X	X		X			X
REDUNCINI								
Kobus sigmoidalis	} A	X	X		X			
Kobus ellipsiprymnus	} L	O				X	X	
Kobus kob	L				X	X		
Redunca sp.	L ?	X			X	X		
Thaleroceros radiciformis	E							X
HIPPOTRAGINI								
Hippotragus gigas	E ?	X	X		X	X		
Oryx sp.	L ?	X						
ALCELAPHINI								
Megalotragus kattwinkeli	E	O	O		X	X		X
Connochaetes africanus	A			X				
Connochaetes sp.	} A	X			X			
Connochaetes taurinus olduvaiensis	} L				X	X		X
Parmularius altidens	} E	X	X					
Parmularius angusticornis	}				X			
Parmularius rugosus	E		O		O	X		X
Damaliscus niro	E				X	X		X
Damaliscus agelaius	A		X		X	X		
Rabaticeras arambourgi	A					X		X
Beatragus antiquus	A	X	X		X			
Alcelaphini, sp. 1								O
Alcelaphini, sp. 2			X					
Alcelaphini, sp. 3					X			
Alcelaphini, sp. 4	E	X	O		O			
Aepyceros melampus	L	X			X			
NEOTRAGINI								
sp. indet.		O			X			
ANTILOPINI								
Antidorcas recki	} A	X	X		X	X		X
Antidorcas sp.	} L ?							X
Gazella sp.	A	X			X			
Antilopini, sp. 1	E	X			X			
CAPRINAE								
? Caprinae, sp. indet.	E	X						

}=one lineage, X=secure record, O=of uncertain horizon or identification. E=extinct lineage, A=ancestral species of an extant lineage, L=living species.

more of a grazer, perhaps akin to the west African *G. rufifrons* rather than to the specialized grazing of the Serengeti *G. thomsoni.*

Fig. 36 shows the percentages of alcelaphine and antilopine bones at the excavated sites at Olduvai. The alcelaphine readings at SHK II and BK II have been brought low by the distorting effects of the herds of *Antidorcas recki* and *Pelorovis oldowayensis* found at these two sites. Otherwise the picture given from FLKNN I onwards would be of increasingly abundant alcelaphines throughout the series of excavated sites, and of *Antidorcas recki* being well-represented higher in Bed I. If these figures reflect hominid hunting preferences, one might deduce that *A. recki* was abandoned as prey after Bed I. If they should indicate the natural occurrence of bovids in the area, they are evidence for a rather dry open bushland or tree savannah plains as the predominant habitat. However, less common bovids, such as buffalo, kob and the *Hippotragus*, indicate the presence of some less arid environments in the Olduvai area. The kob is absent from nearly all of Tanzania and Kenya at the present day.

Size of bovids at Olduvai Gorge

In the past Olduvai Gorge has been noted as a site for giant-sized animals. One important factor contributing to this reputation was the old misidentification of *Pelorovis oldowayensis* as a relative of sheep. Once *Pelorovis* had been recognized as a bovine, its large size became less startling, for its nearest living relative was now the slightly smaller buffalo *Syncerus caffer* and not the very much smaller sheep. Nevertheless, the Olduvai bovids as a whole continue to give the impression of being larger animals than those living today, even if one cannot call them giant. This impression is derived from a number of examples at different taxonomic levels of comparison. Two of the extinct lineages, *Pelorovis* and *Megalotragus*, are larger than surviving members of the same tribes, and *Thaleroceros radiciformis* could also be larger than living reduncines, although this is not certain. *Hippotragus gigas* and *Beatragus antiquus* are larger than surviving members of the same genera, and *Tragelaphus strepsiceros grandis* and the Bed III *Kobus kob* than surviving members of the same species. Also at the species level of comparison, *Damaliscus niro* is larger than its conspecific descendants at later sites in South Africa.

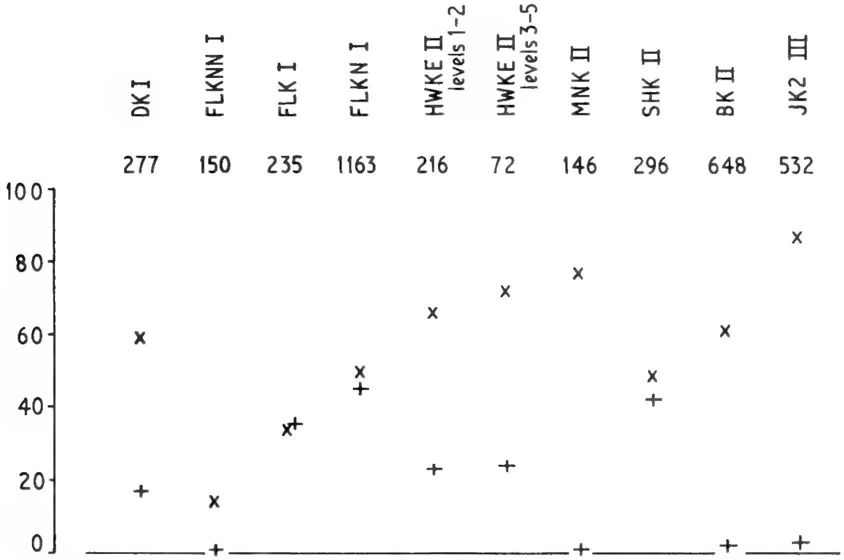

Fig. 36 Percentages of Alcelaphini and Antilopini among the bovid bones identified to tribal level or below at the excavated sites at Olduvai Gorge. The numbers along the top are the bone totals from which the percentages were calculated for each site. X = Alcelaphini, + = Antilopini.

Table 12 Stratigraphical distribution of species

Species List	Bed I	Lower Bed II	Middle Bed II	Upper Bed II
Tragelaphus strepsiceros maryanus	DK, FLKNN, FLK, FLKN	HWKE, *FLKN*	*HWKEE*	
Tragelaphus strepsiceros grandis			MNK, SHK	GRC, BK, RK
Tragelaphus aff. *spekei* or *scriptus*	*London*		SHK	
Taurotragus arkelli				
Pelorovis oldowayensis			HWKE, MNK, (FC), SHK	GRC, *TK*, BK, *PLK*, MR
Pelorovis antiquus				
Syncerus acoelotus	DK, FLK, FLKN	HWKE	MNK, Elephant K, SHK	Kar K, (Rhino K), FKW TK, SC, BK
Kobus sigmoidalis	DK, FLKNN, FLK, London > FLKN, Geol. loc. 63	FLKN, HWK, HWKE	HWKEE, *MNK*	
Kobus ellipsiprymnus				
Kobus kob			MNK, SHK	? MRC, BK
Redunca sp.	DK, FLKN			
Thaleroceros radiciformis				
Hippotragus gigas	DK, FLKNN, FLK, *FLKN*, VEK	*HWKE*	*HWKE*, *MNK*, FLK, SHK	TK, BK
Oryx sp.	FLK, *London*			
Megalotragus kattwinkeli	*DK*, *FLKNN*, *FLK*	*HWKE*	*HWKE*, MNK, SHK	(SC), BK
Connochaetes africanus				
Connochaetes sp.	*FLKNN*, *FLK*, FLKN		HWKEE	
Connochaetes taurinus olduvaiensis			*MNK*, *SHK*	BK
Parmularius altidens	DK, FLKNN, FLK, FLKN, HWK	> FLKN		
Parmularius angusticornis			HWKEE, Long KE, SHK	(SC), (MRC), BK, (DC)
Parmularius rugosus		*HWK*	*HWKE*, *HWKEE*, *SHK*	
Damaliscus niro			Elephant K, SHK	GRC, BK Geol. loc. 54
Damaliscus agelaius		FLKW		
Rabaticeras arambourgi				
Beatragus antiquus	MJTK, FLKN	FLKN, HWKE		Kit K
Alcelaphini, sp. 1				
Alcelaphini, sp. 2		Nairobi		
Alcelaphini, sp. 3			SHK	BK
Alcelaphini, sp. 4	*DK*, FLKN	*HWKE*	*HWKEE*	
Aepyceros melampus	THC		(SHK)	BK
Neotragini, sp. indet.	*FLKN*		FCW	
Antidorcas recki	DK, (THC), KK, *FLKNN*, FLK, VEK, FLKN	*FLKN*, HWK, HWKE	HWKE, HWKEE, *MNK*, Long KW, SHK	FLK, *TK*, BK
Antidorcas sp.				
Gazella sp.	London, KK		HWKEE, FCW, EF-HR, SHK	FLK, BK
Antilopini sp. 1	(DK)		MNK	BK
? Caprinae sp. indet.	London, FLKN			

The large size of most of these forms is manifested most clearly in middle and upper Bed II. Thus the herd of *Pelorovis oldowayensis*, the best-preserved fossils of this species, was found at BK II. The very large alcelaphine teeth are larger in middle and upper Bed II than in Bed III. The largest examples of *Hippotragus gigas* and *Damaliscus niro* occur in Bed II, and the holotype of *Tragelaphus strepsiceros grandis* comes from upper Bed II. Another factor giving one the impression of large bovids in middle and upper Bed II is that both *Connochaetes taurinus* and *Parmularius angusticornis* are larger than their ancestral species in Bed I.

It is difficult to quantify the concept of large bovids at Olduvai Gorge. One has to decide at what stratigraphical and taxonomic levels to make the comparisons, and what measurements or other criteria to use. Two examples of possible comparisons are available from Figs 5 (p. 302). and 15 (p. 345). In Fig. 5 *Tragelaphus strepsiceros grandis* has linear skull dimensions which are on average 17% greater than in the living greater kudu sample used as a standard, although it should be remembered that the greater kudu sample is based on museum specimens which are

d II, vel unknown	Bed III	Beds III–IV undivided	Bed IV	Remarks
				Limb bones indicate two *Tragelaphus* species at DK I and FLK I
	JK1, *JK2*		PDK, BK, CK	Last three entries may not be subsp. *grandis*
			London	
ndon			(LK/RK), WK	Large limb bones at DK I and FLK I not counted as eland
K, *HWK*	London, JK		Berlin	
		(*BK*)	WKE, *GC*	
K	JK2, JK2GP8	(Bos K), (*BK*), VFK	WKE, *GC*	Only teeth in Beds I, lower II, III and IV

				Teeth and limb bones above FLK are taken as transitional to *K. ellipsiprymnus*
	JK2, JK2GP8	(EF-HR)		
	JK2, JK2GP8			Metatarsal at FC West middle II may be reduncine
	JK2			
			Munich	
(HTK)	JK2			

(K)	JK2	TK Fish Gully	GC, GTC	Limb bones at HWK lower II and FC West middle II are of this genus or *Connochaetes* by size
don				
(TK)	London	VEK	London	
?EK, (GHTK)				Teeth and limb bones at MNK middle II and TK upper II are of this species or *Damaliscus niro* by size
------	JK2		HWK	Teeth and limb bones at HWKE lower II may be this species
	JK, JK2, JK2GP8		(NGC), London, (Nairobi)	See note above on *Parmularius angusticornis*
	JK2, JK2GP8	VFK, (*Hoopoe Gully*)		Limb bones at MNK middle II and BK upper II may be this species
	JK2		PDK	
HK				
			Nairobi	
(*irobi*)				

VK	JK2, JK2GP8		London, VEK	Italicized sites have scarce teeth and limb bones not differentiated from *Gazella*. Large Bed I remains taken as *A. recki*
			HEBE	
K, (MLK)				

Key

} = one lineage
Italics = doubtful identification or horizon
Brackets = records based only on known surface specimens
Names of towns = collections containing important material of unknown site

likely to be relatively large males. A similar comparison in Fig. 15 between *Hippotragus gigas* and the living roan, *H. equinus*, shows the former as being 22% larger.

Comparison of the Olduvai bovids with living faunas

It is interesting to examine the Olduvai bovids to see how similar or dissimilar they are to those of the living African fauna. The first step is to distinguish between lineages which are now extinct, lineages which lead to living species but are represented at Olduvai by ancestral species or genera, and lineages in which the Olduvai species are those still alive today. These three categories are distinguished in Table 11 (p. 54) by the letters E, A and L respectively. It should be remembered that our opinions on phylogenies are perhaps more subjective than the species' identifications. The kudu lineage is taken as the living *Tragelaphus strepsiceros* in all the Olduvai horizons but differs at subspecies level. The fragments of *Tragelaphus* aff. *spekei* or *scriptus*, *Redunca* and *Oryx* do not allow the detection of definite differences from living species. The eland *Taurotragus arkelli* and the buffalo *Syncerus acoelotus* are both ancestral to living species. The waterbuck lineage became the living species perhaps as early as Bed I. The kob is the living species, although its Olduvai representatives have differences which could be used to justify a subspecific separation. We regard *Hippotragus gigas* of Olduvai times as probably postdating the separation of its own lineage from that of living *Hippotragus*, but we admit that the Kanjera *Hippotragus* can be interpreted as showing either immigration of *H. equinus* or a late evolutionary transition from *H. gigas*. *Connochaetes africanus* could well be ancestral to *C. gnou*, and the other wildebeest lineage changed into the living *C. taurinus* during Bed II times. We accept *Parmularius* as constituting two lineages. *Damaliscus agelaius*, *Rabaticeras arambourgi* and *Beatragus antiquus* are taken as probably ancestral to living *Damaliscus*, *Alcelaphus buselaphus* and *Beatragus hunteri* respectively, despite the difficulties with the teeth of *D. agelaius* (p. 405). The *Antidorcas* and *Gazella* are probably ancestral to the living springbok and to *Gazella thomsoni* and *G. rufifrons*. We have not attempted to judge the Alcelaphini species 1, 2 and 3 or the very sparse neotragine remains from Olduvai.

Table 13 Number of bovid lineages at Olduvai Gorge compared with two living faunas

	Beds I and Lower II	Middle and Upper Bed II	Beds III and IV	Olduvai Total	Serengeti National Park	Kafue National Park
Tragelaphini	1 (1)	2 (1)	3 (1)	3	3	4
Bovini	1	2	2	2	1	1
Cephalophini	–	–	–	–	4*	3
Reduncini	2	3 (1)	4 (2)	4	3	4
Hippotragini	2	1	1	2	2	2
Alcelaphini	9 (1)	9 (2)	6 (1)	11	4	3
Neotragini	–	1	–	1	4	4
Antilopini	3	3	1	3	2	–
? Caprinae	1	–	–	1	–	–
TOTAL	19 (2)	21 (4)	17 (4)	27	23	21

Brackets surround the numbers of extant species included in the adjacent figures.
* Includes two doubtful records.
The table excludes from the Olduvai columns *Connochaetes africanus* and Alcelaphini sp. 1. *Tragelaphus* aff. *spekei* or *scriptus* is excluded for Bed I, *Taurotragus arkelli* for Bed II, and Alcelaphini sp. 4 for middle and upper Bed II.

Table 13 shows the number of securely identified lineages known from Olduvai as a whole and from the various beds and gives for comparison the numbers of bovid species which have been recorded from the living faunas of two ecologically different areas in tropical Africa, the Serengeti National Park in Tanzania and the Kafue National Park in Zambia (information from Swynnerton 1958 and Ansell 1960). It seems that the total number of lineages at Olduvai exceeds that in either living fauna, although this statement needs some qualifying. One should perhaps reduce the Olduvai total by two or three to allow for such possibilities as the Bed I ? caprine becoming extinct before all the other lineages had evolved, or regional fluctuations of faunas which may have masked lack of sympatry between some of the lineages. On the other hand, this notional reduction would probably need to be counterbalanced by the under-representation of Cephalophini and Neotragini, if not also Tragelaphini, arising from ecological or taphonomical factors. The two living faunas come from areas which contain a number of different habitats, and therefore they probably make a good comparison for the Olduvai fauna in which one can also detect the sampling of several different habitats. In any case the Olduvai fauna is likely to have been richer than the living ones because of the number of extinct lineages it contained. *Pelorovis*, *Thaleroceros*, *Megalotragus*, *Parmularius* and *Damaliscus niro* have no recognized counterparts in extant faunas. *Beatragus* is not quite extinct, but had become restricted to a very small part of Africa by recent centuries. *Antidorcas* no longer inhabits east Africa.

The most striking feature of Table 13 is the large number of alcelaphine lineages at Olduvai in comparison with the living faunas. Generally these Pleistocene alcelaphines were morphologically specialized, as in the case of *Parmularius*, particularly *P. angusticornis*, in comparison with *Damaliscus* and *Rabaticeras*. One can look at the large number of lineages in relation to the account of the behaviour and ecology of living alcelaphines given in the informative review of Jarman (1974). Living alcelaphines (except *Aepyceros melampus* and perhaps *Beatragus hunteri*) are grazers, rather unselective for plant species but much more so for particular parts or growth stages of plants. They have only poorly-defined home areas and are strongly migratory, which must assist in finding grasses at their optimum growth stages. They aggregate into cohesive super-herds which split up temporarily for breeding. Finally, the territory of a male during the nomadic phase is no longer a permanent piece of ground but a temporary area around a group of females. One presumes that this advanced social organization and feeding behaviour have been important in the evolutionary success of the living alcelaphines. Could they have been developed only recently, and could they have played a part in the extermination of *Megalotragus*, *Parmularius* and *Damaliscus niro* and the diminution in the range of *Beatragus*?

Finally, Table 13 shows the number of living species which can be identified at Olduvai, omitting poorly-known forms of uncertain status. It is interesting that the number is so low. Converting the numbers of living species into percentages of the total number of species in each of the beds, one gets the figures of 11% for Beds I and lower II, 19% for middle and upper Bed II and 23% for Beds III and IV. These rising percentages are perhaps spuriously impressive, but probably give a true impression that the Olduvai antelope fauna was becoming increasingly like the living fauna as time advanced through the Pleistocene. Three lineages crossed species boundaries at Olduvai in Beds I and II (*Kobus sigmoidalis*, *Connochaetes* sp. and *Parmularius altidens*), two in Beds III and IV (*Pelorovis oldowayensis* and *Antidorcas recki*) and four have done so at some time after their latest recorded occurrences in Beds III or IV (*Taurotragus arkelli*, *Syncerus acoelotus*, *Damaliscus agelaius* and *Rabaticeras arambourgi*).

Faunal changes at Olduvai Gorge

The conception that there is a faunal break between lower and middle Bed II at Olduvai is now familiar (Leakey 1965 : 4, 75, 76), and one wonders how far the bovids support or refute the idea. Changes which occur in the vicinity of this level are:

Tragelaphus strepsiceros maryanus is last known at HWK East II level 2 in lower Bed II, and *T. s. grandis* first appears in MNK middle Bed II. A tragelaphine maxilla from HWK EE low in middle Bed II has an M^2 of a size to fit *T. s. maryanus* but perhaps too small for later subspecies. More evidence is needed to substantiate the identification for this level.

Pelorovis oldowayensis first appears at Olduvai in HWK East II levels 3–5, the lowest levels of middle Bed II.

A reduncine tooth of the size of *Kobus sigmoidalis* or *K. ellipsiprymnus* last appears in HWK EE low in middle Bed II. Metatarsals, probably reduncine and large enough for waterbuck, appear at MNK and FC West; otherwise this lineage is absent until Bed III.

Kobus kob first appears at MNK in middle Bed II.

Connochaetes taurinus replaces an earlier *Connochaetes* species above the lower part of middle Bed II. It is definitely known from SHK II, while its predecessor is last known from HWK EE II. There is a *Connochaetes* horn core at MNK II, but it is too poorly preserved for identification at species level.

Parmularius altidens is known at FLKN I, while its descendant *P. angusticornis* is known from HWK EE II onwards. A cranium likely to be intermediate between them comes from the clay with root casts at FLKN II.

An early relative or representative of the *Parmularius rugosus* lineage occurs at HWK in lower Bed II and at HWK East and HWK EE in the lower part of middle Bed II. A more evolved form appears higher in middle Bed II.

Damaliscus niro is first known from Elephant K and SHK II.

Horn cores of *Antidorcas recki* are usually without distal divergence at HWK East II level 2 and below. Those from SHK II and later generally have distal divergence.

At least two lineages pass through this period without appreciable change, so far as we know them at present. These are *Hippotragus gigas* and *Beatragus antiquus*. *Damaliscus agelaius* may also do so. The situation is more uncertain with *Megalotragus kattwinkeli*; only teeth and limb bones are known in the period preceding the lower–middle Bed II change, so their species attribution is unknown.

There are some changes in the bovids at other levels in Olduvai Gorge. *Pelorovis oldowayensis* disappears in Bed III or IV, and *P. antiquus* is present in Bed IV. *Parmularius angusticornis* disappears after upper Bed II (but note the interesting Isimila record, p. 390). *Damaliscus agelaius* and *Parmularius rugosus* seem to become more common in Beds III and IV. *Rabaticeras arambourgi* appears in Bed III, *Beatragus antiquus* is not known after upper Bed II, and a larger *Antidorcas* than *A. recki* appears in Bed IV.

It appears then that over the period between FLKN I and SHK II there was quite a substantial change in the bovids which were becoming fossilized in the Olduvai sites. The degree to which the change was sharply localized at the lower/middle Bed II boundary is not yet clear; it might be better placed shortly after the start of middle Bed II. If the fossil bovids do reflect accurately a change in the composition of the then living fauna, they support Leakey's concept of a faunal break. The cause of such a change would have been environmental changes at Olduvai. Local movements of bovid populations and morphological changes on some lineages could produce the fossil record as known to us. *Tragelaphus strepsiceros maryanus* with its very compressed horn cores need have been only a local variant of the kudu. The *Pelorovis* lineage is known to have existed in the Shungura Formation, Omo, at a period before it first became fossilized at Olduvai, and the *Kobus sigmoidalis/ellipsiprymnus* lineage was only temporarily absent from Olduvai during middle and upper Bed II. There is some evidence for ecological instability in part of Bed II with the passing appearance in the HWK group of sites of *Parmularius* aff. *rugosus* and a variety of *Antidorcas recki* with unusually compressed horn cores. We conclude that it is reasonable to postulate a faunal change somewhere near or just above the lower–middle Bed II boundary.

The changes among the alcelaphine species after upper Bed II are not yet sufficiently clear to support the idea of another faunal break. *Damaliscus agelaius* and the *Rabaticeras* are probably ancestral to living alcelaphines whereas the middle and upper Bed II *Damaliscus niro* and *Parmularius angusticornis* were not. Their presence, even alongside *Parmularius rugosus* and the surviving *Damaliscus niro*, helps to give the fauna a more modern aspect. Morphologically, *Damaliscus agelaius* is a species with few advanced characters, and *Parmularius rugosus* is less specialized than *P. angusticornis*. The lower numbers of large alcelaphine teeth and limb bones than at BK II and the smaller size of the large *Megalotragus kattwinkeli* also suggest modernity, but this may be an illusory consequence of a change in hominid hunting preferences.

Bovid extinctions

The evidence for bovid extinctions within the span of Olduvai Beds I–IV is slight. Five lineages which are now extinct survived into Bed IV; these are *Pelorovis*, *Megalotragus*, a lineage of *Parmularius*, *Damaliscus niro* and *Thaleroceros radiciformis*. Terminal populations of *Pelorovis* and *Megalotragus* species have been discovered as late as 11 000 and 15 000–14 000 BP respectively in southern South Africa (Klein 1972 : 141; personal communication), and *Damaliscus niro* certainly survived into the late Pleistocene in the Orange Free State. The times of extinction of *Parmularius rugosus* and *Thaleroceros radiciformis* are not earlier than during the time span of Bed IV, but for these genera there are no late records from other sites. *Hippotragus gigas* survived at Olduvai into Bed III, but has not yet been found in Bed IV. However, it does occur at Elandsfontein and perhaps Florisbad, so the argument is not strong for extinction preceding the end of Bed IV. *Parmularius angusticornis* is the most likely candidate for a species disappearing without issue, an event which would have taken place at the end of upper Bed II. It is also likely that an ovibovine or caprine has become extinct since Bed I times. The two species *Tragelaphus nakuae* and *Menelikia lyrocera*, unrepresented at Olduvai, are last recorded in the Shungura Formation, Omo, in members H and J respectively, equivalent in time to Olduvai Beds I and II.

The main North American extinction of mammals which were mostly large-sized (megafaunal extinction) is known to have taken place close to 11 000 years ago, and the idea has been put forward (P. S. Martin 1967 : 111) that the main Pleistocene extinction in Africa long predated that in the Americas and Australia. The evidence which is now beginning to appear for African bovids does not support this idea.

Correlations with other sites

The contribution of Olduvai bovids to the correlation of different sites, Fig. 37, can be considered in order of their geographical proximity to the Gorge.

The bovids from the **Laetolil** Beds must be earlier than those of Olduvai. Our identifications of this material compared with those of Dietrich are shown in the following table. In this and following lists, the symbol (T) indicates a species represented by dental remains or dental and postcranial remains.

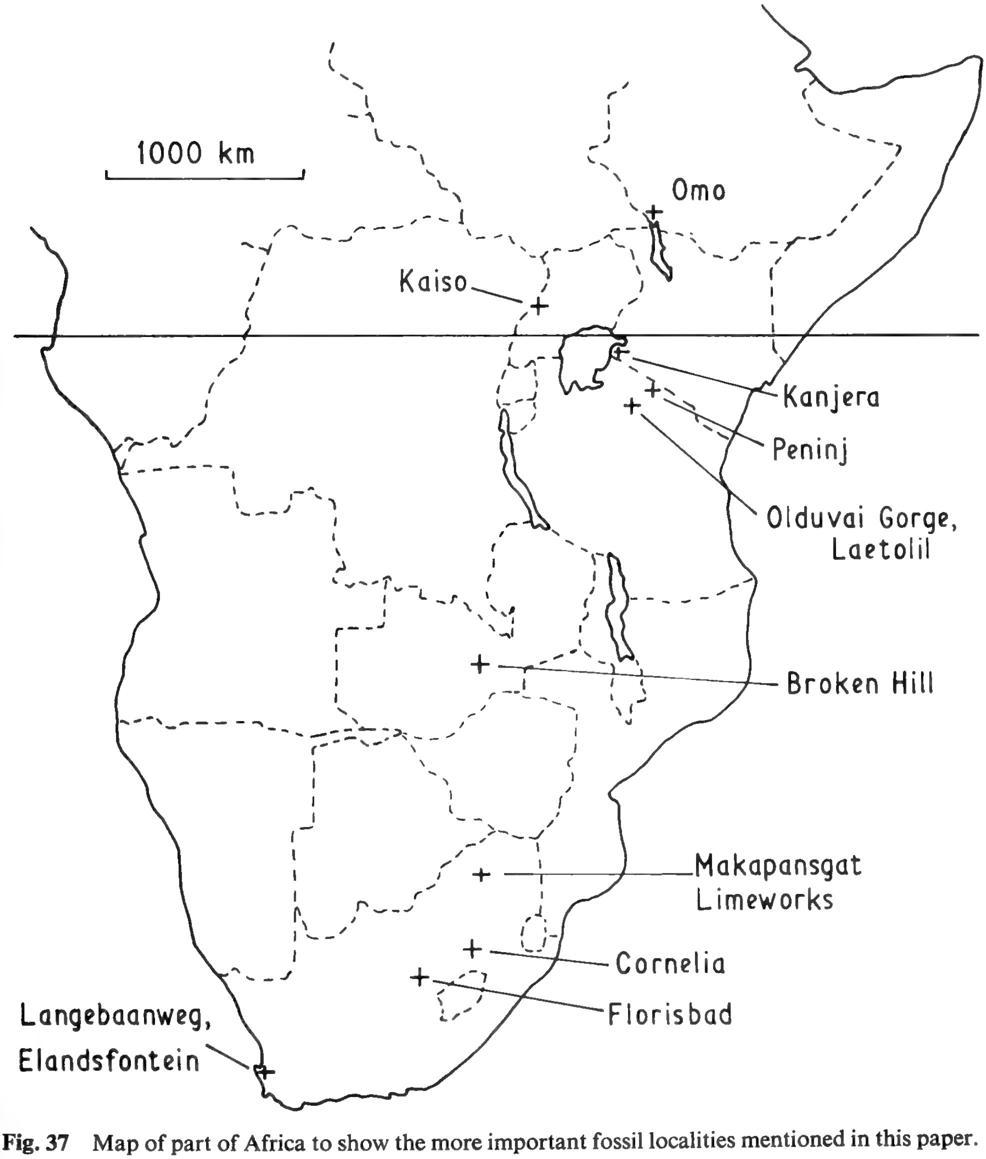

Fig. 37 Map of part of Africa to show the more important fossil localities mentioned in this paper.

Present authors	Dietrich (1942, 1950)
Simatherium kohllarseni	*Simatherium kohllarseni*
Praedamalis deturi	*Praedamalis deturi* *Aeotragus garussi* (T) ? *Hippotragus* sp. (T)
? Hippotragini sp.	*Gazella kohllarseni* Aepycerotinae gen. et sp. indet. (1950 : 30)
? *Parmularius* sp.	Reduncini gen. et sp. indet. (1950 : 36)
Alcelaphini sp. indet. (1959.233)	–
Alcelaphini sp. indet.	*Parestigorgon gadjingeri*
? *Raphicerus* sp. indet.	*Gazella hennigi* (T)
Madoqua avifluminis	*Praemadoqua avifluminis*
? *Antidorcas* sp.	*Gazella hennigi*
Gazella janenschi	*Gazella janenschi*
? Antilopini sp.	*Gazella kohllarseni* (T)
sp. indet.	*Aeotragus garussi*

Simatherium kohllarseni appears to be a stage in the evolution of *Pelorovis oldowayensis*, the alcelaphine cranium 1959.277 would be almost as good an ancestor for *Damaliscus niro* as for the *Parmularius* lineage to which we relate it, early Hippotragini may have been represented, and the horn cores of *Gazella janenschi* are smaller but similar to those of the Olduvai gazelle. All this, together with our difficulty in classifying some ? hippotragine teeth, befits fossils from a primitive or earlier fauna, and according to the K-Ar dating they would be twice as old as Olduvai Bed I. It is interesting that there are no reduncine antelopes in the revised list, and *Madoqua* is notably an antelope of dry country.

Bovid remains of Pleistocene age or later in both the Laetolil and the nearby Eyasi areas are nearly all assignable to living east African species, and include Reduncini. In addition *Pelorovis antiquus* is represented, and there are alcelaphine teeth of a size to match *Megalotragus*. The interesting cranium of *Tragelaphus* sp. cf. *spekei* or *angasi* is also from deposits younger than the Laetolil Beds.

The bovids at **Peninj** come from three different levels in the Humbu Formation, with the exception of the bovine mandibular fragment A67.282 which came from the overlying Moinik Formation. This piece is possibly from *Pelorovis antiquus*.

For the basal sandy clays (BSC) between the top of the Hajaro beds and the Limestone and Basaltic Tuff member the list is:

Tragelaphus strepsiceros ? *grandis* (T)
Connochaetes taurinus olduvaiensis
Aepyceros melampus
Antidorcas ? *recki* (T)

In the middle zone (MZ) sediments immediately above the Limestone and Basaltic Tuff Member there are:

Megalotragus kattwinkeli
Connochaetes taurinus
Parmularius angusticornis
Damaliscus niro

In the upper sandy clays (USC), succeeding the middle zone, are:

Megalotragus kattwinkeli
Connochaetes sp. (a horn core possibly from this level)
Antidorcas ? *recki* (T)

In either MZ or USC are:

Kobus kob
Aepyceros melampus

Of unknown geological horizon are:

Hippotragus gigas
Antidorcas recki
Gazella sp.

The Peninj antelopes all occur at Olduvai. *Parmularius angusticornis* equates with middle and upper Bed II at Olduvai, *Damaliscus niro* with middle Bed II or later, the *Kobus kob* is like those of Bed II and the *Gazella* sp. is the one found in middle and upper Bed II. Obviously the best placing of these deposits according to their bovids is to have MZ correlating with some part of Olduvai middle or upper Bed II. USC is likely to be of the same broad age. If *Pelorovis antiquus* were confirmed for the Moinik Formation, its age might be later than Bed III. The ecology of the area would have been similar to Olduvai.

The bovids make a limited contribution to the correlation of the **Kavirondo Gulf sites** in Kenya.

Species	Implication for correlation
At Kanjera there are:	
Tragelaphus ? *spekei*	perhaps not very old (younger than lower Pleistocene ?)
Pelorovis oldowayensis (T)	Olduvai Beds II–IV
Syncerus sp. (T)	distinctiveness of teeth from *Pelorovis oldowayensis* is reminiscent of Bed II
Kobus sigmoidalis/*ellipsiprymnus*	not before Bed I
Kobus kob	perhaps not very old
Redunca redunca	rather late, but material is scarcely fossilized
Hippotragus gigas	Bed III or earlier
Hippotragus ? *equinus* (T)	perhaps not very old
Alcelaphini, large sp. (T)	
Parmularius angusticornis	middle and upper Bed II
? *Ourebia* sp. (T)	
Antidorcas recki	Bed IV or earlier
Gazella sp.	
At Rawe there are:	
Tragelaphus ? *spekei* (T)	
Kobus kob	later than Olduvai Bed II
At Kagua there is:	
Tragelaphus strepsiceros	
At Kanam East there are:	
Tragelaphus sp. cf. *spekei*	rather early by basal pillars on teeth
Syncerus sp. (T)	
Kobus sp., size of *kob* (T)	
Redunca redunca	not very old
Alcelaphini, 2 spp. (T)	
At Kanam East Hot Springs there are:	
Tragelaphus sp. cf. *spekei*	
Kobus aff. *kob*	
Redunca ? *darti*	coeval with Makapansgat Limeworks
Kobus ? *ancystrocera*	Shungura Formation member G or above, earlier than Olduvai Bed IV
At Kanam Central there are:	
Tragelaphus sp. (T)	
Redunca sp. (T)	
At Kanam West there are:	
Tragelaphus aff. *gaudryi* or *strepsiceros*	
Kobus sp. (T)	
Alcelaphini sp. (T)	
Gazella sp.	
At Kanam West Fish Cliff there is:	
Tragelaphus sp. (T)	
At Kanam Museum Cliff there is:	
Kobus ? *ancystrocera*	Shungura Formation member G or above, earlier than Olduvai Bed IV

It looks as if reedbuck (*Redunca* spp.) and sitatunga (*Tragelaphus* of *spekei* group) have often been in past ages the source species for fossils along the Kavirondo Gulf, and they make no or little contribution to correlation. Apart from this, most material comes from Kanjera and could have an age equivalent to Olduvai Bed II. Some Kanam fossils could be older.

The bovids at **Kaiso** belong to early or late assemblages, for which the species lists are as follows.

Present authors	Cooke & Coryndon (1970)
(a) Early	
Tragelaphus sp. cf. *spekei*	*Strepsiceros* cf. *maryanus* M 26402
Bovini indet. (T)	*Syncerus* sp.
Kobus sigmoidalis	*Pultiphagonides* cf. *africanus*
Aepyceros sp.	*Aepyceros* cf. *melampus*
(b) Late	
Bovini indet. (T)	Bovini incertae sedis *Syncerus* sp. *Hippotragus* sp. M 12595a, M 12601
Kobus aff. *kob*	*Kobus* sp. M 26622 cf. *Parmularius altidens* M 12590
? *Kobus* sp.	*Beatragus* cf. *antiquus* M 26623
Menelikia lyrocera	Various identifications, registered numbers listed previously
Redunca sp. (T)	*Redunca* sp. M 26620, M 26621
Oreonagor/*Connochaetes* sp.	cf. *Menelikia lyrocera* M 12584 (see this paper, p. 368, footnote 3)
Alcelaphini sp.	*Pultiphagonides* cf. *africanus* M 26624 cf. *Damaliscus* sp. cf. *Parmularius altidens*
Aepyceros sp.	*Aepyceros* cf. *melampus* M 12592, M 12596 *Gazella* cf. *wellsi*

In addition there are from the Kazinga Channel *Ugandax gautieri* of unknown age and *Kobus kob* of late Pleistocene age. The bovids of the late fauna are likely to predate Olduvai, and would best fit a time level around member F of the Shungura Formation. This verdict is chiefly based on the *Menelikia lyrocera*, but other bovids are consistent with it. The prominence of reduncines, the weaker representation of alcelaphines and the absence of antilopines implies an ecological situation closer to that of the Shungura Formation up to member G than to Olduvai Gorge. The tragelaphine horn core of the early fauna seems insufficiently primitive to match the accepted age of the fauna well before the Shungura Formation (Cooke & Coryndon 1970 : 220, fig. 17; Maglio 1973 : fig. 12), and the *Kobus sigmoidalis* is notably early.

The Shungura Formation of **Omo** is known to predate and partly overlap Olduvai. In contrast to Olduvai the tragelaphines and reduncines are abundant, while alcelaphines other than impala are poorly represented. The species list is as follows.

	Members				
	B	C–D	E–F	G	H–L
Tragelaphus strepsiceros				O	?
Tragelaphus gaudryi	O	O	X	X	O
Tragelaphus ? *pricei*		O			
Tragelaphus sp. (T)		O	O		
Tragelaphus nakuae	X	X	X	X	O
Taurotragus sp.	O				O
Syncerus sp.	O	X		O	
Pelorovis sp.	O	O	O	O	
Bovini spp. (T)	X	X	O	O	O
Kobus sigmoidalis		O	X	X	
Kobus ellipsiprymnus				O	O
Kobus kob	?	?		?	X
Kobus sp. nov.	X				
Kobus ancystrocera	O	X	O	X	O

	Members				
	B	C–D	E–F	G	H–L
Menelikia sp.		X			
Menelikia lyrocera		?	X	X	X*
Redunca sp. (T)	O	O	O	O	O
Hippotragus sp.				O	
Oryx sp.				O	
Hippotragini sp. (T)		O			
Megalotragus ? kattwinkeli				O	O
Oreonagor/Connochaetes spp.	O			O	
Beatragus antiquus				O	
Parmularius altidens				?	O
Parmularius/Damaliscus sp.		O			
Alcelaphini spp. (T)	O	O	X	O	O
Aepyceros sp. nov.	X	X	X	X	X
cf. *Aepyceros* sp.			O	O	
Neotragini spp.		?	O	O	
Antidorcas recki	O		O	O	O
Gazella praethomsoni			O	O	O
Antilope aff. *subtorta*		O			
'Antilopini sp. 1'					O
Ovibovini sp.		O		O	

In the above list O = rare finds, X = common finds, * = an advanced variety.

During or soon after member G, *Tragelaphus gaudryi* and *T. nakuae* (both unknown at Olduvai) disappear, *T. strepsiceros* appears, *Kobus sigmoidalis* begins changing into *ellipsiprymnus*, *K. kob* becomes common, *Menelikia lyrocera* evolves an advanced variety, alcelaphine genera appear or become commoner and *Antidorcas* becomes more common. All this is a change towards greater faunal and ecological similarity to Olduvai, except that *Menelikia* is unrepresented at Olduvai. The Shungura Formation bovids are generally in accord with the idea that members G–L are contemporary with Olduvai Beds I–III or IV. Thus the boselaphine-like *Tragelaphus nakuae* disappears in member H and is unknown at Olduvai, the *Kobus sigmoidalis–ellipsiprymnus* transition of member G and above also appears in Olduvai Bed I, *K. kob* of member L is rather large as in Bed III, the pair of *Megalotragus* horn cores from member G are more different from those of Olduvai middle Bed II to Bed IV than are those of member K, *Parmularius altidens* is in member H and Bed I and the Antilopini sp. 1 occurs in members K and L and in middle and upper Bed II. The bovid evidence also supports the idea that members B–G predate Olduvai: *Tragelaphus gaudryi* is a smaller and more primitive kudu than *T. strepsiceros*, *T. ? pricei* has anteroposteriorly thicker horn cores than comparable *Tragelaphus* horn cores at Olduvai, the bovine and alcelaphine teeth are generally smaller and the *Aepyceros* and *Antidorcas* horn cores are smaller and more primitive.

The bovids which occur at **Broken Hill**, Zambia, are:

Present authors	Leakey (*in* Clark 1959)
Tragelaphus strepsiceros	*Strepsiceros* sp.
Taurotragus oryx	*Taurotragus* cf. *oryx*
Pelorovis antiquus	*Homoioceros* sp.
Hippotragus sp.	*Oryx* sp.
Connochaetes taurinus	*Connochaetes* spp.
Alcelaphus aff. *lichtensteini*	*Connochaetes* spp.
Antilopini sp.	*Litocranius* sp.

The occurrence of *Pelorovis antiquus* and the likelihood of the hartebeest being only subspecifically different from living *Alcelaphus lichtensteini* both suggest a Pleistocene date later than Olduvai Bed III, and the *Taurotragus oryx* a date later than the level of *T. arkelli* in Olduvai Bed IV.

A number of horn cores almost certainly from Broken Hill includes two examples of *Damaliscus niro*, BM(NH) M 34416–7. They are smaller than at Olduvai or Cornelia and nearer in size to those of Florisbad. The same collection also contains a horn core, M 34418, which looks very like the slightly smaller 'Alcelaphini sp. nov.' recorded from Cornelia and Elandsfontein (p. 67). This species was referred to as 'cf. *Damaliscus* sp.' by Cooke (1974 : 75). Leakey (*in* Clark 1959: 230) recorded *Damaliscus* from Broken Hill.

Broken Hill can be taken as Middle Pleistocene in age, and probably late in this period.

The South African sites can be considered in order of age, starting with the oldest. The bovid material from the Varswater Formation in 'E' Quarry at **Langebaanweg** is as follows:

Tragelaphus sp. cf. *angasi*
Mesembriportax acrae
Simatherium sp.
Kobus sp. (aff. *sigmoidalis* ?)
Alcelaphini spp. A and B
? *Raphicerus* sp.
Gazella aff. *vanhoepeni*
Ovibovini sp.

This is evidently an early fauna. The tragelaphine horn cores are less anteroposteriorly compressed than in living *Tragelaphus*, and resemble the Makapansgat Limeworks BPI M.490 in this character. *Mesembriportax* belongs to the Boselaphini which are now extinct in Africa, the alcelaphines have more primitive teeth than those from Laetolil, and the ? *Raphicerus* is more primitive than at Elandsfontein. The gazelle is alleged to have a resemblance to the Makapansgat Limeworks *G. vanhoepeni* mainly on the prior assumption that Langebaanweg is the older site, so it would be unwise to let it contribute to correlating Langebaanweg. If Laetolil has an age of 3·59–3·77 million years, then Langebaanweg would be somewhat older, and Hendey (1974 : 62) has inferred an age of about 4·5 million years.

The bovid list for **Makapansgat Limeworks** is:

Present authors	Wells & Cooke (1956)
Tragelaphus ? *strepsiceros* (T)	*Strepsiceros* cf. *strepsiceros*
Tragelaphus sp. cf. *angasi*	*Strepsiceros* cf. *angasi*
Tragelaphus pricei	*Cephalophus pricei* (T)
? *Taurotragus* sp. (T)	*Taurotragus* cf. *oryx*
Bovini sp. or spp. (T)	cf. *Syncerus caffer*
Cephalophus sp. cf. *monticola* (T)	cf. *Cephalophus caerulus*
Redunca darti	*Redunca darti* *Redunca* cf. *fulvorufula*
Hippotragus gigas	cf. *Oryx gazella*
Megalotragus sp. (T)	cf. *Pelorocerus helmei*
? *Connochaetes* sp. (T)	cf. *Gorgon taurinus* cf. *Alcelaphus robustus*
Alcelaphini sp.	*Damaliscus* sp. (aff. *albifrons*)
? *Aepyceros* sp.	*Aepyceros* cf. *melampus*
Oreotragus sp.	*Oreotragus major*
? *Raphicerus* sp.	*Cephalophus pricei* (horn core)
Gazella vanhoepeni	*Phenacotragus vanhoepeni* *Gazella gracilior*
Makapania broomi	*Makapania broomi*

Makapansgat Limeworks has a tragelaphine of greater kudu size, a nyala-sized *Tragelaphus* with a primitive horn core cross-section as at Langebaanweg and member C of the Shungura Formation, a *Redunca* which is substantially less advanced than living species or the Elandsfontein reedbuck, a possible *Raphicerus* which is similar to that at Langebaanweg and the *Makapania* which is most similar to *Megalovis latifrons* of the European Villafranchian. This collection could best be given an age between Langebaanweg and Olduvai lower Bed II. This assessment could be altered or refined by the discovery or publication of further fossils, or by the demonstration that the site contains fossils of different ages.

The bovids which we have seen from **Cornelia** are:

Pelorovis antiquus
Megalotragus priscus
Connochaetes ? gnou laticornutus
Damaliscus niro
Alcelaphini sp. nov. (also at Elandsfontein, = cf. *Damaliscus* sp. of Cooke 1974 : 75)
Antilopini sp. (T) (= *Antidorcas wellsi* of Cooke 1974 : 75)
Gen. indet. *helmoedi*

Cooke (1974 : 77) in his much-needed revision of the Cornelia mammals has referred additionally to *Taurotragus* cf. *oryx*, cf. *Tragelaphus strepsiceros*, cf. *Kobus venterae*, *Redunca* cf. *arundinum* and cf. *Sylvicapra grimmia*. Of these the cf. *Kobus venterae* is notable as being earlier than at other sites in South Africa. Cooke believes that the age of the fauna is around that of Olduvai Beds III–IV. We largely concur. The *Pelorovis* suggests a date no earlier than Olduvai Bed IV, and the *Connochaetes* and new species of alcelaphine both suggest a date close to that of Elandsfontein. Cornelia has generally been accepted as slightly earlier than Elandsfontein (Wells 1967 : 101; Cooke 1974 : 79).

The bovid list for **Elandsfontein** is:

Species	Implication for correlation
Tragelaphus sp. nov.	
Taurotragus oryx	later than *T. arkelli* of Olduvai Bed IV
Pelorovis ? antiquus	Olduvai Bed IV or later
Syncerus sp. (postcranial)	
Redunca arundinum	little different from living examples
Hippotragus gigas	a different subspecies from Olduvai
Hippotragus leucophaeus	
Megalotragus priscus	
Connochaetes gnou ? laticornutus	earlier than Florisbad
? *Parmularius* sp.	
Damaliscus niro	Olduvai middle Bed II or later
Rabaticeras arambourgi	Olduvai Bed III or IV
? *Beatragus* sp.	
Alcelaphini sp. nov.	also at Cornelia
Raphicerus sp. nov.	ancestral to one or more of the living species
Antidorcas recki	Olduvai Bed IV or earlier
Antidorcas australis	
Gazella sp.	most like examples in Olduvai middle and upper Bed II

This is the most interesting and informative site in South Africa for comparison with Olduvai. It seems that some part of the assemblage could best correlate with a time level around that of Olduvai Bed IV. There is every likelihood that Elandsfontein has yielded a temporally heterogeneous fauna (Hendey 1974 : 26), and among the bovids the *Syncerus*, *Hippotragus leucophaeus* and *Damaliscus niro* are candidates for being later than the other species.

The bovids at **Florisbad** are:

Tragelaphini sp. (T)
Pelorovis antiquus
Kobus leche
Hippotragus ? gigas (T)
Megalotragus priscus
Connochaetes gnou antiquus
Damaliscus niro
Damaliscus ? dorcas
Antidorcas bondi (T)
Antidorcas marsupialis

The *Connochaetes* is more advanced than at Cornelia or Elandsfontein, and suggests that Florisbad is later than those sites. The rather small horn cores of *Damaliscus niro* and the occurrence of what could be *D. dorcas* are consistent with such a later date. It would be interesting if the *Antidorcas marsupialis* horn cores came from the same low Peat Layer I as the *A. bondi.* The horn cores of the wildebeest (*Connochaetes*) appear to be at about the same level of evolutionary advance in relation to the living form as are the horn cores of *Alcelaphus* aff. *lichtensteini* at Broken Hill. This implies either that Florisbad and Broken Hill have similar ages, or that evolutionary rates have differed in the two lineages.

The bovids from Vlakkraal, Mahemspan, Melkbos and Swartklip need not be listed here as they have diminishing relevance for correlations with Olduvai Gorge. Vlakkraal evidently matches Florisbad very closely, and has the same two pairs of *Damaliscus* and *Antidorcas* species. Mahemspan has two frontlets of *Connochaetes gnou*, one (C.2402) like the Florisbad *C. g. antiquus* and the other (C.2498) more advanced. The latter, together with the horn core of *Alcelaphus buselaphus caama* (Hoffman 1953 : fig. 13), suggest either a later date than Florisbad and Vlakkraal or an admixture of later fossils. Melkbos and Swartklip are both sites under continuing investigation at the South African Museum.

Summary

The significance of the Olduvai bovids

The Olduvai bovids have been interesting from several aspects.

1. They are of Pleistocene age and a large number of lineages is represented. The antelope fauna of northern Tanzania must have been more diverse at that time than in the past few centuries.

2. Many of them would be recognizable to persons familiar with only the living antelopes of Africa. These are the ones which are ancestral to living species, and give information about the forebears of the greater kudu, eland, buffalo, waterbuck, kob, wildebeest, hartebeest, springbok and gazelle.

3. Earlier forms generally have more primitive characters than later ones, as can be seen for example in the horn cores of the Bed I wildebeest compared with those in later beds. However, the fossils sometimes show characters which are more advanced than in their descendants. One of the explanations for this may be that new species have not always evolved from the most advanced subspecies or variety of their parent species.

4. A number of the Olduvai lineages are now extinct or, like *Beatragus* and *Antidorcas*, no longer occur in Tanzania.

5. The higher total number of lineages in the Pleistocene would have necessitated narrower adaptations for many of the species, and this too could contribute to explaining why the Pleistocene forms sometimes appear more advanced than living ones.

6. Many of the bovids are a little larger than their nearest living relatives at tribal, generic or species level.

7. The Olduvai bovids as a whole indicate a rather dry and open environment. Alcelaphini are strongly represented, especially in middle and upper Bed II.

8. There is evidence for faunal changes at Olduvai. The change is very sharp at a level just after the start of middle Bed II. The cause of the change must have been ecological alterations which brought in species new to the Olduvai area as well as morphological evolution in some lineages. Changes at other stratigraphical levels are less sharp.

9. The bovid fauna of Beds III and IV has more resemblance to the living fauna than does that from earlier levels.

10. There is little evidence for extinctions within the time span of Olduvai Beds I–IV. Most of the extinct lineages survived into Bed IV if not later. It seems that a little-known caprine and *Parmularius angusticornis* could have been exterminated (at Olduvai) within the span of Beds I–IV.

11. The bovids contribute to broad faunal correlation of Olduvai with other African fossil localities. Laetolil, Tanzania, has a fauna substantially older than Olduvai, but a few of its fossils are much younger. The Humbu Formation at Peninj, Tanzania, correlates well with middle

and upper Bed II. Kanjera, Kenya, correlates with Olduvai Bed II. The late fauna at Kaiso, Uganda, predates Olduvai, and its bovids would best fit a time level around member F of the Shungura Formation, Omo, Ethiopia. The early fauna need not have been very much earlier. The bovids of the Shungura Formation at Omo support making members G–H equivalent in time to Bed I and member L to Bed III.

In South Africa Langebaanweg is older than Laetolil. Makapansgat Limeworks comes between Langebaanweg and Olduvai lower Bed II, but its fossils may not all be from one time level. Cornelia and Elandsfontein appear to be about the same age as Olduvai Bed IV, but once again there is the problem that Elandsfontein may contain fossils of different geological ages. Florisbad is later than Olduvai Bed IV.

Broken Hill, Zambia, is later than Olduvai Bed III.

Taxonomic changes

The following changes in the nomenclature and classification of Olduvai bovids have been adopted in this paper:

Tragelaphus strepsiceros maryanus and *T. s. grandis* are taken as subspecies of the extant *T. strepsiceros* instead of as separate species.

Homoioceras has become a junior synonym of *Syncerus*, and the bovine previously called *H. antiquus* has become *Pelorovis antiquus*.

Syncerus acoelotus is a new species.

Thaleroceros radiciformis is included in the Reduncini.

Megalotragus kattwinkeli includes the species formerly called *Alcelaphus kattwinkeli*, *Xenocephalus robustus* and *Alcelaphus howardi*.

Pultiphagonides has become a junior synonym of *Connochaetes*, and *C. africanus* is included in the Alcelaphini instead of the Caprinae.

Connochaetes taurinus olduvaiensis is taken as a subspecies of the living blue wildebeest instead of being a separate species.

Parmularius angusticornis includes the species formerly called *Damaliscus angusticornis* and *D. antiquus*.

Damaliscus agelaius is a new species.

Phenacotragus has become a junior synonym of *Antidorcas*.

Antidorcas recki includes *Gazella wellsi*.

We have abandoned three names founded by Schwarz (1932, 1937) for Olduvai antelopes: *Tragelaphus spekei stromeri*, *Taurotragus oryx pachyceros* and *Gazella gazella praecursor*. The holotypes were lost in the Second World War, the only illustrated pieces were a tibia and cervical vertebra of the gazelle, and the descriptions are insufficient to allow existing material to be compared with them.

Many reidentifications have been made of fossil bovids from sites other than Olduvai.

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Index to Parts I and II

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A Revision of the Miocene Hominoidea of East Africa

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A Revision of the Miocene Hominoidea of East Africa

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Contents

Synopsis

Seven species of Lower Miocene apes belonging to the Pongidae and Hylobatidae are revised. Each species is described in detail based on previously-described material and on 368 new specimens from Kenya, and diagnoses are emended to take into account the greater variability now seen to be present in each species.

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The African Dryopithecinae (Pongidae) are divided into two genera, *Proconsul* and *Limnopithecus.* The former is subdivided into two subgenera, *Proconsul* and *Rangwapithecus*, which differ from each other in morphology but overlap in size. The species within each subgenus are distinguished mainly on size. *Limnopithecus* is represented by the single species *L. legetet* Hopwood. The Hylobatidae has only one genus and species, *Dendropithecus macinnesi* (Le Gros Clark & Leakey), which was formerly grouped with *Limnopithecus*. A new subspecies *D. macinnesi songhorensis* is described.

Two of the species of fossil ape are present in basal Miocene deposits at least 22 m.y. old, and one of these and two others survive until the Middle Miocene, about 14 m.y. old. Proposed relationships of *Proconsul* and *Dendropithecus* with the Oligocene primates *Aegyptopithecus* and *Propliopithecus* are supported by the new specimens. The connection between the African Lower to Middle Miocene species and the Eurasian Middle Miocene species are not clear, although there is some evidence for a *Proconsul major–Sivapithecus indicus* link. It is not considered possible to postulate any direct connection between the Miocene and present-day apes, with the possible exception of *Dendropithecus macinnesi* leading to the gibbons.

Introduction

Early Miocene deposits in western Kenya were first discovered in 1909 when G. R. Chesnaye found fossils at Koru and Karungu (Andrews 1911). The first fossil ape specimens were not found until some time later, when Dr H. L. Gordon collected one specimen from Koru in 1926 (Hopwood 1933). The two most prolific Miocene sites in Kenya, Songhor and Rusinga Island, were discovered by Drs L. S. B. Leakey and D. G. MacInnes in 1931–32, and sporadic collecting at these sites (Leakey 1943; MacInnes 1943) was eventually succeeded by the British–Kenya Miocene Expeditions of 1947–51 organized by W. E. Le Gros Clark in England and L. S. B. Leakey in Kenya (Clark & Leakey 1950, 1951; Clark 1950; Leakey & Clark 1955). After the end

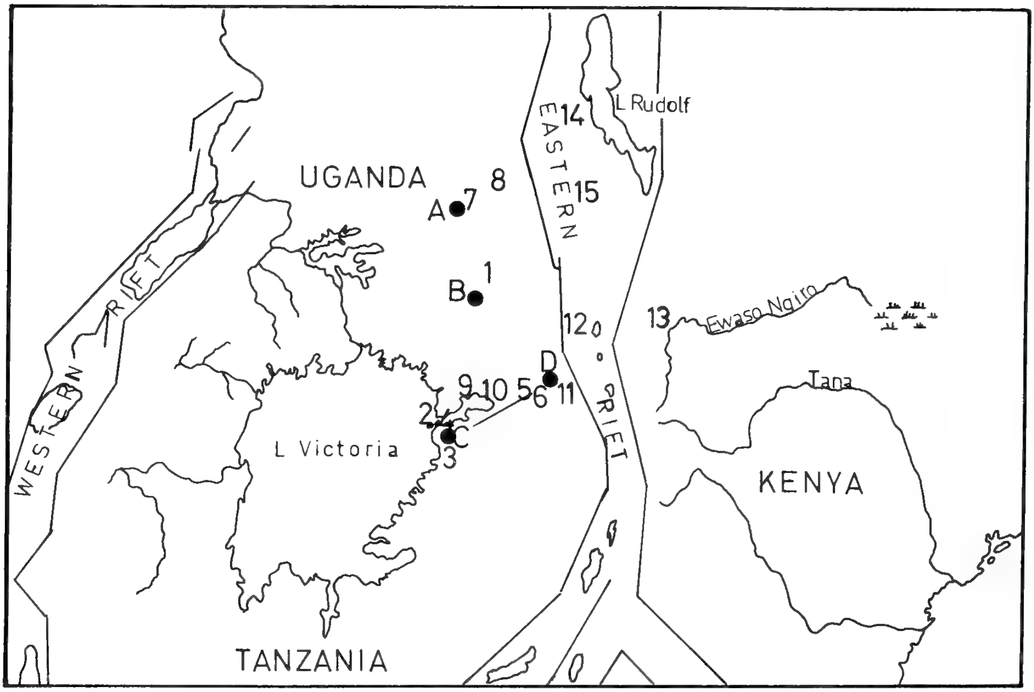

Fig. 1 Locality map of East Africa. Fossil localities: 1 Bukwa, 2 Mfwangano Island, 3 Karungu, 4 Rusinga Island, 5 Songhor, 6 Koru, 7 Napak, 8 Moroto, 9 Ombo, 10 Maboko Island, 11 Fort Ternan, 12 Ngorora, 13 Kirimon, 14 Losidok and Moruorot, 15 Loperot. Miocene Volcanoes: A Napak, B Elgon, C Kisingiri, D Tinderet.

of these expeditions work was continued on an individual basis by L. S. B. Leakey and others (Whitworth 1953, 1961; Leakey 1968; Van Couvering & Miller 1969; Andrews 1970, 1974; Andrews & Van Couvering 1975). A summary of Miocene field work up to the end of 1974 is given in Appendix I (p. 213), and numbers of specimens of hominoid primate found in Appendix II (p. 215). Fossil localities are shown in Fig. 1.

Up to the present time a total of 840 specimens of fossil hominoid primates has been recovered from the Early Miocene deposits of Kenya. Of these 644 represent cranial or dental fragments and are the subject of the present study. Some of the earlier discoveries (276 specimens) have been described previously (Hopwood 1933; MacInnes 1943; Clark & Leakey 1951; Clark & Thomas 1951; Clark 1952; Napier & Davis 1959; Leakey 1967, 1968; Andrews 1970, 1974). The remaining 368 specimens are described for the first time here and in Andrews (1973). A summary of specimens available for study is given in Appendix II (p. 215), and a list of the specimen field numbers used by earlier workers, with their permanent accession numbers used here, is given in Appendix III (p. 216).

Measuring techniques and abbreviations

Measurements were taken with a Helios dial caliper and recorded to the nearest 0·1 mm. All measurements were done at least twice, and a number of representative specimens were measured every 2–3 months. Over a period of 3 years the average measurement error was 1·1 %. The definitions of the measurements are given below. Points on the maxilla and mandible are as defined by Trevor (1950).

Description of measurements

MAXILLA	
Naso–alv. ht	distance between nasospinale and alveolare.
Nasal aperture ht	distance between nasopinale and the top of the nasal aperture.
Nasal ht	distance between nasospinale and nasion.
Zyg. arch position	tooth above which the root of the zygomatic process of the maxilla is positioned.
Zyg. arch ht	distance between the cervical border of the crown of the corresponding tooth and the point of maximum angulation of the zygomatic process of the maxilla.
max. sinus L	maximum anteroposterior length of the floor of the maxillary sinus.
max. sinus B	maximum breadth of the floor of the maxillary sinus.
pal. b at M2 (ext)	external distance between the buccal borders of left and right M2.
Palate L	distance between the posterior (lingual) margins of the central incisors and the distal margins of the third molars.
Palate B at C	internal distance between lingual borders of the crown bases of left and right C.
Palate B at M2	internal distance between lingual borders of the crown bases of left and right M2.
Palate depth at C–P3	depth of palate above cervical borders of crowns of average of C and P3.
Palate depth at M2	depth of palate above cervical borders of crowns of M2.
M1–M3	molar tooth row chord.
P3–M3	premolar–molar tooth row chord.
C–M3	canine–premolar–molar tooth row chord.
MANDIBLE	
Symph. d	maximum length along the mandibular symphysis.
Symph. t	minimum breadth across the mandibular symphysis.
P4 d	vertical depth of the mandibular body at the level of P4.
P4 t	perpendicular breadth of the mandibular body at the level of P4.
M2 d	vertical depth of the mandibular body at the level of M2.
M2 t	perpendicular breadth of the mandibular body at the level of M2.
I–I	distance between the most lingual points of the crown bases of the left and right lateral incisors.
C–C	distance between the most lingual points of the crown bases of the left and right canines.
P4–P4	distance between the most lingual points of the crown bases of the left and right fourth premolars.
M3–M3	distance between the most lingual points of the crown bases of the left and right third molars

Incisors

md	maximum mesiodistal length.
md incis	mesiodistal length across the incisive edge.
md root	mesiodistal length across the root.
bl	buccolingual length.
buc ht	maximum height of the crown measured buccally.
$\frac{\text{md incis}}{\text{md}} \times 100$	index measuring the relative size of the incisive edge on the crown.

Canines

max l	maximum length dimension measured along the long axis of the tooth.
perp b	minimum breadth measured perpendicular to the axis of maximum length.
buc ht	maximum height of the crown measured buccally.
mes ht ($\overline{C}$)	height of the crown at its most mesial point.
mes ridge ($\overline{C}$)	length of the mesial ridge from the top of the cingulum to the tip of the crown.
$\frac{\text{ridge}}{\text{mes ht}} \times 100$	index measuring the symmetry of the crown; a short ridge and low index indicates a highly asymmetrical crown.

Lower P3

max l	as for canine.
perp b	as for canine.
buccal ht mes	maximum height of the crown measured from the most inferior point of the enamel extension on the mesial root to the tip of the crown.
buccal ht dist	the minimum height from the base of the crown on the distal root to the tip of the crown.
$\frac{\text{dist}}{\text{mes}} \times 100$	index measuring the extension of the enamel down the mesial root.

Upper premolars

md	mesiodistal length along the central axis of the crown.
md buc (P3)	maximum mesiodistal length along the buccal edge of the crown.
bl	maximum buccolingual breadth.
buc ht	maximum height of the buccal cusp measured buccally.
ling ht	maximum height of the lingual cusp measured lingually.
$\frac{\text{md}}{\text{md buc}} \times 100$	index measuring the relative buccal extension of the crown.
$\frac{\text{buc ht}}{\text{ling ht}} \times 100$	index measuring the relative projection of the buccal cusp below the lingual one.

Upper molars

md	mesiodistal length along the central axis of the crown.
bl	maximum buccolingual breadth.
$\frac{\text{md}+\text{bl}}{2}$	the crown module, the 'average dimension' of the crown (Schuman & Brace 1954).
$\frac{\text{M2}}{\text{M1}} \times 100$	index measuring the relative size difference between M2 and M1.

Lower molars and P4

md	mesiodistal length along the central axis of the crown.
bl mes	maximum buccolingual breadth across the trigonid.
bl dist	maximum buccolingual breadth across the talonid.
$\frac{\text{md}+\text{bl}}{2}$	as for upper molars.
$\frac{\text{M2}}{\text{M1}} \times 100$	as for upper molars.

Age classes (deposit data; see p. 215)

1	deciduous dentition
2	mixed dentition or isolated unerupted crowns
3	unworn permanent dentition
4	slightly worn permanent dentition
5	moderately worn permanent dentition
6	heavily worn permanent dentition

Other abbreviations

BM(NH)	British Museum (Natural History). Specimens from this Museum are indicated by the single-letter prefix, M.
KNM	Kenya National Museum. Specimens from this Museum are usually designated by a two-letter prefix, indicating the site of origin as follows:
KA	Karungu
KO	Koru
LS	Losidok
MB	Maboko
MO	Moruorot
MW	Mfwangano Island (Site numbers, where known, are indicated by M A, M B, etc.)
OM	Ombo
RU	Rusinga Island (Site numbers, where known, are indicated by R 1, R 2, etc.)
SO	Songhor (Site numbers, where known, are indicated by S 1, S 2, etc.)
WF	Williams Flat
UM–P	Uganda Museum.
YPM	Yale Peabody Museum.

Univariate statistics

In the table of measurements, the mean and number of specimens are given for each tooth. Where the sample size is nearly or greater than ten the following additional statistics are given:

S.D.	standard deviation
Coef. var.	coefficient of variation
S.E.	standard error
95% conf. limits	95% confidence limits.

Calculations were made on the Olivetti desk computer at the Department of Physiology, University of Nairobi.

Multivariate statistics

The method used is that of principal components analysis (Andrews & Williams 1973). It is explained in detail in that paper and in my honours dissertation for the Department of Physical Anthropology, Cambridge (Andrews 1973). The programme used was written by D. B. Williams and it was run on the Cambridge University Titan computer.

The data were divided into three sets for analysis in the computer. These were as follows:

(a) measurements of anterior dentition I1–C and anterior mandibular dimensions and symphysis (22 measurements).

(b) measurements of 'sectorial' dentition C–P4 and mandibular dimensions of this region (28 measurements).

(c) measurements of post-canine teeth P4–M3 and mandibular dimensions of this region (32 measurements).

This division was partly dictated by what measurements were available in the samples of fossil species. The analysis of the post-canine region is based on relatively large samples with few estimated values, and hence it is more reliable than that of the anterior dentition and symphysis which is based on small samples. The grouping was also made on functional grounds, the three regions representing the incisive, the sectorial, and the grinding parts of the dentition respectively.

Acknowledgements

This work was originally intended as a joint project between Dr L. S. B. Leakey and myself. Although his ill-health in the last years of his life, and his death on October 1st, 1972, prevented Louis Leakey's full participation, a large part of the credit for this work must go to him: credit for his persistence and enthusiasm in initiating the work, for his readiness to accept new interpretations of the fossil material even where these ran counter to his own past work, for the generosity with which he made money available to enable the work to go forward, and, not least, for his efforts over the years collecting the fossils that made this study possible. For all these things I am deeply grateful.

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Systematic descriptions

Superfamily **HOMINOIDEA** Gray 1825
Family **PONGIDAE** Elliot 1913
Subfamily **DRYOPITHECINAE** Gregory & Hellman 1939

DIAGNOSIS. Oligocene to Pleistocene apes varying in size of comparable parts from animals a little smaller than a gibbon to those somewhat greater than most gorillas.

Dentition. Differs from that of Ponginae in the following features: incisors less stout, relatively higher crowned and more vertically emplaced; canines less robust; often small diastema between upper C and I2, but functional diastema always less than in Ponginae because of vertical emplacement of the Is; usually no diastema between P_3 and C; upper premolars often relatively broader; upper molars more often with lingual cingulum, crown morphology simpler and usually less crenulated; lower molars more often with buccal cingulum, relatively more elongated.

Mandible. No clear-cut and universal features of distinction from pongines but body often much deeper compared to height of teeth; inferior transverse torus sometimes present but with highly variable degree of development; simian shelf not present on any known specimen. The two sides of the mandibular body usually diverge posteriorly more strongly than in Ponginae and the anterior end of the mandible is always much narrower.

Cranium. The one known skull indicates brain size comparable to living apes of similar bulk. No brow-ridges present. No known major cranial features separate this group from Hominidae on the one hand or Ponginae on the other. The floor of the maxillary sinus is less extensive than in Ponginae. (Emended from Simons & Pilbeam 1965 : 118.)

Genus ***PROCONSUL*** Hopwood 1933

DIAGNOSIS. Primitive apes known only from Africa in early to middle Miocene deposits. They range in dental and cranial size from animals smaller than the gibbon to animals approximately the size of female gorillas. Incisors broader and more spatulate and canines less bilaterally compressed than in *Dryopithecus*. The buccal cusp of P^3 is relatively projecting. Upper molars have well-marked occlusal ridges, usually with at least slight development of the protoconule, and upper molar lingual cingula are prominent, unlike *Dryopithecus* and *Sivapithecus*. Cusp projection and wrinkling of occlusal surfaces are greater than in *Dryopithecus* and *Sivapithecus*. Lower molars always with distinct buccal cingula and greater cusp projection than in *Dryopithecus* and *Sivapithecus*. M_3 elongated, with massive development of the hypoconulid. Genial pit of mandible directed more inferiorly than in *Dryopithecus* and *Sivapithecus*, and there is a large symphyseal superior transverse torus and no inferior torus.

TYPE SPECIES. *Proconsul africanus* Hopwood 1933 : 98.

Subgenus *PROCONSUL* Hopwood 1933

DIAGNOSIS. A group of species covering the full size range of the genus. Incisors are broader and lower-crowned than those of subgenus *Rangwapithecus*, the premolars smaller with more projecting cusps, the upper molars relatively broad and the lower molars less elongated. The M^3 is often reduced and the M_3 often narrows distally so that it is triangular in outline. Cingula are absent or small on the premolars. The body of the mandible is slightly more robust than in *Rangwapithecus*, the alveolar processes of the maxilla considerably more robust, and the floor of the maxillar sinus is reduced in extent.

Proconsul (Proconsul) africanus Hopwood 1933

1932 *Dryopithecus* sp. Keith : 208.
1933 *Xenopithecus koruensis* Hopwood : 97.
1933 *Proconsul africanus* Hopwood : 98.
1950 *Proconsul africanus* Hopwood; Clark & Leakey : 260.
1965 *Dryopithecus (Proconsul) africanus* (Hopwood) Simons & Pilbeam : 129.

DIAGNOSIS. A species of *Proconsul* intermediate in dental size between the siamang and pygmy chimpanzee. Cingula well developed in maxillary cheek-teeth, particularly mesially and lingually; buccal cusp of P^3 strongly projecting; occlusal ridges and protoconule well developed on the upper molars; M^3 typically much reduced, particularly metacone and hypocone. Total length of upper premolar–molar series less than 40 mm, lower less than 45 mm. Skull lightly built, relatively orthognathous, lacking brow ridges of *Pan* species. Subarcuate fossa for the petrosal lobule of cerebellum present. Post-cranial skeleton with some features characteristic of *Pan*, particularly the development of the deltoid crest and the medial epicondyle of the humerus and the conformation of the distal articular surface of the humerus. (Emended from Simons & Pilbeam 1965 : 129.)

HOLOTYPE. Left maxillary fragment with the crowns of C–M3. BM(NH) M 14084.

LOCALITY AND HORIZON. The Lower Miocene of Koru, Rusinga Island, Mfwangano Island, and Songhor; and the Middle Miocene of Fort Ternan. All the localities are in Kenya.

MATERIAL. 118 specimens which cover the complete dentition and mandible, the maxillary, frontal, and temporal regions of the skull, and much of the postcranial skeleton.

Cranial material. M 32363, frontal and maxillary regions of the cranium and complete mandible; KNM-RU 2036, temporal and occipital regions of the cranium with fragments of maxilla and mandible, and a partial forelimb skeleton. (Pl. 1, p. 93.)

Maxillary material. M 14081 with left M^1–M^2; M 14085 with right M^1; KNM-RU 1705 with left C–M^1; RU 1769, ten associated incisors and canines; RU 1792 with left P^3–M^1; RU 1897 with right C; RU 1904 with left M^1–M^2; RU 1919 with left dp^3–dp^4; RU 1973 with right M^1–M^2; RU 2088 with right M^2–M^3 and associated with left P^4–P^3.

Mandibular material. KNM-RU 1680 with right P_4–M_2; RU 1706 with left P_4–M_3; RU 1728 with left P_4–M_3; RU 1824 with left P_4–M_2; RU 1855 with left M_1–M_3 and right P_4–M_3; RU 1899 with left C; RU 1955 with left P_3–M_2; RU 2093 with roots of left dp_3–dp_4; MW 59 with left C; SO 391 with roots of left M_1–M_3. (Pl. 2, fig. 1, p. 97).

Isolated teeth. M 14085, right M^1; M 14087, right M_3; M 32238, right dp^4; M 32362, left I_1; the remaining specimens are listed in Tables 1–22.

Referred material. Two specimens from Fort Ternan (KNM-FT 16, M^1; and FT 29, P^3) are provisionally referred to this species.

DESCRIPTION. The skull of *P. africanus* has been well described by Clark & Leakey (1951 : 16–28) and in the absence of any new cranial material this description will not be enlarged upon.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is small compared with modern apes. The nasal processes are short and the maxillo-premaxillary suture contacts the nasal aperture about half way up the aperture. The body is small and alveolar prognathism is restricted. The nasospinale–alveolare height is low. The incisor roots are set nearly vertically in the body of the premaxilla and the diastema between C and I^2 is short (up to 3 mm) so that essentially there is no functional diastema in this species, even in males.

The alveolar process of the maxilla is fairly robust. The floor of the maxillary sinus is at about the level of the tips of the molar roots so that the latter do not push up into the floor of the sinus. Specimen RU 2036 is exceptional in having one fairly deeply excavated region of the floor of the sinus above M^1. No specimen is complete enough to measure, but it appears that the sinus is restricted laterally. The tuberosities of the alveolar process vary from short in M 32363, possibly a female, to long in M 14084, possibly a male, but in neither case is it possible to make an accurate measurement. The greater palatine foramen is opposite M^3 in both cases. The zygomatic process of the maxilla is above $M^{1/2}$ in all specimens except the immature maxilla RU 2036, in which it is further forward above M^1. There is considerable variation in the height of the zygomatic process; it is low in RU 2036, but this is to be expected in an immature individual; in the two adult specimens on which it is possible to measure this dimension accurately values of 7·1 mm on a possible female (M 32363) and 10·4 mm on a possible male (M 14084) were obtained. The palate is long and narrow. Clark & Leakey (1951 : 16, 24) estimated palate breadths at M^1 for M 14084 and M 32363 both at 24·0 mm; I agree with the former estimate but have a value of 21·0 mm for the latter. By the time it was adult, RU 2036 would probably have had a palate breadth slightly greater than 21·0 mm.

Mandible (Table 2, p. 136–7). The mandibular symphysis is buttressed by a superior transverse torus. An inferior torus is not developed on any specimen, but the medial surface below the superior torus usually passes vertically downwards and only a little anteriorly. In one case (RU 1728) it passes a little posteriorly so that the most posterior part of the symphysis is near the base. The genial fossa is shallow and has a number of genial pits developed. One specimen (RU 1855) has a mental spine with slight impressions a few millimetres posteriorly on both sides of the body that might mark the insertion of the digastric muscle. Clark & Leakey (1951 : 27, 29) refer to this and to a similar tubercle on M 32363 which they say is for the attachment of the mylohyoid raphe, but the mylohyoid line is very distinct on RU 1855 and it clearly crosses the symphysis at the level of the two inferior genial pits well above the base of the mandible (see Fig. 2).

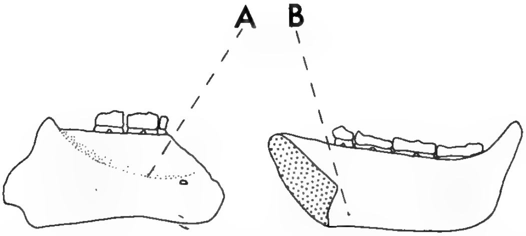

Fig. 2 The mandible of *Proconsul africanus*, × ½. Left, KNM-RU 1680, lateral view; A, line of attachment of buccinator. Right, KNM-RU 1855, medial view; B, position of mylohoid line.

The mandibular body is relatively shallow compared with the symphysis. The mental foramen is situated beneath P_3 just over one third of the way up from the inferior border. Posterior to the mental foramen the buccal surface of the body has a pronounced concavity. In modern apes the buccal cavity follows this concavity, the buccinator muscle attaching along its inferior border, and this appears to be the case here (see Fig. 2). The inferior border is bluntly rounded, thinning out inferiorly posterior to the level of M_3.

The mandibular ramus, by contrast with the body, is very thin. The anterior root overlaps the distal edge of the M_3. The coronoid process is high and pointed, higher than the condyle which follows the usual pongid pattern. Clark & Leakey (1951 : 27) estimate the bicondylar width to be approximately 82 mm. The angle of the mandible is not inflated, and muscle markings on the ramus are indistinct. (See Fig. 4, p. 106.)

Plate 1

Figs 1–3 *Proconsul africanus* (M 32363). Fig. 1, skull and mandible, lateral view. Fig. 2, skull, occlusal view. Fig. 3, mandible, occlusal view.

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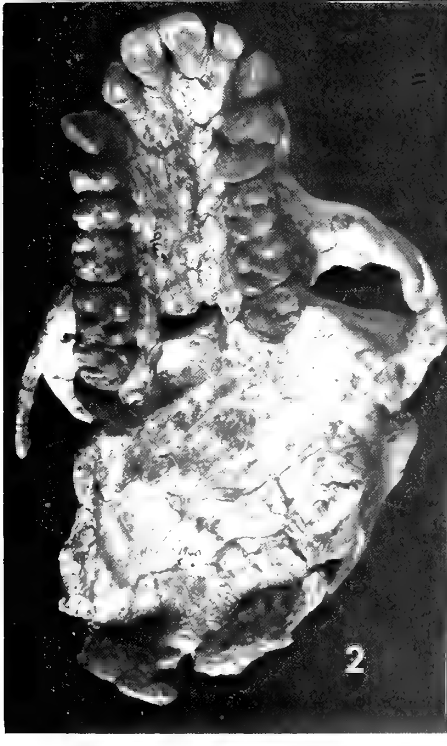

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Upper incisors (Tables 3–4, p. 138–140). The crown of I^1 is relatively broad and spatulate. It is only slightly asymmetrical, and the incisive edge runs nearly the whole width (mediodistal) of the crown. It is usually broader than high, and is also broader than deep. The slimness of the crown is very characteristic, and has been commented on by Clark & Leakey (1951 : 17). The morphology of the crown is simple: an ill-defined basal tubercle is usually present with a swelling running towards the incisive edge. The buccal surface is smoothly convex. Wear is usually confined to the incisive edge, rarely on the lingual surface, and a contact facet develops where the two central incisors meet. In extreme cases lingual wear can pass all the way down the lingual surface to the base of the crown.

The I^2 is smaller and more asymmetrical than I^1. When unworn the crown is usually pointed, the highest point being near the mesial border of the tooth. With wear the tip is flattened so that an incisive edge, directed slightly mesially, is produced. A strongly-developed lingual cingulum is usually present, and running towards the tip of the crown are one or more lingual striations. As on the I^1, wear is usually restricted to the tip of the crown; on one specimen (RU 1964) the distal edge is worn, through contact with the lower canine.

Upper canine (Table 5, p. 141–3). These are short stout teeth, wider than long. The long axis of the canines is only slightly oblique, the angle with the molar–premolar series being about 70°. The most prominent feature is the mesial groove starting from near the tip and increasing in size towards the base, where it ends at the mesial cingulum. The edges of the groove are flattened by wear, the mesial wear facet covering the whole mesial face. The cingulum is well developed and shelf-like. It runs from the buccal border of the mesial groove, at which point there is a distinct tubercle, distally along the lingual margin to the junction of the lingual and distobuccal faces. Wear facets are developed mesially and distally, the former being flat and the latter concave although never cutting deeply into the base of the crown. Frequently there is also a terminal wear facet at the tip of the crown; with increasing wear this usually becomes continuous with the distal facet first and then the mesial facet.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a bicuspid tooth, varying considerably in the extent to which it is mesiodistally compressed. The buccal cusp is always taller than the lingual one. The crown is greatly elongated buccally so that it has a triangular shape, and the enamel is extended slightly up the buccal root. The mesial ridge of the buccal cusp is very well developed and probably had a shearing action against the distal ridge of the P_3. The distal ridge of the buccal cusp is also well developed, giving this cusp a blade-like appearance. The lingual cusp is rounded and lacks mesiodistal ridges. It has a slight buccal ridge which runs transversely to the buccal cusp in a shallow mesial curve. Distal to the transverse ridge is a relatively large distal fovea the distal part of which is a shelf-like cingulum. There is no lingual cingulum. Mesially, there is a shallow, almost vertically oriented, mesial fovea, which becomes flattened during wear. The cusps are worn initially at the tip, the lingual one much more heavily than the buccal one.

The P^4 is similar to P^3 except that it is not elongated buccally, and the buccal cusp is only slightly higher than the lingual. It is relatively broader buccolingually, the index $(bl/md) \times 100$ being about 10% higher than that of P^3. The mesiodistal ridges of the buccal cusps are well developed. The buccal ridge of the lingual cusp is poorly developed and runs mesially as in P^3. The distal cingulum is strongly developed, as in P^3. Wear, as on P^3, is mainly on the lingual cusp.

Upper molars (Tables 8–10, p. 147–153). M^1 has four equal-sized cusps. The crown is sometimes slightly rhomboidal in shape owing to the extension of the cingulum distally, but the M^1 is the most rectangular of all the upper molars. The trigon is well defined. The mesiobuccal ridge of the protocone runs mesially to the protoconule, situated between the base of the protocone and the mesial edge of the tooth. The protoconule has a well-defined distobuccal ridge going in a buccal direction to the tip of the paracone, and also a short mesiobuccal ridge going to the mesial margin of the tooth, where it contacts the mesial marginal ridge. Between these two ridges is a narrow mesial fovea. The trigon basin is limited distally by the crista obliqua, the distobuccal ridge of the protocone, which runs straight into the lingual ridge of the metacone. The ridges of the metaconule do not appear to be developed at all, and the lingual end of the lingual ridge of the metacone is separated from the metaconule, where it is present, by a sulcus. Completing the trigon, the mesial and distal ridge of the paracone and the mesial ridge of the metacone are well developed, but the junction of the ridges between the paracone and the metacone is broken by the very deep buccal main groove.

The hypocone is an isolated cusp standing on the lingual cingulum. There is occasionally a slight ridge connecting it to the crista obliqua, but where the metaconule is developed there is no such ridge. The moderately beaded lingual cingulum runs from the mesiobuccal ridge of the protoconule to the mesial border of the hypocone. The large distal cingulum forms most of the distal fovea, and runs from the distal border of the hypocone to the distal border of the metacone. It is slightly beaded, and often has some minor folding. The buccal cingulum, between the paracone and metacone, is very slight and sometimes does not develop at all.

The M^2 is similar to M^1 except that it is larger. The hypocone and distal cingulum are usually extended distally giving a more characteristic rhomboidal pattern to the M^2. The mesial development of the trigon is the same in M^2 as in M^1, but the crista obliqua is usually cut by a longitudinal sulcus. The metaconule has not been observed on any specimens of M^2. The hypocone is large, and has a slight ridge connecting it to the crista obliqua very close to the tip of the protocone. The cingulum is similarly developed to M^1, but is larger all round, especially distally.

The M^3 is greatly reduced in size. Both metacone and hypocone may be lacking so that the distal end of the tooth is abbreviated and has a bluntly pointed triangular appearance. The mesial development of the trigon is the same as in M^1 and M^2 and the protoconule is usually present. The crista obliqua is faintly present, running from the protocone with many breaks to the buccal border of the tooth. There is a slight cuspule there which may represent the metacone. The hypocone is also hard to identify sometimes, for the distal end of the crown has a number of undifferentiated tubercles, and there are several on the crista obliqua itself. The cingulum is massively developed distally and only slightly smaller lingually. It completes the circuit round the tooth without a break.

Lower incisors (Tables 11–12, p. 154–5). The I_1 is high-crowned and symmetrical. The lingual surface is slightly concave and is unmarked by any ridge or cingulum. The buccal surface is gently convex and featureless. Wear is restricted to the tip of the crown along the incisive edge. The I_2 is a more robust and higher-crowned tooth than I_1. The crown is asymmetrical, the distal edge being convex and the mesial edge nearly straight. The highest point of the crown is at the mesial end of the incisive edge, the latter being relatively much shorter than on I_1. The lingual surface of the crown is concave, as on I_1, but it is marked by a slight lingual pillar running nearly to the tip of the crown.

Lower canine (Table 13, p. 156–8). The unworn lower canine has a characteristic morphology, best seen on specimen RU 2036. The mesial ridge of the crown is long and reaches the base of the crown which is only slightly raised to meet it; the distolingual ridge is also prominent, although it ends a little above the base of the crown, and between the two ridges the lingual face of the crown is a strikingly flat triangular surface. It is ended at the base by a discontinuous lingual cingulum. Distal to the distolingual ridge there is another occurrence of cingulum which constitutes an inconspicuous heel of the canine. A variation to this is seen in the 1948 skull (M 32363); the mesial ridge is reduced in length and runs into a more or less continuous lingual cingulum that is elevated mesially to meet it, very like the condition seen in *Limnopithecus legetet*. The cingulum continues distally around the base of the distolingual ridge and forms a more prominent heel than is found in the first type.

The wear patterns reciprocate those of the upper canine. A distal facet is cut distobuccally, on the buccal side of the distolingual ridge, and this wear facet may be extended to the tip of the crown with two regions of maximum wear, one at the base of the crown producing the distal notch and the other towards the tip of the crown. The crown is not heavily worn on any specimen of this species.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a single cusped tooth, resembling the sectorial type found in gibbons and monkeys but apparently not sectorial in function. The crown is much longer than broad, but is not bilaterally flattened to the extent seen in sectorial premolars. It is set obliquely in the mandibular body, about 60° to the molar–premolar series. The mesial ridge is well developed, running from the tip of the main cusp directly mesially to the end of the lingual cingulum, which is elevated at this point. The distal ridge is also prominent, continuing the line of the mesial ridge distally to the distal cingulum. There is also a distolingual ridge from the tip of the cusp down to, but not contacting, the lingual cingulum. Distally there is a thickened shelf of cingulum which is bounded buccally by the distal ridge, although it slightly overlaps the end of the ridge to form a short and slight distobuccal cingulum. The cingulum is also well developed lingually, running from the mesial ridge to just below the distolingual ridge.

The P_4 is a bicuspid tooth, characteristically broader than long. The long axis of the tooth is set obliquely, paralleling that of P_3. The two main cusps are aligned buccolingually, with sometimes the buccal cusp slightly mesial to the lingual cusp. They are widely separated and are joined by a moderately well-developed transverse ridge which may be homologous with the distal trigonid ridge of the lower molar. There is a short mesial ridge from the buccal cusp which appears to contact the slight buccal cingulum, and then to continue lingually as either ridge or mesial cingulum to the mesial ridge of the lingual cusp. Enclosed within these ridges is a distinct mesial fovea (perhaps homologous with the trigonid basin). There is a broad and deep distal fovea bounded on either side by distal ridges from the two main cusps. These ridges terminate at the distal angles of the talonid in very slight raised points or tubercles. There is a very slight buccal cingulum, hardly more than a line on the enamel, from the mesial ridge of the external cusp to the distobuccal tubercle. Both tubercle and distal basin appear to be cingular structures. There is no sign of any lingual cingulum.

Lower molars (Tables 16–18, p. 163–170). The lower molars are basically five-cusped and are all longer than broad. They increase in both length and breadth from M_1–M_3, so that M_3 has the largest surface area. The M_1 is smaller and narrower than the others. In cusp size the protoconid, hypoconid and metaconid are about equal. The entoconid is rather smaller, so that the hypoconid has a large area of contact with the metaconid, producing the Y-shaped pattern with respect to the protoconid. Also the entoconid is slightly distal to the hypoconid. The hypoconulid is median. Secondary folds or wrinkles are rarely developed.

In most cases the M_1 is slightly broader distally than mesially. Clark & Leakey (1951 : 19) have described the cusps as 'crystalline', and this best describes their appearance. The edges of the 'crystal' are the ridges, which, with few exceptions, are not discrete ridges at all: they are the lines of contact of two faces of the 'crystalline' cusps. The trigonid ridges are the most strongly developed. The distal trigonid ridge runs without a break from protoconid to metaconid, although it is strongly depressed in the midline of the tooth. The mesial trigonid ridge runs mesially to the mesiobuccal cingulum; it then runs lingually and slightly distally until it meets the mesial ridge of the metaconid, and forms the mesial margin of the trigonid basin and of the whole tooth. This development might at one stage have been cingular, but there is nothing to suggest on any of these specimens that it is so. In addition, there is sometimes a third transverse ridge crossing the floor of the trigonid basin, in effect cutting it into two, and this, like the distal trigonid ridge, runs from the tips of the protoconid to the metaconid. In contrast, the talonid ridges are poorly defined. The talonid basin is fairly deep, but, because the talonid cusps are large, have broad areas of contact with each other and intrude into the talonid, the area of the basin is relatively small. There is a small distal fovea behind the entoconid and hypoconulid. The buccal cingulum is only slightly developed. There is a short section on the mesiobuccal border of the protoconid, but the greatest development is in the interval between protoconid and hypoconid. There is also a further slight development between the hypoconid and the hypoconulid.

Plate 2

Fig. 1 *Proconsul africanus*. Mandible, occlusal view (KNM-RU 2036).

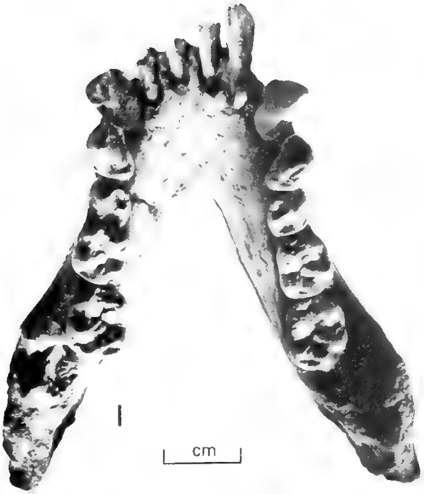
Fig. 2 *Proconsul nyanzae*. Mandible, occlusal view (KNM-RU 2087).

Fig. 3 *Proconsul* (*Rangwapithecus*) *gordoni*. Left mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-SO 1112).

Fig. 4 *Limnopithecus legetet*. Right mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-KO 8).

Fig. 5 *Dendropithecus macinnesi*. Palate, occlusal view (KNM-RU 1850).

Fig. 6 *Dendropithecus macinnesi*. Right mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-RU 2015).



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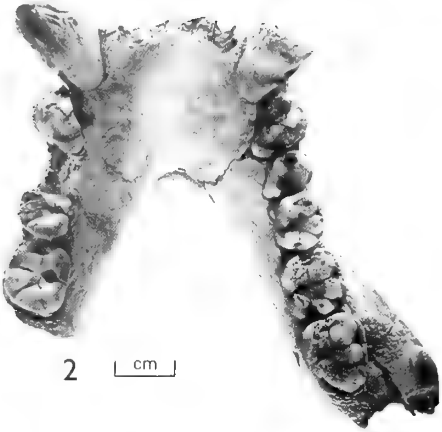

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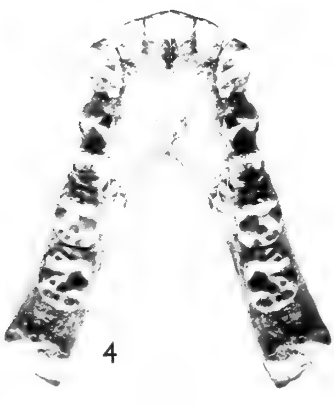

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M_2 is longer and broader than M_1. It is essentially similar in morphology but differs in a few details. The trigonid ridges are less well developed although they can still be seen. The distal trigonid ridge is deeply cut by the longitudinal sulcus. The mesial trigonid ridge is still quite well developed and again meets the mesiobuccal cingulum. The trigonid basin is well developed but opens distally into the talonid basin by the deep longitudinal sulcus. The talonid ridges are more strongly defined than on M_1, especially the entoconid–hypoconulid ridge. The talonid basin is clearly circumscribed by the talonid ridges, although the large basal area of the cusps encroach on it. The distal fovea is very clearly demarcated behind the entoconid–hypoconulid ridge and is rather deep and shelf-like. There is some secondary wrinkling of the talonid. The cingulum is variable, but is rather better developed than on M_1 and is found in the same places.

The M_3 is the largest tooth in the lower molar series. It has conspicuous folding and wrinkling of the whole occlusal area. The trigonid ridges are still more poorly defined than in M_2, and the basin, although distinct from the talonid basin, is rather small. The talonid ridges are also poorly defined, and there does not appear to be any entoconid–hypoconulid ridge. The entoconid is reduced, and appears as one of a series of cuspules along the lingual border between the metaconid and hypoconulid. The hypoconulid is a large heel-like cusp, slightly buccally placed. The talonid in the region of the hypoconulid is particularly strongly wrinkled.

Deciduous dentition (Tables 19–21, p. 171–3). The dp^3 is bicuspid with a faint ridge joining the two cusps. It is slightly elongated buccally, and the buccal cusp is slightly higher than the lingual one. The mesial and lingual cingula are small, but there is a massive distal cingulum.

The dp^4 crown morphology is very similar to that of M^1 except in the absence of the protoconule. It is lower crowned than M^1 and is smaller.

A single isolated dc_1 which is an exact replica, on a smaller scale, of the C for instance of KNM-RU 2036, is fairly certainly referred to this species, both for this reason and because of its size.

The roots of dp_3–dp_4 are present on RU 2093, and RU 1865, which probably is a deciduous dp_4, has comparable root measurements. The five cusps are all isolated from one another, with no ridge development. The hypoconulid is small. The protoconid is slightly in advance of the metaconid, and the hypoconid of the entoconid, giving the crown a skewed appearance. The buccal cingulum is poorly developed.

REMARKS. *Proconsul* (*Proconsul*) *africanus* is the most distinctive of the species assigned to this subgenus. The main points of difference between it and *P.* (*P.*) *nyanzae* and *P.* (*P.*) *major*, apart from its smaller size, may be summarized as follows. The I^1 is relatively slim buccolingually and broad and spatulate mesiodistally; the Cs are slender-crowned pointed teeth, often with marked asymmetry; the P^3 has a slender and strongly-projecting buccal cusp; the M^2 is the largest molar in the maxillary tooth row, but it does not greatly exceed M^1 in size; the M^3 is strongly reduced, both in size and morphology, and it is often limited to the two mesial trigon cusps; the M_3 is elongated, longer than M_2, but the distal end is abbreviated so that the crown is triangular. These points combine to make *P. africanus* readily distinguishable from the other species of *Proconsul*, although it should be remarked that they do not distinguish it from *Limnopithecus legetet*. The latter, however, has other points by which it may be distinguished, notably its very much smaller size, its elongated P_4s, and its rounded molar cusps which lack the 'crystalline' appearance described for *P. africanus*.

An estimate of the size range of *P. africanus* can be obtained from Figs 7–24, p. 176–191. In most dimensions the top of the range for *P. africanus* just meets the bottom of the range of *P. nyanzae*, but for a few teeth, for example the lower molars, there is some overlap. In cases where there is apparently a large gap between the two species it is more likely because of sample inadequacies than a genuine size difference, as, for example, in the lower canines where it is evident that only the bottom half of the population range is represented (Fig. 19). Greenfield (1972) has suggested that a number of specimens presently assigned to *P. nyanzae* represent these missing male *P. africanus*, and on the evidence of dental size alone this is a possibility. However, in terms of dental morphology and of mandibular or maxillary size and morphology it is more probable that the specimens are correctly placed in *P. nyanzae*, and since the dental size evidence is at best equivocal they will be so treated here.

The distribution of *P. africanus* is limited to western Kenya (Fig. 1). It is most common in the deposits of the Hiwegi Formation of Rusinga Island (Van Couvering & Miller 1969), and it also occurs in similar deposits on the neighbouring Mfwangano Island as well as in the lower deposits there equivalent to the Kiahera Formation of Rusinga (Whitworth 1961). These lower deposits are dated as older than 19·6 ± 0·2 m.y. (Van Couvering & Miller 1969). The youngest record of this species is at Fort Ternan, where the deposits are bracketed by dates of 12·5 and 14 m.y. (Bishop, Miller & Fitch 1969), so that the known time range is at least 5·5 million years. On available evidence the morphology of the species does not seem to change over this time period, but the specimens from the two extremes of the time range are fragmentary and might not show any changes that had occurred.

The distribution pattern just outlined is very similar to that of *Proconsul nyanzae*. This similarity must raise the possibility that the two species ought not to be separated. Their basic similarity in morphology indicates that they had diverged from a common ancestor not long previously to their first occurrence in the fossil record, but in view of the size differences between them it seems unlikely that they are conspecific, unless the combined species was exceedingly variable, and the possibility must be raised that more complete material would show a greater degree of morphological difference between them. Alternatively it is possible that the apparent association of the two species is a artifact of poor collecting techniques, and that they might not be actually associated in single fossiliferous horizons. The little evidence available supports this, in that where one species has been found in recent excavations the other is absent (Andrews & Van Couvering 1975), but sample sizes are small, and this is at best negative evidence for lack of association.

Proconsul* (*Proconsul*) *nyanzae Le Gros Clark & Leakey 1950

1943 *Proconsul africanus* MacInnes : 163.
1950 *Proconsul nyanzae* Clark & Leakey : 261.
1950 *Sivapithecus africanus* Clark & Leakey : 261.
1965 *Dryopithecus* (*Sivapithecus*) *sivalensis* (Lydekker) Simons & Pilbeam : 127.
1965 *Dryopithecus* (*Proconsul*) *nyanzae* (Clark & Leakey) Simons & Pilbeam : 130.
1967 *Kenyapithecus africanus* (Clark & Leakey) Leakey : 157.

DIAGNOSIS. A species of *Proconsul* approximating in dental size to the chimpanzee. Canines well developed and often about as large relative to palate and mandible as in the chimpanzees. Strongly sexually dimorphic, particularly in the canines. Lingual cingulum of upper molars beaded, posterior cingulum well developed. M1 very small relative to M2; M3 slightly smaller than M2 but not reduced morphologically and much bigger than M1. P^3–M^3 length between 40 and 50 mm; P_3–M_3 length 45–55 mm. Maximum depth of mandibular body greater than in *P. africanus* (25 mm), but variable. Symphysis and body relatively gracile. (Emended from Simons & Pilbeam 1965 : 130.)

HOLOTYPE. Nearly complete maxilla, but much distorted, with upper dentition except for the incisors. BM(NH) M 16647.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga Island, Mfwangano Island, and Karungu; and the Middle Miocene of Fort Ternan and Maboko Island. All the localities are in Kenya.

MATERIAL. 103 specimens which cover the complete dentition, mandible, maxilla, and parts of the face. Only a few fragments of limb bone can be attributed to this species with any certainty.

Maxillary material. M 16647 palate and maxillary region of face with complete dentition except for the incisors; M 16649 with left P^3–M^1; KNM-RU 1677 complete upper dentition except for the I^2s; RU 1715 with P^4; RU 1718 with P^3–P^4; RU 1803 immature maxilla with I^1, dp^3–dp^4 and M^1, with M^2 unerupted; RU 2031 with broken dp^4 and I^2 unerupted. (Pl. 3, figs 2–3, p. 101.)

Mandibular material. KNM-RU 1674 nearly complete mandible and left maxilla; RU 1676 left tooth row with C–M_3; RU 1678 with P_4–M_2; RU 1679 with P_4–M_1; RU 1710 immature mandible with left P_4–M_2; RU 1711 with P_4–M_1; RU 1716 with unerupted crowns of I_2, C and P_4 exposed; RU 1780 with P_4–M_1; RU 1947 complete mandible and dentition, much distorted;

RU 1982 fragmentary mandible with complete dentition except for the incisors; RU 2087 with left C, P_3 and M_2 and right C–M_2. (Pl. 2, fig. 2, p. 97.)

Isolated teeth. M 32235, right P_3; M 32236, right C; the remaining specimens are listed in Tables 1–22.

Referred material. Six specimens from Fort Ternan (KNM-FT 39 and 28, C; FT 49, I^1 previously assigned to *Kenyapithecus wickeri*; FT 34 and 40, M_3; and FT 2751 distal end of humerus).

DESCRIPTION. This species will be described in conjunction with the next, *P.* (*P.*) *major.*

Proconsul* (*Proconsul*) *major Le Gros Clark & Leakey 1950

1950 *Proconsul major* Clark & Leakey : 261.
1965 *Dryopithecus* (*Proconsul*) *major* (Clark & Leakey) Simons & Pilbeam : 134.

DIAGNOSIS. A species of *Proconsul* with dentition approximately the size of that of the female gorilla. Largest species of *Proconsul*; length of P_3–M_3 may exceed 65 mm. Compared to tooth size, mandibular body much more massive than in *P. nyanzae* and symphysis more massive than in *S. indicus* which otherwise approaches *P. major* in size. M_3 typically larger and longer compared to M_2; much larger than M_1; M^3 larger than M^1, more so than in *P. nyanzae*; the M1 significantly larger than M1 of *P. nyanzae* at 0·02 probability; cingula usually more distinct than in gorilla and simian shelf not developed; crowns of cheek-teeth perceptibly more wrinkled than in *S. indicus.* (Emended from Simons & Pilbeam 1965 : 134.)

HOLOTYPE. Right mandibular body with the crowns of P_4–M_3. BM(NH) M 16648.

LOCALITY AND HORIZON. The Lower Miocene of Songhor and Koru in western Kenya; ? Lower Miocene deposits of Losidok, Moruorot, and Kirimon in northern Kenya; and the Lower Miocene of Napak and ? Middle Miocene of Moroto, Uganda.

MATERIAL. 53 specimens from Kenya which cover parts of the maxilla and most of the upper dentition, all of the mandible and lower dentition except for the I_1 and ascending rami.

Maxillary material. KNM-SO 418 with right P^3–M^1; SO 144 with left P^4; SO 527 with P^3–P^4; SO 529 with right P^3–P^4; SO 542 with right dc, dp^3, dp^4, and M^1, with unerupted crowns of P^3 and P^4, and associated with immature mandible with dp_4 and M_1. (Pl. 4, fig. 3, p. 103.)

Mandibular material. M 14086 with left P_3–M_2 and right P_3–M_2; M 16648 with right P_4–M_3; KNM-SO 396 with right C and left P_4–M_3; SO 404 with left and right mandibular bodies but no teeth; SO 542 see above. (Pl. 4, fig. 4, p. 103; Pl. 5, p. 105.)

Isolated teeth. M 14275, part of molar; M 14297, left I^1; M 14331A, right P^3; M 14331B, left M^3; M 32228, right dc; M 32237, right M_3; the remaining specimens are listed in Tables 1–22, pp. 134–174.

Referred material. One specimen from Moruorot, two from Losidok, and one from Kirimon, all in northern Kenya (MO 26, right mandible with dp_4 and M_1, with I_2 and C in alveolus; LS 7, left maxilla with M^2–M^3; LS 8, left C and Kirimon, C.).

Five specimens from Moroto and 19 from Napak in Uganda have been described by Allbrook & Bishop (1963) and Pilbeam (1969). The material is as follows.

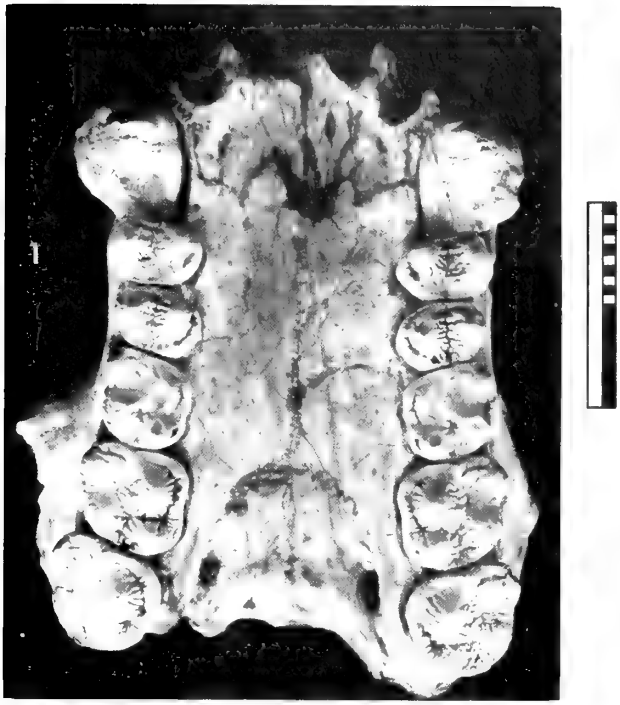
Napak I UM-P 62-03, right C; 62-09, left M^2; 62-13, immature mandible with M_1; 62-14, right M_2; 62-15, left M_2; 62-16 mandible with left P_4–M_1. Napak IV UM-P 64-01, right M^1; 66-41, right M^1; 68-04, P_3. Napak V UM-P 62-04, right C; 62-05, left C; 62-06, mandible with P_4; 62-07, right M^1; 62-08, left M^2; 66-02, right P_4; 66-03, right I^2; 66-20, C ?; 69-01, right P_4; 69-02, right M^1.

Moroto I UM-P 67-36, C. Moroto II UM-P 62-10, mandible with right M_1; 61-11, palate with complete dentition except for tip of right C and lingual half of left P^3; 62-12, left C; 66-01, mandible fragment.

Plate 3

Fig. 1 *Proconsul* (*Rangwapithecus*) *gordoni.* Palate, occlusal view (KNM-SO 700).

Figs 2–3 *Proconsul nyanzae.* Left maxilla with P^3–M^1 (M 16649). Fig. 1, lingual view. Fig. 2, occlusal view.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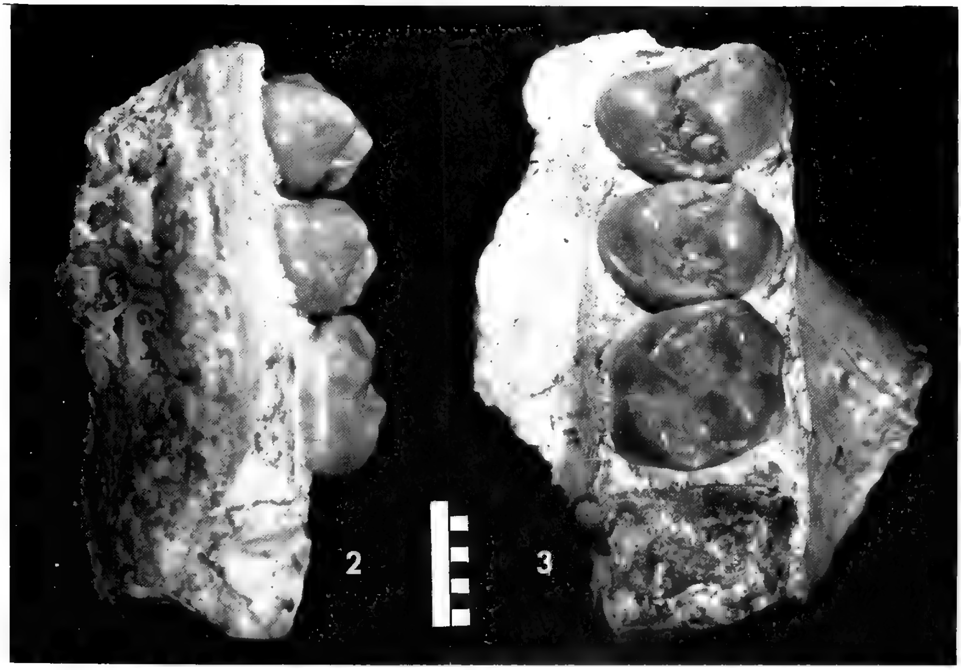
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DESCRIPTION. These two species, *P. major* and *P. nyanzae*, are here assigned a single morphological description. They are almost identical morphologically, but differ in size and distribution. Differences, where they occur, are mentioned in the text.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla was evidently a substantial-sized bone forming most or all of the lateral walls of the nasal aperture. MacInnes (1943 : 164) stated that the base of the nasal aperture lies only just above the alveolus, but although the distance is not nearly as great as in modern pongids, the naso-alv. ht varies from 13 to 16 mm, indicating a robust bone. The comparable value in *P. major* is 16·7 mm, and the index (naso-alv. ht/nasal ht) × 100 is 18 %. The anterior surface of the bone on UM-P 62-11 is swollen in the region of the left central incisor root and heavy wear on this tooth attests to its being well used. There is a considerable diastema (5–7 mm) between the canine and lateral incisor, and this is greatly increased in effect by the procumbency of the incisors which results in a large functional diastema. Nasal height can be estimated for both species, 72 mm in *P. nyanzae* and 98·5 mm in *P. major*. This is similar to values seen in female and male gorillas respectively. However, the nasal aperture is much narrower than in the gorilla, although relatively wider in *P. major* than in *P. nyanzae*: see Table 1. The floor of the nasal aperture is a simple gutter and is angled sharply with the alveolar border of the premaxilla. No nasal spine is visible.

The alveolar process of the maxilla varies from being exceedingly robust in the region of the canine juga to relatively shallow posteriorly. The canine juga are strongly developed so that there are slight concavities anterior (above I^2) and posterior (above P^4) to it. The floor of the maxillary sinus runs from the distal edge of P^4 into the tuberosities of the alveolar process and on into the pterygoid plate. The floor of the sinus is slightly excavated between the roots of the molars but it cannot be said to be divided into separate loculi. The tuberosities project 7–9 mm beyond the distal end of M^3 and are inflated. The greater palatine foramen is opposite M^3. The zygomatic process of the maxilla is set above M^2 in most cases. This is the usual pongid condition. The height of the process is 12–17 mm with the greatest heights in the probably male specimens. The palate is long and narrow and very gorilla-like. The incisor alveolus projects anteriorly to the canines, and the maxillopalatine suture is set relatively far posteriorly (opposite M^3) so that the palate is lengthened both anteriorly and posteriorly. In *P. major* the palate narrows posteriorly, the widest point being between the canines, but in *P. nyanzae* the tooth rows apparently diverge slightly posteriorly. M 16647 is the only intact palate in the latter species, but the posterior distortion makes it impossible to be sure of the actual degree of divergence.

Mandible (Table 2, p. 136–7). The mandibular symphysis is variable both in extent and degree of buttressing. On most specimens of *P. nyanzae* it is deep and fairly gracile but on some of the *P. major* specimens it is more robust. All have a superior transverse torus, and it is the greater development of this that makes the symphysis more robust in *P. major*. The internal surface of the symphysis consists of a long flat slope running posteriorly from the incisor alveolus to the most posterior point of the superior transverse torus, which usually reaches to the level of P_3. At its greatest development, in *P. major*, the superior transverse torus occasionally reaches the level of the mesial quarter of P_4. Below the torus the symphyseal plane runs anteriorly, and is hollowed out slightly in the region of the genial fossa. On specimen RU 1840, which Leakey

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Plate 4

Figs 1–2 *Proconsul* (*Rangwapithecus*) *vancouveringi*. Left maxilla with P^4–M^3 (KNM-RU 2058). Fig. 1, occlusal view. Fig. 2, superior view.

Figs 3–4 *Proconsul major* (KNM-SO 542). Fig. 3, right maxilla with dc-dp^4 and M^1, with superimposed mirror image joined along the palatal suture, occlusal view. Fig. 4, right mandible with roots of dc–dp_3, crowns of dp_4 and M_1, with superimposed mirror image joined along the symphysis, occlusal view.

Figs 5–6 *Limnopithecus legetet*. Left mandible with dp_3–dp_4 (KNM-SO 1073). Fig. 5, occlusal view. Fig. 6, lingual view.

Fig. 7 *Limnopithecus legetet*. Right maxilla with dp^3–dp^4 and M^1, occlusal view (KNM-SO 536).

Fig. 8 *Proconsul* (*Rangwapithecus*) *vancouveringi*. Left maxilla with dp^4 and M^1, occlusal view (KNM-RU 1778).

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(1967) assigned to '*Kenyapithecus africanus*' on the basis of the supposed presence of a chin, the genial fossa is directed almost directly downwards on his reconstruction. When the fossa is directed posteriorly, so that the tongue muscles can attach, the 'chin' disappears. This is shown diagrammatically in Fig. 3. The genial fossa has one or two paired pits, probably marking the attachment of the genioglossus and geniohyoid muscles. The mylohyoid muscle seems to have been attached along the lower lip of the genial fossa, as the mylohyoid line runs directly below the pits and the fossa. A prominent spine is present on specimen SO 396 with clear digastric impressions on either side of it. The digastric fossa and spine extends several millimetres up from the base of the mandible.

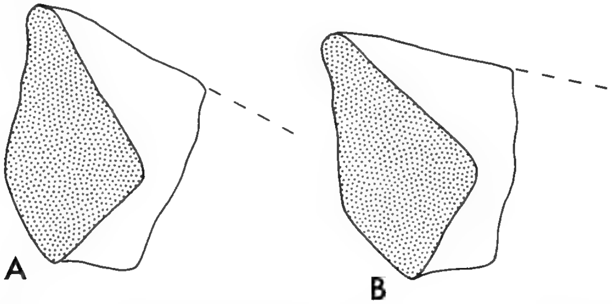

Fig. 3 KNM-RU 1840 '*Kenyapithecus africanus*' mandible, × 1. A, cross-section of the symphysis in the orientation of Leakey (1967 : fig. 5e) with the genial fossa opening downwards and the tooth row sloping downwards. B, alternative orientation showing tooth rows level and genial fossa opening posteriorly. The 'chin' is much less obvious in the second orientation.

The mandibular body varies in the same way as the symphysis. The largest specimens of *P. nyanzae* have body depths as deep as or deeper than *P. major*, but they are more gracile. The mental foramen is single and situated beneath P_3/P_4. The concavity for the buccal cavity is pronounced and in some cases seems to extend surprisingly far towards the base of the mandible. It always extends down to the level of the mental foramen, which is just over one third of the way up from the inferior border of the mandible. The inferior border is bluntly rounded.

The mandibular ramus is preserved in a broken state on specimen RU 1674. It has been described in detail by MacInnes (1943) and Clark & Leakey (1951 : 46–47). It is high and very large relative to the size of the body of the mandible, and has a pronounced posterior slope. A remarkable feature of this specimen is the posterior divergence of the mandible which leads to the bicondylar width of 112 mm. This is similar to values in male chimpanzees. (See Fig. 4.)

Upper incisors (Tables 3–4, p. 138–140). The I^1 is very high-crowned. The mesiodistal length is greater than the buccolingual length but is less than the height. The lingual surface of the tooth is moderately concave and has a broad stout median pillar running half way to the tip of the crown, and composed of a number of ridges that originate from the prominent lingual cingulum. Wear is usually confined to the incisive edge, and in one case only (MB 104) does it extend several millimetres along the lingual surface of the tooth. There are slight differences in shape and morphology accommodated within this sample, but they are not large enough to denote a specific difference.

The I^2 is high-crowned and caniniform. The crown is triangular in shape and only slightly oblique, as the mesial ridge is almost as long as the distal one. There is a small median pillar,

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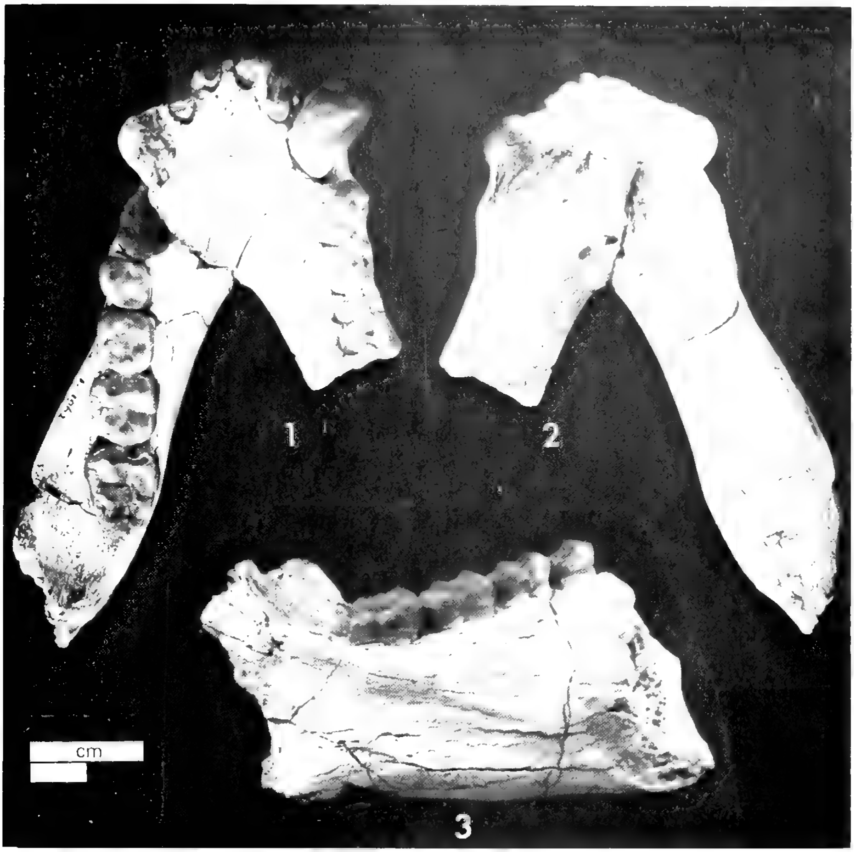
Plate 5

Figs 1–3 *Proconsul major*. Mandible with right C and left P_4–M_3 (KNM-SO 396). Fig. 1, occlusal view. Fig. 2, inferior view. Fig. 3, left mandibular body, lingual view.

Fig. 4 *Proconsul major*. Left I^1, lingual view (M 14297).

Fig. 5 *Proconsul major*. Left M_3, occlusal view (M 32237).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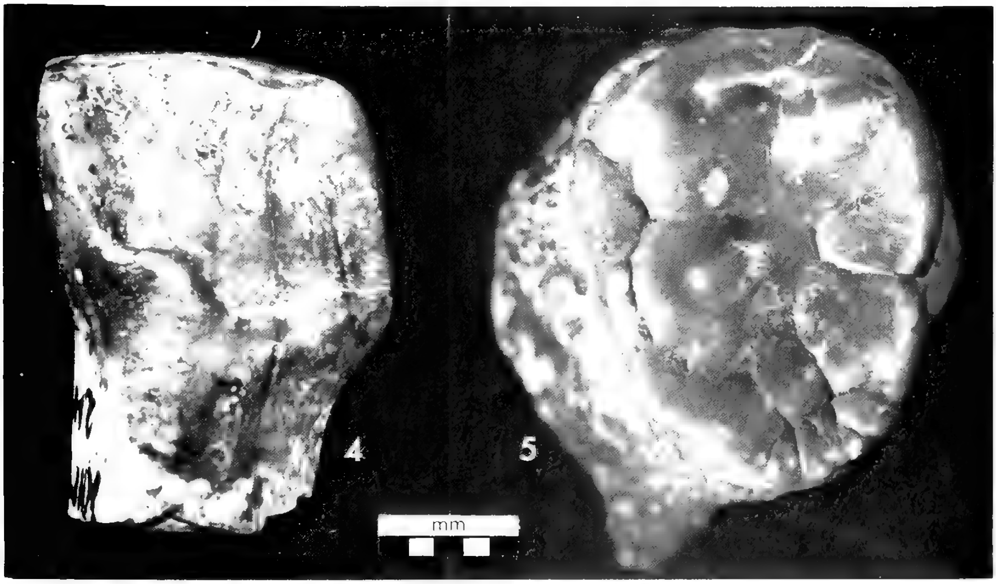
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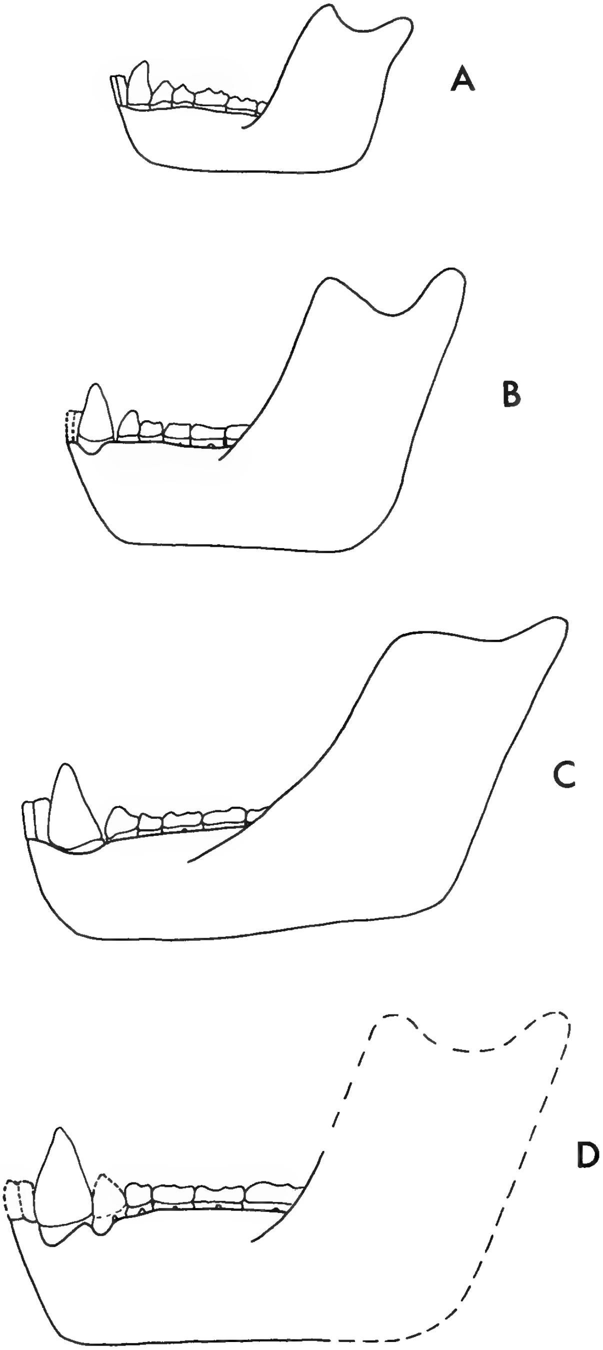


Fig. 4 Mandibular size variation in *Proconsul*, × ⅓. Lateral views of: A, *P. africanus*. B, *P. nyanzae* female. C, *P. nyanzae* male. D, *P. major* male.

consisting, as in I^1, of numerous ridges or striations, but the lingual cingulum is more prominent than in I^1. Distally the cingulum forms a slight heel. With the onset of wear the shape of the tooth alters completely. The tip of the crown is quickly worn flat, and the incisive edge thus produced is concentrated on the mesial side of the tip of the worn incisor. A relatively large mesial contact facet is formed against I^1, and a very deep wear notch is cut into the distal edge of the crown by the lower C.

Upper canine (Table 5, p. 141–3). These are large tusk-like teeth with rounded crown outlines. The crown is moderately bilaterally compressed, and the long axis of the tooth is in line with the molar–premolar tooth row. The crown has a shallow mesial groove running into the lingual cingulum at its mesial edge; the lingual face of the crown is furrowed by grooves and ridges as far as the distal ridge and the lingual cingulum is continuous as far as the distal ridge. Mesial and distal wear facets are developed, the former being a flat facet extending across the mesial groove, and the latter being a deeply-cut concave facet cutting across the distal ridge and quickly obliterating it.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is bicuspid, broader than long, and buccally elongated to give its typical triangular shape. The buccal cusp is higher than the lingual one but less so than in *P. africanus*. There is no ridge development on the occlusal face but there may be secondary wrinkling. Both mesial and distal cingula are prominently developed, and where they meet the mesial and distal ridges of the buccal cusp small tubercles may be developed. There is no lingual cingulum. Wear occurs on both cusps, but the lingual one is worn down more quickly than the buccal one, the latter having the faceting restricted to its lingual face.

The P^4 is similar to the P^3 but tends to have a slightly higher breadth/length index. It is usually smaller than P^3. The lingual cusp is nearly as tall as the buccal one and there is no buccal elongation of the crown. A transverse ridge joining the two cusps is occasionally present but usually the occlusal surface is broken up by secondary wrinkling as in P^3. The mesial cingulum is smaller and the distal cingulum much larger than in P^3.

Upper molars (Tables 8–10, p. 147–153). The M^1 is the smallest molar, and in *P. nyanzae* it is conspicuously smaller than M^2. It has a squarely built crown with all four cusps approximately equal. The cusps are large and occupy most of the occlusal area, resulting in a relatively constricted trigon basin and mesial fovea. The trigon ridges are moderately well developed, and are similar to *P. africanus* in most respects. The talon region of the M^1 is restricted. The hypocone is present as an isolated cusp separated from the protocone by a well-defined sulcus. There is no distal fovea. The cingulum is moderately large. The lingual cingulum runs continuously without a break from the mesial branch of the mesiobuccal ridge of the protocone to a small distal ridge from the hypocone. The cingulum sometimes present on the hypocone is presumably a secondary structure, arising later than the lingual cingulum of the protocone and the hypocone itself, but the two are now continuous. There is also a large distal cingulum running between the distal ridges of the hypocone and the metacone. The buccal cingulum is a small shelf at the base of the buccal main groove in the interval between the paracone and the metacone.

Wear exposes the dentine at the tips of the cusps, on the lingual side initially and much later on the buccal side. There is a fairly steep wear gradient in *P. nyanzae*, in which the dentine may be exposed over the whole lingual surface of M^1 while only just appearing at the tips of the lingual cusps of M^2 and M^3. In *P. major* the wear gradient is less steep.

The M^2 is much larger than M^1 and the ridges are less well defined and the cingulum much larger. There is a small protoconule at the end of the mesiobuccal ridge of the protocone, but the buccal ridges of this cusp are poorly defined. The crista obliqua is low but well defined. It is cut slightly by the distal branch of the longitudinal groove. Where this joins the distinct lingual groove between hypocone and protocone a small distal fovea is produced. The lingual cingulum is very prominent, especially on the protocone, and is moderately strongly beaded. On the hypocone and distally between the hypocone and metacone the cingulum is very large.

The M^3 is smaller than M^2 but it is still a well-developed tooth. This contrasts with *P. africanus* in which the M^3 is much more reduced. The distal cusps are generally slightly reduced in size but are still prominent, and the tooth outline is still predominantly square. The occlusal surface has poorly-defined mesial ridges, although the protoconule is faintly present. The trigon appears very greatly expanded, as there is no mesial fovea, so that it extends mesially all the way to the mesial marginal ridge. The crista obliqua is low and segmented, cut by sulci. The lingual cingulum is smaller than on M^2 and is strongly beaded, breaking at the hypocone and continuing distally as a very large distal cingulum. There is considerable secondary wrinkling over the occlusal surface as a whole.

Lower incisors (Tables 11–12, p. 154–5). The lower incisors are small relative to canine size. The I_1 is a slim high-crowned tooth, wider buccolingually than mesiodistally. All the specimens are heavily worn so little crown morphology can be seen; RU 2030 is the best preserved and is unusual in being much wider mesiodistally than RU 1947 and in having a marked concave curvature of its lingual surface. It resembles a chimpanzee I_1 while the other specimens are more like the gorilla I_1. In addition the other isolated incisors have a surprising amount of lingual wear, sometimes extending beyond the base of the crown, but the two Rusinga specimens have terminal edge wear only. While provisionally referring these specimens to *P. nyanzae*, the heterogeneity of the sample must be noted; even the two Rusinga specimens, one of which is part of a complete dentition clearly representative of *P. nyanzae* (RU 1947), differ greatly from each other.

On specimen RU 1947, where both lower incisors are preserved, I_2 is much larger than I_1. In particular, it is very much thicker buccolingually. It is similar to I_1 in morphology except for the slight mesial skewing of the crown, the distal edge of the crown being slightly convex and the mesial edge nearly straight.

Lower canine (Table 13, p. 156–8). The canine is a large tusk-like tooth on all specimens. This applies even to RU 1674 which is smaller than the others in most other dimensions. The canine is set strongly obliquely to the line of the molar–premolar tooth row. In cross-sectional outline it has a flattened face mesiolingually and a rounded border curving evenly round 270° distobuccally to mesiobuccally. The mesial ridge runs directly mesially, that is down the face of the crown closest to the lateral incisors. It meets the lingual cingulum at a slight elevation, and although the extent of this seems to vary considerably, it is rarely as well developed, and the mesial ridge as shortened, as in *P. africanus*. There is a slight groove immediately lingual to the mesial ridge. There is also a ridge which runs distolingually, but it always ends imperceptibly before it reaches the cingulum. The lingual cingulum is moderately well defined. It is strongest mesially, tapering off distally, and it ends fairly abruptly at the distobuccal angle. Wear occurs distally, starting near the tip and working downwards. This distal facet is usually flattish, and even with heavy wear does not become concave and does not cut deeply into the crown. Wear is only occasionally seen on and across the tip of the crown.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a one-cusped but only moderately sectorial type of tooth. It is elongated, and set obliquely across the line of the molar–premolar series, but the frequent presence of a beak-like process mesially makes the tooth appear less oblique and more mesiodistally aligned, although the roots are always set strongly obliquely. The beak-like process is the result of the fusion of the mesial ridge and the mesiolingual cingulum, both of which are prominent. The prominent mesiolingual cingulum ends at its junction with a varyingly developed lingual pillar, and distally there is a smaller distolingual cingulum not continuous with the mesial part. The lingual surface between the mesial and lingual ridges is typically flat and has a triangular outline. The distal ridge is well defined, running to the distobuccal angle.

The P_4 is bicuspid with the buccal cusp considerably larger than the lingual one. The cusps are set transversely to the general tooth row, but the long axis of the tooth is oblique. The talonid projects distolingually, and the trigonid mesiobuccally, so that the tooth is elongated in these directions. This gives the skewed appearance to the tooth already described for *P. africanus*, and in most other respects also the P_4 is identical to that of *P. africanus*.

Lower molars (Tables 16–18, p. 163–170). The M_1 is smaller than M_2 in both species, but the difference is much greater in *P. nyanzae* than in *P. major*. The mean indices for $(M_2/M_1) \times 100$ are 116% for *P. major* and 124% for *P. nyanzae*. The M_1 is slightly broader distally than mesially. It has five equal cusps, the hypoconulid being fully developed and set slightly buccal to the midline. The cusps appear less 'crystalline' than in *P. africanus*, and are more swollen and bulbous.

The occlusal ridges are correspondingly less well developed. The distal trigonid ridge is deeply depressed in the midline of the tooth and is slightly cut by the longitudinal sulcus, but it is considerably higher than the talonid floor even at its lowest point. The talonid ridges are poorly defined with the exception of the entoconid–hypoconulid ridge. The hypoconid in particular is isolated. The buccal margin of the tooth is formed by the buccal cingulum, and is indented between the buccal cusps. The invaginations are continued into the talonid by grooves, and it is both these factors that give rise to the isolation of the hypoconid. Wear follows the usual pongid pattern, the buccal cusps being worn down and dentine exposed first. Wear is often much heavier in *P. nyanzae* specimens than in *P. major*, and the former species has a steeper wear gradient as described for the M^1.

The M_2 is a much larger tooth than M_1. It is slightly more broad compared to its length. The trigonid and talonid basins are more strongly differentiated by ridges. The trigonid basin is flat and shallow; this is emphasized by the mesial wear pattern of M_2, the hypocone of M^1 being restricted mesially by the medial position of the hypoconulid of the M_1, so that it occludes entirely on the trigonid basin of M_2. The talonid basin is very large, and is completely enclosed by cusps and ridges. The hypoconulid is buccal to the midline. The cingulum is more strongly developed than in M_1, with the consistent occurrence of a small mesiobuccal cingulum on the protoconid and in the interval between the buccal cusps.

The M_3 is bigger than M_2 in all cases, but the size ratio varies considerably. In general, the larger the overall size of the tooth row, the greater the difference in length between M_2 and M_3. The M_3 narrows distally in *P. major*, and has a triangular outline as in *P. africanus*. The entoconid is reduced and is set far back from the metaconid, and the hypoconulid, while not as tall as on the other cusps, is spread out more and occupies a greater surface area of the occlusal surface. In *P. nyanzae* the M_3 is not reduced distally and is a large elongated rectangular tooth.

Deciduous dentition (Tables 19–21, p. 171–3). The upper dc is a small, low-crowned tooth, morphologically rather featureless. There is no mesial groove or ridge formation. The lingual cingulum is massive, and is continuous along the lingual border. There is no diastema between dc and di_2. The long axis of the crown is set in line with the line of the molar–premolar tooth row.

On the dp^3 there are two main cusps. The buccal cusp is higher and much bigger than the lingual one, and the buccal side of the crown is greatly elongated mesiodistally. No ridge development was observed on the relatively worn specimens. The mesial cingulum is well developed mesiobuccally, and the distal cingulum is very well developed, forming a shelf across the distal end of the tooth. The buccal terminations of both cingula are marked by low elevations or tubercles.

The dp^4 is a typically molariform tooth, very similar to M^1. The four cusps are equal, and the ridges connecting them are not strongly developed. The lingual cingulum is less shelf-like than in M^1 but the lingual edge of the tooth is swollen lingually suggesting progressive cingulum development (or loss). The protoconule does not appear to be developed on any specimens.

No crown of the lower dc is known. Measurements of the root of four specimens indicate that it would probably be a small tooth, and there may be some specimens in the collection incorrectly identified as permanent C of a smaller species.

Only one crown of the dp_3 is known, and that an isolated one, so the identification is uncertain. SO 589 is clearly a deciduous tooth judged on its thin enamel, splayed roots, and low crown; it is the same order of size as the root impressions on the immature mandibles, so it is very likely that it belongs to *P. major*. The mesial and distal ridges are poorly developed. The lingual ridge is more distinct, but there is no tubercle or second cusp present where it meets the lingual cingulum. The cingulum is massive, but is present as a swelling lingually rather than as a shelf. The talonid basin is rather shallow and poorly defined.

The dp_4 is a typically molariform tooth very like M_1. It is lower-crowned and lower-cusped than M_1, the hypoconulid is smaller, the buccal cingulum is much less well developed, and the tooth is more elongated. Also the talonid breadth exceeds the trigonid breadth more than in M_1. The cusps are set well in from the margins of the tooth so that the occlusal surface is restricted. A striking feature of this tooth is the elongated trigonid region mesial to the metaconid. This arises partly because the protoconid is set far mesial to the metaconid, and partly because the trigonid basin is relatively very extensive. The isolated tooth recorded as of *P. major* from Rusinga

Island is the largest of the specimens and as such has been retained in *P. major* even though it is the only specimen of this species now known from this site (RU 1767).

REMARKS. The main difference between *P. nyanzae* and *P. major* is one of size, but that this is not a consistent difference can be seen by reference to the tables of measurement (Tables 1–21). Nearly all the teeth could just be encompassed within the range of a single species with slightly greater than gorilla-type sexual dimorphism, but this assumes, naturally, that the large specimens are male and the small female. The distribution of this hypothetical species is not so easily explained, however, for the large specimens are all found at Songhor and Napak, while the small ones come from these two sites and Rusinga Island. It is most unlikely that in the good Rusinga sample no males have been found, so it must be assumed that the size difference in this instance cannot be attributed to sexual dimorphism, but must be owing to some level of taxonomic difference.

Part of this problem centres on whether there is any *P. nyanzae* at Songhor or not. Clark & Leakey (1951) assigned specimens from Songhor to this taxon, but Pilbeam (1969 : 71) reassigned some of the Songhor mandibular specimens as small *P. major*. The maxillary specimens had already been reassigned by Leakey to his taxon '*Kenyapithecus africanus*'. At this stage, therefore, there was a complex situation: large maxillary specimens only were put in *P. major* and these were clearly not representative of its full range of variation; all large and small mandibular specimens from Songhor were put in *P. major*, representing a more plausible range of variation for a species of this size; maxillary specimens only (from Songhor) were still in '*K. africanus*', and some odd fragments of *P. nyanzae* were left over. Accepting Pilbeam's reassignment of mandibular specimens, it seems most reasonable to follow suit with the maxillary specimens and refer all the Songhor pongids of this size to the one taxon *P. major*. This is the position adopted here. Apart from Songhor there remains one specimen probably belonging to *P. major* from Rusinga Island. This is specimen KNM-RU 1767, a lower deciduous molar. (The clavicle fragment from Rusinga Island mentioned by Clark & Leakey (1951 : 98) is a fragment of a crocodile limb bone.) The deciduous molars can be identified with more certainty now as *P. major* because the same tooth is preserved together with the first permanent molar on the mandible SO 541 which clearly belongs to this taxon.

In addition to the size differences there are a number of morphological differences that will be summarized briefly here. On the maxilla the nasal aperture is relatively broader in *P. major* than in *P. nyanzae*, the palate is relatively longer and narrower, the tooth rows converge posteriorly while in *P. nyanzae* they diverge, and the floor of the maxillary sinus is simple in *P. major* and more complex in *P. nyanzae*. On the mandible the main difference is the degree of robusticity, both the symphysis and body of the mandible of *P. major* being considerably more robust than those of *P. nyanzae*. This is emphasized by the nature of the sexual dimorphism of both; the larger males of *P. nyanzae* have mandibles nearly as deep as those of male *P. major* but more gracile and the small females of *P. major* have mandibles as shallow as those of female *P. nyanzae* but more robust. In the dentition there are also a number of differences, but also some striking similarities. The incisors and canines are morphologically identical, and when the canine lengths are plotted in a frequency diagram for both taxa together a bimodal distribution is obtained (but with 'males' at Songhor and 'females' at Rusinga as already discussed). In the premolars, the lower premolars are more bilaterally compressed in *P. nyanzae* than in *P. major*, but the uppers are similar. The first molar, especially the lower, is characterized by its small size relative to M2 in *P. nyanzae*. However, the difference is not all that great between it and *P. major*, which also has a relatively small first molar. The M_3 is relatively more elongated in *D. major* and the distal cusps are characteristically atrophied, while in *P. nyanzae* it is a broad rectangular tooth not reduced at all. Similarly the M^3 is relatively large in *P. nyanzae* and reduced in *P. major*.

There were thus two populations of large pongids in the Kenya Miocene, one centred on the southern sites around the Rangwa volcano (Rusinga and Mfwangano Islands and Karungu) and the other on the northern sites around the Tinderet volcano (Songhor and Koru) and Napak and Moroto. Whether these were subspecies belonging to one highly variable species, or separate but obviously closely related species, it is not possible to tell on the available dental evidence.

Hopefully when more postcranial bones are known a definite answer may be forthcoming. In the meantime, on the basis of the differences between them, the two species will be retained.

Brief comment might be made here of Leakey's (1967) taxon *Kenyapithecus africanus*. There is no justification for retaining this species, and as discussed above the specimens assigned to it have been variously reassigned to *Proconsul nyanzae* and *P. major*. For most of the specimens this course needs no justification, but some explanation is considered necessary for the reassignment of specimen M 16649 to *P. nyanzae*. This was described by Clark & Leakey (1951 : 63) as the type specimen of *Sivapithecus africanus*, mainly on the grounds of the near-absence of molar cingula, and, hence, similarity with the Asian dryopithecines then assigned to the genus *Sivapithecus*. This similarity was accepted by Simons & Pilbeam (1965 : 127) who actually included it in the hypodigm of one of their Asian species, *Dryopithecus* (*Sivapithecus*) *sivalensis*. Leakey (1967 : 157) subsequently removed it from the Dryopithecinae by describing it as a species of *Kenyapithecus*, ancestral to *K. wickeri* from Fort Ternan. Finally, Pilbeam (1969 : 115–123) discussed the whole problem in great detail, and concluded that most of the '*K. africanus*' specimens had best be described as *Dryopithecus* sp. indet., that phylogenetic relationship with *Ramapithecus* species (including '*Kenyapithecus*' *wickeri*) was improbable, and that the most likely relationship was with *D.* (*S.*) *sivalensis*. I agree with Pilbeam on nearly all of his conclusions, including his phylogenetic ones, but I do not see any reason for separating these specimens from their contemporaries in Kenya by referring them to an unknown species of *Dryopithecus*. The crown morphology of the molars and premolars is very similar to that of *P. nyanzae*: both P^4 and M^1 have small lingual cingula; the protocone and protoconule development of M^1 is identical to that of *D. nyanzae*; the M^1 is extremely small relative to the premolars and also, judged on the roots, to M^2; the canine root is very large, indicating a large crown; there is a posterior canine fossa associated with the large canine root; and the height and position of the zygomatic process are within the known range of variation of *P. nyanzae*. The main differences from *P. nyanzae* are that the tooth crowns are less crenulated, the cingula, though present, are smaller, and the M^1 is extremely small relative to the other teeth. I think the similarities outweigh the differences and that most of the '*K. africanus*' specimens, including M 16649, belong with *P. nyanzae*, which could well be ancestral to the later-occurring *S. sivalensis*.

Subgenus ***RANGWAPITHECUS*** Andrews 1974

DIAGNOSIS. A group of species approximating in size to the gibbon and siamang. Incisors high-crowned and relatively very narrow compared with subgenus *Proconsul* s. str. Upper molars and premolars elongated, the molars usually longer (mesiodistally) than broad, low-cusped and the occlusal surface often with more secondary wrinkling than in *Proconsul* s. str. Upper molars increase in size from M^1 to M^3 and premolars from P^3 to P^4, unlike *Proconsul*. No reduction of M^3. Lower molars and premolars also elongated. The molars have a marked wear gradient, such that M1 may have dentine exposed on the occlusal surface when M3 is only just coming into wear, unlike the condition in *Proconsul*. Strong lingual cingula are developed on all the upper molars and premolars, and the premolars also have a prominent distal cingulum. Zygomatic process is set very low over M1/2. The floor of the maxillary sinus is greatly extended. Mandibular body and symphysis relatively deep and robust.

TYPE SPECIES. *Proconsul* (*Rangwapithecus*) *gordoni* (Andrews), 1974 : 189 & 680.

Proconsul* (*Rangwapithecus*) *gordoni (Andrews 1974)

DIAGNOSIS. A species of *Proconsul* intermediate in dental size between the siamang and pygmy chimpanzee; similar in size to *P. africanus*. Upper teeth similar to those of *P.* (*R.*) *vancouveringi* as described in the subgeneric diagnosis, differing only in their larger size. In the lower dentition the incisors are very high-crowned and narrow; the canine is high-crowned and bilaterally compressed; the P_3 is very bilaterally compressed with nearly parallel buccal and lingual sides; the P_4 is elongated; the M_1–M_3 are also elongated, the cusps are low, the buccal cusps are divided by deep buccal sulci like the condition in the gorilla, the occlusal ridges and buccal cingulum are poorly defined, and secondary wrinkling is often present. P3–M3 lengths are: upper 40 mm, lower 44 mm for single specimens. M^1–M^3 length is 29 mm.

HOLOTYPE. Palate with complete left and right maxillary bodies and C–M^3. KNM-SO 700. (Pl. 3, fig. 1, p. 101.)

LOCALITY AND HORIZON. The Lower Miocene of Songhor with a few specimens from Rusinga and Mfwangano Islands, Kenya.

MATERIAL. 79 specimens which cover the complete mandible and maxilla except for the ascending ramus of the former and the nasal and zygomatic process of the latter.

Maxillary material. KNM-SO 401 with left P^4–M^1; MW 52 with left M^1–M^2 (this specimen is lost, but a cast is preserved in Nairobi).

Mandibular material. KNM-SO 374 with left P_4–M_2; SO 377 with left P_3–P_4; SO 463 with right M_1–M_3 (may be same individual as SO 700); SO 464 with right M_3; SO 486 with left M_2; SO 540 with left dp_4 and roots of M_1; SO 908 with right M_2; SO 1112 with left P_3–P_4, M_2, and roots of I_2–C, M_1, M_3.

Isolated teeth. M 16337, left M_3; the remaining specimens are listed in Tables 1–22.

DESCRIPTION. This species will be described together with the next, *P.* (*R.*) *vancouveringi*.

Proconsul* (*Rangwapithecus*) *vancouveringi (Andrews 1974)

DIAGNOSIS. A small species of *Proconsul* approximately the dental size of the siamang. It is like *P.* (*R.*) *gordoni* in morphology, as defined in the subgeneric diagnosis, but differs from it in size. The M^1 is significantly different from the M^1 of *P.* (*R.*) *gordoni* at greater than the 0·001 level of probability. The tooth row lengths are M^1–M^3, 22 mm, and P^3–M^3, estimated at 31 mm for a single specimen.

HOLOTYPE. Fragment of maxilla with left P^4–M^3. KNM-RU 2058.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga and Mfwangano Islands and Songhor. It is also provisionally identified from the Middle Miocene deposits at Maboko Island. All the localities are in Kenya.

MATERIAL. Seven specimens as follows: KNM-RU 1778, maxillary fragment with left dp^4–M^1 and P^3–P^4 exposed in crypts; KNM-RU 1801, left M^1; KNM-RU 2058, maxilla with left P^4–M^3; KNM-MW 48, left M^3; KNM-SO 942, right M^3; KNM-SO 944, right M^1; KNM-SO 1134, right M^1. (Pl. 4, figs 1–2, 8, p. 103.)

Referred material. Three specimens from Maboko Island. KNM-MB 53 left P^3; KNM-MB 125 left M^1; KNM-MB 148 left dp^4.

DESCRIPTION. This species and *P.* (*R.*) *gordoni* are so similar in morphology that they can be described together. Their only major difference is one of size, but this difference is great enough for there to be little doubt that the species are distinct.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is restricted in extent in *P.* (*R.*) *gordoni* compared with modern apes, and is slightly less extensive than comparable-sized *P. africanus*. The nasal processes of the premaxilla are not complete on any specimen, but they appear to make up most of the wall of the nasal aperture. The body of the premaxilla is short, and the index (naso-alv. ht/M^1–M^3) × 100 is 35·0 %. The incisor roots are moderately procumbent, and the functional diastema would appear to be small, an anomalous situation in view of the large canines.

The alveolar process of the maxilla is shallow in both species. The maxillary sinus is greatly expanded posteriorly, although its forward limit is rather far back, above M^1. It is relatively wide, although the full width is not apparent in specimen SO 700 or RU 2058 because the zygomatic processes are broken off. The floor of the sinus is deeply excavated between the roots of the molars in a manner more nearly approaching modern pongids than any other Kenya Miocene species. This may be evidence of progressive sinus expansion in these species such as has occurred in living apes, particularly the orang-utan (Cave & Haines 1940). The tuberosities of the alveolar process are extremely short in both species, projecting 4 mm beyond the distal border of M^3 in SO 700. The greater palatine foramen is anterior in position, being opposite the mesial border of M^3.

Both these features are quite variable in modern pongids. The zygomatic process of the maxilla is set both relatively far anteriorly and inferiorly. Two specimens of *P.* (*R.*) *gordoni* and one of *P.* (*R.*) *vancouveringi* have the root of the zygomatic process above $M^{1/2}$. A double log regression of the height of the zygomatic process on the upper tooth row length distinguishes these two species from the regression for the three species of *P.* (*Proconsul*).

The overall size of the nasal aperture corresponds with that of *P. africanus*, but it appears relatively broader in relation to height. The palate is relatively long and narrow in *P.* (*R.*) *gordoni*. It widens posteriorly, and the width at M^3 is 114% of the width at M^1.

Mandible (Table 2, p. 136–7). The symphysis is preserved on one specimen of *P.* (*R.*) *gordoni* (KNM-SO 1112). It is extremely deep, and although gracile in its general construction has a massive superior transverse torus which gives a high value for the robusticity index [(t/d) × 100 = 56%]. The medial surface both above and below the torus is concave (Fig. 5) so that the superior torus is a shelf-like structure analogous to the inferior simian shelf of modern pongids. The mandibular body is deep and gracile. The buccal surface below M_1 runs slightly laterally for about 14 mm from the alveolar margin and then slopes vertically down to the inferior margin 12 mm beyond. The inferior border of the body is relatively sharply angulated in contrast to the bluntly rounded border of most pongids, in keeping with the greater body depth. The root of the mandibular ramus overlaps most of M_3.

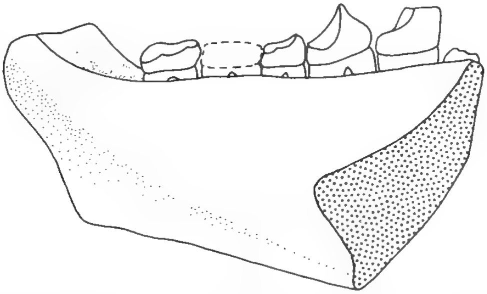


Fig. 5 The mandible of *Proconsul* (*Rangwapithecus*) *gordoni*, KNM-SO 1112, showing the almost shelf-like superior transverse torus. × 1.

Upper incisors (Tables 3–4, p. 138–140). The incisors are relatively high-crowned. The I^1 appears narrow as a result of buccolingual compression. The crown is strongly mesially skewed, and the incisive edge is relatively short, occupying the mesial $\frac{3}{4}$ of the crown. The lingual surface of the crown is prominently striated, particularly in the middle portion of the crown, and there is a well-developed lingual cingulum at the base. Wear is concentrated at or near the incisive edge; the top of the lingual surface is worn a little but on the available specimens the wear does not extend down onto the striated and swollen base of the crown.

The I^2 is a robust tooth, extremely mesially skewed so that the incisive edge has a slope of nearly 45°. The one specimen available is very worn, but the striations of the crown and development of the cingulum appear similar to the condition in I^1. The skewing of this tooth and the strong distal slope of the incisive edge both have the effect of increasing the available space for the top of the lower canine in occlusion. This could mean that the functional diastema between the upper canine and I^2, which is usually enlarged by the procumbancy of the incisors, may here be enlarged because the incisor crowns are skewed mesially.

Upper canine (Table 5, p. 141–3). The upper C is bilaterally compressed but rather low-crowned in comparison with length of crown. The long axis is only slightly oblique. There are no mesial ridges, but the distal ridge is very prominent, and is prolonged distally into a blade-like flange. This separates the broadly convex buccal surface from the slightly concave lingual surface. The mesial groove is very deep and is a striking feature of these teeth. There is only a slight distolingual cingulum present. Wear is both mesial and distal, the former producing a flat wear facet across the mesial groove, and the latter a deep concave facet lingually across the distal flange, quickly obliterating it. So heavy is the distal wear that a distinct notch may be cut.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is bicuspid, as usual in pongids, but it shows signs of molarization. The buccal cusp is only a little higher than the lingual one and the crown outline is nearly rectangular, mainly the result of massive distal cingular development. The buccal half of the crown is only slightly larger mesiodistally than the lingual half. The mesial cingulum is strongly developed, and runs in parallel with the buccal ridge, so that the mesial fovea is well developed, nearly horizontal, but narrow. The ridges on *P.* (*R.*) *vancouveringi* are slightly better developed than on *P.* (*R.*) *gordoni*, and the cusps themselves are relatively cristodont, consisting of sharply-edged inverted triangles separated from each other by a deep V notch. There is a moderate lingual cingulum, starting at the midpoint of the lingual surface of the lingual cusp, and increasing distally until it runs into the large distal cingulum. The distal fovea enclosed by the cingulum is deep and well defined. There is also a slight buccal cingulum continuous with both mesial and distal ones, so that the tooth is almost completely encircled by cingulum.

The P^4 is even more molarized than the P^3 and is unusual in being larger than P^3. The increase is brought about by massive cingulum development. The cusps are nearly equal in size. The lingual cusp has two distinct ridges, one running mesially to the mesial cingulum and the other running without a break to the mesial side of the tip of the buccal cusp. Enclosed between the ridges is a narrow mesial fovea. Distally there are no ridges but there is considerable occlusal wrinkling, nearly as much as in M^3. The cingulum is very strongly developed. The mesial cingulum forms the margin of the mesial fovea, but continues past the mesial ridge of the buccal cusp to form a slight and discontinuous buccal cingulum. There is a large lingual cingulum, continuing from the lingual end of the mesial ridge of the lingual cusp and running into the large distal cingulum.

Upper molars (Tables 8–10, p. 147–153). The upper molars are four-cusped. The hypocone is large, and is often larger than some of the trigon cusps. The order in size is usually protocone–hypocone–paracone–metacone. The teeth are usually longer than broad. The relatively greater length is due partly to the expansion of the trigon, the paracone and metacone being widely separated, and partly to the large size of the hypocone. In *P.* (*R.*) *gordoni* the paracone is some way mesial to the protocone and the hypocone some way distal to the metacone, and this gives the teeth a diamond-shaped outline. The cusps have a sharp-edged 'crystalline' appearance and the ridges are well developed. Neither of the conules appears to be present. In *P.* (*R.*) *vancouveringi* the crown is more circular in outline and the protocone relatively much bigger. The hypocone is still large but it is smaller than the protocone.

The wear on the molars is a conspicuous feature of these two species, the wear gradient being very high. In *P.* (*R.*) *gordoni* SO 700 has the M^1 with moderate areas of dentine exposed on the lingual cusps, M^2 with evident signs of wear but no dentine exposed, and M^3 newly erupted with only slight traces of wear mesially. In *P.* (*R.*) *vancouveringi* RU 2058 is more heavily worn and has dentine exposed continuously along the lingual half of the crown of M^1; M^2 has dentine exposed on the protocone, and M^3 appears only slightly worn with no dentine exposed at all.

On M^1 the trigon is greatly expanded mesiodistally. The mesiobuccal ridge of the protocone divides into the mesiobuccal and distobuccal ridges of the protoconule and these both run slightly mesially to the bottom of the mesial border and half way up the border of the paracone respectively. Neither of them makes contact with the tip of the paracone. Between the two ridges is a narrow and inconspicuous mesial fovea. The distobuccal ridge of the protocone joins the lingual ridge of the metacone without a break to make the crista obliqua. The mesial and distal ridges of the paracone, and the mesial ridge of the metacone, are distinct but low and are deeply depressed, but not cut, by the buccal main groove.

The hypocone is very large and completely isolated. It stands on and is a part of the distal cingulum, which in *P.* (*R.*) *gordoni* appears to made up of two parts. The internal part stops short at the hypocone, but a thin external shelf of the distal cingulum does not stop at the distal margin of the hypocone, but continues around it and joins up with the lingual cingulum. Only the first of these is present in *P.* (*R.*) *vancouveringi*. The lingual cingulum is massive and is continuous all round the protocone. The main part of it merges into the hypocone but a small segment of it continues round the hypocone as already mentioned. The distal cingulum is similar to that of P^4

and ends buccally at a small angulation at the base of the cusp. A slight buccal cingulum is developed in the gap between the two buccal cusps. The cingulum is slightly beaded, and the occlusal surface of the whole tooth has fine wrinkles all over it. The wrinkling is quickly destroyed by wear and cannot have had much functional significance on this tooth.

The M^2 is a much larger tooth than M^1 and relatively broader, but is otherwise quite similar. The degree of wrinkling, which is much stronger, probably had more functional significance than that present in M^1. The lingual cingulum is not continuous around the hypocone, but breaks off as it reaches the distal border of the hypocone. The buccal cingulum is much more prominent and is continuous around the paracone.

The M^3 is a very large tooth, bigger than M^1 and M^2. It is also still relatively elongated although not as much as is M^1. There has been some morphological reduction, as the metacone and sometimes the hypocone are both reduced in size, but this is compensated for by great enlargement of the protocone. The trigon can hardly be distinguished except the mesiolingual portion of it between the protocone and protoconule which is sometimes developed. Apart from this the mesial and distal foveae appear continuous over the trigon. The cingulum is large, and the hypocone stands as an elevation on it, with no cingulum around its border. The buccal margin is conspicuous and shelf-like, and contacts the distal cingulum past the metacone. With the development of the protoconule, the elongation of the crown, and the moderate distal taper, the M^3 looks rather like a lower molar.

Lower incisors (Tables 11–12, p. 154–5). The lower incisors are very high-crowned and buccolingually compressed. They are quite exceptional for pongids in this respect and it is important to find incisors associated with posterior dentition in order to check the assignment to *P.* (*R.*) *gordoni* of the six isolated I_1 and seven I_2. The crowns are perfectly symmetrical and of simple construction with a narrow medial pillar on the lingual face but no striations. Wear is along the incisive edge only. There is no buccal wear such as would occur in overbite, and presumably the slight amount of wear lingually on the I^1 could be due to occlusion with the buccal edge of the incisive surface of the lower.

The I_2 is very like the I_1, and is more buccolingually compressed than is usual in pongid I_2s. The crown is only moderately mesially skewed and has a long incisive edge. A slight medial pillar is often developed. Wear is again confined to the incisive edge.

Lower canine (Table 13, p. 156–8). The lower canine is a very high-crowned, slender tooth. It has a moderate distobuccal curvature enhanced by the long mesial ridge. Only one specimen has the canine in place (SO 1112) and in this the crown is half broken away, but it does not appear that the crown is at all strongly laterally divergent. The root is very long and reaches nearly to the base of the mandible. The ends of the root sockets converge inferiorly and nearly meet below the incisor roots at the symphysis.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a very distinctive tooth. It has a sharply triangular crown, long and low-crowned. It is also strongly bilaterally compressed, so much so that the nearly straight buccal and lingual faces are parallel, joining front and back in bluntly rounded surfaces. The lingual face of the crown between the mesial and lingual ridges is flat, and as the distolingual ridge is nearly as far distal as the distal ridge, the lingual face is greatly expanded. The ridges are massive and rounded rather than sharp and distinct, and they enclose a small and shallow distal heel which also connects up with the slight lingual cingulum. There are too few specimens to be able to conclude much on the kind of wear on the P_3, but, from its morphology and that of the upper and lower C, it is likely that at least a moderate degree of sectoriality is present.

The P_4 is a bicuspid tooth that is longer than broad. Linked with this elongation the crown is less obliquely set in the tooth row. The buccal and lingual cusps are equal in height, the buccal one being slightly in advance of the other. They are not connected by any ridge, but as they are set so close together in the narrow crown a depression is isolated mesially. The crown is elongated distally with a prominent distal cingulum, and this region has much secondary wrinkling. The buccal cingulum is also prominent, although usually not continuous. It is largest on the mesiobuccal angle of the buccal cusp, may continue thinly around this cusp, and is large again distal to this, where it joins the distal cingulum.

Lower molars (Tables 16–18, p. 163–170). The M_1 is an elongated narrow tooth. It is set rather obliquely with the buccal cusps mesial to the corresponding lingual ones. The trigonid ridges are poorly developed so that the trigonid basin is not separated from the talonid basin. There is a very slight trace of the distal trigonid ridge but it appears no stronger than the secondary wrinkling which is a feature of the talonid surface. The buccal ridges are strongly indented into the talonid basin, so that the buccal cusps are isolated from each other. Large diamond-shaped foveae are produced buccally with the buccal margin of the crown being provided by the cingulum. The system of grooves follows the usual pattern, but the occlusal surface shows a tendency to be broken up into secondary wrinkles and folds. The cingulum is strongly developed, but is less shelf-like and fills the gap between the two buccal cusps. When it is completely unworn the cingulum may be beaded. The cusps do not project very high above the occlusal plane, so with wear they are quickly worn down to this level. Wear initially is at the tips of the cusps, but as it continues the elaboration of the crown comes into effect as the wear crosses the folds and wrinkles in the trigonid and talonid basins. The wear gradient is similar to that described for the upper molars.

The M_2 is similar to M_1 in general morphology and in the indented buccal margin. The trigonid basin is completely undifferentiated from the talonid. The only trigonid ridge is a slight mesial one. There is a moderate entoconid–hypoconulid ridge with a distal fovea beyond it. The wrinkling and folding are conspicuous, particularly in the region of the trigonid and mesial part of the talonid. The hypoconulid is more buccally placed, and is isolated similarly to the other buccal cusps with a large triangular infilling of cingulum between it and the hypoconid.

The M_3 is a very large tooth, much larger than M_1 or M_2. The M_3 has very strongly developed folding and wrinkling covering the whole occlusal surface. There is no division into separate compartments as the ridges are poorly developed and appear as part of the secondary folding. The hypoconulid is buccally placed exactly in line with the protoconid and hypoconid, and is isolated in the same way as they are. There is no reduction of the distal end of the tooth so the crown lacks the triangular shape characteristic of the M_3 in species of *Proconsul* s. str. The buccal cingulum is the most strongly developed of the lower molars and is nearly continuous along the buccal edge.

Deciduous dentition (Tables 19–21, p. 171–3). One isolated di^2 is referred to *P.* (*R.*) *gordoni* on the basis of size. It is high-crowned and mesiodistally compressed. The tip is pointed and there is only a very short incisive edge mesial to the tip. The lingual cingulum is relatively well developed.

Two isolated dc are referred to *P.* (*R.*) *gordoni* on the basis of size. They are low-crowned, featureless teeth. There is no ridge or groove formation. They have a massive lingual cingulum, shelf-like along most of its length and extremely swollen lingually. There is a slight elevation of the cingulum about one third of the way distally from the mesial origin of the cingulum.

The dp^3 is a bicuspid tooth. The specimen is not associated with any permanent teeth and its allocation to *P.* (*R.*) *gordoni* is based on size. The buccal cusp is much larger than the lingual one, but is so heavily worn it is difficult to say how much taller it was. There is a faint ridge connecting the cusps. Mesial to it the mesial cingulum is fairly strongly developed and distally the distal cingulum is more strongly developed, although not to the extent that might have been expected for a milk tooth of this species.

The dp^4 of *P.* (*R.*) *vancouveringi* is a most unusual tooth. It is extremely elongated; the breadth/length index is 85·7%, much lower than for M^1. Apart from that, the crown is similar to the associated M^1 except that it is lower-crowned, the cusps are lower, and the lingual cingulum is poorly developed. The measurements for this specimen (KNM-RU 1778) are mesiodistal length 6·3 mm and buccolingual breadth 5·4 mm. A second specimen of this tooth was recovered from the later deposits of Maboko Island (KNM-MB 148). It is almost identical in size and morphology to the Rusinga specimen despite the probable age difference of several million years between the two sites. A single tooth, SO 945, might be a dp^4 of *P.* (*R.*) *gordoni*, but it is very uncertain and no account can be given until better material is available.

The dp_4 is a molariform tooth with very distinctive morphology. It is elongated and narrow. The protoconid is far mesial to the metaconid and has a mesial trigonid ridge running mesiolingually to a very slight elevation that probably represents the paraconid. The trigonid basin is well developed and triangular in shape, and mesial to it is a small mesial fovea. The mesial end of the tooth is therefore very long and constitutes part of the elongation of the crown. The rest is made up by the lengthened talonid, a relatively large space separating the protoconid–metaconid from the hypoconid–entoconid. The hypoconulid is small and does not much affect the length of the crown. The effect of narrowness of the crown is enhanced by the way the cusps are set in from the lingual and buccal edges, particularly the latter. In addition, the buccal cingulum is only slightly developed.

REMARKS. *Proconsul* (*Rangwapithecus*) *gordoni* and *P.* (*R.*) *vancouveringi* are so similar that there is little doubt that they are closely related. The question that remains to be answered, however, is whether they are specifically distinct. Such a distinction must be based almost entirely on the size difference between them, but there is an additional difference in their geographical ranges. The size differences are indicated in Tables 6–10 (p. 144–153) and in Figs 12–16, and these give an indication of the degree of difference between them, but the only sample large enough to enable a statistical test to be made is that for M^1. A sample of 13 is available for this tooth, and these divided clearly into two groups on the bivariate (breadth/length) plot in Fig. 14 (p. 182). Significance tests on the two samples gave values of t of 9·9 for mesiodistal length and 13·8 for buccolingual breadth, and, therefore, probabilities of very much less than 0·001 that the two samples represented one statistical population (Andrews 1974 : 188). Furthermore, the two samples differ in their distributions. That referred to *P.* (*R.*) *gordoni* is known almost exclusively from Songhor (72 specimens) with only one good specimen known from Mfwangano and a few isolated teeth from Rusinga. The much smaller sample of *P.* (*R.*) *vancouveringi* is known by isolated teeth from Rusinga, Mfwangano, and Songhor, but the two more complete specimens are both from Rusinga. This largely allopatric distribution, coupled with the big size difference, is felt sufficient to justify the distinction at the species level.

Genus ***LIMNOPITHECUS*** Hopwood 1933

DIAGNOSIS. Primitive apes of Miocene age from Africa. Dental size slightly smaller than *Hylobates*. Central incisors relatively large and broad. Canines well developed, the lower with short mesial ridge and very asymmetrical. P^3–P^4 low-crowned, cusps of approximately equal size. P_3 single-cusped but low-crowned, P_4 elongated. Molar cusps low and rounded. Distinct buccal cingulum on the lower molars, occlusal ridges poorly developed, and distinct size increase from M_1 to M_3. Distinct lingual cingulum on the upper molars, cingulum not crenulated, slight protoconule developed, occlusal ridges moderately well defined, and increase of molar size in sequence M^1–M^3–M^2. The M^3 is slightly reduced in size. P_3–M_3 length averages 26–27 mm. The mandible is relatively short.

TYPE SPECIES. *Limnopithecus legetet* Hopwood 1933 : 97.

Limnopithecus legetet Hopwood 1933

1933 *Limnopithecus legetet* Hopwood : 97.
1943 *Limnopithecus evansi* MacInnes : 153.
1963 *Pliopithecus* (*Limnopithecus*) *legetet* (Hopwood) Simons : 881.

DIAGNOSIS. As for genus.

HOLOTYPE. Distorted mandible with M_1–M_2. BM(NH) M 14079.

LOCALITY AND HORIZON. The Lower Miocene of Songhor, Koru, Ombo, and Rusinga Island; and the Middle Miocene of Fort Ternan and Maboko, Kenya. The Oligo-Miocene of Bukwa, and the Lower Miocene of Napak, Uganda.

MATERIAL. 116 specimens which cover the complete dentition, the premaxilla, the portion of the maxillary body between C and M^1, and the mandible except for the ascending ramus.

Maxillary material. KNM-SO 421 with left P^3; SO 443 with right C–M^1; SO 535 with right M^2–M^3; SO 536 with right dp^3–dp^4 and M^1; SO 537 with left M^1–M^2; SO 538 with left C–P^3. (Pl. 4, fig. 7, p. 103.)

Mandibular material. M 14079 with right M_1–M_2; M 14080 with left dp_3–dp_4; M 14284 with right P_3–P_4; M 32227 with left P_3; KNM-SO 376 with right M_1; SO 385 with right P_4–M_2; SO 386 with left P_3 and right M_1–M_3; SO 387 with left M_1–M_2; SO 388 with right M_2; SO 444 with right M_2–M_3; SO 455 with right M_3; SO 482 with right M_1–M_2; SO 532 with right M_2–M_3; SO 533 with right P_3; SO 534 with right M_1–M_2; SO 1073 with left dp_3–dp_4; SO 1075 with right C–P_3; KNM-KO 6 with right M_3; KO 7 with left M_2; KO 8 with I_1–M_2; KO 11 with dp_3; KNM-RU 1708 with right M_2–M_3; RU 1916 with right P_3–P_4; RU 2078 with right M_1; KNM-OM 35 mandibular symphysis. (Pl. 4, figs 5–6, p. 103; Pl. 6, p. 119.)

Isolated teeth. M 14332, right I^1; the remaining specimens are listed in Tables 1–22.

Referred material. 37 specimens attributable to *L. legetet* are known from Napak, Uganda. Some of these are mentioned by Bishop (1964 : 1329–1330), and one, UM-P 64-02, has been recently described by Fleagle (1975). Thirteen specimens from Fort Ternan are provisionally referred to *L. legetet*. There are KNM-FT 19–24, left mandible with C–M_3 and associated right P_4–M_2 and M^3 (Pl. 6); FT 11 left I^1; FT 12 edentulous mandible; FT 14 immature mandible with M_1; FT 15 left C; FT 17 left M_1; FT 18 right P_4; FT 25 right I_2. Seven specimens from Maboko Island are provisionally referred to *L. legetet*, KNM-MB 109 M^2, 147 M^1, 149 M_2, 151 I^2, 152 M^3, 153 I_2 and 156 C^1.

DESCRIPTION. This description is based entirely on the Kenya specimens. There are a number of specimens probably belonging to this species from Napak, Uganda, but I have not been able to include these here.

Maxilla and premaxilla (Table 1, p. 134–5). Maxillary specimens are fewer and more fragmented than the mandibular ones. Only one specimen has the molars associated with any of the anterior teeth. The premaxilla is preserved on a number of specimens, but is never complete. The nasal process ascends the side of the nasal aperture, and it looks as though it may connect up with the nasal bones, i.e. complete the side of the aperture, but all the specimens are broken before this point is reached so it is impossible to establish this. It appears that the aperture was probably high and narrow.

The alveolar process of the maxilla is low and gracile. On the large specimens there are relatively prominent canine juga associated with the canine root and distinct concavities posterior to them (canine fossae). The maxillary sinus is long and narrow. Its anterior end is above P^4 and it extends beyond M^3. It is excavated between the roots of M^2 and M^3, but there is no division into loculi. It does not seem to extend laterally into the zygomatic process, and medially it is limited by the nasal cavity which may be relatively broad. In this it is like the condition in dryopithecines and differs from that of *Dendropithecus macinnesi*, in which the sinus floor is wide and the nasal cavity narrow. The root of the zygomatic process is above M^2 and does not appear to be close to the alveolar border. On two specimens the zygomatic process still curves laterally at 4 mm above the alveolar border, so the actual height must be greater than this. On the one specimen measurable it is 5·6 mm.

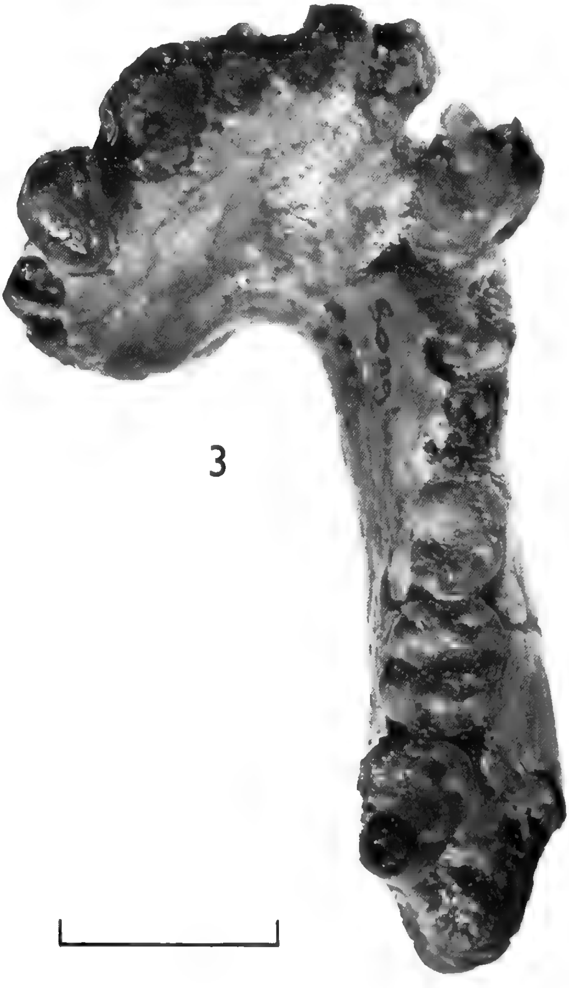
Mandible (Table 2, p. 136–7). Despite the large sample the mandibular symphysis is preserved entire on only a few specimens. Its morphology is similar to that of the other Kenya dryopithecines. The internal surface slopes evenly down from the incisor alveolus and reaches its most posterior extent slightly below the midline at the superior transverse torus; from there it slopes very slightly anteriorly with a broad shallow genial concavity. The development of genial pits varies but usually consists of two pairs, the pairs being divided by the symphysis. The most posterior extent of the symphysis reaches the level of mid-P_3. The anterior surface of the mandible on either side of the symphysis is gently convex, but on the specimens with large canines the canine juga are prominent so that the anterior face is flattened and sharply divided from the posterior body of the mandible.

Plate 6

Fig. 1 *Limnopithecus legetet.* Right mandible with I_1–M_2, lingual view (KNM-KO 8).
Fig. 2 cf. *Limnopithecus legetet.* Left mandible with C–M_3, occlusal view (KNM-FT 20).
Fig. 3 *Limnopithecus legetet.* Mandible with left P_3, right C and M_1–M_3, occlusal view (KNM-SO 386).

1

2



3

The mandibular body is fairly robustly built. It becomes slightly shallower posteriorly. Laterally the mental foramen is set below P_3/P_4 about $\frac{3}{8}$ of the way up from the inferior border. The lateral surface of the body is slightly concave between the canine juga and the root of the ramus. The latter rises steeply and overlaps most of the last molar. The lingual surface of the body is marked by the mylo-hyoid line which is often extremely prominent; it passes down to the inferior border of the body and crosses the symphysis along the inferior edge. The mandibular ramus is not preserved on any specimen. The root of it overlaps M_3 and at this point is rising nearly vertically, so it is likely that the whole ramus was nearly vertical and lacked any great posterior slope.

Upper incisors (Tables 3–4, p. 138–140). The I^1 is a broad spatulate tooth. The crown is mesiodistally appreciably broader than thick. It is also higher than broad but not by much and the effect is of a low-crowned tooth. The lingual surface is flat to slightly concave, with a rounded swelling arising from a prominent basal cingulum. The large cingulum, which leads into mesial and distal marginal ridges, makes the lingual surface appear hollowed out. The height of the lingual cingulum varies but it is usually quite high so that it limits the lingual face. Wear begins along the incisive edge and on the lingual surface of the crown immediately above it. In its early stages it hits up against the lingual swelling and slowly cuts into it. Eventually wear obliterates all trace of the swelling and cuts a broad channel through the lingual cingulum.

By contrast with the I^1 only one specimen of the I^2 is known. It is assigned to this species because it is small, relatively broad, and low-crowned. The mesiodistal dimension is actually larger than the buccolingual one. The lingual face is nearly flat, and is bordered by the same combination of basal cingulum and mesiodistal marginal ridges seen in I^1. The crown is strongly mesially angulated, but even though this specimen is unworn there is a considerable incisive edge.

Upper canine (Table 5, p. 141–3). The crowns are bilaterally flattened and blade-like in appearance. The roots are long and often have a pronounced buccal curve. The crown has a rounded and indistinct mesial ridge, which forms the buccal margin of a shallow mesial groove. There is a very broad and rounded lingual pillar (rather than a ridge) immediately distal to the mesial groove, and distal to this the crown is flat to slightly concave. The distal ridge is more strongly developed and is incipiently blade-like. The buccal surface of the crown is evenly convex. The crown appears symmetrical when viewed buccally, but there is a slight distal curve to the tip of the crown. The lingual cingulum is well developed. It is largest mesially and where it contacts the mesial ridge a tiny tubercle is sometimes present. Distal to this it forms the end of the mesial groove, and there is a distinct elevation of the cingulum at the top of the lingual pillar. Distally the cingulum is low and narrow.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a bicuspid tooth. The buccal cusp is bigger and more conical than the lingual one but the difference in height is not marked. The crown outline is nearly rectangular, and the crown is only slightly longer buccally than lingually because there is a small lingual and bigger distolingual cingulum developed that fills out the lingual side of the crown. There is a shelf-like distal cingulum ending buccally in a small tubercle on the distal ridge of the buccal cusp. There is no ridge developed on the occlusal surface.

The P^4 is very similar to the P^3 and is slightly the larger in the one specimen on which both teeth are present. The two cusps are nearly equal in height, and are connected by a low transverse ridge running between the tips of the cusps. There is a slight lingual cingulum running from the mesial edge of the lingual cusp, becoming wider distally, and the distal cingulum is shelf-like.

Upper molars (Tables 8–10, p. 147–153). In M^1 the paracone and metacone are equal in size. The protocone is larger in basal outline but even before wear it is a little lower than the paracone and the metacone; it is situated just distal to the line of the paracone. The development of the hypocone is variable: in some it appears as part of the cingulum and is continuous with it, although it has a conical outline like the other cusps, and it is nearly as big as the paracone. In others, however, the hypocone is more independent of the cingulum and even has a slight cingulum developed on its lingual border. In all cases the hypocone lies slightly distal to the metacone and slightly lingual to the protocone.

The trigon is well defined although the trigon ridges are low and rounded. The mesiobuccal ridge of the protocone is a massive ridge running obliquely forwards towards the protoconule. This is sometimes absent but usually it can just be seen. The mesiobuccal ridge of the protoconule is short so that the mesial fovea is extremely restricted and could have had little functional purpose in occlusion. The distobuccal ridge of the protocone branches almost immediately into a buccal branch to the metacone (crista obliqua) and smaller distal branch to the hypocone. The distal fovea is well developed and is divided from the distal cingulum by a well-marked transverse ridge running from the distal edge of the tip of the metacone to the bottom of the mesial border of the hypocone. The lingual cingulum is well developed. It starts on the mesial border of the protocone, reaching its maximum thickness on the lingual border of this cusp. It is sometimes continuous around the hypocone, joining up with the well-developed distal cingulum just described. There is also a slight buccal cingulum, most strongly developed in the interval between the paracone and the metacone.

There is no complete upper tooth row preserved, but on the basis of comparison of single teeth it appears that M^2 is the largest molar. The metacone on M^2 is slightly reduced in size and is lingually displaced relative to the paracone so that the distobuccal corner of the tooth is slightly cut away. The hypocone is also reduced relative to the protocone and may also be *lingually* displaced so that the distolingual corner is extended. The occlusal ridges are more distinct than on M^1, and in particular the mesial branch of the mesiobuccal ridge of the protocone is often better developed. The cingulum is more strongly developed than in M^1, but is similar in morphology and is always most strongly developed lingually.

Most of the differences seen between M^2 and M^1 are even more exaggerated in M^3. The protocone is very large and the hypocone small and sometimes vestigial. The metacone is usually present, but very reduced. The cingulum forms a complete ring around the tooth, and it is largest distolingually.

Lower incisors (Tables 11–12, p. 154–5). The I_1 crown is well preserved in the half mandible KO 8. It has a symmetrical, relatively broad mesiodistal crown. It is also relatively low-crowned although still higher than broad. The crown morphology is simple. The lingual face is slightly concave and lacks any cingulum or lingual swelling. The buccal face is gently convex. Wear is concentrated along the incisive edge, and in one specimen passes down on to the lingual face.

The I_2 is also relatively broad mesiodistally, having a similar breadth/length index as in I_1, but in this case it is even more remarkable a feature, for usually in pongids the I_2 is relatively much narrower than the I_1. The morphology is also very close to that of I_1, except for the asymmetry resulting from the bulging of the distal edge of the crown.

Lower canine (Table 13, p. 156–8). The canine is variable in size. In some cases where a small canine is associated with small posterior teeth and a gracile mandible, and a large canine with large posterior teeth and robust mandible, it is possible to attribute the variability to sexual differences, but there are many cases where the sex is uncertain. It is bilaterally compressed and the long axis is set obliquely to the line of the molar–premolar tooth row. The mesial ridge is extremely short and gives the crown a skewed and incisiform look. Lingual and distal ridges are faintly outlined, and the former also meets the cingulum at a distinct elevation. The lingual cingulum is narrow but quite distinct. It is most strongly developed at its mesial end, and it diminishes rapidly beyond its contact point with the lingual ridge so that the distal end of the crown, which is slightly prolonged into a heel-like process, apparently has no cingulum.

Lower premolars (Tables 14–15, p. 159–162). The P_3 has one principal cusp. It is only moderately bilaterally compressed, unlike the C, and the long axis is only slightly obliquely placed relative to the molar–premolar tooth row. It is set close to the canine, and on some specimens the mesial end of P_3 overlaps the distal end of the C. The pattern of three distinct ridges on the occlusal surface is very characteristic of this species. The mesial and distal ridges arise from the tip of the cusp and follow the line of the main axis of the molar–premolar series to the mesial and distal borders of the tooth. There they link up with a narrow lingual cingulum which completes a semicircle around the lingual border. More or less perpendicular to these two ridges is a lingual ridge, homologous probably with the distal ridge of the primitive trigonid of the molar. Where it meets the lingual cingulum the latter is raised up in a distinct tubercle.

On all available specimens the crown of P_4 is longer than broad. There is some indication that on the larger specimens the crown is relatively broader but more material is needed to be certain. Related to this, the long axis of the tooth is slightly oblique on the large specimens but is in line with the molar tooth row in the small gracile specimens. The two cusps are approximately equal in size and height. The buccal cusp is set in front of the lingual cusp, and they are connected by a moderately distinct transverse ridge. There is a small fovea mesial to this ridge. Distally there is an elongated fovea bounded on each side by distal ridges from the two main cusps, and at the distal angle of the fovea these ridges are raised into low inconspicuous tubercles. There are slight traces of buccal cingulum on the mesiobuccal face of the buccal cusp, and along the buccal edge of the distal basin. The cingulum becomes higher distally until it contacts the distobuccal tubercle which is probably then a cingular structure.

Lower molars (Tables 16–18, p. 163–170). The M_1 is five-cusped and always longer than broad. It is the smallest molar, and differs morphologically from the others by having the hypoconulid centrally placed and the talonid usually broader than the trigonid. The protoconid is often slightly in advance of the metaconid. It is set relatively far in from the buccal border and this distance is increased by the development of the buccal cingulum, which is thickest at the buccal border of the protoconid. The metaconid, the other trigonid cusp, rises steeply up from the lingual border of the tooth. The mesial and distal trigonid ridges enclose a small trigonid basin which is often referred to as the anterior fovea. That it is actually the trigonid basin, however, is established by the ridge homologies. In some specimens the basin is poorly developed or even absent altogether.

The talonid cusps of M_1 all appear isolated. On some specimens two longitudinal ridges are faintly apparent between the protoconid and the hypoconid and between the metaconid and the entoconid, but both are deeply cut by sulci. The hypoconulid is completely isolated. There is no sign of any ridge connecting hypoconulid and entoconid, and as a result of this there is no distal fovea differentiated. The development of the cingulum varies but is usually well developed on the buccal side of the lower molars. It is most strongly developed on the buccal border of the protoconid and in the interval between the protoconid and hypoconid.

The M_2 is the broadest of the molars. It is bigger than M_1 but smaller than M_3. It is similar in morphology to M_1 but the trigonid and talonid ridges are slightly better defined. The trigonid basin is nearly always apparent. The cingulum is more strongly developed, again on the protoconid and in the interval between it and the hypoconid. On one specimen there is a small cuspule on the cingulum between the protoconid and hypoconid, and in this specimen the cingulum is continuous around the buccal border of the hypoconid. The hypoconulid varies in position, but is more buccally placed than in M_1.

The M_3, the biggest of the molars, is elongated and relatively narrow. The trigonid ridges are no better developed than in M_2, but the talonid ridges are absent altogether and the enlarged hypoconulid occupies the whole of the distal end of the tooth. The cingulum is continuous buccally past the protoconid and hypoconid, but always remains narrow.

Deciduous dentition (Tables 19–21, p. 171–3). The di^1 is a low-crowned spatulate tooth. The lingual surface has a massive lingual cingulum merging into a short pointed lingual pillar that stops before it reaches the incisive edge. The buccal surface is smooth and rounded. In both specimens available the mesiodistal length exceeds the buccal height.

The upper dc is a low-crowned tooth. The lingual cingulum is massive and more shelf-like than in the di^1. One of the specimens has a slight lingual elevation of the cingulum connecting up with a lingual ridge to the tip of the crown but the other has no trace of either of these features. There is no mesial groove. The mesiodistal length is approximately equal to the buccal height.

The dp^3 has a marked buccal elongation, and the buccal cusp is considerably higher than the lingual one. There is an indistinct ridge connecting the two cusps. The distal cingulum is slightly developed. There are two buccal roots and a single lingual one.

The dp^4 is almost identical to M^1 except that it is smaller, lower crowned, and has thinner enamel. Ridge development is similar but the protoconule cannot be seen. The lingual cingulum is less shelf-like but relatively larger than on M^1. The crown is less rectangular than M^1 as the mesial and distal surfaces converge towards the lingual border.

The crown of dp_3 is almost bicuspid, although the buccal cusp is much larger than the lingual one. The cusps are joined by a sharp ridge running distolingually from the main cusp to the lingual one. There is a ridge running mesially from the buccal cusp to the mesial point of the crown, where there is a slight tubercle developed. The distal ridge of the buccal cusp is less distinct, but it also has a tubercle at its distal end. The lingual cingulum is well developed. The crown is elongated and bilaterally compressed.

The dp_4 is similar to M_1 but more elongated. The talonid width is relatively greater than the trigonid width, and the protoconid is well in advance (mesially) of the metaconid. There is no sign of paraconid development. The buccal cingulum is only slightly developed.

REMARKS. The taxon *Limnopithecus legetet* was first described from very inadequate material from Koru (Hopwood 1933). It was said at that time that it was a gibbon-like primate, in contrast to the chimpanzee-like morphology of *Proconsul africanus*. Little evidence was put forward to substantiate this view, but the contrary evidence of the differences between the milk dentitions of *L. legetet* and *Hylobates* was pointed out (Hopwood 1933a : 440). It was not mentioned, however, that *L. legetet* resembled pongids rather than hylobatids in the milk dentition.

In 1943 a second species, *L. evansi*, was described (MacInnes 1943 : 152). That such a split could be made depended solely on the inadequacy of the material on which *L. legetet* had originally been based, and discovery of further material made it quite obvious that the specific distinction of *L. evansi* was invalid (Clark & Leakey 1951).

The description of a third species, *L. macinnesi* (Clark & Leakey 1951), which was also said to have many hylobatine characters, seemed to confirm the family classification of *Limnopithecus*. However, in their discussion on the origin of *Proconsul*, Clark & Leakey (1951) concluded that an ancestor of *Proconsul* might have looked something like *Limnopithecus* and that the two genera were really not greatly different. They considered that *L. macinnesi* was too specialized in its C–P_3 morphology, but that as these specializations were absent in *L. legetet*, the latter served as a good model of the ancestral condition for *Proconsul* (Clark & Leakey 1951 : 111). This is so true that it is surprising that they put the two species of *Limnopithecus* together at all, for while *L. legetet* is morphologically very like the much larger *Proconsul* species, *L. macinnesi* has many features that link it with the gibbons.

What has been so misleading in this whole question of the status of *Limnopithecus* is a largely unconscious bias towards linking species of similar size. Size is not a valid criterion for a generic diagnosis, and it was not used explicitly in the earlier diagnoses of *Limnopithecus*, but because the morphological variation between all hominoid species, both fossil and Recent, is so small, species of similar size tend to look very much alike and so are grouped together. This essentially was the basis for the original linking of *L. legetet* and '*L.*' *macinnesi*, both with each other and with the Recent gibbons. If size is ignored, however, and morphological similarities alone considered, it is at once evident that the greatest degree of similarity of *L. legetet* is with *Proconsul africanus*, not with '*L.*' *macinnesi*. This is shown by the following list of characters which are shared by *L. legetet* and *P. africanus*, but for which '*L.*' *macinnesi* has the contrary condition. Maxillary sinus long and narrow; nasal aperture broad; mandibular symphysis with a superior transverse torus; incisors broad and low-crowned; I^1 spatulate; C rounded, not bilaterally compressed, and lacking a double mesial groove on the uppers; P_3 triangular in shape, not bilaterally compressed, grinding function rather than sectorial, low-crowned; M^1 square, not very much broader than long; M^3 very reduced relative to M^2; M_1 with strong buccal cingulum; M_3 elongated, crown compressed distally, and with a large heel-like hypoconulid.

In contrast to this there are only a few characters in which *L. legetet* resembles '*L.*' *macinnesi* to the exclusion of *P. africanus*. These are: C with short mesial ridge; P_4 elongated, longer than broad; and molars with low bulbous cusp formation. None of these are absolute differences from other species of dryopithecine, and they are of relatively minor significance compared with the extreme sectorial development of the C–P_3 complex of '*L.*' *macinnesi*. The postcranial material also, although it is not being covered in this paper, and there are only two specimens available for *L. legetet*, indicates an affinity between the latter and *P. africanus*, very different from the elongated and gracile long bones of '*L.*' *macinnesi* (Clark & Thomas 1951). The latter, indeed, is the strongest evidence for linking '*L.*' *macinnesi* with the ancestry of the gibbons, and it is on this basis, together with the sectorial specializations just mentioned, that it is retained in the Hylobatidae (see next section) while *L. legetet* is removed to the Pongidae, Dryopithecinae.

Family **HYLOBATIDAE** Blyth 1875

Genus ***DENDROPITHECUS*** Andrews & Simons 1977

DIAGNOSIS. Small anthropoid apes approximating in dental size to the siamang. Incisors high-crowned and strongly mesiodistally compressed. Canines blade-like, in males with double mesial grooves, showing a striking degree of sexual dimorphism. P_3 sectorial *sensu stricto*, as in gibbons. P^3 has strongly projecting buccal cusp. Lower molars have the cusps arranged around the periphery of the crowns, connected by well-defined ridges and enclosing large trigonid and talonid basins. Buccal cingulum of lower molars slightly developed. Upper molars of simple construction, with well-defined trigon and relatively small hypocone. Prominent lingual cingulum. M_3 slightly larger than M_2. M^3 usually reduced. Palate long and narrow and maxillary sinus well developed. Body and symphysis of mandible robust, well-developed superior transverse torus and usually also an inferior torus projecting posteriorly at least to the extent of the superior torus and often further. Dentally very similar to *Pliopithecus*, but having higher-crowned incisors, more strongly bilaterally compressed canines, more sectorial P_3, more projecting buccal cusp on P^3, and lower molars with stronger ridge formation and delineation of the talonid basin. Differs from *Pliopithecus* postcranially, particularly in the length and slenderness of the long bones. All the postcranial bones lack conspicuous muscular markings.

TYPE SPECIES. *Dendropithecus macinnesi* (Clark & Leakey), 1950 : 262.

Dendropithecus macinnesi (Le Gros Clark & Leakey 1950)

1950 *Limnopithecus macinnesi* Clark & Leakey : 262.
1963 *Pliopithecus* (*Limnopithecus*) *macinnesi* (Clark & Leakey) Simons : 881.
1970 *Aegyptopithecus* sp. Simons; Andrews : 539.
1977 *Dendropithecus macinnesi* (Clark & Leakey) Andrews & Simons : 162.

DIAGNOSIS. As for genus.

HOLOTYPE. The greater part of both mandibular bodies, lacking the symphysis, and containing P_3–P_4 and M_2–M_3 on both sides. BM(NH) M 16650.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga, Mfwangano, Karungu, Songhor and Koru, Kenya.

MATERIAL. 160 specimens which cover all of the maxilla and dentition and the mandible except for the ascending ramus. Postcranial material in direct association with cranial remains are known.

Maxillary material. KNM-RU 1774 with left and right C–M^3; RU 1799 with right M^1–M^3 and associated fragmentary skull fragments; RU 1806 ten associated teeth; RU 1849 associated upper and lower dentition with left I^1 and right I^1–M^3; RU 1850 associated upper and lower dentition, complete palate with C–M_3 both sides; RU 1915 with right M^2–M^3; RU 2086 with right P^4–M^2; KNM-SO 539 with left I^1–P^4. (Pl. 2, fig. 5, p. 97.)

Mandibular material. M 16650 with left and right P_3–P_4 and M_2–M_3; M 14083 symphysis with left P_3; KNM-RU 900 with right I_1–I_2 and left I_1–M_1; RU 1725 with right M_1–M_3; RU 1726 with right M_2–M_3; RU 1727 with left P_3–M_1; RU 1804 with right M_1–M_2; RU 1810 with roots C–C and right P_3; RU 1844 with left M_2; RU 1849 with right M_2–M_3 (see maxilla); RU 1850 with left M_2 and right M_1–M_3 (see maxilla); RU 1857 with right P_4–M_1 and M_3; RU 1893 with right P_3–P_4 and M_2; RU 1901 with right M_1–M_3 and nine associated teeth; RU 1925 with left M_1; RU 1935 with right P_3–P_4; RU 1962 with left C; RU 1972 with right C–P_3; RU 1978 with left M_3; RU 2001 symphysis; RU 2015 left and right bodies with right P_3–M_3 and left M_2–M_3; KNM-MW 51 symphysis with roots of right P_3–M_1; MW 53 with left P_3–M_2; KNM-SO 378 with right P_4–M_3; SO 405 symphysis with right C and two isolated teeth; SO 530 with right P_3 and M_1–M_2. (Pls 2, p. 97 and 7, p. 127.)

Isolated teeth. M 14082, right M^1; M 16381, right dp_4; M 18788, right I^1; M 32230, right C; M 32231, left P^3; M 32232, left C; M 32233, left C; M 32234, right P_3; M 32237, left P^3; M 32238, left C; the remaining specimens are listed in Tables 1–22.

DESCRIPTION. The following description is based entirely on the specimens from Rusinga and Mfwangano Islands. The Songhor specimens are divergent in a number of characters, and this probably signifies a taxonomic difference which will be commented on after the description.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is a relatively small bone. The nasal processes are not complete on any specimen, but it appears from the convergence of the maxillo-premaxillary suture with the lateral margin of the nasal cavity that they extend no further than two-thirds of the way up the nasal aperture. Alveolar procumbency appears well developed, but only a single female individual is measurable: naso-alv. ht is 6·1 mm and the index (naso-alv. ht/M^1–M^3) × 100 is 32·5%. The incisor roots are inclined anteriorly, and this, in combination with a short true diastema of 2·3 mm, produces a much larger functional diastema similar to that of modern apes.

The nasal aperture appears to have been narrow, reaching a maximum breadth on RU 1850 of only 12 mm. The floor of the aperture is a narrow gutter, uncomplicated by any grooves posteriorly. After having been divided in two by the nasal septum, the floor of the nasal cavity continues at a constant width of 11 mm in RU 1849, and an estimated 12 mm in RU 1774.

The alveolar process of the maxilla is fairly shallow. It is mainly occupied by the maxillary sinus, which is very large. The anterior wall of the sinus is above P^3, and it extends posteriorly into the tuberosities of the alveolar process beyond M^3. The floor of the sinus extends into the widely-flaring zygomatic process on the right side of RU 1774, and on all the specimens it penetrates down into the spaces between the roots of the molars so that the ends of the roots, with a thin bony covering, penetrate up into the sinus. The tuberosities of the alveolar process on specimen RU 1850 are very small and rounded, extending no more than 2 mm beyond M^3. On RU 1774, on the other hand, the tuberosity on the intact side is prolonged posteriorly into an angular process nearly 7 mm beyond M^3. The maxillary sinus extends into this process. The greater palatine foramen enters the palate posterior to M^3 in this specimen, but in RU 1850 it enters opposite the mesial border of M^3.

The zygomatic process of the maxilla is above M^2 in both specimens, but whereas in RU 1850 the height of the process above the base of the crown of M^2 must have been at least 6 mm, in RU 1774 it is only 2·4 mm. Since these are both adult female individuals, the feature is evidently extremely variable in this species.

The palate is not preserved intact on any specimen, although much of it is preserved on RU 1850. It is relatively long and narrow, and the indices for breadth over length are all less than 50%. The tooth rows diverge slightly from P^3 to M^3, and the index of breadth at M^2 over breadth at C is 106%.

Mandible (Table 2, p. 136–7). The mandibular symphysis is extensive and well buttressed. It is fairly deep, and the index of (t/d) × 100 for five individuals is 46%. There is a well-developed superior transverse torus about one-third of the way from the inferior border. Above this the lingual border of the symphysis runs straight to the incisor alveolus, while below it the border is moderately concave due to development of the genial fossa. This is shallow and on most specimens lacks any tubercle development. The inferior border of the symphysis is sharply rounded and an inferior transverse torus is usually present. Where the inferior torus is well developed the most posterior part of the symphysis is usually at the inferior border. The buccal border of the symphysis is gently and evenly convex from the inferior border to the incisor alveolus.

Posterior to the symphysis the body of the mandible gets shallower. The depth of the body at M_2 is 73% of the symphyseal depth, but the robusticity of the body remains very similar to that of the symphysis. The type mandible, described by Clark & Leakey (1951 : 76), gives a misleading picture of the construction of the mandibular body owing partly to the crushing to which this specimen has been subjected and partly to its unusually gracile construction. Most other specimens are considerably more robust than the type specimen. There is a single mental foramen about one-third of the way up from the inferior border of the mandible. The line of attachment of the buccinator muscle lining the outside wall of the buccal cavity is prominent and follows the usual hominoid pattern. Medially, the mylohyoid line is not easily seen except on one specimen (RU 1857), and again follows the usual pattern.

The mandibular ramus is not preserved on any specimen. The root of the ramus arises opposite

M_3 and overlaps the distal quarter of it. The pterygoid fossa is incompletely preserved on two specimens and appears very deep. The thickness of bone posterior to M_3 decreases sharply so that at the pterygoid fossa it is extremely thin but with a thickened buttress running along the inferior border. In addition, the inferior border starts to swing out inferiorly, posterior to the level of M_3, and this could indicate that the angle of the mandible was inflated.

Upper incisors (Tables 3–4, p. 138–140). The I^1 is a slim high-crowned spatulate tooth. The crown is usually asymmetrical with the distal border convex and the highest point of the crown at the mesial end of the incisive edge. The latter is appreciably shorter than the greatest mesiodistal length. The lingual surface is gently concave and usually has only the slightest trace of a lingual pillar. The cingulum is small and usually no lingual tubercle is developed. The buccal surface is convex and unmarked. The crown is worn along its incisive edge and down the lingual surface, abrasion of the latter having the effect of keeping the incisive edge always sharp. The I^1 of the Songhor population is much broader and more spatulate.

The I^2 is high-crowned like the I^1 and has a pointed apex. The incisive surface is that part mesial to the apex of the crown. The mesiodistal length is much reduced in comparison with the I^1. The lingual surface is simple, gently convex, and lacking any trace of lingual tubercle or pillar. The crown thus appears spatulate when unworn, but the effects of wear drastically alters this; the incisive surface is worn down, sharpening the tip of the crown into a dagger-like point, and the distolingual surface develops a deep wear notch from wear against the lower C. In these conditions it is not always easy to distinguish the worn I^2 from a small canine. (See Fig. 6.)

Upper canine (Table 5, p. 141–3). The upper canines show marked variation in both morphology and size. The large teeth, which are associated with molars in three specimens, are extremely characteristic of this species and are different from all other hominoids known. The large (presumably male) upper canine is a blade-like tooth deeply furrowed by grooves. The mesial ridge is very prominent and has a deep groove on either side of it; one is the mesial groove normally found on the lingual margin of the ridge, while the other is on the buccal margin. (The mesial ridge is identified from the origin of the lingual cingulum at its base.) Distal to the grooves both surfaces of the crown are slightly concave, the lingual face more so than the buccal. The two faces meet at the distal ridge which is narrow and prolonged into a knife-like flange. The lingual face of the crown is marked by numerous striations, while yet another shallow groove is typically present midway across the buccal face. The lingual cingulum is small and broken up by the vertical striations of the lingual surface. It is largest mesially and becomes smaller distally, usually not reaching the distal ridge. The wear on these large canines is characteristically distolingual, cutting across the lingual face of the distal flange-like ridge. There is also a flat wear facet developed mesially across the lingual mesial groove of the upper canine, made by the action of the lower canine. (See Fig. 6.)

The smaller (female) canines also have a knife-like appearance but the mesial ridge and single mesial groove are only moderately developed. The buccal surface is convex and not marked by any groove, and the lingual surface is only slightly striated and is flat rather than concave. The distal ridge is still pronounced, but it is not extended distally as in the larger teeth. The cingulum is slightly better developed and continues all the way to the distal ridge. The range of variation of the upper canine is extremely large, far greater than is seen in any other comparable-sized primate. This is reflected in the high values for standard deviation and coefficient of variation. The breadth/length index is low on both large and small teeth.

The Songhor population has canines as large as or larger than the Rusinga one. Some of the large ones, however, lack the double mesial groove and are less bilaterally compressed and more tusk-like.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a specialized tooth as part of the sectorial complex. The buccal cusp is much larger than the lingual one, and it is bilaterally compressed

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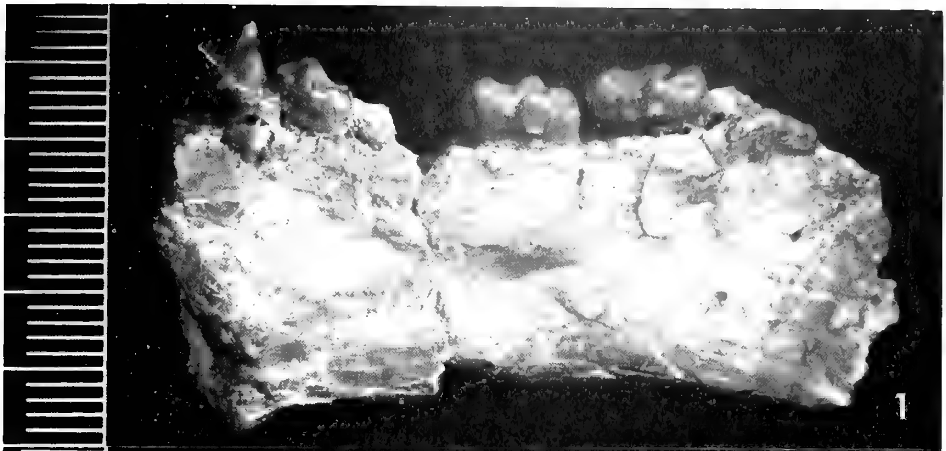
Plate 7

Figs 1–4 *Dendropithecus macinnesi* (M 16650). Figs 1–2, right mandible, lingual and occlusal views. Figs 3–4, left mandible, buccal and lingual views.



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with sharp ridges running mesially and distally. The mesial ridge occludes against the back of the single-cusped P_3 and the distal ridge against the buccal cusp of P_4. The mesiodistal length is greater at the level of the buccal cusp than at the lingual cusp. In overall shape the P^3 is mesiodistally compressed with a higher breadth/length ratio than P^4. The morphology of the occlusal surface is simple. There is at least one transverse ridge, and in one specimen two, but this does not reach the tip of either cusp. The lingual cusp is skewed mesially relative to the buccal one and is set directly on the mesial border of the tooth. There may be a slight mesial cingulum, but the lingual cingulum is completely lacking and only the distal cingulum is at all well developed.

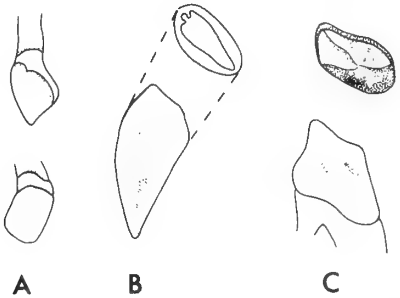

Fig. 6 Anterior teeth of *Dendropithecus macinnesi*, × 1. A, lingual and buccal views of I^2. B, lingual view and cross-section of large male canine crown. C, buccal and occlusal view of P_3.

The P^4 is the same size as the P^3 but lacks its buccal elongation and projecting buccal cusp. The mesiodistal length is slightly greater, so that the buccolingual breadth being the same, the breadth/length ratio is lower. Two transverse ridges are developed on the occlusal surface. There is a very slight mesial fovea cut off by the first of these ridges. The cingulum is strongly developed on the lingual and distal edges of the P^4 and runs from the mesial border of the lingual cusp to the distal border of the buccal one, where it forms a slight tubercle on the distobuccal corner.

The P^3 and P^4 of the Songhor population are relatively very small compared with the Rusinga sample. They are much less sectorially specialized and in fact are remarkably similar to the premolars of *L. legetet*.

Upper molars (Tables 8–10, p. 147–153). The M^1 is a symmetrical tooth, the four cusps being nearly equal in size and only the hypocone differing by being slightly smaller. The crown is always broader than long, more so than is usually found for second and third molars, which are both larger and more elongated than the first. The occlusal surface is crossed by a number of very well-defined ridges. The mesiobuccal ridge of the protocone is a robust but short ridge and divides into two at the base of the protocone. The resulting two ridges would appear to be homologous with the mesial and distal ridges of the protoconule (Korenhof 1960) and the point of division homologous with the protoconule itself, but this cusp is never developed in this species. The distal ridge of the protoconule runs directly buccally to the tip of the paracone. Bounded distally by these ridges, and mesially by the mesial marginal ridge of the tooth and a short mesial ridge from the paracone, is a narrow mesial fovea. This is limited to the buccal half of the crown by the conformation of the ridges; functionally, it constitutes part of an occlusal basin the mesial part of which is continued by the distal cingulum of the P^4.

The distobuccal ridge of the protocone, or crista obliqua, is also well defined. It connects the protocone and metacone, usually without a break. Together with the distal ridge of the protoconule, just described, it delimits the trigon basin which is completed buccally by the rather cristodont formation of the paracone and metacone. The ridges of the hypocone are variously developed, but there are commonly two, neither as well defined as the preceding ridges. There is a ridge running mesially to the distal border of the protocone, and another running buccally to the base of the metacone, sometimes almost reaching the tip of this cusp.

The lingual cingulum is strongly developed. Mesially it runs from the end of the mesial ridge of the protocone, encircles the protocone, and continues without a break onto the lingual border of the hypocone. At the distolingual corner of the hypocone there is a break and there is a short distance without any cingulum until the start of the distal cingulum. This is a broad shelf forming the distal part of the tooth beyond the buccal ridge of the hypocone. Where it connects with the metacone a small tubercle may be developed distobuccally on this cusp. A similar tubercle may be present on the mesiobuccal corner of the paracone where the mesial marginal ridge impinges on it, and in view of this similarity it is possible that the mesial fovea originates partly from the mesial cingulum. There is also a small buccal cingulum developed in the gap between paracone and metacone.

The M^2 is extremely similar to the M^1, differing only in being larger and in having more distinct occlusal ridges and cingula. The crown is more oblique due to the reduction in size of the metacone. The greatest buccolingual breadth is therefore across the paracone–protocone. The lingual cingulum is sometimes continuous with the distal cingulum around the base of the hypocone.

The morphology of the M^3 is again very similar to that of M^1. The metacone and hypocone are both much reduced, but usually present, so that the tooth is often triangular, the apex being at the distal end. The protocone is very much the largest cusp and the lingual cingulum is massive. Despite the reduction distally, the M^3 is still larger than M^1 and is still relatively longer.

Lower incisors (Tables 11–12, p. 154–5). The I_1 is high-crowned and symmetrical. The morphology is simple; the lingual face is concave and lacks any trace of a cingulum, and the buccal face is convex. The I_2 crown is strongly asymmetrical, the mesial edge being concave and the distal edge convex. This curvature is continued in the root, so that the whole tooth is curved, especially so in the Songhor specimens. The lingual face of the crown is simple, unmarked by any ridges, and has only the slightest trace of a cingulum at the base of the crown.

Lower canine (Table 13, p. 156–8). In morphology the lower C is very like that of *Limnopithecus legetet*, and in size they overlap considerably. Hence it is difficult to assign small canines to either species. Those specimens from Rusinga Island, of the same size and with similar indices to RU 1850, I have arbitrarily assigned to *Dendropithecus macinnesi*, leaving only a few very small specimens from Rusinga with *L. legetet*. The position for Songhor is more difficult; the large canines fairly clearly belong to *Dendropithecus macinnesi*, but the smaller ones, which could be of either, I have assumed are more likely to belong to *L. legetet* because at Songhor this species is much more common than *D. macinnesi*. The errors introduced by this approach are not likely to be great. They are that the frequency proportion of *L. legetet* to *D. macinnesi* at Songhor may be slightly weighted in favour of the former, and that the means for the lower canine dimensions of the latter may be slightly biased in favour of the larger specimens.

The crown of the C is slender and slightly distally curved. The breadth/length index is low. The only ridge well developed is the mesial one, which is short, and the base of the crown curves up mesially to meet it. There is no cingulum. During wear, a deep notch may be cut buccodistally by the upper canine on both male and female individuals.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a highly specialized tooth, almost caniniform and strongly sectorial. It is strongly bilaterally compressed, has a single acutely pointed cusp, and is set sharply obliquely from the axis of the molar series. The breadth/length index is very low. The enamel extends far down the cervical border of the mesial root, and with wear a flattened elongated wear facet develops on the mesiobuccal surface. The mesial extension of the enamel is shown by the index (distal ht/mesial ht) × 100 in Table 14. (See Fig. 6.)

The ridges are well developed. The mesial ridge is particularly prominent, and in M 16650 it has a distinct tubercle at its junction with the lingual cingulum not present in the other specimens. The mesial ridge meets the cingulum at its highest point along the crown. The lingual ridge is also well developed, and between these two ridges and the cingulum the lingual surface of the tooth is distinctly concave. The junction of the lingual ridge with the cingulum varies from a perfect junction at an elevation of the cingulum to an incomplete junction at a low and diffuse elevation. The distal ridge is less well developed than the others. Between it and the lingual ridge the surface is again deeply concave, and passes down onto a small basal talonid. The degree of excavation of the talonid depends on degree of wear, the lingual cusp of the P^3 occluding on this surface.

The P_3 of the Songhor specimens is more robust and probably less specialized sectorially. It is a very big tooth, correlated with the large canines of this subspecies. By contrast the P_4 is very much smaller.

The P_4 is a highly specialized tooth, more a part of the sectorial complex than of the molar row. It has two main cusps arranged perpendicular to the line of the molars, but the long axis of the tooth is set obliquely to this, at a somewhat smaller angle than the P_3, so that the mesiodistal length is only 80–90% of the maximum length. As in the P_3 the enamel is extended down the cervical border of the mesial root. The crown is longer than broad. The buccal cusp is more strongly developed than the lingual cusp. It is always greater in bulk and in some specimens it is considerably higher as well. The two cusps are joined by a well-defined transverse ridge. The buccal cingulum is only slightly developed mesially, but increases distally. It starts mesially at the end of the mesial buccal ridge and descends almost vertically to below the buccal cusp. It then starts to ascend slightly and increase in size until it ends prominently in the distobuccal tubercle. A small distal cingulum is developed between two distal tubercles.

Lower molars (Tables 16–18, p. 163–170). The M_1 is an oval-shaped tooth with rounded corners. It is slightly broader distally than mesially. All the cusps are interconnected by a well-developed ridge system. The protoconid is slightly in advance of the metaconid and is joined to it by a fairly high and distinct ridge, the distal trigonid ridge, which forms a prominent boundary between the trigonid and the talonid basins. The former is small and is bounded mesially by a low and poorly-developed ridge, the mesial trigonid ridge. It is relatively shallow and set well above the level of the talonid basin. The trigonid as a whole is constricted in this tooth. The talonid ridges are mostly well developed, and the talonid basin therefore appears completely encircled by ridges, except for the lingual border which opens in a broad and deep V-shaped depression between the metaconid and the entoconid. The size of the talonid basin is somewhat constricted, however, by the medial position of the hypoconulid which occupies the distal part of the talonid basin. The cingulum is relatively more strongly developed in M_1 than on the other molars. It starts at the mesial ridge of the protoconid, increasing to the buccal border of the protoconid where it is large and shelf-like. It is continuous around the hypoconid and ends at the buccal border of the hypoconulid.

The M_1 in the Songhor population is smaller and less elongated than that of the typical Rusinga subspecies. This is quite a striking difference and casts doubt on their inclusion in one species, and will be discussed in more detail in the next section, p. 131.

The M_2 is much larger and squarer than M_1. The protoconid is level with the metaconid and the two cusps are widely separated. The mesial trigonid ridge is not developed, but the distal trigonid ridge is prominent and cut by a longitudinal valley. The trigonid basin is large and broad, because the protoconid is widely separated from the metaconid, and it is fairly shallow. The distal ridges of the protoconid and the hypoconid are not developed, and deep grooves pass between these cusps. The entoconid–hypoconulid ridge is low but well defined with a large distal fovea behind it, also worn by the hypocone of the M^2. The talonid basin is large, broad and shallow, partly the result of the more buccally placed hypoconulid. The buccal cingulum is less distinct and is slightly cut by the buccal main groove; it is very small on the protoconid, reaching its maximum development in the interval between the protoconid and the hypoconid.

The M_3 is the largest tooth in the molar series. It is similar to M_2 except that the hypoconulid is extremely buccally displaced, being about in line with the other buccal cusps, and the cingulum is slightly more distinct. Ridge development is the same as in M_2.

Deciduous dentition (Tables 19–21, p. 171–3). The di^2 are high-crowned caniniform teeth, strongly mesiodistally compressed. There is a moderately long incisive edge mesial to a sharp lingual crest. The lingual crest arises from a rather small lingual pillar, which in turn arises from the massive shelf-like lingual cingulum. One of the specimens has a distal wear notch near the tip of the crown, indicating the cutting action of the lower deciduous canine.

The crown of the upper dc is relatively high compared with maximum length. It is rather featureless except for sharp mesial and distal ridges, giving it the blade-like appearance of the permanent canine, and shelf-like lingual cingulum.

The dp^4 is typically molariform, very like M^1. It is only the small size, the thinness of the enamel, and the splayed roots that suggest the two isolated specimens are milk teeth of this species.

The lower dc is very like the permanent lower canine. It is relatively high-crowned for a milk tooth, and has the short mesial ridge characteristic of canines. The lingual cingulum is more strongly developed, however, and the enamel is thin.

The dp_4 is an extremely elongated tooth. The protoconid–entoconid ridge is strongly oblique and the trigonid is elongated and narrow. The talonid ridges are prominent, encircling the very large talonid basin. The cingulum is hardly developed at all. This tooth is strikingly different from the dp_4 of *Limnopithecus legetet* and is equally different from that of other dryopithecines.

REMARKS. This species shows such a remarkable degree of variation that it is difficult to know how to handle it taxonomically. The population from Rusinga and Mfwangano Islands show a higher degree of sexual dimorphism than any other primate I am familiar with, including baboons and gorillas, and the many differences of the Songhor specimens increases that variability still further. Because of the coherent nature of the Rusinga and Mfwangano samples they clearly belong together, but some degree of differentiation appears to be recognizable in the Songhor sample. This is attributed here to a subspecies difference based on the combination of broader and more spatulate incisors in the Songhor sample, more tusk-like canines, larger and more robust P_3, shorter and broader P_4 and M_1–M_3, smaller upper premolars and molars, and deeper mandibular bodies.

Dendropithecus macinnesi macinnesi (Le Gros Clark & Leakey 1950)

TYPE AND DIAGNOSIS. As for species.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga and Mfwangano Islands, and Karungu, Kenya.

Dendropithecus macinnesi songhorensis subsp. nov.

1943 *Limnopithecus legetet* Hopwood; MacInnes: 151.

DIAGNOSIS. A subspecies of *D. macinnesi* distinguished from the type subspecies by the following features: I^1 relatively broader, less high-crowned and more spatulate; I^2 by contrast relatively small; C less bilaterally flattened, large and tusk-like; upper premolars and molars similar in morphology but much smaller, and the M^3 cusps, though reduced in size, all well developed; P_3 less bilaterally flattened with less enamel extension onto the mesial root, very large and robust; P_4 similar in morphology but much smaller; M_1 with relatively large buccal cingulum, oblique transverse ridges (protoconid is mesial to metaconid and hypoconid to entoconid), and the hypoconulid medially placed. I^1, Cs and P_3 are all relatively very large compared with the molars and P4. The mandible is deep and less robust than the type subspecies.

HOLOTYPE. KNM-SO 378, right mandible with the crowns of P_4–M_3 well preserved.

LOCALITY AND HORIZON. The Lower Miocene of Songhor and Koru, Kenya.

MATERIAL. 31 specimens. M 14083 mandible and symphysis with left P_3; KNM-SO 378 mandible with right P_4–M_3; SO 405 symphysis with right C; SO 530 mandible with right P_3 and M_1–M_2; SO 539 maxilla with left I^1–P^4. M 14082, right M^1, and M 18788, right I^1, are provisionally assigned to this subspecies, as are all of the Songhor specimens listed as *D. macinnesi* in Tables 1–21.

HOMINOIDEA INDETERMINATE

There are a number of specimens which cannot satisfactorily be placed into any of the extant hominoid species from the East African Lower Miocene. These specimens are too fragmentary to be named, or for their affinities to be assessed, so all that can be done here is to place them on record by means of brief descriptions.

M 32309 (Chianda Uyoma, collected by W. E. Owen in October 1935). It is a left upper C with the crown and much of the root intact and well preserved. The crown is low-crowned and has a peg-like appearance as a result of its massive lingual cingulum development. The mesial groove is broad and shallow, the distal ridge is small, and both are dwarfed by the shelf-like lingual cingulum which connects them without a break. The tip of the crown is worn almost flat, and the facet continues distally onto the much narrower distal wear facet. Mesially there are faint traces of wear on either side of the mesial groove. Dimensions of this tooth are: maximum length 7·9 mm, perpendicular breadth 6·0 mm, buccal height 9·1 mm. This specimen was found by Mr C. Madden in the BM(NH) collections.

KNM-LS 1 (Losidok 1 : 1951). Described by Clark (1952 : 276) as *P. africanus*. This specimen is a right lower C, well preserved but moderately worn; the extreme tips of root and crown are broken. Its dimensions are: maximum length 8·7 mm, perpendicular breadth 5·4 mm; index (b/l) × 100 is 62·1 %. It is slightly smaller than most *P. africanus* canines and is considerably more strongly bilaterally compressed. Crown and root have a marked buccodistal curvature, enhanced by the short mesial ridge. The lingual cingulum is prominent. The crown is moderately worn with a well-developed distobuccal wear facet cutting into the top of the root.

KNM-MO 1 (Moruorot 1 : 1951). This specimen is a left mandible fragment with M_3 and roots of M_1–M_2. It is weathered and part of the bone cortex is missing on the medial surface of the body. M_3 is weathered and most of the enamel is missing on the lingual edge of the crown. Mandibular dimensions at M_2 are: depth 17·8 mm, thickness 10·5 mm; index (t/d) × 100 is 58·6 %. M_3 dimensions are: md 9·2 mm, bl mes 7·3 mm, bl dist 6·7 mm; bl/md is 79·4 %. A very approximate estimate of M_1–M_3 length is 25 mm. The size of both mandible and teeth is small for *P. africanus*, although the morphology of M_3 is almost certainly pongid rather than hylobatid. The M_3 was apparently only slightly bigger than M_2.

KNM-SO 1236 (Songhor 760 : 1972). This specimen was found with SO 1237 at an exposure of red beds in the Mtete Valley near Songhor. It is a mandible fragment with the symphysis and part of the left body with root of C and root sockets of all the incisors and left P_3–P_4. The body and symphysis are broken inferiorly but the depth was probably not greater than 18 mm. The thickness at the symphysis is 14·7 mm, giving a high index of 81·7 %. The central incisor roots are much shorter buccolingually than the lateral incisors (approximately $\frac{2}{3}$ the length). The canine root dimensions are 10·0 mm for length and 6·0 mm for breadth, giving an index of 60 % comparable to the value for KNM-LS 1.

KNM-SO 1237 (Songhor 761 : 1972). This specimen is a right upper C, weathered but intact. The tip of the root is broken. The crown is moderately worn, with a flat facet across the tip passing into a facet down the distal edge narrowing towards the base of the crown. In this and in its general morphology this specimen from Songhor is almost identical to M 32309 from Chianda Uyoma. The dimensions are 8·4 mm for length and 6·3 mm for breadth, giving an index of 75 %. The lingual cingulum is very prominent on this specimen. This and KNM-SO 1236 were found within 2 ft of each other and at the same level, and it is likely that they go together, especially as no other primate specimens were found at this locality.

Measurements, univariate statistics, and bivariate plots

Tables of measurement

Tables 1–22 give dimensions of all cranial material of Kenya fossil apes. Each table covers just one body part; for instance there is a separate table for the maxilla, the mandible and for each tooth in the dentition. Within each table there are subdivisions by species with the specimens listed singly. In Tables 3–18, which cover the main part of the collection, the specimen dimensions are followed by sample statistics: the mean, the number of specimens, the standard deviation, the coefficient of variation, the standard error, and the 95% confidence limits of the sample (the last few parameters were not calculated on small samples). Index ratios are given as percentages in every case.

Table 1 Maxillary measurements.

	D. macinnesi KNM-RU						*P.* (*R.*) *gordoni* KNM-SO		*P.* (*R.*) *vancouveringi* KNM-RU
	1774	1799	1849	1850	1901	2986	401	700	2058
naso-alv. ht	–	–	–	6·1	–	–	–	10·0	–
ht/M^1–M^3	–	–	–	32·5	–	–	–	35·0	–
nasal aperture									
ht	–	–	–	–	–	–	–	21·0	–
b	–	–	–	12·0	–	–	–	15·4	–
b/ht	–	–	–	–	–	–	–	73·3	–
zyg. arch									
position	–	M^2	–	M^2	–	M^2	M^1	M^1	M^2
ht	–	2·4	–	6·0	–	8·0	3·5	4·7	4·3
max. sinus									
L	–	26·6	–	23·8	–	–	–	31·0	18·7
B	–	14·0	–	11·5	–	–	–	14·0	15·0
B/L	–	52·6	–	48·3	–	–	–	46·7	80·0
pal. b at M^2 (ext)	–	–	–	31·7	–	–	–	39·2	–
B/pal b at M^2 (ext)	–	–	–	36·3	–	–	–	37·0	–
palate									
L	–	–	–	35·0	–	–	–	53·4	–
B at C	–	–	–	14·9	–	–	–	21·4	–
M^2	–	–	–	15·4	–	–	–	22·0	–
B at C/M^2	–	–	–	96·8	–	–	–	97·0	–
B at M^2/L	–	–	–	44·1	–	–	–	41·3	–
depth at C–P^3	–	–	–	2·6	–	–	–	2·5	–
M^2	–	–	–	4·3	–	–	–	5·4	–
M^1–M^3	18·6	16·5	19·6	19·0	20·0	27·7	–	28·6	22·5
P^3–M^3	27·6	–	29·1	27·0	–	–	–	39·6	–
C–M^3	33·7	–	–	33·8	–	–	–	51·0	–

L. legetet			*P. africanus*				*P. nyanzae*			*P. major*	
KNM-SO				KNM-RU			KNM-RU				UM-P
421 535	443	537 538	M 14084	1705 2036	1792	M 32363	1965 M 16647	1674	1677	M 16649	62-11
4·6	5·2	5·9	–	11·0	10·1	11·1	16·0	–	–	–	16·7
–	–	–	–	–	–	41·5	–	–	–	–	45·5
–	–	–	–	–	–	23·0	37·0	–	–	–	36·0
–	–	–	–	–	–	14·0	19·0	–	–	–	30·2
–	–	–	–	–	–	60·8	51·4	–	–	–	84·0
M^2	M^2	M^2	$M^{1/2}$	M^1	$M^{1/2}$	M^2	M^2	M^2	M^2	M^1	M^2
5·6	4·0	4·0	10·4	6·0	–	7·1	17·0	14·0	12·0	11·0	14·0
–	–	–	–	–	–	–	–	32·0	–	–	46·0
7·5	7·4	6·0	–	10·5	–	11·2	–	–	19·0	18·0	17·0
–	–	–	–	–	–	–	–	–	–	–	37·0
–	–	–	–	–	–	–	59·0	–	–	–	61·0
–	–	–	–	–	–	–	–	–	–	–	28·0
–	–	–	51·0	–	–	45·0	66·0	–	–	–	79·0
–	–	–	–	–	–	19·0	30·5	–	–	–	37·0
–	–	–	26·0	–	–	23·6	32·0	–	–	–	34·4
–	–	–	–	–	–	42·2	95·5	–	–	–	108·6
–	–	–	51·0	–	–	52·4	48·5	–	–	–	43·6
–	–	–	4·0	–	4·7	5·1	7·0	–	–	–	4·0
–	–	–	5·9	–	6·1	6·8	10·2	–	–	–	7·5
–	–	–	25·0	–	–	25·8	33·2	28·4	33·2	–	36·7
–	–	–	38·1	–	–	36·5	46·8	41·5	48·5	–	54·6
–	–	–	49·5	–	–	44·4	61·9	–	–	–	73·7

Table 2 Mandibular measurements.

	symphysis			body at P_4			body at M_2			$\frac{M_2\ d}{\text{symph}\ d}$	$\frac{M_2\ d}{P_4\ d}$	M_1–M_3	P_3–M_3	C–M_3	I–I	C–C	P_4–P_4	M_3–M_3
	d	t	t/d	d	t	t/d	d	t	t/d									
D. macinnesi																		
RU **900**	23·9	10·1	42·3	18·1	6·7	37·0	16·0	8·6	53·7	66·9	88·4	–	–	–	–	–	–	–
1726	–	–	–	–	–	–	15·6	7·9	50·7	–	–	23·0	–	–	–	–	–	–
1727	–	–	–	16·8	7·7	45·8	–	–	–	–	–	–	–	–	–	–	–	–
1844	–	–	–	–	–	–	16·3	7·3	44·8	–	–	–	–	–	–	–	–	–
1850	–	–	–	15·4	7·7	50·0	14·1	8·2	58·2	–	91·5	20·2	29·5	35·7	–	–	–	–
1857	21·1	11·2	53·1	17·3	8·2	47·4	15·6	8·4	53·9	74·0	90·2	22·9	34·5	41·8	–	–	–	–
1901	–	–	–	–	–	–	17·0	8·5	50·0	–	–	22·0	–	–	–	–	–	–
2001	22·2	9·5	42·7	15·4	6·7	43·5	–	–	–	–	–	–	–	–	–	–	–	–
2015	22·5	10·3	45·8	19·0	9·0	47·4	17·3	9·1	52·6	77·0	91·0	23·5	34·8	41·4	–	–	–	–
M **16650**	–	–	–	18·6	7·3	39·3	17·8	7·8	43·8	–	95·8	21·6	34·3	41·6	–	–	–	–
MW **51**	17·1	8·0	46·8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
53	–	9·6	–	17·4	7·6	43·7	16·6	7·0	42·2	–	95·4	–	–	–	–	–	–	–
Mean	21·4	9·8	46	17·3	7·6	44	16·3	8·1	50	73	93	22·2	33·3	40·1	–	–	–	–
Number	5	6	5	8	8	8	9	9	9	3	6	6	4	4	–	–	–	–
P. (R.) gordoni																		
SO **463**	–	–	–	27·0	10·2	37·8	25·0	11·6	46·4	–	88·0	29·0	–	–	–	–	–	–
464	–	–	–	–	–	–	16·1	10·5	65·2	–	–	–	–	–	–	–	–	–
1112	33·2	18·5	55·7	29·7	12·0	40·4	25·7	14·5	56·4	77·0	86·0	28·3	43·5	64·3	–	–	–	–
Mean	33·2	18·5	56	28·4	11·1	39	22·3	12·2	56	77	87	28·7	43·5	64·3	–	–	–	–
Number	1	1	1	2	2	2	3	3	3	1	2	2	1	1	–	–	–	–
L. legetet																		
SO **376**	16·0	7·4	46·3	14·7	6·4	43·6	13·6	5·4	39·8	84·9	92·6	–	–	–	–	–	–	–
385	–	–	–	14·4	6·2	43·0	15·0	6·3	42·0	–	107·0	18·5	27·5	–	–	–	–	–
386	21·4	7·8	36·5	16·4	7·2	43·9	15·3	8·1	52·9	71·6	93·3	18·3	27·5	33·8	11·0	9·6	17·4	–
387	–	–	–	–	–	–	16·2	7·8	48·2	–	–	21·7	–	–	–	–	–	–
388	–	–	–	–	–	–	17·8	8·1	45·5	–	–	–	–	–	–	–	–	–
452	17·0	7·4	43·5	14·3	5·9	41·3	–	–	–	–	–	–	–	–	–	–	–	–
481	–	–	–	–	–	–	16·4	8·3	50·6	–	–	–	–	–	–	–	–	–
533	17·4	7·5	43·1	14·0	6·0	42·9	–	–	–	–	–	–	–	–	–	–	–	–
534	–	–	–	–	–	–	12·8	6·2	48·4	–	–	–	–	–	–	–	–	–

Mean		17·4	7·5	43	14·8	6·4	43	15·1	7·2	48	82	97	19·1	27·3	33·3	11·0	9·6	17·4	–
Number		7	7	7	6	6	6	8	8	8	3	4	4	3	2	2	1	1	–
P. africanus																			
M	**32363**	30·0	12·0	40·0	22·2	10·1	45·5	19·3	11·9	61·6	64·4	87·0	30·0	43·3	50·8	–	–	–	–
RU	**1680**	–	–	–	23·0	10·1	43·9	22·4	9·7	43·3	–	97·5	–	–	–	–	–	–	–
	1706	–	–	–	–	–	–	–	–	–	–	–	29·4	42·3	49·3	–	10·2	18·3	–
	1728	27·0	11·6	43·0	23·1	10·7	46·3	21·0	11·9	56·6	77·7	91·0	25·2	36·5	43·3	–	–	–	–
	1855	26·7	12·2	45·8	20·8	11·0	52·9	19·8	11·5	58·1	74·6	95·2	27·2	40·0	48·0	13·5	13·8	22·1	31·3
	1864	24·6	11·4	46·3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	1955	23·6	11·5	48·7	19·6	10·2	52·0	20·1	11·7	58·2	85·2	102·6	–	–	–	–	–	–	–
	2036	24·0	11·8	49·2	19·2	9·8	51·0	18·4	12·3	66·8	76·7	95·9	29·6	43·4	51·2	–	15·4	16·9	20·4
SO	**372**	27·5	12·8	46·5	22·0	9·7	44·1	–	–	–	–	–	–	–	–	–	–	14·2	21·4
	391	–	–	–	–	–	–	17·3	10·2	59·0	–	–	–	–	–	–	–	–	–
Mean		26·2	11·9	46	21·4	10·2	48	19·8	11·3	58	76	95	28·3	39·1	48·5	13·5	13·8	20·7	31·3
Number		7	7	7	6	6	6	6	6	6	5	6	6	6	6	1	3	4	3
P. nyanzae																			
RU	**1674**	40·2	17·5	43·6	31·9	14·4	45·2	32·8	16·3	49·7	81·8	102·9	31·3	44·7	57·5	21·0	19·0	27·0	32·4
	1676	–	–	–	–	–	–	–	–	–	–	–	36·8	54·5	68·7	–	–	–	–
	1678	–	–	–	28·0	14·4	51·4	24·7	14·7	59·5	–	88·3	33·5	48·1	–	–	–	–	–
	1711	35·5	16·2	45·6	30·4	13·0	42·7	–	–	–	–	–	–	–	–	–	–	–	–
	1740	40·0	18·0	45·0	37·0	14·0	37·8	–	–	–	–	–	–	–	–	–	–	–	–
	1840	36·4	18·3	50·2	–	–	–	–	–	–	–	–	–	–	–	17·6	15·3	–	–
	1947	38·5	19·3	50·2	30·7	11·8	38·4	28·5	14·7	51·6	76·1	92·9	35·0	53·1	66·7	–	–	–	–
	1982	–	–	–	–	–	–	–	–	–	–	–	37·4	–	–	–	–	–	–
	2087	39·1	17·5	44·8	33·2	13·6	40·0	29·0	14·9	51·4	74·2	87·4	31·7	47·5	59·3	21·0	20·2	30·0	37·9
Mean		38·3	17·8	47	31·9	13·5	42	28·8	15·2	53	77	93	34·3	48·0	63·1	19·9	18·2	28·5	35·2
Number		6	6	6	6	6	6	4	4	4	3	4	6	5	4	3	3	2	2
P. major																			
M	**14086**	41·3	22·1	53·5	36·2	15·6	43·1	34·9	14·8	42·4	84·6	96·5	35·3	53·0	66·0	–	–	–	–
	16648	–	–	–	–	–	–	–	–	–	–	–	44·4	65·6	–	–	–	–	–
SO	**396**	52·4	29·1	55·6	40·5	19·8	48·9	35·5	20·9	58·9	67·8	87·7	41·4	66·0	78·0	15·5	20·2	33·0	–
	404	39·4	22·5	57·1	33·2	17·2	51·8	29·3	19·2	65·5	74·4	88·2	33·5	53·2	63·6	–	19·4	25·2	31·1
Mean		44·4	24·1	55	36·6	17·5	48	33·2	18·3	55	75	90	38·7	59·5	69	15·5	19·8	29·1	31·1
Number		3	3	3	3	3	3	3	3	3	3	3	4	4	3	1	2	2	1

Table 3 Measurements of upper I1.

	md	bl	bl	md		incis	root	buc ht	md
			md	incis	root	md	md		buc ht
D. macinnesi									
M 18788*	6·4	4·3	67·2	5·2	4·5	81·2	70·3	7·5	85·4
RU 1651	6·0	4·9	81·6	4·2	4·3	70·0	71·7	9·0	66·7
1798	4·7	3·9	83·0	–	2·8	–	59·6	6·1	77·0
1806	4·7	4·2	89·5	3·2	3·6	68·1	76·5	6·0	78·4
1849	5·0	4·2	84·0	3·3	3·7	66·0	74·0	7·3	68·5
1850	4·9	4·3	87·8	3·5	3·3	71·5	67·4	6·9	71·0
1858	5·1	4·2	82·4	4·5	3·2	88·2	62·8	6·7	76·1
1901	5·2	4·9	94·2	3·8	3·6	73·0	69·2	7·0	74·3
SO 380*	6·4	4·7	73·4	–	–	–	–	–	–
417*	6·6	4·7	71·2	5·8	4·5	87·9	68·2	7·4	89·2
453*	6·3	4·5	71·4	5·2	4·4	82·5	69·7	6·9	91·3
Mean	5·1	4·4	86	3·8	3·5	73	69	7·0	73
Number	7	7	7	6	7	6	7	7	7
P. (R.) gordoni									
RU 1833	8·4	5·8	69·0	6·6	5·9	78·6	70·2	10·2	82·4
SO 551	6·9	5·1	73·9	6·2	4·5	89·9	65·2	10·2	67·6
552	6·7	5·3	79·1	5·1	4·3	76·1	64·2	8·9	75·3
553	7·6	5·7	74·9	6·2	5·9	81·6	77·7	9·3	81·7
Mean	7·4	5·5	74	6·0	5·2	82	69	9·5	78
Number	4	4	4	4	4	4	4	4	4
L. legetet									
M 14332*	5·2	3·6	69·3	4·8	3·4	92·4	65·4	5·3	98·1
RU 1826	4·3	3·4	79·1	–	3·3	–	76·8	–	–
2075	4·4	3·8	86·3	–	3·1	–	70·5	–	–
SO 476	4·8	3·7	77·0	4·0	3·1	83·3	64·6	5·3	90·6
483	5·0	4·0	80·0	–	4·2	–	84·0	–	–
489	5·4	4·0	74·1	–	3·2	–	59·3	6·2	87·1
490	5·4	3·9	72·3	4·4	3·1	81·5	58·5	6·0	90·0
504	5·1	4·3	84·4	4·2	3·9	82·3	76·5	5·3	96·2
548	5·0	3·8	76·0	4·0	3·5	80·0	70·0	5·7	87·7
565	4·8	3·7	77·1	–	3·4	–	70·8	5·8	82·7
1085	5·1	3·7	72·6	–	3·9	–	76·5	5·5	92·7
Mean	4·9	3·8	78	4·2	3·5	82	71	5·7	90
Number	10	10	10	4	10	4	10	7	7
S.D.	0·37	0·28	4·69	–	0·40	–	8·15	–	–
Coef. var.	7·6	7·4	6·0	–	11·4	–	11·5	–	–
S.E.	0·12	0·09	1·48	–	0·13	–	2·58	–	–
95% conf.	4·1	3·2	67	–	2·6	–	53	–	–
limits	5·7	4·4	89	–	4·4	–	89	–	–

*Not included in calculation of sample parameters.

Table 3 (*cont.*)

	md	bl	bl	md		incis	root	buc ht	md
			md	incis	root	md	md		buc ht
P. africanus									
M 32363	7·0	6·1	87·2	6·6	5·3	94·3	75·7	8·9	78·7
RU 1769	7·8	5·8	74·4	6·6	5·5	84·6	70·5	8·6	90·7
1831	7·5	5·4	72·0	–	5·4	–	72·0	9·2	81·5
1933	7·5	5·7	76·0	5·9	5·7	78·7	76·0	7·5	100·0
1968	7·5	5·4	72·0	–	4·4	–	58·7	–	–
1979	7·3	5·7	72·4	5·5	5·0	75·4	68·5	10·1	72·3
2036	7·7	5·1	66·2	6·6	4·9	85·8	63·8	8·5	90·5
2040	6·8	5·5	80·8	–	5·0	–	73·5	–	–
Mean	7·4	5·6	75	6·2	5·2	84	69	8·8	87
Number	8	8	8	5	8	5	8	6	6
P. nyanzae									
RU 1677	9·2	7·0	76·1	8·4	6·1	91·3	66·3	10·4	88·5
1681	9·8	7·2	73·5	7·7	6·8	78·6	69·4	11·0	89·1
1685	8·3	6·9	83·1	5·5	6·4	66·3	77·2	11·9	69·7
1712	8·6	6·8	79·0	7·0	6·1	81·4	70·9	10·2	84·4
1713	9·0	6·7	74·5	–	6·5	–	72·2	11·5	78·3
1714	9·0	7·2	80·0	7·8	6·7	86·6	74·5	10·9	82·6
1803	9·5	–	–	7·2	–	75·8	–	10·6	89·6
1951	9·4	6·5	69·2	–	7·0	–	74·5	–	–
1975	9·4	6·4	68·1	7·4	7·3	78·7	77·6	10·6	88·7
1996	10·4	8·6	82·7	–	8·9	–	85·6	10·7	97·2
MB 104*	9·8	7·4	75·5	7·7	7·3	78·5	74·5	11·0	89·0
Mean	9·3	7·0	76	7·3	6·9	80	74	10·9	85
Number	10	9	9	7	9	7	9	9	9
P. major									
M 14297	11·0	8·3	75·5	9·0	7·8	81·8	71·0	12·6	87·3
UM-P 62-11	10·8	9·0	83·4	–	–	–	–	–	–
Mean	10·9	8·7	79	9·0	7·8	82	71	12·6	87
Number	2	2	2	1	1	1	1	1	1

* Not included in calculation of sample parameters.

Table 4 Measurements of upper I2.

	md	bl	bl	md	root	buc ht	md
			md	root	md		buc ht
D. macinnesi							
RU 1825	4·0	4·9	122·5	3·7	92·5	6·5	61·5
1849	3·5	4·4	125·8	–	–	5·8	60·3
1850	3·4	4·3	126·4	–	–	6·2	54·8
1901	4·1	4·8	117·1	–	–	6·6	62·2
1906	3·0	4·6	153·2	–	–	–	–
1938	2·9	4·0	138·0	–	–	–	–
1969	4·3	4·4	102·3	3·2	74·4	7·0	61·4
MW 41	3·9	5·5	141·0	3·0	77·0	6·6	59·1

Table 4 (*cont.*)

	md	bl	bl/md	md root	root/md	buc ht	md/buc ht
D. macinnesi (*cont.*)							
SO 417*	3·4	4·2	123·6	–	–	6·1	50·8
461*	3·9	4·4	112·9	3·2	82·1	6·4	61·0
1048*	4·0	4·4	110·0	2·8	–	5·8	–
Mean	3·6	4·6	128	3·3	81	6·5	60
Number	8	8	8	3	3	6	6
P. (R.) gordoni							
SO 550	5·8	6·0	103·4	4·8	82·7	7·4	78·4
Mean	5·8	6·0	103	4·8	83	7·4	78
Number	1	1	1	1	1	1	1
L. legetet							
SO 546	3·6	3·5	97·2	–	–	4·7	76·6
Mean	3·6	3·5	97	–	–	4·7	77
Number	1	1	1	–	–	1	1
P. africanus							
M 32363	5·0	6·0	120·0	–	–	7·0	71·4
RU 1769	5·6	5·9	105·3	3·7	66·0	7·1	78·9
1964	4·2	5·1	121·4	3·5	83·4	–	–
1998	5·5	6·2	112·8	4·0	72·7	7·3	75·3
2019	4·3	5·4	125·6	–	–	–	–
2036	5·1	5·1	100·0	3·4	66·7	6·6	77·3
MW 47	4·7	5·2	110·8	3·6	76·6	–	–
57	5·4	5·4	100·0	4·1	75·9	6·7	80·6
SO 549	4·5	4·8	106·7	3·8	84·5	5·2	86·5
Mean	4·9	5·5	111	3·7	75	6·7	78
Number	9	9	9	7	7	6	6
P. nyanzae							
RU 1674	5·5	6·2	112·8	–	–	7·5	73·3
1690	6·2	6·8	109·8	–	–	9·2	67·4
1704	6·6	6·9	104·5	–	–	9·0	73·4
2031	6·8	6·9	101·4	–	–	–	–
2035	5·8	6·1	105·2	–	–	8·0	72·5
2039	7·3	7·7	105·4	–	–	9·6	76·1
Mean	6·4	6·8	107	–	–	8·7	73
Number	6	6	6	–	–	5	5
P. major							
SO 554	7·3	7·5	102·7	–	–	9·5	76·8
UM-P 62-11	8·6	9·6	111·6	–	–	10·9	78·9
66-03	8·2	10·1	123·1	–	–	–	–
Mean	8·0	9·1	112	–	–	10·2	78
Number	3	3	3	–	–	2	2

* Not included in calculation of sample parameters.

Table 5 Measurements of upper C.

	max l	perp b	b/l	buc ht	max l / ht
D. macinnesi **(Rusinga Island)**					
M 32233	8·7	6·6	75·8	–	–
M 32230	8·9	6·3	70·7	–	–
RU 1649	6·1	4·7	77·0	7·6	80·3
1666	6·7	5·0	74·6	–	–
1682	9·6	6·6	68·6	–	–
1774	7·2	5·5	76·4	–	–
1775	8·5	6·1	71·8	–	–
1806	8·4	6·4	76·3	12·0	70·0
1843	8·3	5·6	67·5	–	–
1849	9·2	6·1	66·4	14·9	61·7
1850	7·0	5·4	77·2	–	–
1860	7·3	5·2	71·2	–	–
1875	6·5	4·9	75·4	–	–
1883	7·0	4·7	67·1	8·2	85·4
1895	8·8	6·2	70·5	–	–
1905	8·9	6·2	69·6	–	–
1948	8·6	6·2	72·1	15·8	54·4
1963	6·6	4·9	74·2	–	–
1966	9·9	6·4	64·6	16·1	61·5
1985	7·3	5·0	68·5	8·6	84·9
1988	9·3	5·7	61·3	–	–
2020	7·1	5·2	73·2	8·9	79·8
2041	8·2	6·1	74·4	9·3	88·2
2068	6·6	4·6	69·7	–	–
Mean	7·9	5·6	72	11·3	70
Number	24	24	24	9	9
S.D.	1·16	0·67	4·31	–	–
Coef. var.	14·7	8·2	8·6	–	–
S.E.	0·24	0·14	0·90	–	–
95% conf.	5·5	4·2	63	–	–
limits	10·3	6·0	81	–	–
D. macinnesi **(Songhor)**					
SO 402	8·3	6·5	78·3	–	–
414	7·5	5·6	74·6	10·1	74·3
417	8·4	6·6	78·6	–	–
519	7·6	5·7	75·0	–	–
520	7·8	5·8	74·4	11·0	70·9
539	6·9	5·7	82·6	–	–
580	7·7	5·7	74·0	–	–
581	8·0	5·7	71·2	–	–
582	8·8	6·1	69·3	14·8	59·4
952	7·2	5·5	76·4	–	–
1137	7·6	5·6	73·7	10·4	73·0
Mean	7·8	5·9	76	11·6	69
Number	11	11	11	4	4
S.D.	0·55	0·37	3·94	–	–
Coef. var.	7·1	6·3	5·2	–	–
S.E.	0·17	0·11	1·18	–	–
95% conf.	6·6	5·1	67	–	–
limits	9·0	6·7	85	–	–

Table 5 (*cont.*)

	max l	perp b	b/l	buc ht	max l/ht
P. (R.) gordoni					
SO 419	11·3	8·4	74·4	–	–
467	10·9	7·5	68·8	11·0	99·1
521	10·6	7·5	70·8	–	–
531	11·4	8·3	72·9	–	–
700	12·4	8·0	64·5	–	–
RU 1686	10·3	7·0	68·0	–	–
1788	11·4	8·2	72·0	–	–
Mean	11·0	7·8	72	11·0	99
Number	7	7	7	1	1
S.D.	0·80	0·50	4·95	–	–
Coef. var.	7·3	6·4	6·9	–	–
S.E.	0·28	0·18	1·75	–	–
95% conf.	9·1	6·3	60	–	–
limits	12·9	9·8	84	–	–
L. legetet					
RU 1995	6·0	4·8	80·0	8·6	69·8
SO 370	5·6	4·5	80·4	7·4	75·7
403	5·4	4·2	77·8	7·0	77·1
421	6·0	4·3	71·7	–	–
423	5·7	4·6	80·7	7·9	72·1
443	5·4	4·5	83·3	–	–
538	5·2	4·0	76·9	–	–
572	6·1	4·9	80·4	9·0	67·8
573	6·8	5·2	76·5	–	–
Mean	5·8	4·6	79	7·9	73
Number	9	9	9	5	5
S.D.	0·49	0·37	3·36	–	–
Coef. var.	8·4	8·1	4·3	–	–
S.E.	0·16	0·12	1·12	–	–
95% conf.	4·7	3·7	71	–	–
limits	6·9	5·5	8·7	–	–
P. africanus					
M 14084	11·4	8·2	72·0	15·2	75·0
M 32363	9·9	8·2	82·8	12·9	76·7
RU 1688	8·3	6·7	80·7	9·8	84·7
1705	9·0	7·3	81·1	–	–
1707	8·9	7·0	78·7	10·6	84·0
1723	10·7	7·7	72·0	–	–
1769	9·4	7·1	75·5	–	–
1797	10·8	7·4	68·5	–	–
1830	9·5	7·5	78·9	–	–
1871	9·2	7·7	83·7	–	–
1897	11·2	8·4	75·0	–	–
1900	8·2	6·8	83·0	–	–
1912	9·3	7·0	75·3	–	–
1913	9·1	6·7	73·6	–	–
1942	9·7	7·1	73·2	–	–
1974	7·7	6·9	89·6	10·4	74·1

Table 5 (*cont.*)

	max l	perp b	b/l	buc ht	max l / ht
P. africanus (*cont.*)					
2049	9·4	7·0	74·5	11·6	81·0
2088	12·6	8·7	69·1	–	–
MW 46	9·1	6·9	75·8	–	–
Mean	9·7	7·4	77	11·8	81
Number	19	19	19	6	6
S.D.	0·61	5·47	–	–	–
Coef. var.	12·5	8·2	7·1	–	–
S.E.	0·28	0·14	1·25	–	–
95% conf.	7·2	6·1	65	–	–
limits	12·2	8·7	89	–	–
P. nyanzae					
M 16647	15·1	11·6	76·8	21·0	71·9
RU 1677	13·8	10·9	79·0	19·0	72·6
1684	14·4	11·2	77·8	17·2	83·7
1687	11·7	9·8	83·8	–	–
1763	13·5	11·1	82·2	–	–
1812	12·2	9·0	73·8	–	–
1813	14·2	11·5	80·9	–	–
1815	12·1	10·1	83·5	–	–
1845	12·7	10·0	78·6	–	–
1971	12·3	10·2	82·9	–	–
Mean	13·2	10·5	80	19·1	76
Number	10	10	10	3	3
S.D.	1·16	0·85	3·29	–	–
Coef. var.	8·8	8·1	4·1	–	–
S.E.	0·37	0·27	1·04	–	–
95% conf.	10·6	8·6	73	–	–
limits	15·8	12·4	87	–	–
P. major					
SO 584	16·2	13·3	82·1	–	–
585	19·5	14·7	75·4	–	–
LS 8	17·2	12·2	70·9	–	–
UM-P 62-03	18·7	15·7	84·0	25·0	70·8
62-04	19·3	16·0	83·0	22·0	87·7
62-05	18·8	16·1	85·6	22·5	83·5
62-11	18·6	15·7	84·4	27·6	67·3
62-12	17·6	16·1	91·5	22·0	80·0
Mean	18·2	15·0	82	23·8	79
Number	8	8	8	5	5
S.D.	1·14	1·47	6·33	–	–
Coef. var.	6·3	9·8	7·7	–	–
S.E.	0·40	0·52	2·24	–	–
95% conf.	15·5	11·5	67	–	–
limits	20·9	18·5	97	–	–

Table 6 Measurements of upper P3.

	md		bl	bl	md ling	height		buc ht	md + bl	P³
	buc	ling		md	md buc	buc	ling	ling ht	2	M¹
D. macinnesi										
M 32231	4·3	3·9	6·5	158·5	90·7	6·5	4·0	162·5	5·3	–
M 32337*	4·1	3·6	7·0	184·1	87·8	6·0	3·0	200·0	5·4	–
RU 1774	4·5	3·6	6·9	170·4	80·0	7·1	4·2	169·0	5·5	80·9
1849	4·5	4·0	7·0	164·8	88·9	6·9	4·5	153·3	5·6	81·2
1850	4·1	3·5	6·8	179·0	85·4	6·8	3·5	194·3	5·3	79·1
SO 417*	4·5	4·0	5·8	136·5	88·9	5·5	2·6	210·5	5·0	–
Mean	4·3	3·8	6·8	168	87	6·8	4·1	170	5·5	80
Number	4	4	4	4	4	4	4	4	4	3
P. (R.) gordoni										
RU 1894	5·6	4·9	7·4	142·4	87·5	6·3	5·2	121·1	6·4	–
SO 700	5·8	5·5	8·3	146·9	94·8	7·0	4·8	145·9	7·0	84·4
Mean	5·7	5·2	7·9	145	91	6·7	5·0	134	6·7	84
Number	2	2	2	2	2	2	2	2	2	1
P. (R.) vancouveringi										
RU 1778	5·3	5·3	6·8	128·3	100·0	5·2	4·8	108·2	6·1	88·4
MB 53	5·3	5·3	6·7	126·4	100·0	6·0	5·6	107·1	6·0	–
Mean	5·3	5·3	6·8	127	100	5·6	5·2	108	6·1	88
Number	2	2	2	2	2	2	2	2	2	2
L. legetet										
SO 421	4·2	3·4	5·9	155·3	80·9	3·7	3·3	112·1	4·9	–
443	3·3	3·0	5·3	168·0	90·9	4·2	2·7	155·6	4·2	73·7
538	4·0	3·0	5·1	145·6	75·0	–	–	–	4·3	–
1086	3·6	3·0	4·6	139·2	83·4	3·8	2·5	152·0	4·1	–
Mean	3·8	3·1	5·2	148	83	3·9	2·8	141	4·4	74
Number	4	4	4	4	4	3	3	3	4	1
P. africanus										
M 14084	7·4	5·1	9·4	149·2	68·9	8·4	5·1	164·8	7·8	89·0
M 32363	6·2	5·1	9·8	172·0	82·2	8·5	5·1	166·8	7·7	89·0
RU 1705	5·6	4·2	8·7	177·7	75·0	6·2	4·3	144·1	6·8	85·0
SO 596	5·6	4·5	7·8	154·4	80·4	6·1	3·5	174·3	6·4	–
Mean	6·2	4·7	8·9	163	77	7·3	4·5	163	7·2	88
Number	4	4	4	4	4	4	4	4	4	4
P. nyanzae										
M 16647	7·7	6·5	11·3	159·1	84·4	10·9	6·3	173·0	9·2	87·6
16649	8·5	6·6	12·5	164·2	77·6	8·7	6·1	142·7	10·0	91·8
RU 1674	6·8	5·3	10·5	173·6	77·9	7·2	4·5	160·0	8·3	87·2
1677	7·8	6·3	10·9	154·6	80·8	11·1	6·7	165·6	9·0	87·4
1718	6·8	5·7	10·3	164·9	83·9	7·9	5·7	138·5	8·3	–
1874	7·2	6·3	11·1	164·4	87·5	8·9	5·6	160·0	8·9	–
Mean	7·5	6·1	11·1	163	82	9·1	5·8	157	9·0	89
Number	6	6	6	6	6	6	6	6	6	4

*Not included in calculation of sample parameters.

Table 6 (*cont.*)

	md		bl	bl/md	md ling/md buc	height		buc ht/ling ht	md + bl/2	P³/M¹
	buc	ling				buc	ling			
P. major										
M 14331*	9·1	8·2	13·1	150·5	90·2	10·7	6·9	155·0	10·9	–
SO 418	8·6	5·4	10·6	151·4	62·8	–	–	–	8·3	80·5
527	8·0	5·6	10·0	147·0	70·0	–	–	–	8·4	–
529	8·2	7·0	11·7	153·9	85·4	9·8	6·1	160·6	9·7	–
UM-P 62-11	10·6	8·1	14·6	155·2	76·4	–	–	–	12·0	99·2
Mean	8·9	6·5	11·7	149	74	9·8	6·1	161	9·6	90
Number	4	4	4	4	4	1	1	1	4	2

* Not included in calculation of sample parameters.

Table 7 Measurements of upper P4.

	md	bl	bl/md	height		buc ht/ling ht	md + bl/2	P⁴/M¹
				buc	ling			
D. macinnesi								
RU 1774	4·2	6·7	159·7	5·2	3·4	152·9	5·5	80·9
1806	4·3	6·8	158·1	3·9	2·8	139·2	5·6	81·2
1849	4·3	7·3	169·8	5·1	4·7	108·4	5·8	84·1
1850	3·8	6·8	179·0	4·3	3·8	113·2	5·3	79·1
2076	4·4	7·2	163·7	–	–	–	5·8	–
2086	3·8	7·5	197·5	–	–	–	5·7	76·0
SO 417*	4·3	6·1	141·9	4·7	3·6	130·6	5·2	–
Mean	4·1	7·1	172	4·6	3·6	129	5·5	81
Number	6	6	6	4	4	4	6	5
P. (R.) gordoni								
SO 401	5·6	7·2	128·7	–	–	–	6·4	80·0
488	5·6	7·9	141·1	–	–	–	6·8	–
700	6·0	8·0	133·3	5·4	4·7	114·8	7·0	84·2
1081	5·3	7·2	135·9	5·1	4·4	115·9	6·3	–
Mean	5·6	7·6	135	5·3	4·6	115	6·7	82
Number	4	4	4	2	2	2	4	2
P. (R.) vancouveringi								
RU 1778	5·6	6·7	119·6	5·2	5·2	100·0	6·2	89·8
2058	4·9	6·2	126·5	–	–	–	5·6	83·6
Mean	5·3	6·5	123	5·2	5·2	100	5·9	86
Number	2	2	2	1	1	1	2	2
L. legetet								
SO 443	3·4	5·3	155·8	3·7	3·0	123·0	4·4	77·2

* Not included in calculation of sample parameters.

Table 7 (*cont.*)

	md	bl	bl	height		buc ht	md + bl	P^4
			md	buc	ling	ling ht	2	M^1
P. africanus								
M 14084	5·7	9·0	158·0	7·4	5·7	129·7	7·4	84·0
32363	5·2	9·8	188·4	–	–	–	7·5	85·0
RU 1705	4·9	8·5	173·6	5·1	4·1	124·3	6·7	84·0
1733	5·8	9·9	170·9	7·7	5·8	132·8	7·9	–
2036	4·9	8·5	173·6	5·8	4·9	118·3	6·7	76·0
2088	5·5	9·4	171·0	–	–	–	7·5	82·0
MW 43	5·8	9·5	163·9	7·5	5·9	127·0	7·7	–
82	5·5	8·5	154·5	–	–	–	7·0	–
SO 524	5·6	9·6	171·5	6·4	6·0	106·8	7·6	–
Mean	5·4	9·2	170	6·7	5·4	123	7·3	82
Number	9	9	9	6	6	6	9	5
P. nyanzae								
M 16647	6·7	11·7	174·6	8·4	5·9	142·3	9·2	87·6
16649	7·7	12·0	155·8	6·9	6·3	109·3	9·9	91·6
RU 1674	6·1	11·2	183·6	6·0	4·2	142·8	8·6	91·4
1677	7·0	10·8	154·2	8·4	7·0	120·0	8·9	86·4
1691	6·8	9·6	141·1	7·0	4·9	143·0	8·2	–
1715	7·3	10·8	140·8	7·2	6·6	109·1	9·1	–
1718	6·4	10·6	165·8	7·4	6·5	113·9	8·5	–
1719	6·4	10·4	162·5	7·4	6·6	112·1	8·4	–
1732	7·7	11·5	149·3	7·2	6·8	106·0	9·6	–
2005	6·0	11·0	183·3	–	–	–	8·5	–
2037	6·2	10·9	175·9	–	–	–	8·6	–
Mean	6·8	11·0	163	7·3	6·1	122	8·9	89
Number	11	11	11	9	9	9	11	4
S.D.	0·61	0·66	14·72	–	–	–	–	–
Coef. var.	9·0	6·0	9·0	–	–	–	–	–
S.E.	0·18	0·20	4·44	–	–	–	–	–
95% conf.	5·3	9·5	130	–	–	–	–	–
limits	8·1	12·5	196	–	–	–	–	–
P. major								
SO 418	6·1	11·2	183·5	6·0	4·2	143·0	8·7	84·5
441	7·4	11·5	155·3	5·5	4·0	137·3	9·5	–
527	6·4	10·2	159·3	–	–	–	8·3	–
529	7·6	11·6	152·9	7·8	5·5	141·9	9·6	–
UM-P 62-11	7·9	14·7	186·0	–	–	–	11·3	93·3
69-01	7·5	13·6	181·2	–	–	–	10·6	–
Mean	7·2	12·1	170	6·4	4·6	141	9·7	95
Number	6	6	6	3	3	3	6	2

Table 8 Measurements of upper M1.

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$
D. macinnesi				
RU 1669	5·4	7·1	131·6	6·3
1774	6·0	7·5	125·0	6·8
1788	6·0	7·0	116·7	6·5
1796	5·7	7·7	135·1	6·7
1799	5·5	6·9	125·4	6·2
1806	6·0	7·8	130·0	6·9
1849	6·2	7·5	121·0	6·9
1850	5·8	7·5	129·3	6·7
1901	6·2	8·1	130·6	7·1
1946	5·6	7·7	137·7	6·7
1991	6·2	7·4	119·3	6·8
2028	6·0	7·5	125·0	6·8
2086	6·5	8·4	129·2	7·5
M 14082	5·7	6·6	115·8	6·2
Mean	5·9	7·5	127	6·8
Number	14	14	14	14
S.D.	0·31	0·47	6·61	0·34
Coef. var.	5·3	6·3	5·2	5·0
S.E.	0·08	0·12	1·77	0·09
95% conf.	5·2	6·5	113	6·1
limits	6·6	8·5	141	7·5
P. (R.) gordoni				
MW 52	8·4	8·0	95·3	8·2
SO 401	8·1	7·9	97·5	8·0
487	8·4	7·9	94·1	8·2
700	8·5	8·1	95·3	8·3
930	8·1	8·5	104·9	8·3
931	8·1	8·0	98·8	8·1
932	7·8	8·0	102·6	7·9
Mean	8·2	8·1	98	8·1
Number	7	7	7	7
S.D.	0·24	0·21	4·05	0·15
Coef. var.	2·9	2·6	4·1	1·9
S.E.	0·09	0·08	1·53	0·06
95% conf.	7·6	7·6	88	7·7
limits	8·8	8·6	108	8·5
P. (R.) vancouveringi				
RU 1778	7·0	6·8	97·2	6·9
1801	6·4	6·6	103·0	6·5
2058	6·8	6·5	95·6	6·7
SO 944	6·8	6·4	94·2	6·6
1134	6·5	6·5	100·0	6·5
MB 125	7·1	6·7	94·4	6·9
Mean	6·8	6·6	97	6·7
Number	6	6	6	6
S.D.	0·27	0·15	2·48	0·18
Coef. var.	4·0	2·2	2·6	2·7
S.E.	0·11	0·06	1·42	0·07
95% conf.	6·1	6·2	91	6·3
limits	7·5	7·0	103	7·1

Table 8 (*cont.*)

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$
L. legetet				
SO 413	4·9	6·6	134·7	5·8
443	5·1	6·2	121·6	5·7
536	5·3	6·5	122·8	5·9
537	4·8	5·9	123·0	5·4
926	5·1	6·2	121·6	5·7
Mean	5·0	6·3	125	5·7
Number	5	5	5	5
S.D.	0·19	0·28	4·02	0·19
Coef. var.	3·8	4·5	3·3	3·3
S.E.	0·09	0·12	1·8	0·08
95% conf.	4·5	5·5	110	5·2
limits	5·5	7·1	132	6·2
P. africanus				
M 14081	7·0	8·4	120·0	7·7
14084	7·9	9·6	121·5	8·8
14085	7·8	8·9	114·1	8·4
32363	7·8	9·5	121·9	8·7
RU 1705	7·4	8·6	116·2	8·0
1741	8·4	9·8	116·7	9·1
1742	8·5	9·8	115·3	9·2
1795	8·0	9·0	112·5	8·5
1904	7·4	8·7	117·6	8·1
1934	7·6	9·9	130·2	8·8
1936	7·7	9·1	118·2	8·4
1973	7·1	8·0	112·8	7·6
2036	7·8	9·8	125·6	8·8
2088	8·6	9·6	111·6	9·1
MW 61	8·2	9·8	119·4	9·0
SO 528	7·0	8·5	121·3	7·8
Mean	7·8	9·2	118	8·5
Number	15	15	15	15
S.D.	0·48	0·61	5·11	0·51
Coef. var.	6·2	6·6	2·8	6·0
S.E.	0·12	0·16	1·32	0·13
95% conf.	6·8	7·9	108	7·4
limits	8·8	10·5	128	9·6

Table 8 (*cont.*)

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$
P. nyanzae				
M 16647	9·2	11·7	127·2	10·5
16649	10·2	11·6	113·7	10·9
RU 1674	8·4	10·3	123·8	9·4
1677	9·4	11·2	119·1	10·3
1696	11·0	12·2	110·9	11·6
1720	9·7	11·5	118·6	10·6
1721	10·7	12·4	115·9	11·6
1803	9·2	9·8	106·5	9·5
1929	10·3	11·3	109·6	10·8
MB 107	10·6	11·3	106·6	11·0
Mean	9·9	11·3	115	10·7
Number	10	10	10	10
S.D.	0·86	0·79	7·36	0·77
Coef. var.	8·7	7·0	6·4	7·2
S.E.	0·27	0·25	2·33	0·24
95% conf.	7·9	9·5	98	9·0
limits	11·8	13·1	132	12·4
P. major				
SO 418	9·3	11·3	121·5	10·3
542	10·5	12·8	121·9	11·7
933	11·4	12·2	107·0	11·8
934	10·1	11·6	114·9	10·9
939	9·7	10·9	112·4	10·3
UM-P 62-07	11·4	13·9	122·0	12·7
62-11	11·7	12·7	108·5	12·1
64-01	12·0	13·9	115·8	13·0
66-41	12·0	14·0	116·6	13·0
69-02	11·0	13·3	121·0	12·2
Mean	10·9	12·7	116	11·8
Number	10	10	10	10
S.D.	0·96	1·13	5·55	1·01
Coef. var.	8·8	8·9	4·8	8·6
S.E.	0·30	0·36	1·76	0·32
95% conf.	8·2	10·2	103	9·5
limits	13·1	15·2	129	11·7

Table 9 Measurements of upper M2.

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$	$\frac{M^2}{M^1}$
D. macinnesi					
RU 1669	5·8	7·1	122·4	6·5	103·2
1774	6·7	8·0	119·4	7·4	108·8
1776	6·6	7·8	118·1	7·2	–
1799	5·8	6·9	119·0	6·4	103·2
1806	7·4	8·8	119·0	8·1	117·4
1849	7·1	8·1	114·2	7·6	110·2
1850	6·7	8·0	119·4	7·4	110·4
1862	7·0	8·9	127·2	8·0	–
1866	6·4	8·2	128·1	7·3	–
1901	7·2	8·5	118·1	7·8	109·8
1915	6·6	8·0	121·2	7·3	–
2028	6·4	7·8	121·9	7·1	–
2086	7·2	8·7	120·9	8·0	107·0
Mean	6·7	8·1	121	7·4	109
Number	13	13	13	13	8
S.D.	0·50	0·60	3·73	0·53	–
Coef. var.	7·5	7·4	3·1	7·2	–
S.E.	0·14	0·17	1·03	0·15	–
95% conf.	5·6	6·8	113	6·2	–
limits	7·8	9·4	129	8·6	–
P. (R.) gordoni					
MW 52	9·2	8·6	93·5	8·9	108·4
SO 375	10·0	10·4	104·0	10·2	–
449	9·6	10·4	108·3	10·0	–
700	9·6	10·0	104·2	9·8	118·0
938	9·5	10·0	105·3	9·8	–
Mean	9·6	9·9	103	9·7	113
Number	5	5	5	5	2
P. (R.) vancouveringi					
RU 2058	7·8	7·4	94·8	7·6	113·3
L. legetet					
SO 436	5·4	7·1	131·4	6·3	–
535	5·8	7·0	120·8	6·4	–
537	5·1	6·3	123·6	5·7	105·5
927	5·4	6·8	126·0	6·1	–
929	5·4	6·8	126·0	6·1	–
935	5·8	7·0	120·8	6·4	–
936	5·4	6·9	127·9	6·2	–
MB 109	5·6	6·8	121·3	6·2	–
Mean	5·5	6·8	125	6·2	106
Number	8	8	8	8	1
S.D.	0·24	0·24	3·81	0·23	–
Coef. var.	4·4	3·5	3·6	3·7	–
S.E.	0·08	0·09	1·35	0·08	–
95% conf.	4·9	6·2	116	5·7	–
limits	6·1	7·4	134	6·7	–

Table 9 (*cont.*)

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$	$\frac{M^2}{M^1}$
P. africanus					
M 14081	7·5	9·4	125·3	8·5	110·0
14084	9·2	11·3	122·8	10·3	117·0
32363	9·2	10·8	117·4	10·0	115·0
RU 1671	7·8	9·7	124·3	8·8	–
1672	8·1	9·5	117·3	8·8	–
1747	8·9	10·9	122·4	9·9	–
1835	8·9	10·8	121·2	9·9	–
1861	8·9	10·2	114·7	9·6	–
1872	9·3	11·0	118·3	10·2	–
1873	8·4	10·5	125·0	9·5	–
1904	7·7	9·4	122·0	8·6	106·0
1954	7·9	9·3	117·8	8·6	–
1973	7·9	9·3	117·8	8·6	–
1981	7·8	9·6	123·0	8·7	–
2016	8·7	10·1	116·1	9·4	–
2026	9·8	12·0	122·4	10·9	–
2036	8·1	9·9	122·2	9·0	102·0
2088	9·8	11·0	112·3	10·4	114·0
SO 946	9·2	11·6	126·2	10·6	–
1078	8·1	10·2	126·0	9·2	–
Mean	8·5	10·3	120	9·5	111
Number	20	20	20	20	6
S.D.	0·72	0·82	3·99	0·76	–
Coef. var.	8·5	8·0	3·3	8·0	–
S.E.	0·16	0·18	0·89	0·17	–
95% conf.	7·0	8·6	112	7·9	–
limits	10·0	12·0	129	11·1	–
P. nyanzae					
M 16647	12·2	13·4	109·8	12·8	122·0
RU 1674	9·9	11·5	116·1	10·7	114·0
1677	12·0	13·5	112·5	12·8	124·0
1803	10·5	11·8	112·3	11·2	118·0
KA 6	11·1	12·5	112·6	11·8	–
Mean	11·3	12·5	113	11·9	120
Number	5	5	5	5	4
P. major					
SO 381	12·1	14·2	117·3	13·2	–
382	12·8	16·0	125·0	14·4	–
485	14·7	16·8	114·3	15·8	–
LS 7	10·8	14·6	135·1	12·7	–
UM-P 62-08	15·1	17·0	112·5	16·2	–
62-11	13·1	14·0	106·9	13·6	112·0
Mean	12·7	14·9	119	13·8	112
Number	6	6	6	6	1

Table 10 Measurements of upper M3.

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{M^3}{M^1}$
D. macinnesi					
RU 1670	7·0	8·0	114·3	7·5	–
1774	6·2	7·9	127·3	7·1	104·4
1799	5·2	6·6	126·9	5·9	95·2
1806	6·7	7·9	117·9	7·3	105·8
1849	6·4	7·9	123·3	7·2	104·3
1850	6·6	7·8	118·1	7·3	109·0
1901	6·9	8·5	123·2	7·7	108·4
1915	5·8	7·6	131·0	6·7	–
2054	7·0	8·2	117·1	7·6	–
SO 457*	6·3	8·0	127·0	7·2	–
Mean	6·4	7·8	122	7·1	105
Number	9	9	9	9	6
S.D.	0·62	0·52	6·01	0·55	–
Coef. var.	9·7	6·7	4·9	7·8	–
S.E.	0·21	0·17	2·00	0·18	–
95% conf.	5·0	6·6	108	5·8	–
limits	7·8	8·9	136	8·4	–
P. (R.) gordoni					
RU 1692	12·2	11·7	96·0	12·0	–
SO 700	10·3	10·7	103·9	10·5	127
943	9·9	9·7	98·0	9·8	–
Mean	10·8	10·7	99	10·8	127
Number	3	3	3	3	1
P. (R.) vancouveringi					
RU 2058	8·3	7·5	90·4	7·9	117·9
MW 48	7·2	7·4	102·8	7·3	–
SO 942	7·8	8·1	103·8	8·0	–
Mean	7·8	7·7	99	7·7	118
Number	3	3	3	3	1
L. legetet					
SO 412	4·8	5·7	118·7	5·3	–
459	5·6	7·0	125·1	6·3	–
462	5·7	7·1	124·6	6·4	–
535	5·5	6·3	114·4	5·9	–
940	5·5	7·2	130·9	6·4	–
941	5·4	6·8	126·0	6·1	–
Mean	5·4	6·7	123	6·0	–
Number	6	6	6	6	–
S.D.	0·32	0·58	6·71	0·50	–
Coef. var.	5·9	8·6	5·4	8·3	–
S.E.	0·13	0·24	2·74	0·21	–
95% conf.	4·6	5·2	108	4·7	–
limits	6·2	8·2	140	7·3	–

Table 10 (*cont.*)

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$	$\frac{M^3}{M^1}$
P. africanus					
M 14084	7·9	10·5	132·9	9·2	105·0
32363	8·4	11·0	130·9	9·7	111·0
RU 1821	7·6	9·9	130·2	8·8	–
1920	7·9	10·5	132·9	9·2	–
1922	8·8	10·9	123·9	9·9	–
2088	9·3	11·5	123·8	10·4	114·0
SO 442	8·5	11·4	134·1	10·0	–
Mean	8·3	10·8	130	9·6	110
Number	7	7	7	7	3
S.D.	0·59	0·56	4·08	0·56	–
Coef. var.	7·1	5·2	3·1	5·8	–
S.E.	0·22	0·21	1·54	0·21	–
95% conf.	6·8	9·4	120	8·2	–
limits	9·8	12·2	140	11·0	–
P. nyanzae					
M 16647	11·1	14·1	127·0	12·6	120·0
RU 1674	10·1	12·6	124·8	11·4	121·0
1677	11·8	13·9	117·8	12·9	125·0
1697	12·4	14·8	119·3	13·6	–
1836	12·0	13·1	109·1	12·5	–
1910	10·1	12·5	123·8	11·3	–
2061	11·7	14·0	119·6	12·9	–
Mean	11·3	13·6	120	12·5	122
Number	7	7	7	7	3
S.D.	0·92	0·86	5·92	0·83	–
Coef. var.	8·1	6·3	4·9	6·6	–
S.E.	0·35	0·32	2·24	0·32	–
95% conf.	9·0	11·5	105	10·5	–
limits	13·6	15·7	135	14·5	–
P. major					
M 14331	14·6	17·8	121·9	16·2	–
LS 7	10·4	13·6	130·8	12·0	–
UM-P 62-11	12·7	14·3	112·6	13·5	112·0
Mean	12·6	15·2	121	13·9	112
Number	3	3	3	3	1

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* Not included in calculation of sample parameters.

Table 11 Measurements of lower I1.

	md	bl	bl/md	md		incis/md	root/md	buc ht	md/buc ht
				incis	root				
D. macinnesi									
RU 900	2·7	3·7	137·0	2·7	1·9	100·0	70·4	5·1	52·9
SO 395*	3·3	4·0	121·3	3·3	2·5	100·0	75·7	6·6	50·0
Mean	2·7	3·7	137	2·7	1·9	100	70	5·1	53
Number	1	1	1	1	1	1	1	1	1
P. (R.) gordoni									
SO 428	4·3	4·7	109·3	4·0	3·1	93·0	72·1	10·1	42·6
473	3·9	4·4	112·8	3·9	3·0	100·0	76·9	7·7	50·7
475	5·6	4·8	85·7	5·2	4·6	92·9	80·7	10·3	54·4
555	5·9	4·9	83·1	5·6	4·8	94·9	81·4	8·4	70·2
556	4·7	4·8	102·1	4·7	3·5	100·0	74·5	10·7	43·9
563	4·3	4·8	111·7	4·3	3·5	100·0	81·4	10·1	42·6
Mean	4·8	4·8	101	4·6	3·8	97	77	9·6	51
Number	6	6	6	6	6	6	6	6	6
L. legetet									
SO 545	2·3	3·4	147·8	–	1·7	–	73·9	–	–
1076	2·8	3·0	107·1	–	–	–	–	–	–
KO 8	2·9	3·0	103·5	2·6	2·0	89·6	69·7	4·8	60·4
Mean	2·7	3·1	119	2·6	1·9	90	71	4·8	60
Number	3	3	3	1	2	1	2	1	1
P. africanus									
M 32362*	3·5	4·6	131·3	–	–	–	–	–	–
32363	3·7	4·9	132·4	3·7	3·2	100·0	86·5	9·9	37·3
RU 1769	4·1	5·2	126·9	3·8	3·0	92·7	73·2	8·4	48·8
2036	4·0	5·0	125·0	–	–	–	–	–	–
2090	4·6	5·5	119·5	–	–	–	–	–	–
Mean	4·1	5·2	126	3·8	3·1	96	80	9·2	43
Number	4	4	4	2	2	2	2	2	2
P. nyanzae									
RU 1947	4·6	6·2	134·8	4·6	4·1	100·0	89·1	9·5	48·4
2030	6·0	5·8	96·7	5·5	4·6	91·7	76·7	9·7	62·8
MW 40	5·5	6·1	110·9	–	–	–	–	–	–
42	5·3	6·5	122·6	–	–	–	–	–	–
KA 5	5·0	5·8	116·0	–	–	–	–	–	–
Mean	5·3	6·1	115	5·1	4·4	96	83	9·6	55
Number	5	5	5	2	2	2	2	2	2
P. major									
UM-P 62-06	6·4	8·0	125·0	6·2	4·8	96·9	75·0	14·0	45·7

* Not included in calculation of sample parameters.

Table 12. Measurements of lower I2.

	md	bl	bl/md	md/root	root/md	buc ht	md/buc ht
D. macinnesi							
RU 900	2·9	4·3	148·3	2·0	68·9	5·6	51·8
1952	3·0	4·7	157·0	–	–	6·0	50·0
1953	3·4	4·3	126·4	–	–	–	–
1993	3·0	4·0	133·3	2·5	83·4	4·7	63·8
2017	3·7	4·3	116·2	3·0	81·1	5·9	62·7
2064	3·7	4·0	108·1	2·4	64·9	6·0	61·7
SO 517*	3·2	4·7	147·8	2·6	81·3	6·0	53·3
544*	3·5	4·7	134·3	3·0	85·7	6·0	58·3
Mean	3·3	4·3	132	2·7	75	5·6	59
Number	6	6	6	4	4	5	5
P. (R.) gordoni							
SO 383	4·5	5·3	117·8	3·8	84·5	11·3	39·8
557	4·2	4·5	107·2	3·3	78·6	7·2	58·3
558	4·7	5·5	117·0	3·6	76·6	–	–
559	4·6	5·0	106·3	3·6	78·3	7·5	61·3
560	4·8	5·6	116·7	3·8	79·2	7·0	68·6
562	4·5	5·3	117·8	3·8	81·4	11·3	39·8
Mean	4·6	5·2	113	3·6	79	8·9	52
Number	6	6	6	6	6	5	5
L. legetet							
SO 384	3·4	3·8	111·8	2·9	91·2	5·6	60·7
411	3·4	4·2	123·6	–	–	5·2	65·4
547	3·5	4·0	114·2	2·6	74·3	4·7	74·5
KO 8	2·9	3·2	110·2	2·6	89·7	5·2	55·7
Mean	3·3	3·8	115	2·7	85	5·2	64
Number	4	4	4	3	3	4	4
P. africanus							
M 32363	4·2	6·0	142·9	3·1	73·8	11·8	35·6
RU 1769	4·4	6·0	136·3	3·0	68·2	11·5	38·3
2036	4·6	5·5	119·6	2·7	58·7	9·4	48·9
SO 561	4·2	6·2	147·7	2·6	61·9	8·3	50·6
Mean	4·4	5·9	137	2·9	66	10·2	43
Number	4	4	4	4	4	4	4
P. nyanzae							
RU 1716	5·0	6·4	128·0	4·0	80·0	12·2	41·0
1730	4·7	6·8	144·8	3·8	80·8	9·9	47·4
1947	5·2	7·8	150·0	4·1	78·8	11·1	46·8
1982	5·6	8·0	142·8	4·4	78·8	–	–
Mean	5·1	7·2	143	4·1	80	11·1	46
Number	4	4	4	4	4	3	3
P. major							
SO 454	7·0	8·4	120·0	–	–	11·0	64·0
1135	4·7	7·0	149·0	4·2	89·4	11·5	40·8
Mean	5·9	7·7	135	4·2	89	11·3	52
Number	2	2	2	1	1	2	2

* Not included in calculation of sample parameters.

Table 13 Measurements of lower C.

	max l	perp b	b/l	buc ht	mesial		ridge/ht	max l/buc ht
					ht	ridge		
D. macinnesi								
M 32232	8·2	5·5	67·0	–	–	–	–	–
32338	7·0	4·6	65·7	8·5	6·8	4·1	60·3	82·4
RU 900	7·5	5·0	66·7	12·0	8·2	7·3	89·0	62·5
1650	6·2	4·1	66·1	8·4	5·0	3·0	60·0	73·8
1699	8·3	5·9	71·1	11·8	7·5	5·1	68·0	70·4
1700	8·2	5·4	65·8	12·0	9·0	7·2	80·0	68·4
1701	8·5	6·0	70·6	14·6	11·8	9·0	76·2	58·2
1702	6·6	3·9	59·1	9·3	7·4	5·1	68·9	71·0
1781	6·5	4·2	64·7	8·3	6·0	3·6	60·0	78·3
1811	9·2	5·8	63·0	11·0	7·2	4·2	58·3	83·6
1850	6·5	4·1	63·1	8·7	6·2	4·0	64·5	74·7
1857	9·2	6·0	65·2	–	–	–	–	–
1880	8·0	5·3	66·2	–	–	–	–	–
1902	7·8	5·6	71·8	12·0	9·8	6·8	69·1	65·0
1962	8·5	5·3	62·4	–	–	–	–	–
1972	8·5	5·4	63·5	13·5	7·7	5·1	66·2	63·0
1990	6·7	4·6	68·6	7·6	5·2	3·2	61·6	88·2
2007	7·6	4·8	63·2	–	–	–	–	–
2012	6·8	4·0	58·9	–	–	–	–	–
2013	8·0	5·5	68·7	–	–	–	–	–
2023	6·9	4·0	58·0	8·3	5·4	3·5	64·6	83·2
2024	6·4	4·0	62·5	8·5	6·5	4·2	64·6	75·3
2062	8·3	5·6	67·5	–	–	–	–	–
2063	6·5	4·1	63·1	8·9	6·1	4·9	80·3	73·1
SO 405*	7·5	5·0	66·7	9·1	–	–	–	82·5
429*	7·3	5·0	68·5	10·1	6·8	3·9	57·4	72·2
518*	7·6	5·0	65·8	9·7	6·5	3·8	58·5	78·4
574*	7·1	5·8	81·7	10·2	8·9	7·3	82·1	69·6
576*	8·2	5·3	64·6	10·1	7·0	3·5	50·0	81·2
1047*	7·5	5·1	68·0	10·1	6·8	4·3	63·3	74·5
1099*	7·7	5·6	72·7	8·1	5·9	3·7	62·7	95·0
Mean	7·6	5·0	65	10·3	7·3	5·1	69	73
Number	24	24	24	16	16	16	16	16
S.D.	0·94	0·76	3·70	2·20	1·86	1·75	8·86	8·48
Coef. var.	12·4	15·2	5·7	21·3	25·5	34·2	12·8	11·6
S.E.	0·20	0·16	0·77	0·57	0·48	0·45	2·29	2·19
95% conf.	5·6	3·4	57	5·6	3·3	1·3	50	55
limits	9·6	6·6	73	15·0	11·3	8·9	88	91
P. (R.) gordoni								
SO 373	11·3	8·5	75·2	15·7	12·7	10·4	81·9	72·0
1112	11·3	7·4	65·5	–	–	–	–	–
Mean	11·3	8·0	70	15·7	12·7	10·4	82	72
Number	2	2	2	1	1	1	1	1

* Not included in calculation of sample parameters.

Table 13 (*cont.*)

	max l	perp b	b/l	buc ht	mesial		ridge	max l
					ht	ridge	ht	buc ht
L. legetet								
RU 1749	5·9	3·7	62·7	–	–	–	–	–
SO 386	6·7	4·6	68·7	–	–	–	–	–
398	6·1	4·3	70·5	9·4	7·2	5·0	69·4	64·9
452	6·2	4·4	71·0	–	–	–	–	–
516	6·4	4·4	68·7	9·5	7·2	4·6	63·9	67·4
567	6·0	4·3	71·6	7·8	6·0	4·0	66·7	76·9
568	5·1	3·7	72·6	6·4	5·2	2·9	55·7	79·7
569	6·0	4·4	73·4	7·4	5·6	2·4	42·8	81·1
570	7·0	4·5	64·3	9·6	6·6	3·5	53·1	72·9
571	6·0	4·3	71·7	9·1	6·7	5·1	76·1	65·9
1050	5·5	3·7	67·2	7·5	5·6	2·8	50·0	73·4
1075	6·0	4·4	73·4	9·5	7·0	4·5	64·2	63·2
1102	5·8	3·7	63·7	8·2	6·0	3·9	65·1	70·8
1136	6·8	4·7	69·2	9·7	7·4	5·1	69·0	70·1
KO 8	4·6	3·4	73·9	5·8	4·7	2·7	57·4	79·3
Mean	6·0	4·2	70	8·3	6·2	3·9	61	74
Number	16	16	16	13	13	13	13	13
S.D.	0·62	0·46	4·69	1·29	0·85	0·96	9·10	8·64
Coef. var.	10·3	10·9	6·7	15·6	13·7	24·6	14·9	11·7
S.E.	0·15	0·11	1·17	0·36	0·23	0·27	2·52	2·40
95% conf.	4·6	3·2	60	6·9	4·3	1·8	41	55
limits	7·4	5·2	80	12·5	8·1	6·0	81	93
P. africanus								
M 32363	9·6	6·1	63·5	12·4	9·0	5·8	64·5	77·4
RU 1698	9·1	6·3	69·3	13·6	10·3	6·4	62·2	66·8
1769	8·6	6·2	72·1	12·3	9·4	7·8	83·0	69·9
1785	8·1	6·0	74·2	10·7	7·9	6·1	77·2	75·6
1899	9·3	6·6	71·0	12·7	9·0	6·4	71·1	73·2
1914	9·4	6·2	66·0	12·3	9·2	6·0	65·2	76·4
1999	8·6	6·7	77·9	–	–	–	–	–
2036	8·4	6·2	73·8	11·5	9·3	7·5	80·7	74·1
2071	8·6	7·1	82·6	–	–	–	–	–
MW 45	9·4	7·0	74·4	–	–	–	–	–
59	8·4	6·8	81·0	–	–	–	–	–
160	8·8	5·7	64·8	11·5	7·9	6·3	79·8	76·5
KO 9	10·4	7·9	76·0	14·5	11·0	8·3	75·4	71·7
Mean	9·0	6·5	73	12·4	9·2	6·7	73	74
Number	13	13	13	9	9	9	9	9
S.D.	0·63	0·58	5·90	1·14	1·04	0·89	7·76	3·51
Coef. var.	7·0	8·9	8·1	9·2	10·9	13·3	10·6	4·8
S.E.	0·18	0·16	1·64	0·38	0·33	0·30	2·59	1·17
95% conf.	7·6	5·2	60	9·8	6·9	4·7	56	65
limits	10·4	7·8	86	15·0	11·5	8·7	91	82

Table 13 (*cont.*)

	max l	perp b	b/l	buc ht	mesial		ridge/ht	max l/buc ht
					ht	ridge		
P. nyanzae								
M 32236	12·2	9·5	77·9	–	13·3	11·3	85·0	–
RU 1674	11·3	8·4	74·2	16·9	10·0	7·5	75·0	66·9
1676	12·6	9·6	76·2	18·1	15·7	12·7	80·9	69·6
1717	10·9	8·2	75·2	–	–	–	–	–
1740	13·1	8·7	66·3	–	–	–	–	–
1791	11·5	9·3	80·8	–	–	–	–	–
1840	13·7	11·2	81·7	–	–	–	–	–
1889	12·8	10·0	78·1	–	–	–	–	–
1926	12·3	9·7	78·8	–	–	–	–	–
1947	12·8	10·3	80·5	18·0	15·8	12·4	78·5	71·1
1960	14·2	11·1	78·2	14·7	14·4	11·8	82·0	96·5
1982	13·6	10·2	75·0	20·7	15·1	12·0	79·5	65·7
2010	11·0	8·5	77·3	–	–	–	–	–
2024	12·9	9·4	72·8	–	–	–	–	–
2034	12·0	9·2	76·6	16·0	13·8	11·7	84·7	75·0
2048	12·4	8·9	71·8	–	–	–	–	–
2087	11·6	8·5	73·3	15·1	14·6	12·0	82·2	76·8
MW 39	11·3	7·9	69·9	–	–	–	–	–
44	13·3	9·4	70·7	–	–	–	–	–
Mean	12·4	9·4	75	17·1	14·1	11·4	81	75
Number	19	19	19	7	8	8	8	7
S.D.	0·96	0·92	4·16	–	–	–	–	–
Coef. var.	7·7	9·8	5·6	–	–	–	–	–
S.E.	0·22	0·21	0·95	–	–	–	–	–
95% conf.	10·4	7·5	66	–	–	–	–	–
limits	14·4	11·3	84	–	–	–	–	–
P. major								
M 14086	13·5	9·5	70·4	–	–	–	–	–
SO 396	14·7	11·2	76·1	21·0	17·0	15·6	91·7	70·0
404	13·1	9·0	68·7	–	–	–	–	–
Mean	13·7	9·9	72	21·0	17·0	15·6	92	70
Number	3	3	3	1	1	1	1	1

Table 14 Measurements of lower P3.

	max l	perp b	b/l	buccal ht		dist/mes
				mes	dist	
D. macinnesi						
M 14083*	5·6	3·7	66·1	5·1	3·6	70·5
16650	8·0	4·9	61·3	9·0	6·8	75·6
32234*	8·4	4·8	57·2	–	–	–
RU 900	6·6	4·2	63·7	7·0	5·4	77·2
1664	7·3	4·4	60·2	–	–	–
1727	7·5	4·3	57·5	–	–	–
1893	7·3	4·2	57·6	–	–	–
1898	8·3	5·1	61·5	7·0	5·5	78 6
1935	7·2	4·3	59·7	8·3	5·3	63·8
1972	8·2	4·6	56·1	8·4	5·7	67·9
MW 53	6·7	4·1	61·2	6·3	4·5	71·4
SO 405*	7·9	4·7	59·5	7·9	5·6	70·9
530*	7·4	4·5	60·8	6·6	4·8	72·7
Mean	7·5	4·5	60	7·7	5·5	72
Number	9	9	9	6	6	6
S.D.	0·61	0·34	2·40	–	–	–
Coef. var.	8·1	7·6	4·0	–	–	–
S.E.	0·20	0·11	0·80	–	–	–
95% conf.	5·6	3·7	54	–	–	–
limits	8·4	5·3	66	–	–	–
P. (R.) gordoni						
SO 377	8·5	4·6	54·2	8·1	6·6	81·5
588	10·2	5·8	56·8	8·5	–	–
948	8·5	5·3	62·4	7·7	6·5	84·4
1112	10·3	5·9	57·3	–	–	–
Mean	9·4	5·4	58	9·0	7·3	82
Number	4	4	4	3	2	2
L. legetet						
M 14284*	4·9	3·6	73·4	4·2	3·7	88·1
32227*	5·1	3·4	65·6	4·3	3·7	86·1
RU 1916	6·0	3·5	58·4	5·5	3·9	70·8
SO 386	5·5	3·9	70·9	5·3	4·6	86·7
474	6·4	3·6	56·3	6·4	4·7	73·4
525	6·6	4·0	60·6	6·9	4·6	66·6
533	6·2	4·2	67·7	6·0	4·4	73·3
1075	5·5	3·6	65·5	6·3	4·8	76·2
Mean	5·9	3·8	65	5·9	4·5	77
Number	7	7	7	7	7	7

* Not included in calculation of sample parameters.

Table 14 (*cont.*)

	max l	perp b	b/l	buccal ht		dist/mes
				mes	dist	
P. africanus						
M 32363	8·5	5·6	65·8	9·5	7·1	75·0
RU 1762	8·1	5·2	64·2	7·1	5·4	76·0
1955	8·1	5·1	62·9	7·4	6·0	81·1
1958	8·0	5·1	63·7	9·3	6·9	74·2
2008	9·0	5·7	63·3	–	–	–
2036	8·5	6·0	70·6	9·0	6·6	73·4
Mean	8·4	5·4	65	8·4	6·4	76
Number	6	6	6	5	5	5
P. nyanzae						
M 32235	11·6	7·0	60·3	10·0	6·5	65·0
RU 1674	8·6	6·5	75·6	11·0	6·2	56·3
1676	9·6	6·9	71·9	9·6	8·1	84·4
1711	11·3	6·8	60·2	–	–	–
1765	10·0	6·0	60·0	–	–	–
1782	11·0	6·6	60·0	11·1	7·9	71·2
1924	12·9	6·8	52·7	11·6	6·9	59·4
1947	12·2	7·3	59·8	9·4	7·1	75·5
1982	11·6	6·9	59·4	11·7	7·7	65·8
2087	11·0	6·9	62·7	9·6	7·5	78·2
Mean	11·0	6·8	63	10·5	7·2	70
Number	10	10	10	8	8	8
S.D.	1·27	0·34	6·73	–	–	–
Coef. var.	11·6	5·0	10·7	–	–	–
S.E.	0·40	0·11	2·13	–	–	–
95% conf.	8·1	6·0	48	–	–	–
limits	13·9	7·6	78	–	–	–
P. major						
M 14086	12·2	7·0	57·4	11·9	9·2	77·3
16648	13·8	8·9	64·5	–	–	–
SO 465	16·2	9·6	59·2	–	–	–
466	16·0	9·2	57·5	15·2	11·6	76·3
1114	12·2	8·2	67·2	–	–	–
1242	12·0	7·5	62·5	–	–	–
Mean	13·6	8·4	61	13·5	10·4	77
Number	6	6	6	2	2	2

Table 15 Measurements of lower P4.

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$	$\frac{P_4}{M_1}$
D. macinnesi					
M 16650	5·9	5·6	94·9	5·7	–
RU 900	4·6	5·2	113·1	4·9	84·5
1727	5·4	5·1	94·4	5·3	80·3
1758	5·2	4·7	90·5	4·9	–
1857	5·0	4·6	92·0	4·8	78·7
1882	5·6	4·4	78·6	5·0	–
1893	5·4	4·6	85·2	5·0	–
1901	6·1	4·9	80·3	5·5	87·3
1935	5·2	4·7	90·3	5·0	–
2015	5·4	5·0	92·6	5·2	83·9
MW 53	4·6	4·1	89·2	4·4	78·7
SO 378*	4·1	5·1	124·4	4·6	86·8
Mean	5·3	4·8	91	5·1	82
Number	11	11	11	11	6
S.D.	0·47	0·41	9·08	0·36	–
Coef. var.	8·9	8·5	10·0	7·1	–
S.E.	0·14	0·12	2·74	0·11	–
95% conf.	4·2	3·9	71	4·3	–
limits	6·4	5·7	111	5·9	–
P. (R.) gordoni					
SO 374	6·1	5·3	86·9	5·7	80·3
377	5·6	5·6	100·0	5·6	–
590	6·3	5·1	81·0	5·7	–
591	6·4	5·7	89·1	6·1	–
592	7·4	5·5	74·3	6·5	–
593	6·1	6·4	105·0	6·3	–
1112	6·2	6·7	108·0	6·5	–
Mean	6·3	5·8	92	6·1	80
Number	7	7	7	7	1
L. legetet					
M 14284*	4·2	4·0	95·3	4·1	–
RU 1916	4·9	4·2	85·7	4·5	–
SO 385	4·8	3·7	77·1	4·3	84·3
595	5·0	4·4	88·0	4·7	–
KO 8	4·7	4·0	85·1	4·4	83·1
Mean	4·8	4·1	84	4·5	84
Number	4	4	4	4	2

* Not included in calculation of sample parameters.

Table 15 (*cont.*)

	md	bl	$\frac{\text{bl}}{\text{md}}$	$\frac{\text{md}+\text{bl}}{2}$	$\frac{P_4}{M_1}$
P. africanus					
M 32363	6·2	6·7	108·0	6·5	82·0
RU 1706	6·4	6·7	104·8	6·6	87·0
1824	6·2	6·6	106·4	6·4	88·0
1868	6·1	6·4	104·9	6·3	–
1955	5·6	6·3	112·5	6·0	77·0
2036	5·7	6·2	108·8	6·0	77·0
2044	5·8	6·0	103·4	5·9	–
MW 56	6·0	6·6	110·0	6·3	–
Mean	6·0	6·4	108	6·3	82
Number	8	8	8	8	5
P. nyanzae					
RU 1674	6·5	7·8	120·0	7·2	86·7
1676	8·1	8·1	100·0	8·1	89·0
1678	6·9	7·2	104·3	7·1	85·5
1679	7·3	7·8	106·8	7·6	83·5
1710	7·9	7·4	93·7	7·7	85·8
1711	6·8	7·5	110·3	7·2	83·8
1716	8·2	8·4	102·2	8·3	–
1731	8·7	7·5	86·3	8·1	–
1780	6·6	7·7	116·7	7·2	80·9
1947	7·7	8·3	107·7	8·0	94·2
1982	8·6	7·7	89·4	8·2	84·5
2087	6·4	6·7	104·7	6·6	83·6
MW 55	7·0	7·8	111·4	7·4	–
Mean	7·4	7·7	104	7·6	86
Number	13	13	13	13	10
S.D.	0·81	0·45	10·07	0·53	3·67
Coef. var.	10·9	5·9	9·7	7·0	4·3
S.E.	0·22	0·13	2·79	0·15	1·16
95% conf.	5·6	6·7	82	6·4	78
limits	9·2	8·7	126	8·8	94
P. major					
M 14086	7·7	8·9	115·6	8·3	86·5
16648	9·0	9·7	107·8	9·4	84·7
SO 396	8·9	9·7	109·0	9·3	83·0
416	9·4	10·3	109·6	9·9	–
UM-P 62-06	8·5	8·7	102·2	8·6	–
62-13	8·6	9·1	105·8	8·9	90·0
62-16	7·9	9·0	113·9	8·5	84·2
66-02	7·8	9·0	115·2	8·4	–
Mean	8·5	9·3	110	8·9	86
Number	8	8	8	8	5

Table 16 Measurements of lower M1.

	md	bl		bl mes	bl dist	md + bl mes
		mes	dist	md	bl mes	2
D. macinnesi						
RU 900	6·2	5·3	–	85·5	–	5·8
1727	7·2	6·0	6·1	83·2	101·7	6·6
1773	7·1	5·4	5·6	76·0	103·7	6·3
1798	6·7	5·3	5·5	79·2	103·8	6·0
1804	6·3	4·8	–	76·2	–	5·6
1849	7·0	5·4	–	77·2	–	6·2
1850	6·1	5·3	5·4	86·8	101·9	5·7
1852	6·8	5·3	5·5	78·0	103·8	6·1
1857	6·7	5·5	5·7	82·2	103·7	6·1
1901	7·0	5·5	5·7	78·6	103·7	6·3
1925	6·5	4·9	–	75·4	–	5·7
1994	6·5	5·3	–	81·6	–	5·9
2015	6·9	5·4	5·7	78·2	105·6	6·2
2065	6·7	5·4	5·5	80·6	101·9	6·1
MW 53	6·2	–	5·0	–	–	5·6
SO 378*	5·6	4·9	5·0	87·5	102·1	5·3
530*	6·0	4·9	5·1	81·7	104·1	5·5
Mean	6·7	5·3	5·6	80	103	6·0
Number	15	14	10	14	9	15
S.D.	0·35	0·28	0·28	3·54	1·26	0·29
Coef. var.	5·2	5·3	5·0	4·4	1·2	4·8
S.E.	0·09	0·07	0·08	0·95	0·42	0·08
95 × conf.	5·9	4·7	5·0	73	100	5·4
limits	7·5	5·9	6·2	87	106	6·6
P. (R.) gordoni						
RU 1768	8·8	6·9	7·1	78·4	103·0	7·9
SO 374	7·9	6·2	6·2	78·5	100·0	7·1
434	7·8	5·9	6·1	75·7	103·4	6·9
445	7·7	5·9	–	76·6	–	6·8
463	8·4	6·0	6·1	71·4	101·6	7·2
507	7·6	6·0	6·0	78·9	100·0	6·8
522	8·5	6·8	6·8	80·0	100·0	7·7
904	8·3	6·2	6·4	74·7	103·2	7·2
905	8·6	6·6	6·9	76·8	104·5	7·6
Mean	8·2	6·3	6·5	77	102	7·2
Number	9	9	8	9	8	9
S.D.	0·44	0·39	0·42	2·62	1·80	0·40
Coef. var.	5·4	6·2	6·5	3·4	1·8	5·6
S.E.	0·15	0·13	0·15	0·87	0·64	0·13
95% conf.	7·2	5·4	5·5	71	98	6·3
limits	9·2	7·2	7·5	83	106	8·1

* Not included in calculation of sample parameters.

Table 16 (*cont.*)

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md} + \text{bl mes}}{2}$
		mes	dist			
L. legetet						
M 14079	5·6	4·6	4·9	82·2	106·5	5·0
RU 1984	5·7	4·6	4·7	80·7	102·2	5·2
2078	5·6	4·6	4·7	82·2	102·2	5·1
SO 376	5·6	4·3	4·5	76·9	104·7	5·0
385	5·7	4·5	4·6	79·0	102·3	5·1
386	5·6	4·2	4·1	75·0	97·6	4·9
387	6·0	4·8	5·0	80·0	104·2	5·4
425	6·0	4·8	4·9	80·0	102·2	5·4
426	5·5	4·1	4·5	74·5	109·7	4·8
435	6·1	5·1	5·1	83·6	100·0	5·6
482	5·5	4·5	4·7	81·9	104·4	5·0
534	5·6	4·4	4·6	78·5	104·6	5·0
597	6·1	5·0	5·2	82·0	104·0	5·6
598	5·5	4·1	4·3	74·5	104·8	4·8
599	5·1	4·0	4·3	78·4	107·5	4·6
900	6·1	4·6	4·7	75·4	102·2	5·4
KO 8	5·8	4·7	4·8	81·0	102·0	5·3
WF 1	6·3	5·0	5·0	79·4	100·0	5·7
Mean	5·7	4·5	4·7	79	104	5·2
Number	18	18	18	18	18	18
S.D.	0·30	0·33	0·31	2·93	2·88	0·31
Coef. var.	5·1	7·3	6·6	3·7	2·8	5·9
S.E.	0·07	0·08	0·07	0·68	0·67	0·07
95% conf.	5·1	3·8	4·0	73	98	4·5
limits	6·3	5·2	5·4	85	110	5·9
P. africanus						
M 32363	8·5	7·2	7·3	84·7	101·4	7·9
RU 1680	8·0	6·5	–	81·2	–	7·3
1706	8·0	7·1	7·4	88·8	104·2	7·6
1728	7·4	6·7	–	90·6	–	7·1
1824	7·7	6·9	–	89·5	–	7·3
1955	8·4	7·2	7·0	85·7	97·2	7·8
1980	8·3	7·2	–	86·7	–	7·8
2036	8·4	7·1	7·4	84·5	104·2	7·8
2093	8·2	6·9	–	84·2	–	7·6
SO 901	7·7	7·0	6·7	90·9	95·7	7·4
903	8·6	7·3	7·5	84·9	102·8	8·0
Mean	8·1	7·0	7·2	87	101	7·6
Number	11	11	6	11	6	11
S.D.	0·38	0·24	–	4·34	–	0·29
Coef. var.	4·7	3·4	–	5·0	–	3·8
S.E.	0·12	0·07	–	1·31	–	0·09
95% conf.	7·2	6·5	–	78	–	7·0
limits	8·8	7·5	–	97	–	8·2

Table 16 (*cont.*)

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md + bl mes}}{2}$
		mes	dist			
P. nyanzae						
RU 1674	9·1	7·4	7·9	81·3	106·8	8·3
1676	9·7	8·4	8·5	86·6	101·2	9·1
1678	9·1	7·4	7·9	81·3	106·8	8·3
1679	9·8	8·3	8·5	84·7	102·3	9·1
1710	9·2	7·5	7·6	81·5	101·3	8·4
1711	9·2	8·0	8·0	87·0	100·0	8·6
1780	9·5	8·2	8·5	86·3	103·7	8·9
1789	9·5	8·1	8·1	85·3	100·0	8·8
1818	9·5	7·8	7·9	82·2	101·2	7·7
1822	9·4	7·8	7·9	83·0	101·2	8·6
1947	9·2	7·8	8·3	84·8	107·8	8·5
1982	10·1	9·2	9·1	91·1	98·9	9·7
2000	9·6	8·3	8·5	86·4	102·3	9·0
2032	10·6	9·0	8·9	84·9	98·9	9·8
2087	8·4	7·3	7·3	86·9	100·0	7·9
Mean	9·5	8·0	8·2	85	102	8·7
Number	15	15	15	15	15	15
S.D.	0·50	0·56	0·48	2·71	2·88	0·58
Coef. var.	5·3	7·0	5·9	3·2	2·8	6·7
S.E.	0·13	0·14	0·12	0·70	0·74	0·15
95% conf.	8·4	6·8	7·2	79	96	7·5
limits	10·6	9·2	9·2	91	108	9·9
P. major						
M 14086	9·8	9·4	9·5	95·9	101·1	9·6
16648	12·1	10·0	10·4	82·7	104·0	11·1
SO 396	11·7	10·7	10·6	91·5	99·1	11·2
470	11·2	10·4	10·2	92·9	98·1	10·8
472	11·7	10·4	10·5	88·9	101·0	11·1
542	11·2	9·7	8·9	86·6	91·8	10·5
915	11·3	10·0	10·2	88·5	102·0	10·7
916	12·0	10·0	–	83·3	–	11·0
917	12·4	10·5	10·8	84·7	102·8	11·5
1113	10·7	9·5	9·8	88·9	103·2	10·1
UM-P 62-13	10·8	9·0	9·2	83·4	102·2	9·9
62-14	12·1	10·2	10·5	84·3	102·9	11·2
62-15	12·7	10·6	11·0	83·5	103·8	11·7
62-16	10·7	9·4	9·4	87·8	100·0	10·1
Mean	11·5	10·0	10·1	88	101	10·8
Number	14	14	13	14	13	14
S.D.	0·79	0·52	0·66	4·18	3·27	0·63
Coef. var.	6·9	5·0	6·6	4·7	3·2	5·8
S.E.	0·21	0·14	0·18	1·12	0·91	0·17
95% conf.	9·8	8·9	8·7	79	94	9·4
limits	13·2	11·1	11·5	97	108	12·2

Table 17 Measurements of lower M2.

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md}+\text{bl mes}}{2}$	$\frac{M_2}{M_1}$
		mes	dist				
D. macinnesi							
M 16650	7·9	6·7	–	84·8	–	7·3	–
RU 1725	7·8	6·7	6·5	86·0	97·0	7·3	–
1726	7·8	6·6	6·5	84·7	98·5	7·2	–
1803	7·0	5·8	5·7	82·9	98·3	6·4	114·3
1844	7·0	6·2	–	88·7	–	6·6	–
1847	7·9	6·5	–	82·2	–	7·2	–
1849	8·2	6·2	6·5	75·6	104·8	7·2	–
1850	7·1	6·2	6·1	87·3	98·4	6·7	117·9
1893	7·6	6·1	6·4	80·3	104·9	6·9	–
1901	7·4	6·6	6·7	89·2	101·4	7·0	111·1
1992	7·5	5·9	5·9	78·7	100·0	6·7	–
2003	7·6	6·0	6·1	78·9	101·7	6·8	–
2015	7·8	6·6	6·8	84·6	103·0	7·2	116·1
2046	7·6	6·3	6·0	82·9	95·3	7·0	–
2053	7·0	6·0	5·9	85·8	98·4	6·5	–
MW 53	7·5	5·8	–	77·4	–	6·7	119·6
SO 378*	5·7	5·7	5·6	100·0	98·3	5·7	107·4
405*	7·2	6·3	6·5	87·5	103·2	6·8	–
530*	6·9	5·7	5·6	83·7	98·5	6·3	114·5
Mean	7·5	6·3	6·3	83	100	6·9	115
Number	16	16	12	16	12	16	5
S.D.	0·37	0·32	0·35	4·03	3·05	0·30	–
Coef. var.	4·9	5·1	5·6	4·9	3·1	4·4	–
S.E.	0·09	0·08	0·10	1·00	0·88	0·07	–
95% conf.	6·7	5·6	5·5	74	94	6·3	–
limits	8·3	7·0	7·1	92	107	7·4	–
P. (R.) gordoni							
SO 374	9·2	7·4	7·1	80·4	95·9	8·3	117·0
420	9·7	7·8	7·7	80·4	98·7	8·8	–
463	10·0	7·6	7·3	76·0	96·1	8·8	122·0
486	9·2	7·6	7·4	82·6	97·3	8·4	–
523	9·2	7·5	7·2	81·6	96·0	8·4	–
906	9·5	6·8	7·1	71·6	104·3	8·2	–
907	9·2	7·8	–	84·8	–	8·5	–
908	9·6	7·6	7·8	79·2	102·7	8·6	–
909	10·2	7·8	8·1	76·5	103·8	9·0	–
1112	9·6	8·3	8·5	86·5	102·2	9·0	–
Mean	9·5	7·6	7·6	80	100	8·6	120
Number	10	10	9	10	9	10	2
S.D.	0·36	0·38	0·49	4·4	3·55	0·29	–
Coef. var.	3·8	5·0	6·5	5·5	3·6	3·4	–
S.E.	0·11	0·12	0·16	1·40	1·18	0·09	–
95% conf.	8·7	6·7	6·7	70	92	7·9	–
limits	10·3	8·5	8·5	90	108	9·3	–

* Not included in calculation of sample parameters.

Table 17 (*cont.*)

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md}+\text{bl mes}}{2}$	$\frac{M_2}{M_1}$
		mes	dist				
L. legetet							
M 14079	6·3	5·8	6·0	92·1	103·4	6·1	122·0
RU 1708	6·2	5·3	5·4	85·5	101·9	5·8	–
1739	6·0	5·2	5·3	86·7	101·9	5·6	–
SO 385	6·2	5·2	5·0	83·9	96·2	5·7	111·8
386	6·0	5·2	5·1	86·7	98·0	5·6	114·3
387	6·7	5·9	5·8	88·1	98·4	6·8	126·0
388	6·7	6·1	5·8	91·1	95·1	6·4	–
411	7·2	6·1	6·1	84·8	100·0	6·7	–
424	6·3	5·2	5·2	82·5	100·0	5·8	–
444	6·5	5·6	5·7	86·2	103·6	6·1	–
458	6·7	5·5	5·4	82·2	98·3	6·1	–
482	6·2	5·2	5·2	83·9	100·0	5·7	–
532	6·8	6·1	6·0	89·7	98·4	6·5	–
534	5·9	5·0	4·8	84·8	96·0	5·5	–
910	6·0	4·9	4·7	81·7	95·9	5·5	–
911	5·9	5·0	5·0	84·8	100·0	5·5	–
912	7·0	6·0	5·9	85·8	98·5	6·5	–
913	6·1	5·3	5·2	86·9	98·1	5·7	–
1098	6·2	5·4	5·4	87·0	100·0	5·8	–
KO 7	6·9	5·5	5·7	79·7	103·6	6·2	–
8	6·3	5·4	5·4	85·7	100·0	5·9	111·4
Mean	6·4	5·5	5·4	85	99	6·0	117
Number	21	21	21	21	21	21	5
S.D.	0·38	0·39	0·41	2·88	2·50	0·41	–
Coef. var.	5·9	7·1	7·6	3·4	2·5	6·9	–
S.E.	0·08	0·08	0·09	0·64	0·55	0·09	–
95% conf.	5·7	4·7	4·5	79	94	5·2	–
limits	7·1	6·3	6·3	91	104	6·8	–
P. africanus							
M 32363	10·0	8·8	8·5	88·0	96·6	9·4	119·0
RU 1680	9·5	8·0	–	84·2	–	8·8	120·0
1683	10·5	8·5	8·3	81·0	97·6	9·5	–
1706	9·8	8·3	8·2	84·7	98·8	9·1	120·0
1728	9·0	7·5	7·5	83·4	100·0	8·3	117·0
1823	9·8	8·5	8·6	86·8	101·2	9·2	–
1824	10·1	8·6	8·5	85·1	98·9	9·4	129·0
1945	9·9	7·9	7·9	79·8	100·0	8·9	–
1955	9·4	7·6	–	80·9	–	8·5	109·0
1959	9·5	8·0	7·9	84·2	98·8	8·8	–
2036	9·6	8·0	8·2	83·4	102·5	8·8	113·0
2045	9·0	7·8	7·4	86·6	94·9	8·4	–
Mean	9·7	8·1	8·1	84	99	8·8	116
Number	12	12	10	12	10	12	7
S.D.	0·43	0·41	0·42	2·49	2·18	0·38	–
Coef. var.	4·4	5·1	5·2	3·0	2·2	4·3	–
S.E.	0·13	0·12	0·13	0·72	0·67	0·11	–
95% conf.	8·7	7·2	7·1	78	94	8·0	–
limits	10·7	9·0	9·1	89	104	9·6	–

Table 17 (*cont.*)

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md} + \text{bl mes}}{2}$	$\frac{M_2}{M_1}$
		mes	dist				
P. nyanzae							
RU 1674	10·5	8·4	9·0	80·0	107·2	9·5	115·0
1676	12·7	10·9	11·2	85·8	102·8	11·8	130·0
1678	11·4	9·3	9·5	81·5	102·1	10·4	125·0
1694	10·7	10·1	10·1	94·4	100·0	10·4	–
1695	12·7	10·7	10·4	84·3	97·2	11·7	–
1710	11·2	9·7	9·7	86·6	100·0	10·5	125·0
1734	13·0	11·1	11·3	85·4	98·3	12·1	–
1736	11·4	9·9	9·6	86·8	97·0	10·7	–
1839	12·0	10·8	–	90·0	–	11·4	–
1947	11·6	10·4	10·4	89·7	100·0	10·9	130·0
1982	13·0	11·7	11·1	90·0	94·9	12·4	128·0
2087	10·0	8·5	8·4	85·0	98·9	9·3	118·0
MB 108	11·7	11·1	–	94·9	–	11·4	–
Mean	11·7	10·2	10·1	87	100	11·0	124
Number	13	13	11	13	11	13	7
S.D.	0·97	1·01	0·93	4·44	3·33	0·93	–
Coef. var.	8·3	9·9	9·2	5·1	3·3	8·5	–
S.E.	0·27	0·28	0·28	0·23	1·00	0·26	–
95% conf.	9·6	8·0	8·0	77	93	9·0	–
limits	13·8	12·4	12·2	97	107	11·0	–
P. major							
M 14086	11·9	10·5	10·0	88·2	99·0	11·2	106·0
16648	14·8	12·7	12·8	85·8	100·9	13·8	124·0
SO 396	13·4	13·0	12·2	97·0	93·9	13·2	118·0
415	15·2	14·3	13·7	94·1	94·0	14·8	–
914	13·4	11·1	10·9	82·8	98·2	12·3	–
Mean	13·7	12·3	11·9	90	98	13·5	116
Number	5	5	5	5	5	5	3

Table 18 Measurements of lower M3.

	md	bl		bl mes	bl dist	md + bl mes	M_3
		mes	dist	md	bl mes	2	M_1
D. macinnesi							
M 16650	8·0	6·7	6·5	83·7	97·0	7·2	–
RU 1724	8·2	6·4	6·1	78·0	95·4	7·3	–
1726	8·4	6·5	6·0	77·4	92·3	7·5	–
1737	7·9	6·4	5·9	81·0	92·2	7·2	–
1738	6·8	5·0	4·5	73·5	90·0	5·9	–
1849	8·2	6·2	5·9	75·6	95·2	7·2	–
1850	7·3	–	–	–	–	–	–
1857	8·1	6·9	–	85·2	–	7·5	123·0
1901	8·2	6·7	6·1	81·7	91·0	7·5	119·0
1970	7·4	5·6	4·9	75·7	87·5	6·5	–
2015	8·7	7·2	6·7	82·7	93·1	8·0	129·0
2025	6·6	5·5	5·2	83·4	94·6	6·1	–
2079	9·1	7·0	6·6	76·9	94·3	8·1	–
MW 49	8·3	6·6	6·0	79·6	90·0	7·5	–
SO 378*	6·5	5·3	4·9	81·5	92·5	5·9	111·3
Mean	7·9	6·4	5·9	80	92	7·2	124
Number	14	13	12	13	12	13	3
S.D.	0·70	0·64	0·68	3·67	2·44	0·66	–
Coef. var.	8·8	10·0	11·5	4·6	2·7	9·3	–
S.E.	0·19	0·18	0·20	1·02	0·74	0·18	–
95% conf.	6·4	5·0	4·4	72	87	5·8	–
limits	9·4	7·8	7·4	88	97	8·6	–
P. (R.) gordoni							
SO 450	9·5	7·0	6·7	73·6	95·7	8·8	–
463	11·9	8·3	7·8	69·8	94·0	10·1	140·2
464	10·3	6·9	6·7	67·1	97·2	10·1	–
921	11·7	8·7	8·0	74·4	91·9	10·2	–
1112	11·1	8·3	–	74·7	–	9·7	–
Mean	10·9	7·8	7·3	72	94	9·8	140
Number	5	5	4	5	4	5	1
L. legetet							
RU 1708	6·3	5·0	4·8	79·4	96·0	5·7	–
SO 387	6·5	5·1	4·5	78·4	88·2	5·8	118·4
388	7·4	6·2	–	83·7	–	6·8	–
444	7·3	5·5	5·3	75·3	96·4	6·4	–
481	6·5	5·2	4·4	80·0	84·6	5·9	–
532	6·8	6·0	5·6	88·2	93·4	6·4	–
918	6·8	5·9	5·5	86·7	93·2	6·4	–
919	7·7	5·9	5·6	76·6	95·0	6·8	–
KO 6	6·6	5·6	5·2	84·9	93·9	6·1	–
Mean	6·9	5·6	5·1	82	92	6·3	118
Number	9	9	8	9	8	9	1
S.D.	0·48	0·43	0·48	4·57	3·93	0·41	–
Coef. var.	6·9	7·7	9·4	5·6	4·3	6·5	–
S.E.	0·16	0·14	0·17	1·52	1·39	0·14	–
95% conf.	5·8	4·6	4·0	72	83	5·4	–
limits	8·0	6·6	6·2	92	101	7·2	–

Table 18 (*cont.*)

	md	bl		$\frac{\text{bl mes}}{\text{md}}$	$\frac{\text{bl dist}}{\text{bl mes}}$	$\frac{\text{md}+\text{bl mes}}{2}$	$\frac{M_3}{M_1}$
		mes	dist				
P. africanus							
M 14087	12·0	9·5	8·8	79·2	92·6	10·8	–
32363	11·3	9·0	7·9	79·7	97·8	10·2	129·0
RU 1706	11·5	8·3	7·9	72·2	87·8	9·9	130·0
1728	10·2	8·4	8·1	82·4	96·4	9·3	131·0
1820	10·9	8·7	8·3	79·8	95·4	9·8	–
1855	10·0	8·1	7·8	81·0	95·8	9·0	–
1927	10·3	9·0	8·6	87·5	95·6	9·7	–
1931	11·5	8·8	8·3	76·6	94·4	10·2	–
Mean	11·0	8·7	8·2	80	94	9·8	130
Number	8	8	8	8	8	8	3
S.D.	0·73	0·45	0·36	5·34	3·09	0·66	–
Coef. var.	6·6	5·2	4·4	6·8	3·3	6·7	–
S.E.	0·26	0·16	0·13	1·89	1·09	0·23	–
95% conf.	9·3	7·6	7·3	66	87	8·2	–
limits	12·7	9·8	9·1	92	101	11·4	–
P. nyanzae							
RU 1674	12·0	9·2	9·2	76·7	100·0	10·6	127·8
1676	14·1	12·1	11·5	85·8	95·0	13·1	144·0
1678	13·5	10·2	9·3	75·6	91·2	11·1	133·9
1735	13·7	12·1	11·3	88·4	93·4	12·9	–
1764	14·8	11·6	10·4	78·4	89·7	13·2	–
1923	14·3	10·9	10·2	76·3	93·6	12·6	–
1947	14·0	11·3	10·7	80·7	94·8	12·7	149·5
1982	15·3	12·7	11·5	83·0	90·6	13·0	134·1
2087	11·3	9·4	8·4	83·2	89·4	10·4	131·8
Mean	13·6	11·1	10·3	81	93	12·2	137
Number	9	9	9	9	9	9	6
S.D.	1·28	1·23	1·11	4·52	3·35	1·14	–
Coef. var.	9·4	11·1	10·8	5·58	3·6	9·3	–
S.E.	0·43	0·41	0·37	1·51	1·12	0·38	–
95% conf.	10·6	8·3	7·7	70	85	9·6	–
limits	16·6	13·9	12·9	92	101	14·8	–
P. major							
M 16648	18·1	13·2	11·3	72·9	85·6	15·7	141·5
32237*	16·5	13·5	12·2	81·8	90·4	15·0	–
SO 396	17·3	14·2	12·1	82·1	85·3	15·8	141·0
920	16·8	13·1	12·2	77·9	93·2	15·0	–
Mean	17·4	13·5	11·9	78	88	15·5	141
Number	3	3	3	3	3	3	2

* Not included in calculation of sample parameters.

Table 19 Measurements of upper and lower dp3–dp4.

		md	bl	bl dist	$\frac{\text{bl}}{\text{md}}$	buc ht	$\frac{\text{bl dist}}{\text{bl mes}}$
Upper dp3–dp4							
D. macinnesi							
RU 1790	dp^4	4·9	5·8	–	118·2	–	–
2057	dp^4	4·6	5·8	–	125·9	–	–
P. (R.) gordoni							
SO 89	dp^3	4·6	6·2	–	134·8	4·8	–
945	dp^4	6·3	7·8	–	124·0	–	–
P. (R.) vancouveringi							
RU 1778	dp^4	6·3	5·4	–	85·7	–	–
L. legetet							
SO 536	dp^3	3·3	4·3	–	130·2	–	–
	dp^4	4·2	5·3	–	126·2	–	–
1095	dp^4	4·5	5·0	–	111·1	–	–
P. africanus							
M 32238	dp^4	6·5	7·5	–	115·2	–	–
RU 1919	dp^3	3·9	5·4	–	138·4	–	–
	dp^4	5·4	6·0	–	111·1	–	–
P. nyanzae							
RU 1693	dp^4	7·0	8·2	–	117·1	–	–
1803	dp^3	5·8	6·5	–	112·0	–	–
	dp^4	6·8	7·6	–	111·8	–	–
2031	dp^3	6·0	7·4	–	123·2	–	–
	dp^4	7·9	9·2	–	116·0	–	–
P. major							
SO 397	dp^4	8·9	9·9	–	111·2	–	–
542	dp^3	7·0	7·3	–	104·3	–	–
	dp^4	9·1	9·4	–	103·3	–	–
1101	dp^4	9·1	10·3	–	113·3	–	–
Lower dp3–dp4							
D. macinnesi							
M 16381	dp_4	5·9	3·8	4·1	64·4	–	107·9
P. (R.) gordoni							
SO 540	dp_4	8·1	5·2	5·6	64·3	–	107·7
923	dp_4	7·5	5·7	6·1	76·2	–	107·1
924	dp_4	7·4	4·7	4·9	63·5	–	104·2
925	dp_4	7·3	4·5	4·9	61·6	–	109·0
L. legetet							
M 14080	dp_3	4·7	3·1	–	66·0	–	–
	dp_4	5·0	3·9	4·2	78·1	–	107·8
SO 455	dp_4	4·9	3·5	3·7	71·5	–	105·5
1073	dp_3	4·7	3·2	–	68·2	4·5	–
	dp_4	5·4	3·8	4·2	70·4	–	110·6
1096	dp_3	4·2	2·5	–	59·6	–	–
1097	dp_3	4·0	2·6	–	65·0	–	–
KO 11	dp_3	4·8	3·3	–	68·8	4·0	–

Table 19 (*cont.*)

		md	bl	bl dist	bl/md	buc ht	bl dist/bl mes
Lower dp3–dp4 (*cont.*)							
P. africanus							
RU 1865	dp_4	6·9	5·0	5·4	72·5	–	108·0
2093	dp_3	5·9	4·6	–	78·0	–	–
	dp_4	6·5	5·2	–	80·0	–	–
P. major							
SO 451	dp_4	10·6	7·3	7·7	68·9	–	105·2
542	dp_3	8·3	–	–	–	–	–
	dp_4	9·3	6·9	7·5	74·2	–	108·8
589	dp_3	8·5	5·7	–	67·1	7·5	–
922	dp_4	9·4	7·6	7·0	80·9	–	92·0
RU 1767	dp_4	10·5	8·0	8·6	76·2	–	107·3
MO 26	dp_3	8·1	–	–	–	–	–
	dp_4	8·2	6·6	6·8	80·4	–	103·1
UM-P 62-13	dp_3	8·5	–	–	–	–	–
	dp_4	9·8	7·8	–	79·5	–	–

Table 20 Measurements of upper di1–di2.

		md	bl	bl/md	buc ht
D. macinnesi					
RU 1869	di^2	1·9	2·1	110·5	3·5
1903	di^2	1·6	1·8	107·8	3·8
SO 1238	di^2	1·5	2·0	133·3	3·6
P. (R.) gordoni					
SO 575	di^2	2·7	2·8	103·8	4·3
L. legetet					
SO 564	di^1	4·4	2·7	61·4	–
1133	di^1	4·2	2·6	62·0	–

Table 21 Measurements of upper and lower dc.

	max l	perp b	b/l	buc ht
Upper dc				
D. macinnesi				
RU 1888	4·5	3·4	75·6	5·5
P. (R.) gordoni				
SO 577	5·3	4·4	83·0	5·8
578	5·5	4·3	78·2	5·8
L. legetet				
SO 460	4·6	3·8	82·6	4·7
566	4·0	3·3	82·5	3·9
P. nyanzae				
RU 2031	5·8	4·4	75·9	–
P. major				
M 32228	7·1	5·8	81·6	–
SO 371	8·4	6·6	78·6	9·4
542	8·1	5·8	71·6	9·4
Lower dc				
D. macinnesi				
RU 1887	3·8	2·6	68·4	4·8
P. africanus				
RU 1787	5·5	4·4	80·0	7·8
P. nyanzae				
RU 1710	6·0	4·1	68·3	–
P. major				
SO 542	7·5	5·0	66·6	–
MO 26	7·0	4·7	67·2	–
UM-P 62-13	7·5	5·0	66·7	–

Table 22 Measurements of specimens from Fort Ternan.

		md	**bl**	$\frac{\mathbf{bl}}{\mathbf{md}}$
P. africanus				
KNM-FT 16	M^1 or M^2	7·7	9·7	126·0
KNM-FT 29	P^3	5·7	9·2	161·4
P. nyanzae				
KNM-FT 28	C_1	12·5	8·8	70·4
KNM-FT 34	M_3	12·3	10·2	82·9
KNM-FT 35	P_3	13·1	7·4	56·5
KNM-FT 39	C^1	15·5	11·7	75·5
KNM-FT 40	M_3	13·0	10·7	82·3
KNM-FT 49	I^1	9·9	6·8	68·7
L. legetet				
KNM-FT 11	I^1	6·2	4·2	67·7
KNM-FT 14	M_1	6·0	4·1	68·4
KNM-FT 15	C^1	7·5	5·8	77·3
KNM-FT 17	M_1	6·3	5·2	82·5
KNM-FT 18	P_4	4·3	3·8	88·4
KNM-FT 19	M^3	4·8	6·4	133·3
KNM-FT 20–24	C_1	5·6	3·7	66·1
	P_3	5·6	3·8	67·8
	P_4	4·7	4·1	87·2
	M_1	6·2	4·8	77·4
	M_2	7·0	5·3	75·6
	M_3	6·4	4·9	76·5
KNM-FT 25	I_2	3·1	4·3	138·5

Bivariate plots

Figures 7–24, p. 176–191, show the length and breadth dimensions of all the species of East African Miocene apes. In every case the mesiodistal length, or maximum length in the case of the Cs and P_3, is along the horizontal axis, and buccolingual breadth, or perpendicular breadth, is along the vertical axis. The symbols are as follows:

x	*Dendropithecus macinnesi*
⦸	*Proconsul* (*Rangwapithecus*) *gordoni*
⊗	*P.* (*R.*) *vancouveringi*
□	*Limnopithecus legetet*
●	*Proconsul africanus*
○	*P. nyanzae*
■	*P. major*
◎	*P. nyanzae* from Fort Ternan
▣	*L. legetet* from Napak
⧈	*L. legetet* from Fort Ternan

Specimens of uncertain affiliation are denoted by a letter signifying the sites of origin. These are as follows:

L	Losidok
mb	Maboko Island
S	Songhor
FT	Fort Ternan
UM	Uganda

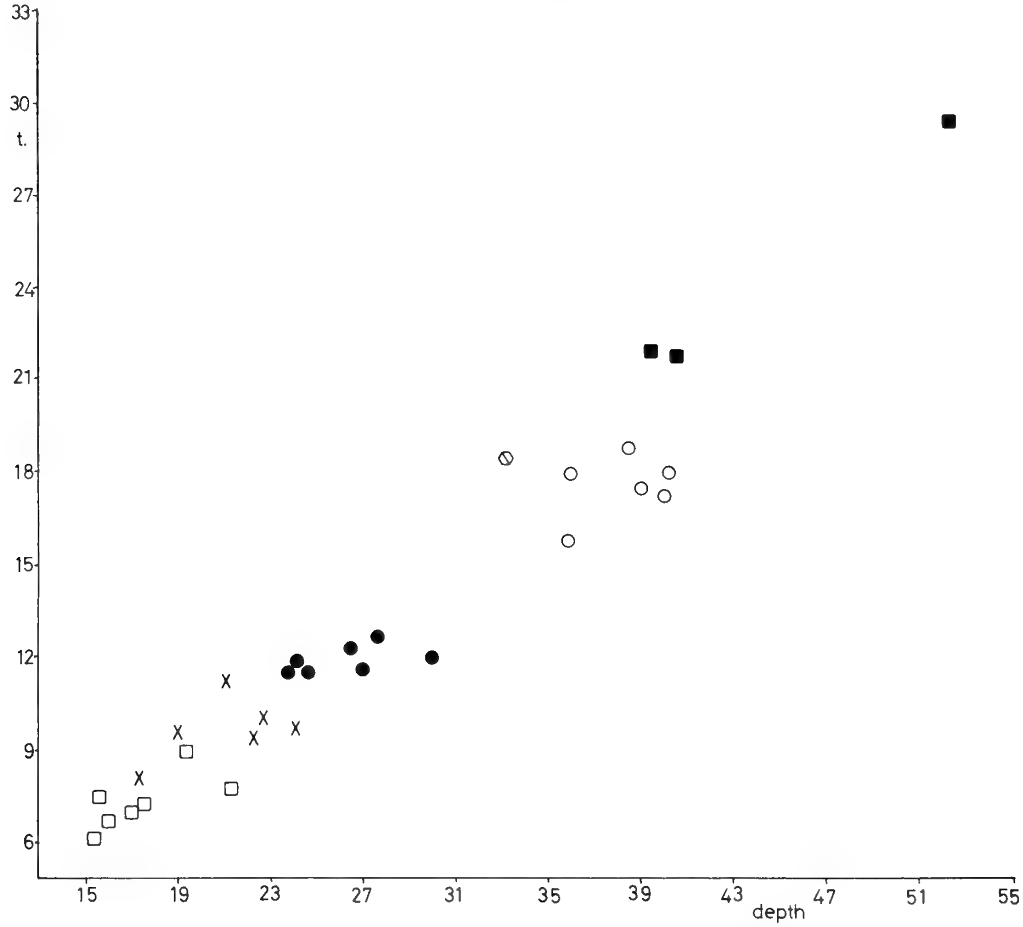

Fig. 7 Bivariate plot of symphysis.

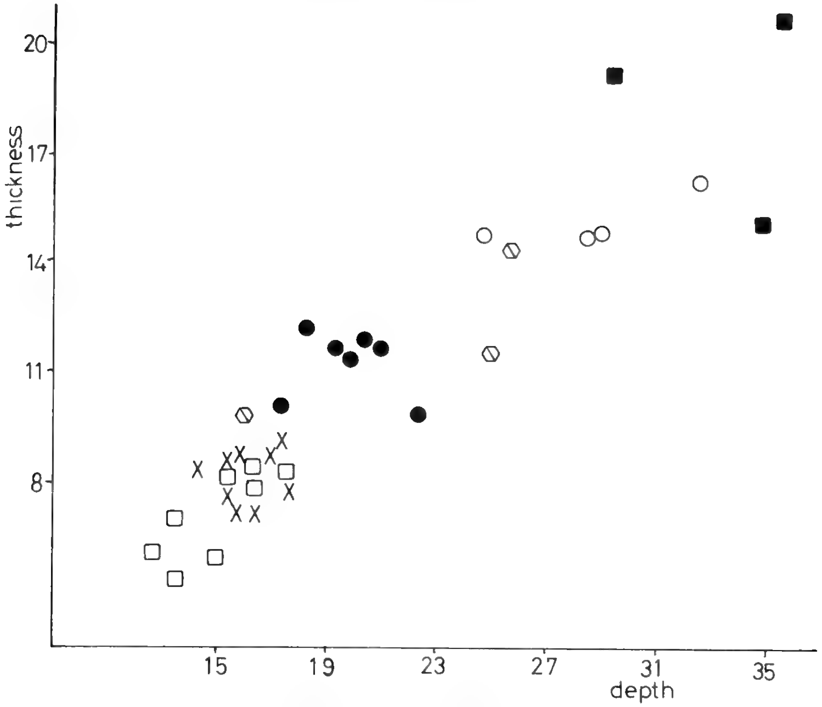

Fig. 8 Bivariate plot of mandible at M_2.

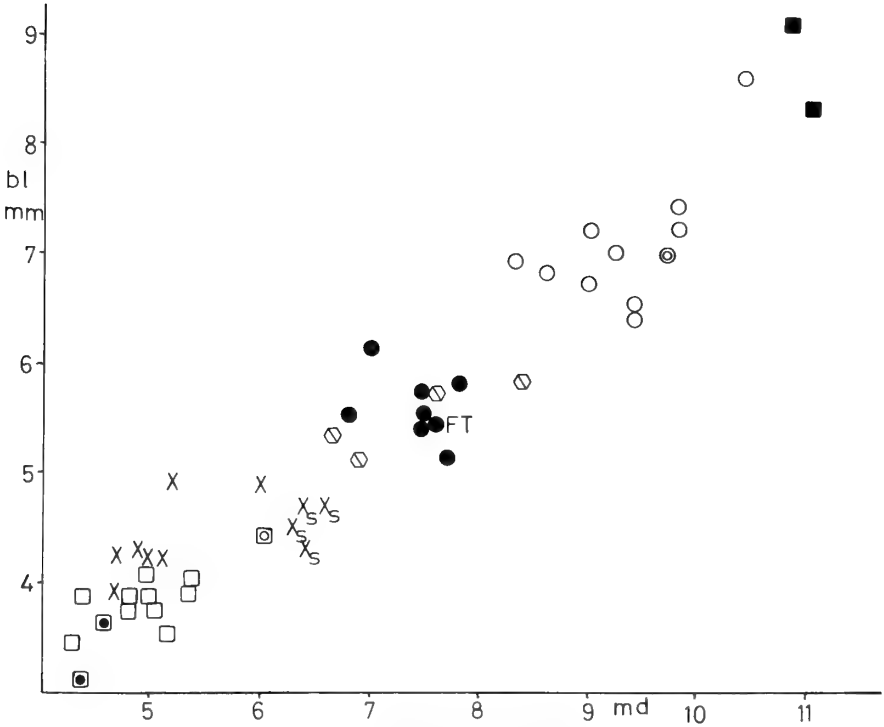

Fig. 9 Bivariate plot of I^1.

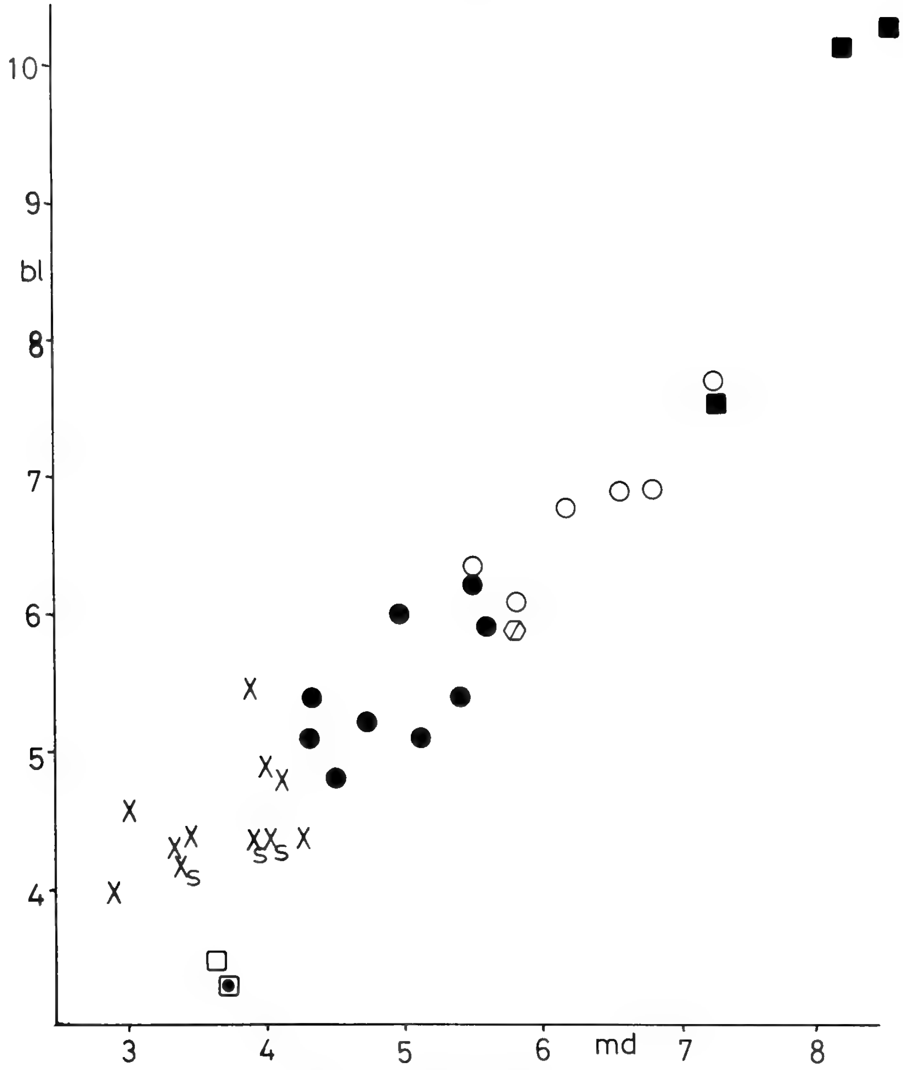

Fig. 10 Bivariate plot of I^2.

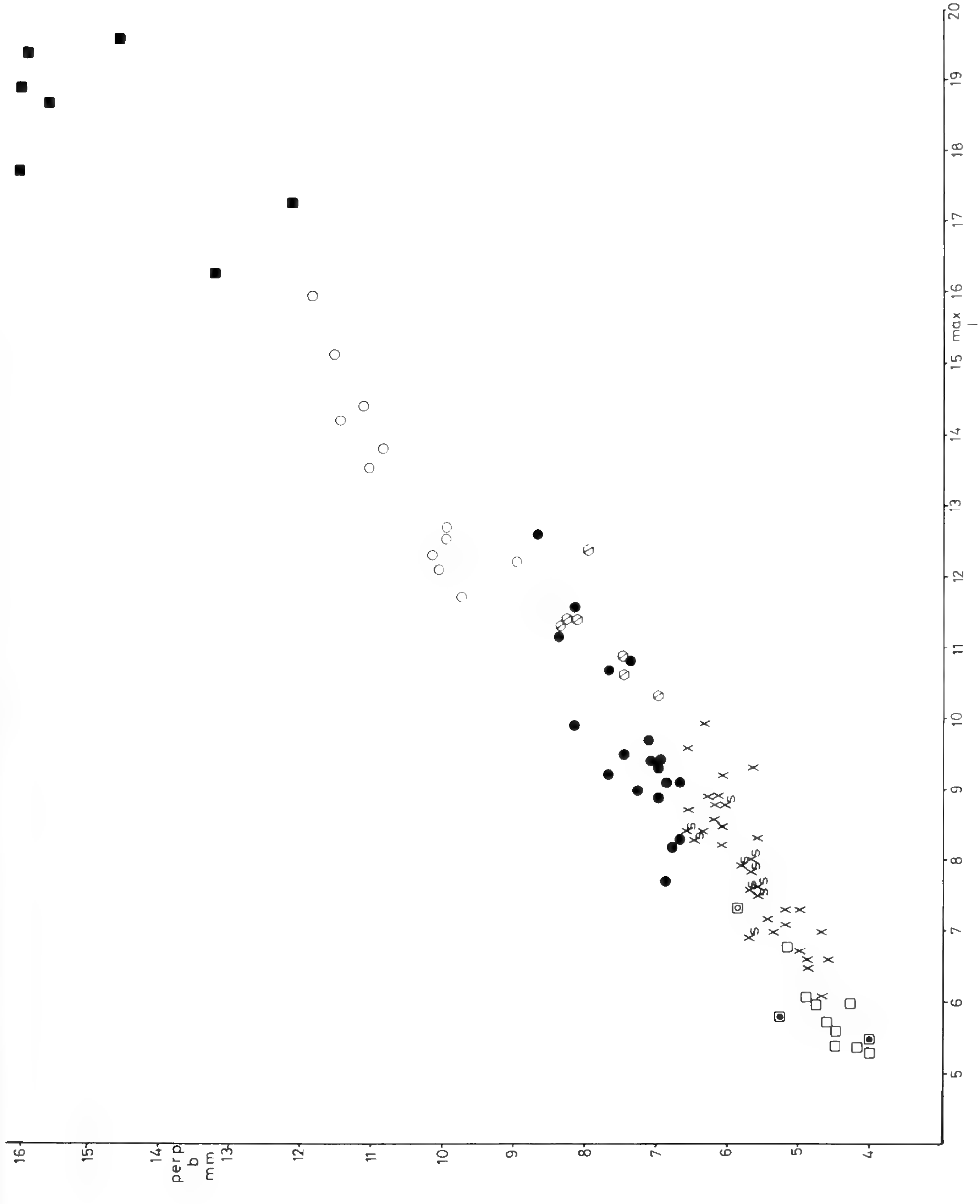

Fig. 11 Bivariate plot of upper C.

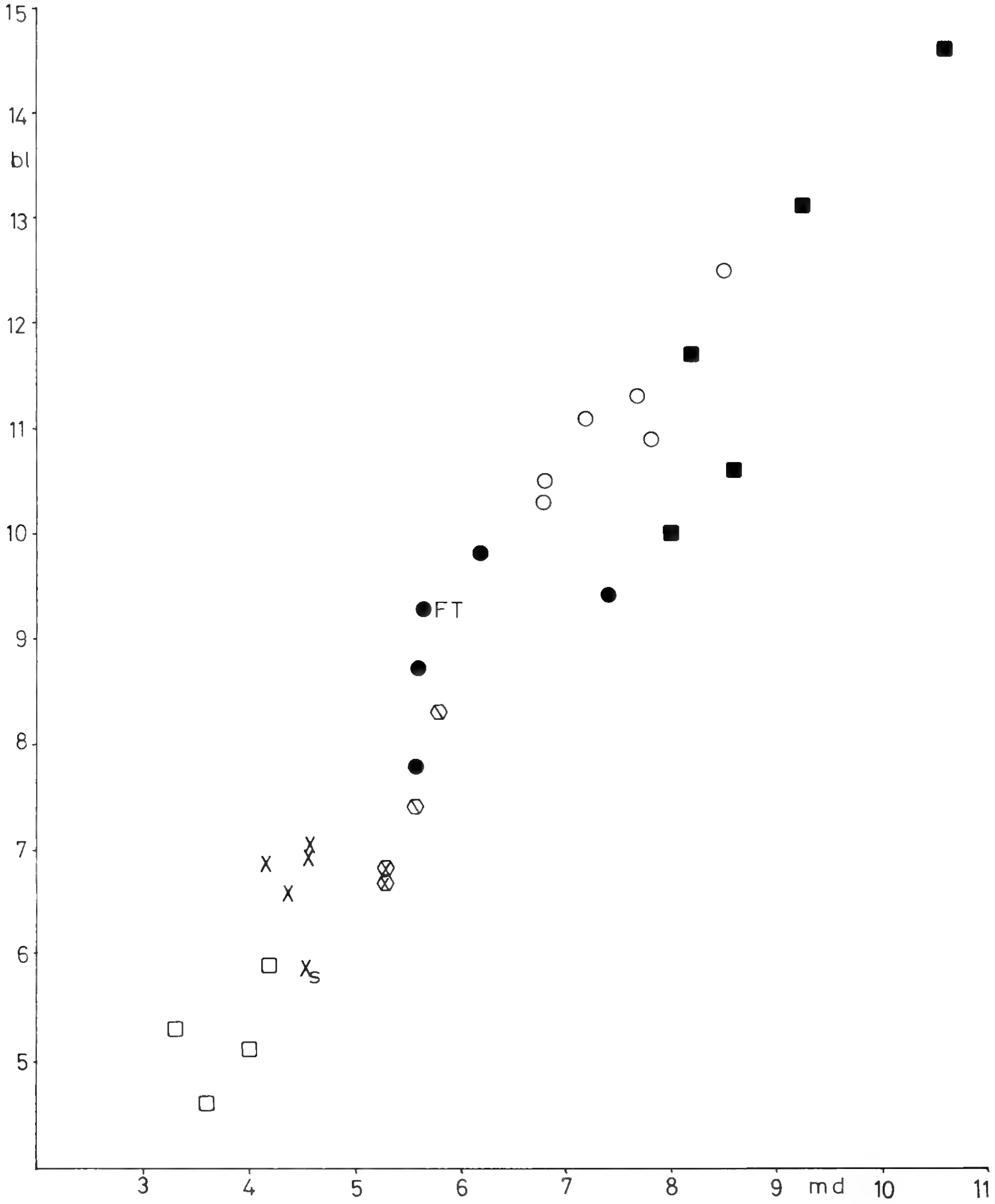

Fig. 12 Bivariate plot of P³.

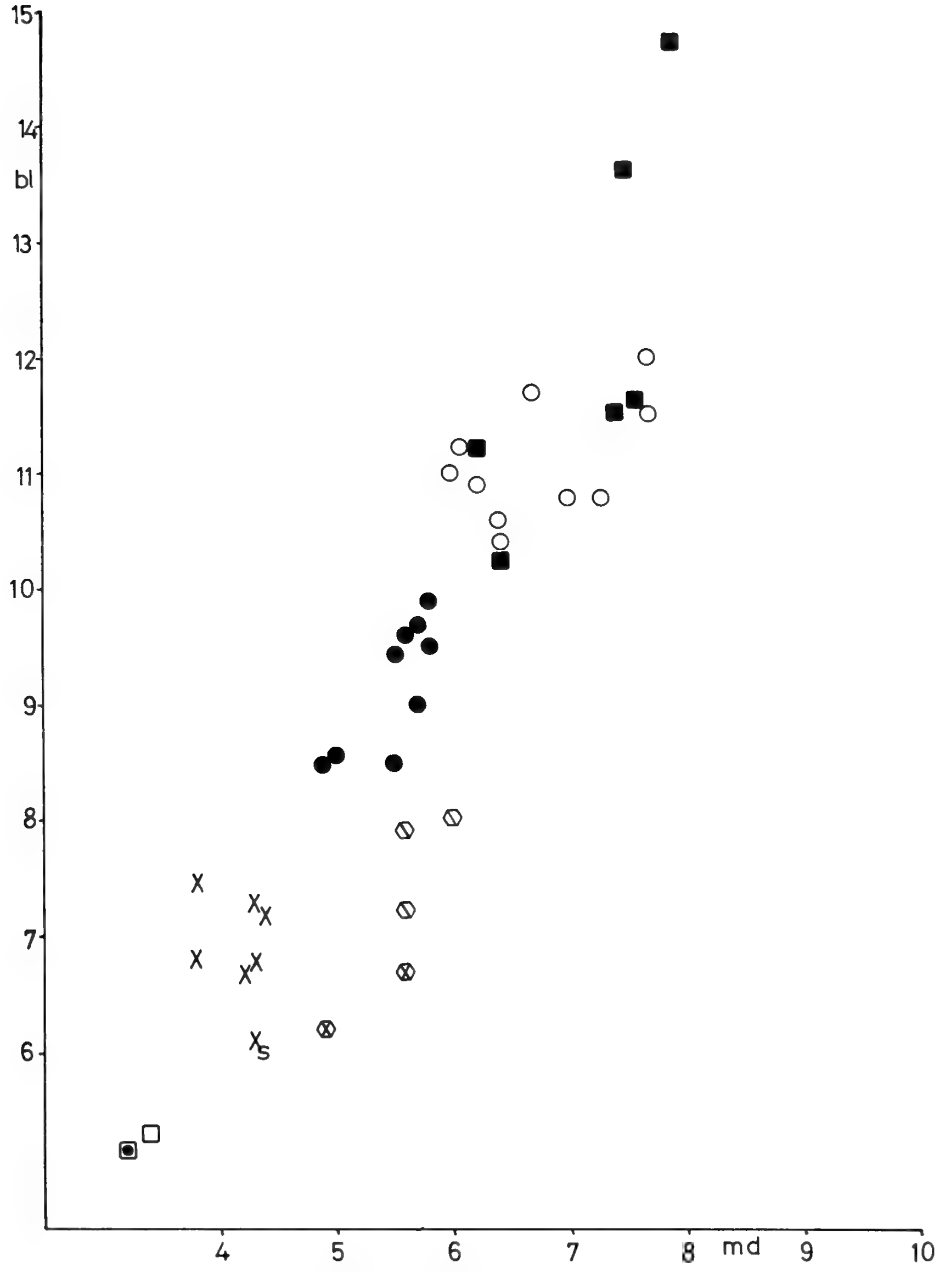

Fig. 13 Bivariate plot of P^4.

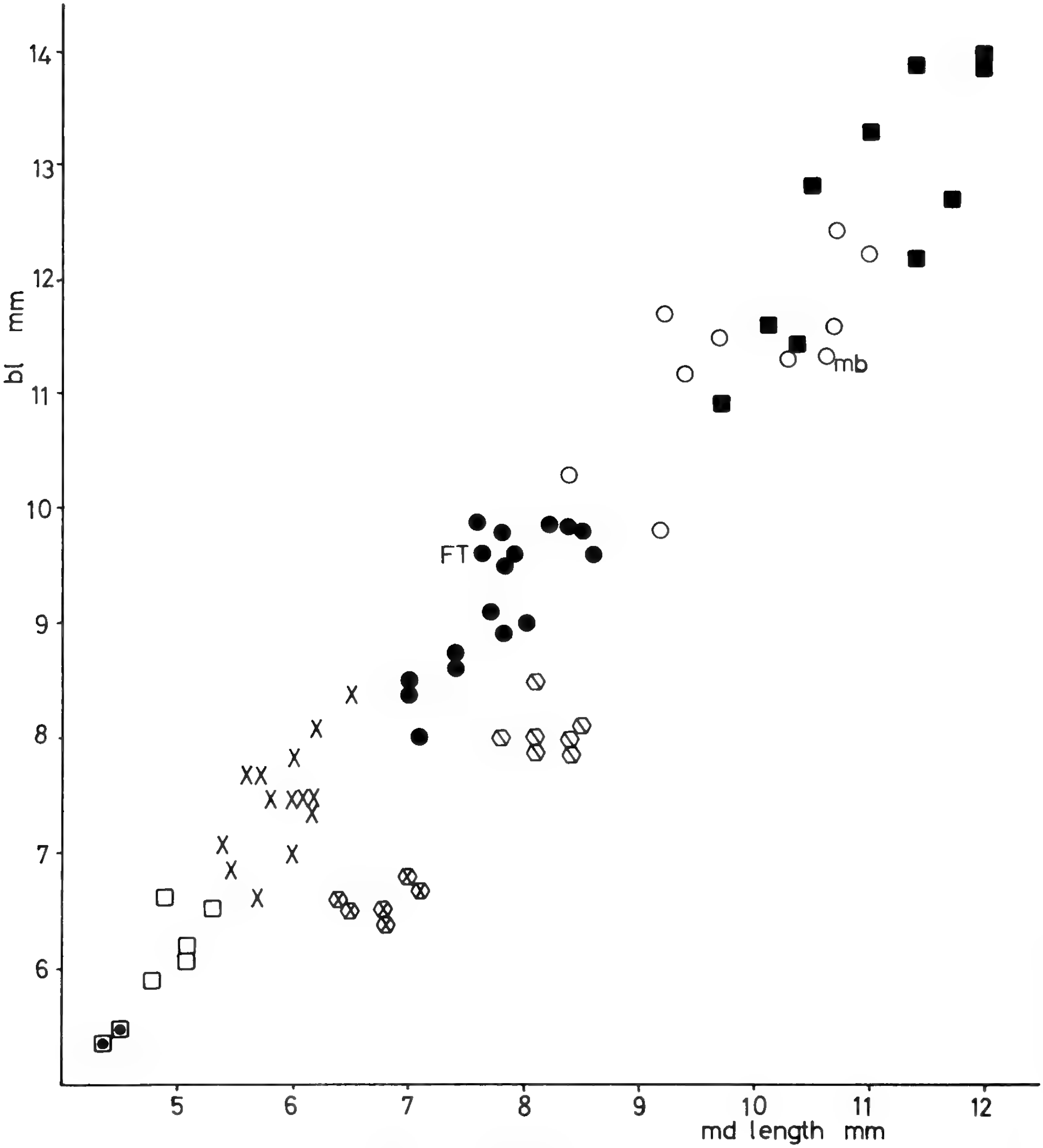

Fig. 14 Bivariate plot of M¹.

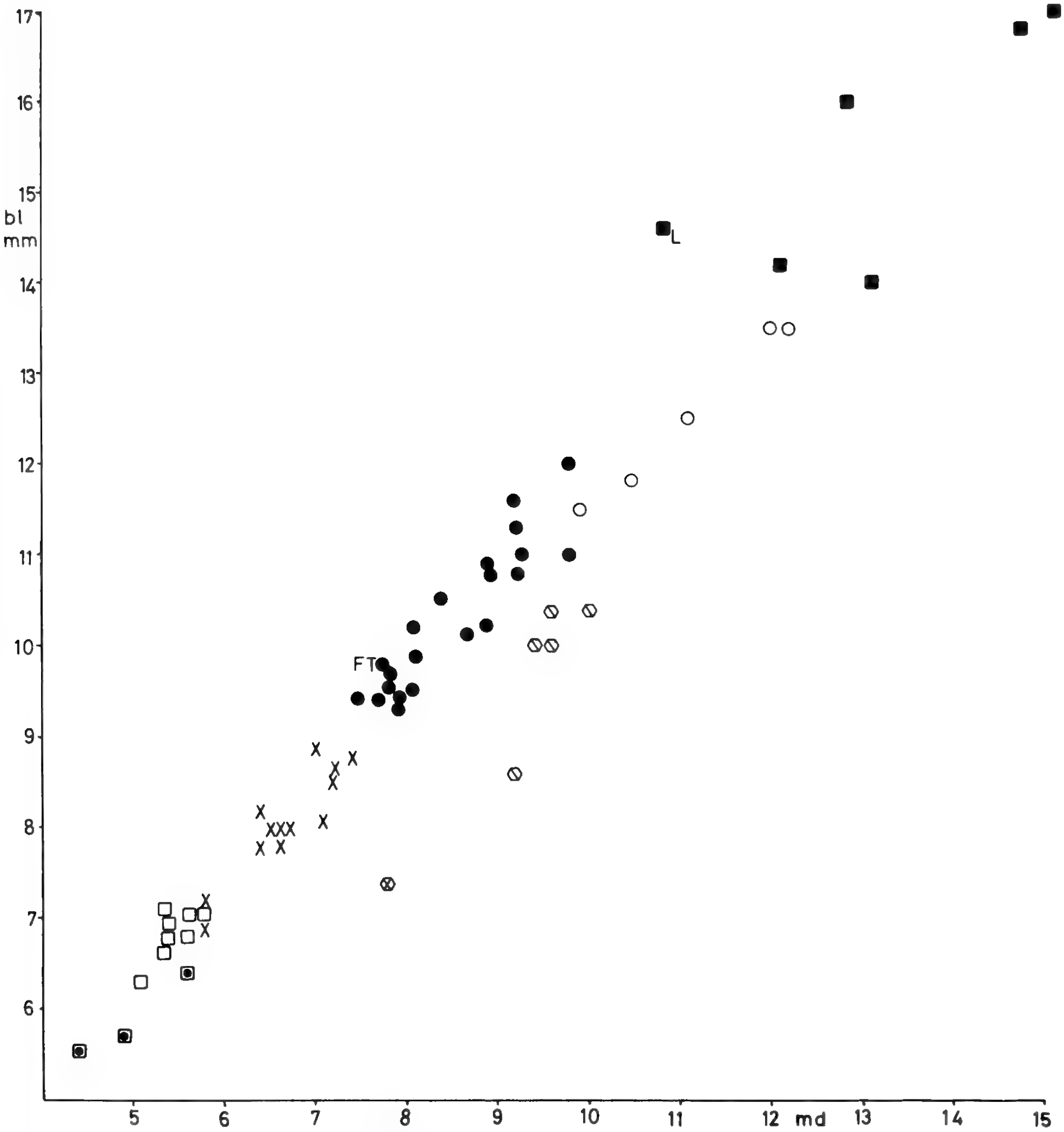

Fig. 15 Bivariate plot of M^2.

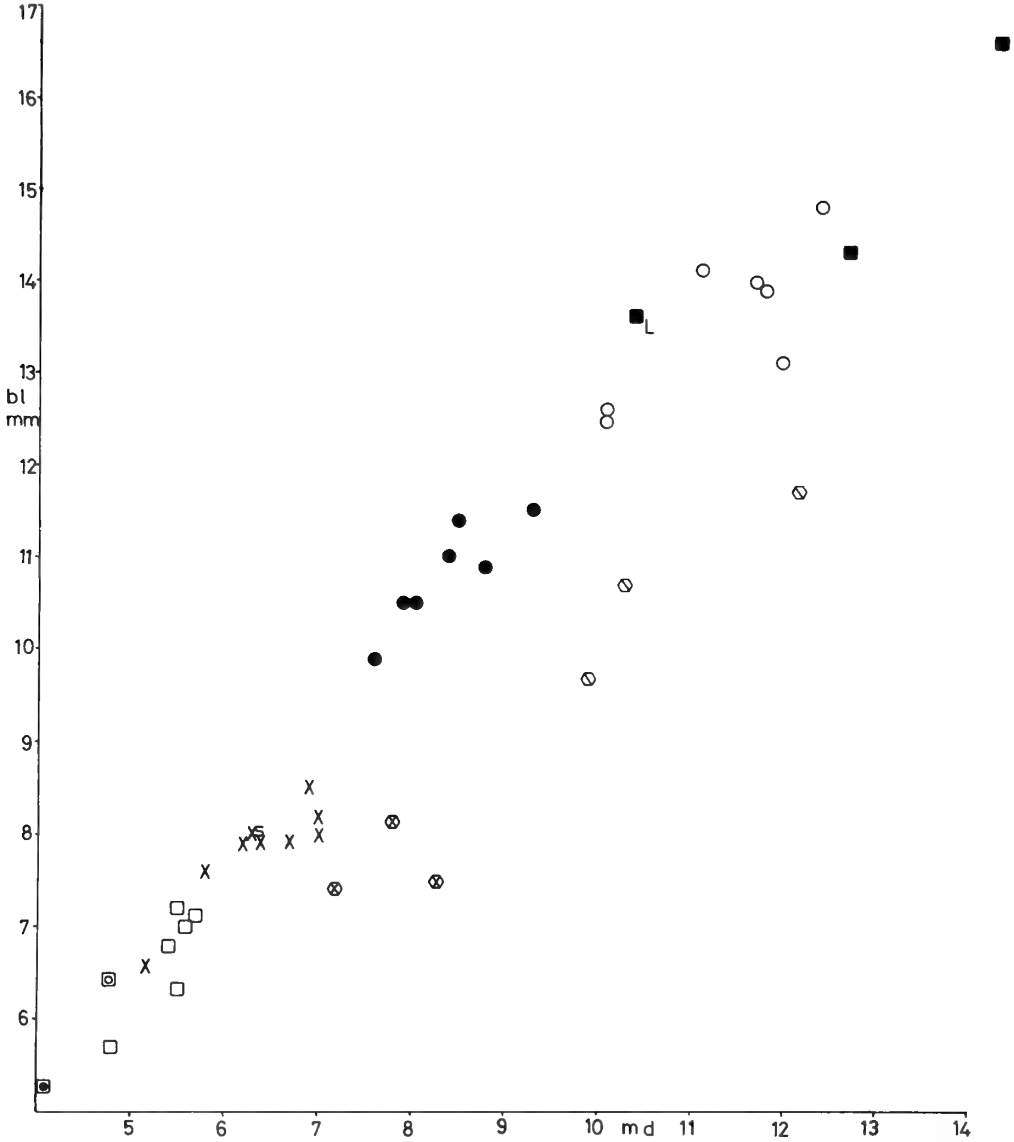

Fig. 16 Bivariate plot of M^3.

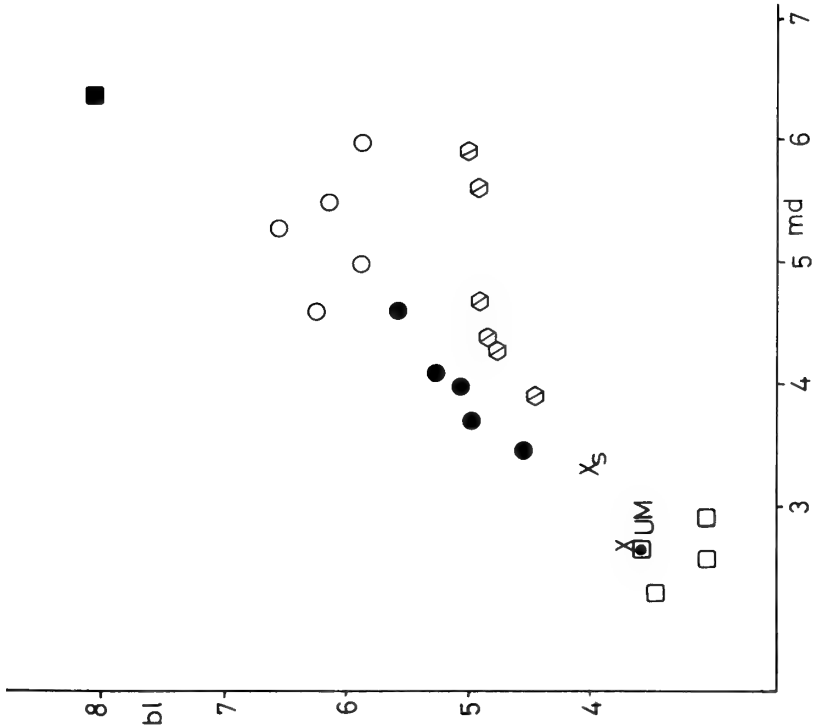

Fig. 17 Bivariate plot of I_1.

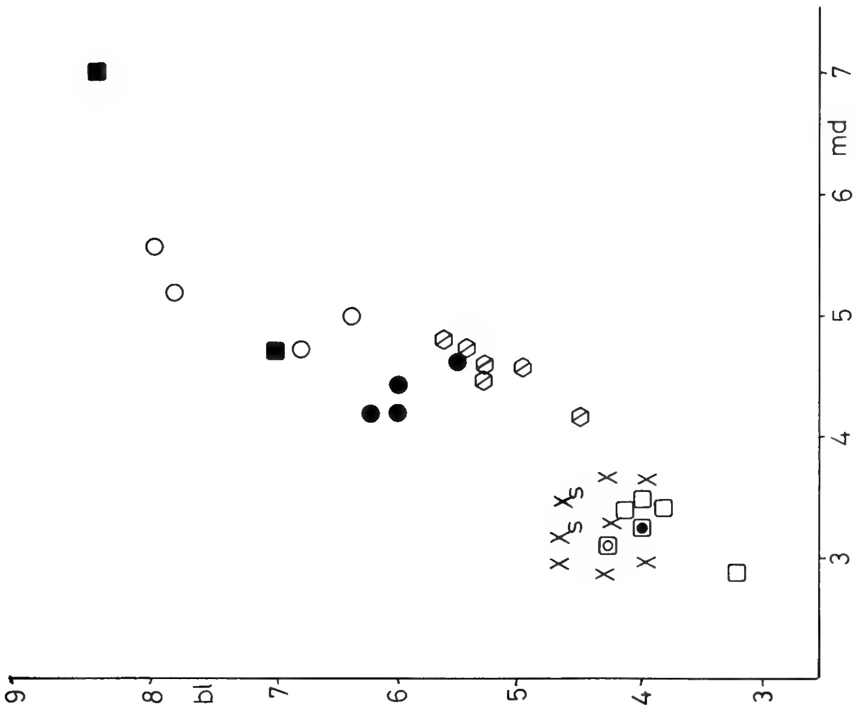

Fig. 18 Bivariate plot of I_2.

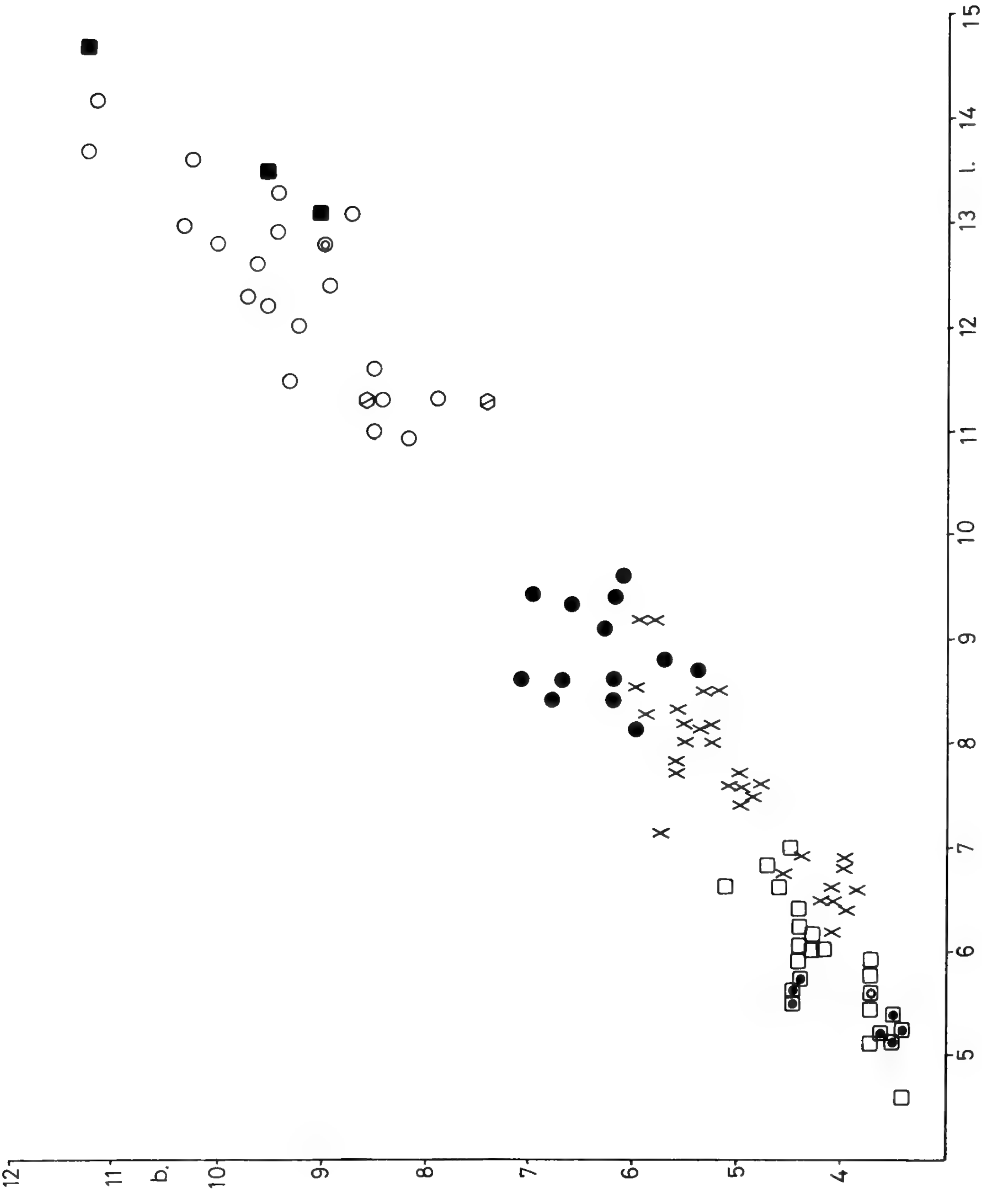

Fig. 19 Bivariate plot of lower C.

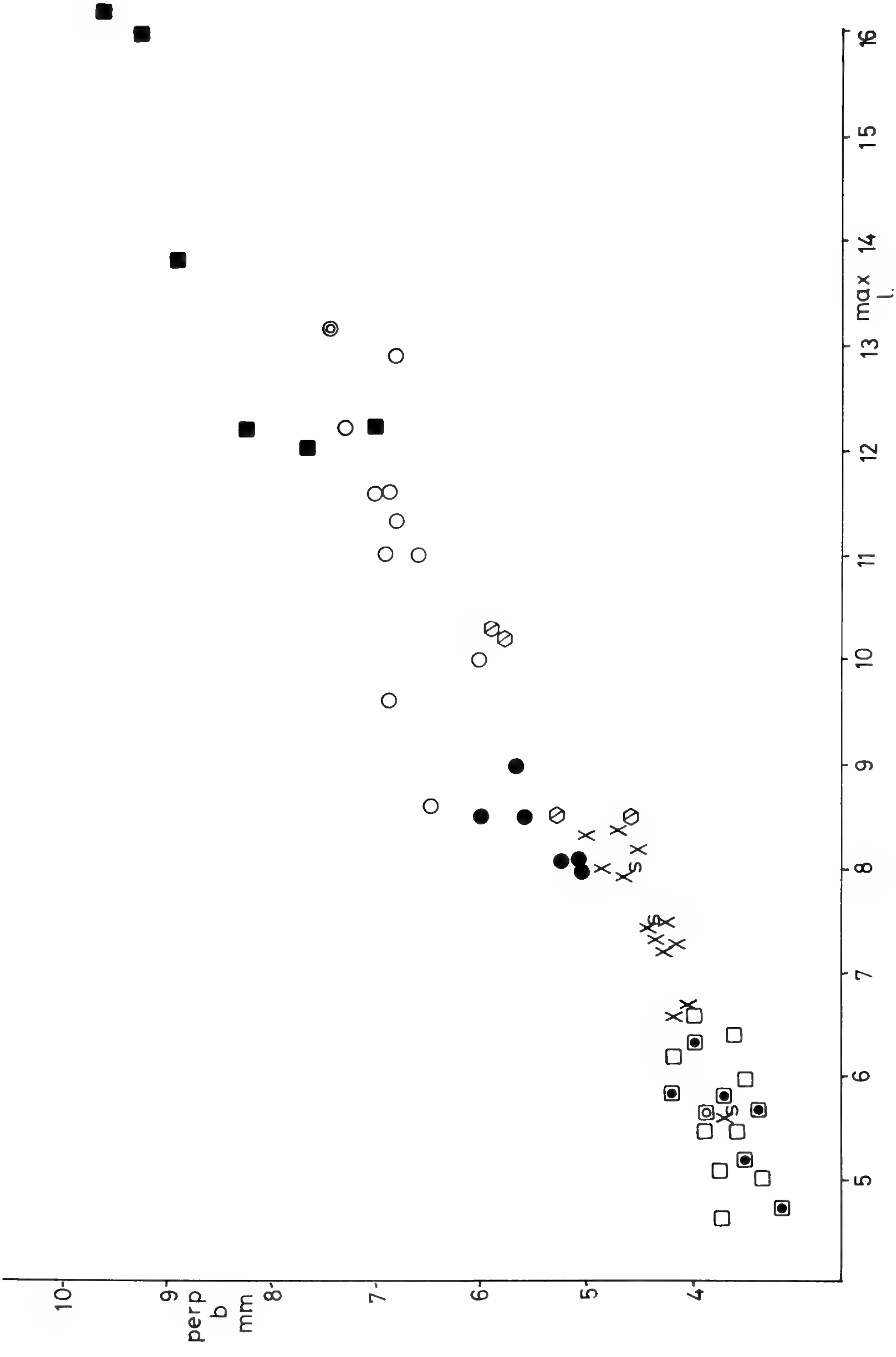

Fig. 20 Bivariate plot of P_3.

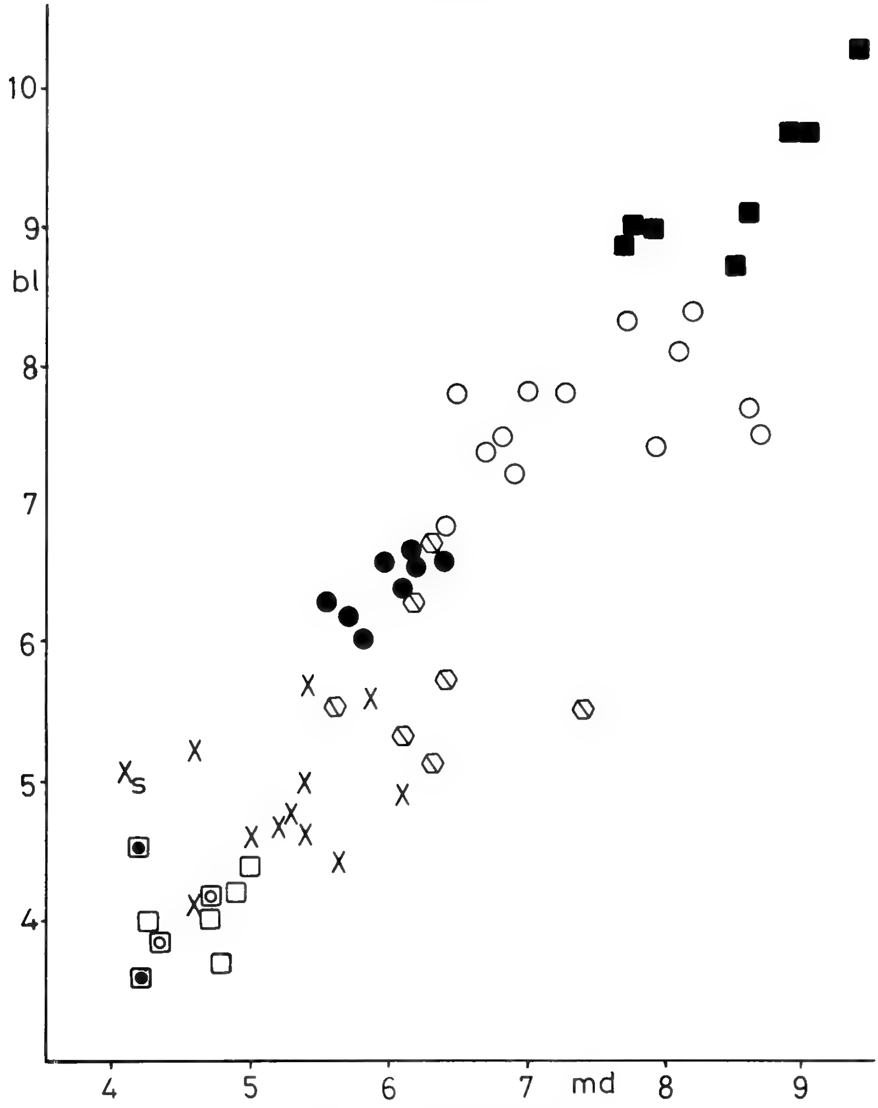

Fig. 21 Bivariate plot of P_4.

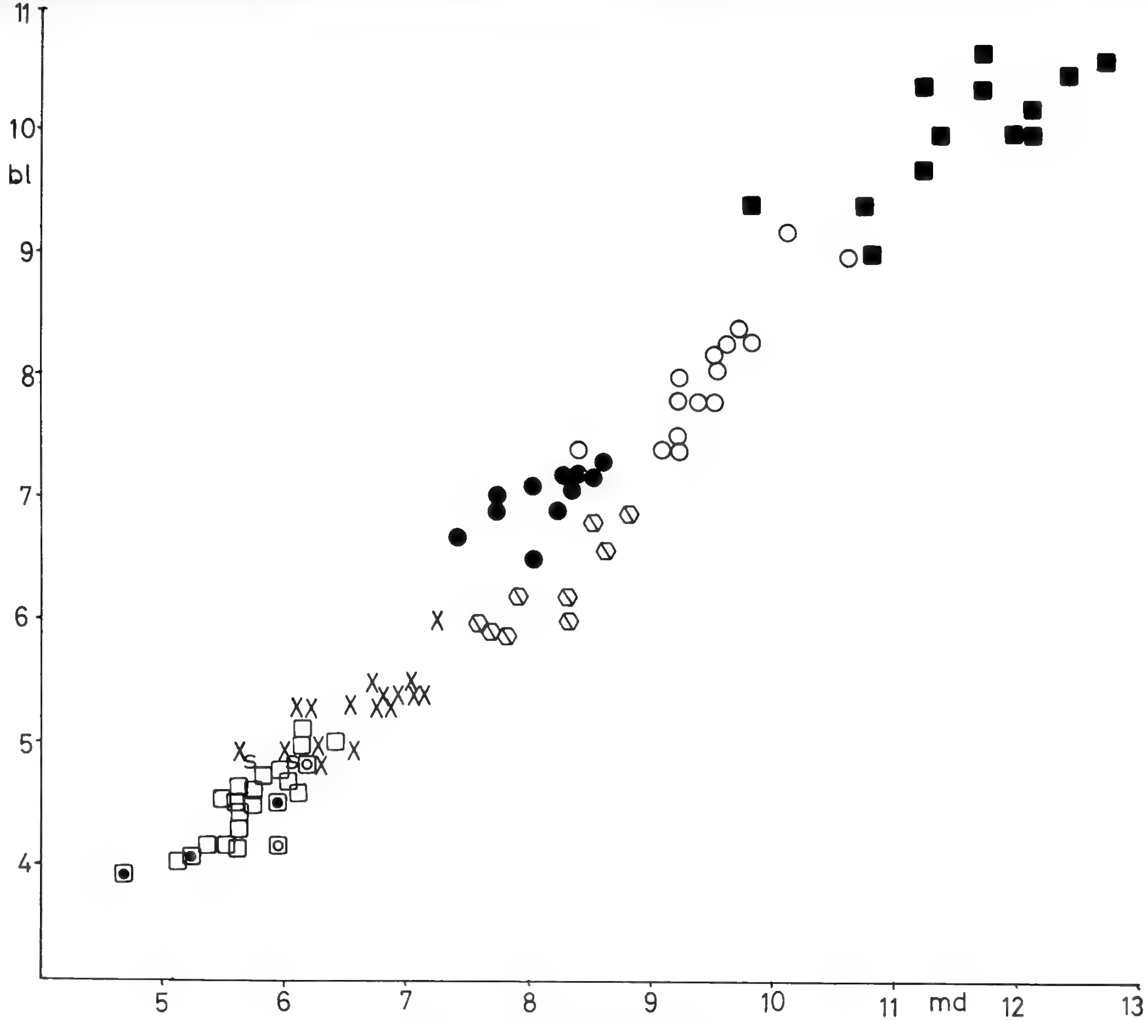

Fig. 22 Bivariate plot of M_1.

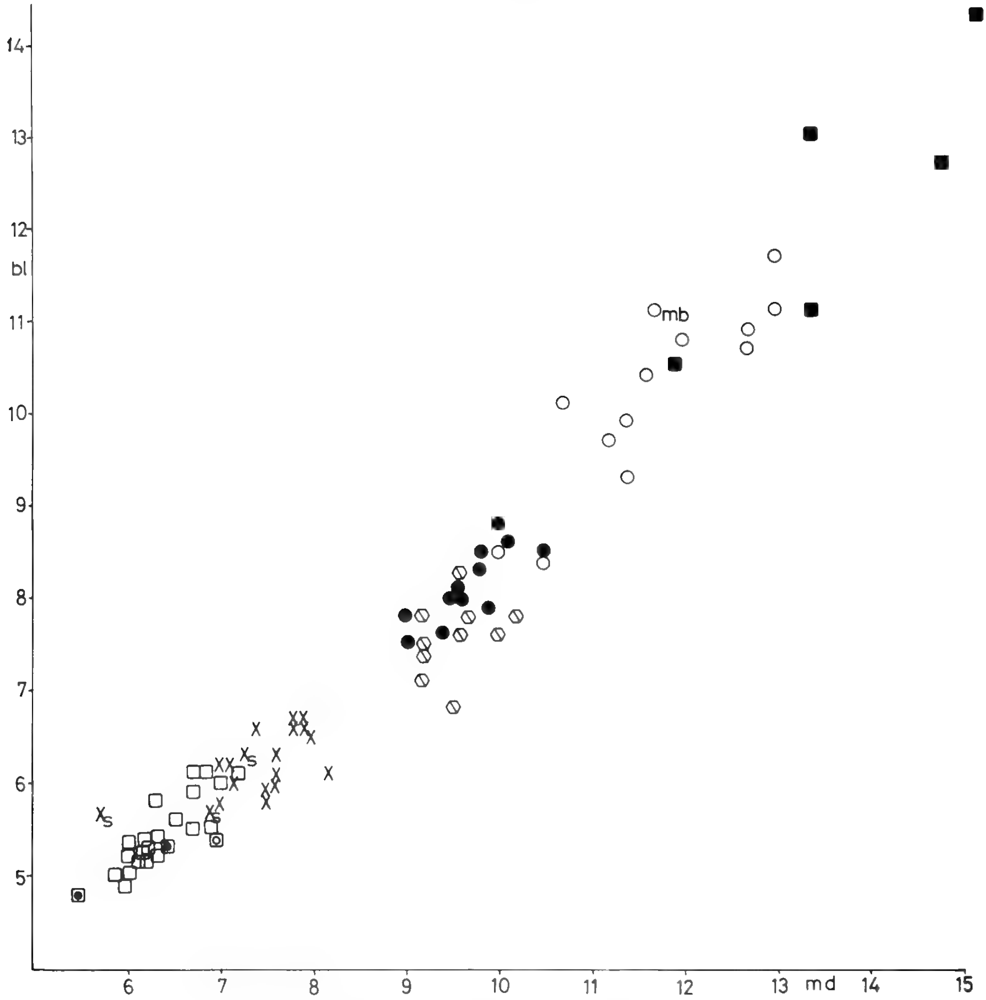

Fig. 23 Bivariate plot of M_2.

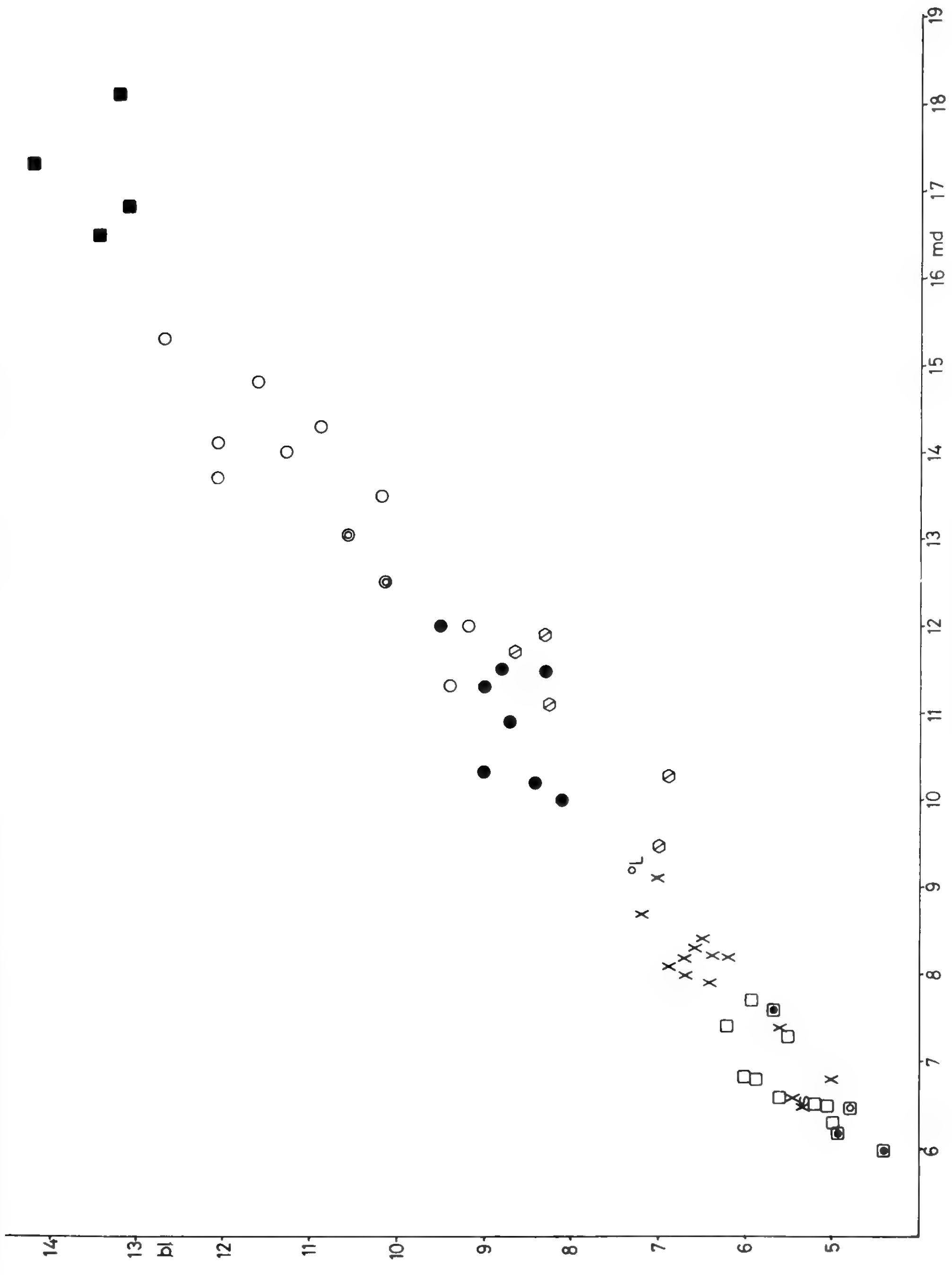

Fig. 24 Bivariate plot of M_3.

Morphological comparison of fossil and modern apes

Seven species of fossil ape are recognized from the Miocene of East Africa (Clark & Leakey 1951; Simons & Pilbeam 1965; Pilbeam 1969; Andrews 1970, 1974; Andrews, Simons & Pilbeam 1977). Six of these are placed here in two genera of the Dryopithecinae (Pongidae), *Proconsul* and *Limnopithecus*. The former is further divided into two subgenera, *P.* (*Proconsul*) and *P.* (*Rangwapithecus*), and five species, while the latter is restricted to one species, *Limnopithecus legetet*. The seventh species was formerly included also in *Limnopithecus*, but it has now been transferred to a newly-named genus, *Dendropithecus*, which is classified with the Hylobatidae.

The closest relatives to the East African fossil apes are two groups in the Oligocene of Egypt and the Middle Miocene of Europe and Asia. Comparison with the Oligocene forms is here restricted to *Aegyptopithecus zeuxis* and *Propliopithecus* species (Schlosser 1911; Simons 1965). The European Miocene apes comprise the dryopithecines *Dryopithecus fontani* and *D. laietanus* and the hylobatids *Pliopithecus antiquus* and *P. vindobonensis* (Lartet 1856; Zapfe 1960; Simons & Pilbeam 1965). The two species of *Pliopithecus* will be considered here as one morphological unit, and *D. laietanus* will be ignored as there are so few specimens representing it. From Greece there is the recently-described *Dryopithecus macedoniensis* (de Bonis *et al.* 1974). Two species of *Sivapithecus* are known from Asia, *S. sivalensis* and *S. indicus* (Simons & Pilbeam 1965).

A summary of some of the morphological features distinguishing the fossil and modern ape species is given in Table 23, p. 200–1. This list is by no means exhaustive, but it does include many of the points of difference between the fossil and modern species and also between the fossil species themselves. These points are commented on in the following sections which follow the headings of the table fairly closely.

Maxilla and premaxilla. The premaxilla in modern pongids is relatively long. In the fossil pongids it is very much shorter, and the index values for naso-alv. length are less than half those of modern pongids (Table 23, no. 1). It seems that the larger fossil species have relatively higher values of this index, presumably an allometric relation, but unfortunately there are too few specimens measurable for this feature to establish the presence of such a relation. *P.* (*R.*) *gordoni* has a lower index than the similar-sized *P. africanus*, and this might be correlated with the narrower incisors of the former. It is very possible that, when more specimens are found, *P.* (*R.*) *gordoni* will be found to have a different allometric size relation to the species of *P.* (*Proconsul*). In the hylobatids, *Dendropithecus macinnesi* has lower index values than *Pliopithecus* spp., and both are generally lower than modern gibbons.

The height of the zygomatic process is directly correlated with facial height in modern pongids. It varies in its position over the molar teeth from M^1 to M^3, and it also varies both in position and in height with age of the individual. Zygomatic width does not appear highly correlated with zygomatic height: in hylobatids the siamangs tend to have more widely flaring zygomatic arches combined with relatively low zygomatic heights, while gibbons have higher, narrower zygomatic regions, as do pongids. Of the fossil pongids, *P.* (*Proconsul*) appears to be at least as variable as modern apes in this feature. The few specimens of *P.* (*Rangwapithecus*) differ from both in having low and more widely flaring zygomatic processes, more like the condition in the siamang. In all cases the process is above either M^1 or M^2, but in *P. africanus* more of the specimens have the M^1 condition while in *P. nyanzae* more have the M^2 position.

The alveolar processes of the maxilla are long in modern pongids and they are often continued posteriorly beyond M^3 as tuberosities. The length of the tuberosity in absolute terms is greatest in gorillas, intermediate in chimpanzees, and least in the orang-utan and hylobatids. Relative to the length of the tooth row, however, the tuberosity is extremely small in the orang-utan and longer in the chimpanzees. The position of the greater palatine foramina is variable within a single species, varying from a position 7 mm beyond M^3 to opposite the middle of M^3 in gorillas of both sexes. It is set more posteriorly in the gorilla than the chimpanzee, in which it is placed no more than 3–4 mm beyond the M^3 at maximum. In the fossil apes the alveolar tuberosities are less strongly developed and the greater palatine foramina are not found posterior to M^3, even in *P. major*. There appears to be no correlation with sex in these features, and indeed one of the specimens with alveolar tuberosities most strongly developed is a probable female of *D. macinnesi* (KNM-RU 1774).

All hominoids preserve the primitive primate heritage of maxillary and sphenoidal sinuses (Cave & Haines 1940). This condition is present in hylobatids, but it has been complicated in various ways in pongids. In the orang-utan the maxillary sinus has expanded at the expense of the sphenoidal sinus, occupying an enormous area in the maxilla and the sphenoid, and extending posteriorly into the pterygoid and palatine processes and temporal bone and superiorly into the frontal bone. No explanation is given by Cave & Haines (1940) for this extensive pneumatization but it is interesting, for the orang-utan has the least robust skull of the living pongids. The chimpanzee and gorilla share with man the development of the ethmoidal sinus, an offshoot of which is the twin frontal sinus (Cave 1961). They also have extensive maxillary and sphenoidal sinuses, the former penetrating down between the roots of the molars so that the floor of the sinus is divided up into many loculi.

Of the Kenya Miocene apes, *P.* (*R.*) *gordoni* has conspicuously the most extensive maxillary sinus, as judged by the area of the floor of the sinus. It is followed closely by *P.* (*R.*) *vancouveringi* (Table 23, no. 2). The floor of the sinus penetrates deeply between the roots of the molars, although no separate loculi are formed, and it extends laterally into the zygomatic processes of the maxilla. By contrast the species of *P.* (*Proconsul*) appear to have more restricted maxillary sinuses, especially *P. africanus*. *Dendropithecus macinnesi* has a fairly extensive maxillary sinus, the floor penetrating between the molar roots nearly as deeply as in *P.* (*R.*) *gordoni*, but it does not extend as far laterally as in the latter species. A fronto-ethmoidal sinus like that of the African apes and man is known in *P. major* (Pilbeam 1969). The apparent parallelism of maxillary sinus development between *P.* (*R.*) *gordoni* and the modern apes, particularly the orang-utan, is interesting, but it is probably of little taxonomic significance. Similarly with the relatively small maxillary sinus of *P.* (*Proconsul*); but the presence of a true frontal sinus in *P. major* is probably significant in that the true frontal sinus (cf. Cave 1961) is only known in *Pan* and in hominids, and is absent in the orang-utan and gibbon and all other primates.

Palatal shape in modern pongids is very distinctive. The intercanine distance is as great as or greater than the intermolar distances so that the palate has a rectangular appearance. In hylobatids, and most of the fossil apes, the palate is narrower anteriorly, only *P. major* differing from these and resembling the modern apes (Table 23, nos 3–4).

Mandible. The mandibular symphysis in pongids has been the subject of much controversy. Symphyseal cross-sections have been discussed in great detail by Goodman (1968), but so great is the variability in morphology that it is not possible to distinguish absolutely between the three living pongid species. All are alike in having an inferior transverse torus, which stretches posteriorly as far as P_4/M_1 in the orang-utan and to M_1 in the gorilla and sometimes in the chimpanzee (Goodman 1968). (I distinguish here between the inferior transverse torus, which is some way removed from the inferior edge of the symphysis and which has the digastric impressions on its inferior surface, and the simian shelf which is an infolding of the inferior edge of the mandible at the symphysis and which has the digastric impressions medially or even slightly superiorly.) The development of an inferior shelf (simian shelf) is much less common in the gorilla than in the chimpanzee and orang-utan. Correlated with this is the shallower and constricted genial fossa in the gorilla compared with the deeply indented fossa in the other two.

The symphysis of most of the dryopithecines differs strikingly from that of the modern apes. None of these Miocene pongids has anything approaching a simian shelf, although the inferior transverse torus may be developed in some Eurasian species, for example *S. indicus* and *D. fontani*. In the African species the superior transverse torus is always well developed and is relatively larger on the larger species, reaching its maximum development in *P.* (*R.*) *gordoni* and *P. major*. The Miocene pongids had more robust symphyses than modern pongids (Table 23, no. 5), but despite these differences all the Miocene pongids fall on the same log regression line (symphysis thickness plotted against mandibular tooth row length C–M_3) with the modern pongids, indicating that the same allometric relation holds throughout. *Dendropithecus macinnesi* differs from the dryopithecines, but resembles the Oligocene *Aegyptopithecus zeuxis*, in having an inferior torus that often projects posteriorly further than the superior torus. The development of the inferior torus varies greatly, but it is as distinctive a feature as it is in modern apes. It is particularly well developed on the Songhor specimens of *D. macinnesi*.

The body of the mandible in modern pongids shows very great variation in size between males and females. It gets shallower posteriorly in both pongids and hylobatids, but more so in the latter. The degree of robusticity is much less in the hylobatids, and in the pongids it is least in the orang-utan which tends to have a relatively deep gracile mandible. The divergence of the tooth rows is greatest in the gorilla mainly because the breadth across the canines is less in this species than in the other pongids. Both chimpanzee and orang-utan have rather broad parallel tooth rows. The degree of robustness of the mandibular body of the Miocene pongids follows closely that of the symphysis (Table 23, no. 6). The variation in size is at least as great as in modern pongids of equivalent size, and often greater. Like the symphysis the body of the mandible in Miocene pongids is often more robust than in modern apes. The mandibular tooth rows diverge more strongly in the fossil apes, although the modern pongid condition is approached by *P. major* (Table 23, no. 8).

Incisors. Compared with other groups of mammals, hominoid primates have relatively large incisors. The central incisors are broad and spatulate, and the upper ones often have a central pillar or tubercle. The lateral incisors are asymmetrical, but while the uppers are often more or less pointed, the lowers always retain a flat incisive edge continuous with that of the central incisors. Chimpanzees and orang-utans have relatively larger incisors than other pongids.

The dryopithecines have relatively small incisors compared with modern pongids. *P. major* and the two Indian species of *Sivapithecus* have the largest I^1s relative to M^1 size (Table 23, no. 30). The other species all have smaller incisors relative to M1, but they are of approximately the same relative breadth as those of modern pongids (Table 23, no. 9) and in some cases are broader, e.g. the species of *P.* (*Proconsul*). It would appear, therefore, that it is in the buccolingual dimensions that the fossil pongid incisors are smaller than those of modern pongids, or in other words that the incisors were less stout. This is emphasized by the fact that the crown heights are relatively higher in the fossil pongid incisors, especially in *P.* (*R.*) *gordoni* and the Asian *Sivapithecus sivalensis*, than in the modern pongids (Table 23, no. 10). In addition, there is a greater size difference between I^1 and I^2 in *P.* (*Proconsul*) than in other dryopithecines or in modern pongids, the I^1 being spatulate and the I^2 more of a narrow blade (Table 23, nos 11 and 12). This is not the case in *P.* (*R.*) *gordoni*. The Miocene hylobatids, *Dendropithecus macinnesi* and *Pliopithecus* species, are similar to modern hylobatids in most of these features, but differ in the incisors being higher-crowned. As a whole the hylobatids have smaller incisors relative to M1, relatively narrower and higher crowns, and less spatulate I^1s compared with pongids. These features are also shared by the isolated incisors attributed to *Aegyptopithecus zeuxis*. Nearly all of the incisor samples of Miocene apes are small and little can be said about variability. The bivariate plots (Figs 9–10 and 17–18) show the size variation which is of the same order as that of equivalent-sized modern apes. Morphological variation is less than that of modern apes, probably as a result of lack of representation in the smaller samples.

Canines. The canines are variable in size but are always pointed tusk-like teeth in modern pongids. The crown of the upper canine is bilaterally flattened, although this is not necessarily reflected in the dimensions at the base of the crown. The long axis of the tooth is in line with or only slightly divergent from the line of the premolar series. The lower canine is more oblique. It is also more asymmetrical since the mesial ridge is well developed and the distal ridge is not; the upper canines have both mesial and distal ridges well developed and continuous over the apex of the tooth. The upper canines are worn both mesially and distally, the former by occlusion with the lower canine, producing a flat wear facet, and the latter by occlusion with the P_3, producing a concave wear facet cutting across the distal ridge. In living pongids this grinding action of the flat surface of the P_3 against and into the concave facet of the upper canine cannot be described as sectorial because it blunts rather than sharpens the canine. The wear on both the C and the P_3 starts at the tip and in some individuals never passes along the crown, so that both teeth are worn flat. This condition has been referred to by Wolpoff (1971). More usually, however, wear facets are formed along the edges of the crown.

In hylobatids the distal wear facet is distolingual. The anterobuccal face of the P_3 occludes against the lingual edge of the distal ridge of the upper canine, so that attrition has the effect of sharpening the canine tip and the edge of the distal ridge. This means that throughout the effective life of the tooth the upper canine is maintained with a sharp distal cutting edge. This condition has been described for the Cercopithecoidea (Zingeser 1969; Every 1970), in which the P_3 acts as a grindstone to sharpen the point and distal edge of the upper C, as canine honing, by which the unworn pointed tip of the canine is maintained by wear.

The canines in dryopithecines tend to be less tusk-like and less robust than in modern pongids, but this is a qualitative assessment and is not reflected in any of the indices. This arises because the indices are based (necessarily) on the dimensions of the base of the crown (Table 23, no. 13), and these are quite similar between fossil and modern pongids. The crown above the base tapers more in the fossil canines, and this makes them appear less robust, but it has not been found possible to illustrate this by any repeatable measurement or index. The fossil hylobatids differ strongly from the modern ones in having lower-crowned canines and in displaying a higher degree of sexual dimorphism. They are similar in having the truly sectorial C–P_3 complex found among the Hominoidea only in the Hylobatidae; the wear of the P_3 on the upper C of *D. macinnesi* has a sharpening action on the distal edge of the canine. What is known of *Aegyptopithecus zeuxis* suggests that it resembles the hylobatids in canine morphology.

Morphological variations are greater in the fossil apes than those seen in the modern ones. This is particularly true of cingulum development, which may be strongly developed or absent altogether within one species. Mesial groove development in the upper canines is also variable; it is most striking in *D. macinnesi* in which the upper canine in males has two prominent mesial grooves and in females has one shallower groove. The bivariate plots for the canines are shown in Figs 11 and 19. Much larger samples were available than for the incisors, and it is probable that something approaching the full range of variation is present for both canines in *Dendropithecus macinnesi*, *Limnopithecus legetet* and *P. nyanzae*, and for the upper C in *P. africanus* and *P. major*. The lower C ranges for *P. africanus* and *P. major* are obviously too limited, either as a result of sample bias or of incorrect identification of isolated teeth. In either event, more complete material, in which canines are definitely associated with molars, is necessary before the whole picture can emerge.

Lower third premolar. P_3 is usually one-cusped in modern pongids, but a smaller lingual tubercle is often developed on the lingual ridge. The axis of the tooth is set obliquely to the molar tooth row, and the enamel at the anterior end of the long axis (the mesiobuccal angle of the tooth) is extended inferiorly down the mesial root of the tooth. In hylobatids, the tooth is more in line with the molars, but it still has the inferior extension of the enamel on the buccal side of the tooth. Also in hylobatids the lingual ridge is poorly developed. The function of P_3 in hylobatids is completely different from that in pongids, as just discussed in the last section. In pongids the tooth is undergoing molarization in a manner similar to, but much less advanced than, that of hominids, and there is a lot of variation in the extent to which molarization has occurred. Variations occur particularly in the degree of development of the lingual cingulum, and in the breadth/length index, which varies from 60% to 80% in the chimpanzee and gorilla and from 50% to 60% in hylobatids.

In the Miocene pongids the morphology and variability of the P_3 is very similar to that of the modern pongids. Correlated with the blade-like crown of the canines is the probably greater degree of sectoriality in the fossil pongids (Table 23, no. 18). This is particularly marked in *P.* (*R.*) *gordoni* and *P. nyanzae* in which sectoriality in function is correlated with two P_3 indices, the breadth/length index and the mesial extension of enamel index (Table 23, nos 19 and 20). The height of the crown would also appear to be correlated, but in this case in the fossil hylobatids it is very high-crowned (*D. macinnesi* and *Pliopithecus* spp.) while in *Hylobates* itself it is low-crowned (Table 23, no. 21). Unfortunately there is no crown of the P_3 of *Aegyptopithecus zeuxis* yet known. The degree of molarization in the fossil pongids appears to be rather less than in modern ones. A small lingual cusp is sometimes developed, particularly in *L. legetet*, but it is by no means common. Lingual cingula are usual in the fossil P_3s. In the bivariate plot for this tooth (Fig. 20) it can be seen that, so wide are the ranges of variation, there is considerable overlap between the larger species of *P.* (*Proconsul*). The relatively elongated crown in *P.* (*R.*) *gordoni* is also shown in this figure.

Finally, in the discussion of the P_3, special mention must be made of *P.* (*R.*) *gordoni*. If the specimens known are correctly attributed to this species it differs strongly from the other dryopithecines and from other pongids, but once again the differences are not reflected in the indices, except in the degree of bilateral compression (Table 23, no. 19). The tooth is very big, both in mesiodistal length and in height; the lingual and buccal borders are nearly parallel, and there is no mesial angulation of the anterior end of the crown as seen in most fossil and living pongid species. In this respect the crown resembles those of hylobatids, but whereas in the latter the long axis of the crown is nearly in line with the axis of the molar tooth row, in *P.* (*R.*) *gordoni* the long axis of the P_3 is strongly oblique. The wear facet is nearly perpendicular to the long axis at the anterior end of the crown, which faces anterobuccally so that the distal wear on the upper C must have been lingual rather than distal. As a result the distal edge of the upper C would have been sharpened by the lingual wear rather than blunted by distal wear, i.e. the wear would have been sectorial.

Lower fourth premolar. The P_4 is always bicuspid in modern pongids, the buccal cusp being the larger of the two. The talonid is well developed. The roots are set obliquely in the mandible, paralleling the orientation of the P_3. In hylobatids the crown is longer than broad; in the orang-utan it is nearly square; while in the chimpanzee and gorilla the crown is usually broader than long. In the Miocene pongids, the P_4 is so variable that it is hard to generalize on its morphology. The long axis of the tooth is nearly always set obliquely to the molar tooth row, paralleling the long axis of the P_3. Different degrees of obliqueness result in widely different breadth/length ratios if mesiodistal length is used, for the greater the obliqueness the shorter is the mesiodistal length and the wider is the buccolingual breadth. This shows up in the breadth/length ratio (Table 23, no. 22) and can be seen in individual detail in the tables of measurements (Tables 1–21) and in the bivariate plot for this tooth (Fig. 21). The plotted points are particularly widely scattered for *Dendropithecus macinnesi*, *P.* (*R.*) *gordoni* and *P. nyanzae*. As in P_3, there is extensive overlap between the species of *P.* (*Proconsul*).

Upper premolars. In modern pongids the upper premolars are always bicuspid, and the buccal cusp projects further than the lingual one. This difference is more pronounced in the P^3 than the P^4. Also in P^3 the buccal side of the crown is slightly more expanded up the mesiobuccal root in a similar fashion to the P_3. Both upper premolars are three-rooted, the mesiobuccal root being more prominent than the distobuccal one. The P^3 is bigger than the P^4 and is also more variable in size.

In the Miocene pongids the same general pattern emerges with the only variations being in *P.* (*Rangwapithecus*). In this the two upper premolars have a greater degree of molarization: the two cusps are nearly equal in height, the P^3 has no pronounced buccal expansion, the distal cingulum is greatly expanded, and P^4 is larger than P^3 (Fig. 25). In addition, the breadth/length index is lower as a result of the large distal cingulum and despite the presence of a well-developed lingual cingulum on both premolars. These differences are all illustrated in Table 23, nos 24–28. The fossil hylobatids have relatively small upper premolars with strongly projecting buccal cusps, especially on P^3. The breadth/length ratios are very high as well, seemingly independent of lingual cingulum development. The P^3 is approximately the same size as P^4. The main feature shared with modern hylobatids is the projecting buccal cusp on P^3, which is correlated with the sectorial development of upper C and P_3 (Figs 12–13).

Upper molars. Upper molars of pongids and hylobatids are usually broader than long. They are four-cusped with a well-developed hypocone in addition to the three trigon cusps. Supernumerary cusps are uncommon, the so-called carabelli cusp being the most frequent. Variations in the ridge development and the projection of the cusps is similar to that described for lower molars. Wear is usually much heavier lingually than buccally, matching the buccal wear of the lower molars, but it rarely reaches the same extent as in lower molars where the whole buccal side may be worn away down to the roots.

There is more variation in the relative sizes of the upper molars than there is in the lowers. In

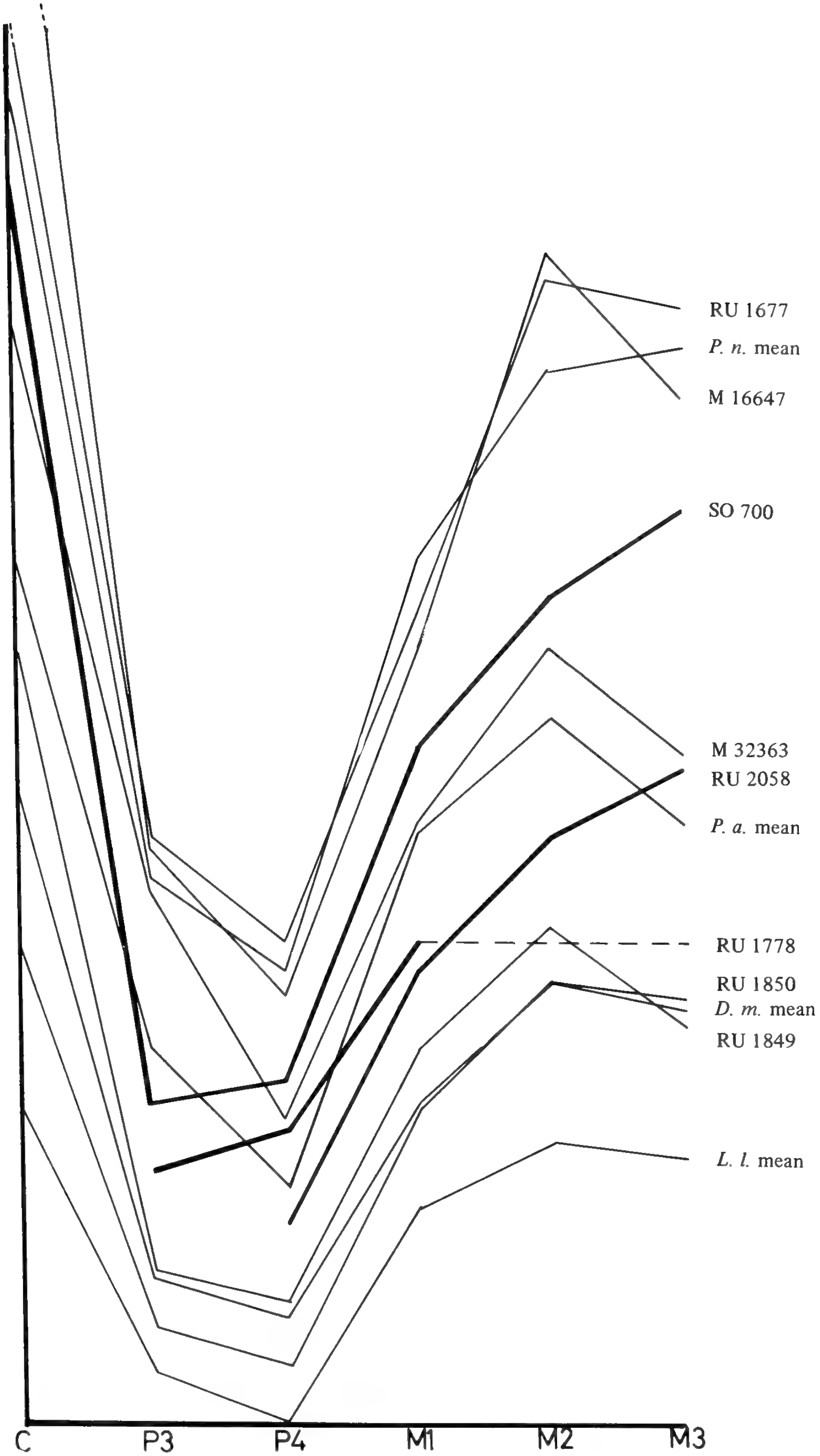

Fig. 25 Relative sizes of C–M³ in Miocene apes, crown module. '*P. n.* mean' is the mean value for *Proconsul nyanzae* with two individual series, M 16647 and RU 1677; SO 700 represents the type specimen of *P.* (*R.*) *gordoni* and RU 2058 of *P.* (*R.*) *vancouveringi*; '*P. a.* mean' is the mean value for *P. africanus* with one individual value M 32363; '*D. m.* mean' is the mean value for *Dendropithecus macinnesi* with two individual values RU 1849 and 1850; '*L. l.* mean' is the mean value for *Limnopithecus legetet*.

the chimpanzees the M^1 is usually the longest tooth, although not always the biggest, because in buccolingual breadth M^2 usually exceeds M^1. M^3 is nearly always reduced. In the gorilla M^2 is usually bigger than M^1, and M^3 is often the longest tooth but is relatively narrower. This variability in relative sizes of the upper molars is a function of variability in the posterior molars, the values for coefficient of variation increasing from M^1 to M^3. In hylobatids the M^3 is usually smaller than M^2, but marginally bigger than M^1. The M^3 is nearly always reduced relative to M^2 in the dryopithecines (Fig. 25). The species follow a consistent pattern, although the degree of reduction of M^3 does vary considerably. Unlike the modern apes, where the M^3 is often smaller than M^1, the dryopithecines have M^3 almost invariably larger than M^1, but smaller than M^2. This pattern is shown in Fig. 25 and in Table 23, no. 33. *L. legetet* and *P. africanus* have the most greatly reduced M3s and *P. nyanzae* the least, while both species of *P.* (*Rangwapithecus*) have greatly enlarged M^3s which are by far the biggest of the upper molars. The contrast between the two subgenera is seen in Fig. 25.

The three trigon cusps of M^1–M^2 tend to be of equal size in the species of *P.* (*Proconsul*). In *P.* (*Rangwapithecus*) the protocone is larger than the others. Perhaps linked with this, the protoconule is developed in the former subgenus but absent in the latter. The ridges connecting the cusps are similar to the modern ape pattern in all species, and it is only the protoconule and cingulum development that distinguishes the upper molars of the fossils.

Another noticeable feature of the upper molars of *P.* (*Rangwapithecus*) is in the breadth/length index (Table 23, nos 29 and 32). In nearly all cases the upper molars are longer than broad, in striking contrast to other dryopithecines in which they are broader than long. There is a very slight increase in the breadth/length index from M^1 to M^3, but nothing like as big as the increases in other dryopithecines and modern pongids. This difference in shape sets them apart from other dryopithecines in the bivariate plots (Figs 14–16). Particularly in Fig. 14 the two species of *P.* (*Rangwapithecus*) can be seen to form discrete clusters below the other dryopithecine samples.

The development of the lingual cingulum in the modern pongids is moderately variable. It is relatively most strongly developed in the concolor gibbon. Of the pongids it is most consistently developed in the gorilla, mostly on the protocone but also on the hypocone. In the chimpanzee the cingulum is confined to the protocone and is larger on M^2 than on M^1. Although smaller on M^3 it is relatively more extensive, running distally nearly to the hypocone. The orang-utan rarely has any cingulum developed. The upper molars of the African dryopithecines are unique in pongids in consistently having a well-developed lingual cingulum. Even some specimens of *P. nyanzae* and *P. major*, formerly assigned to '*Kenyapithecus africanus*', have a slight lingual cingulum on the M^1.

The hypocone is usually a small cusp set directly on the lingual cingulum. Its origin from the cingulum is often clearly seen. In many cases, however, the hypocone itself has a small lingual cingulum encircling it and connecting with the distal cingulum. This is particularly evident in *P. nyanzae*, *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi*. The last two species also have a very large distal cingulum, and this may be connected with the expansion of the lingual cingulum. The Miocene hylobatids, like the African dryopithecines, have massive lingual cingula on their upper molars. The hypocone is less obviously a cingular structure, although this is not to say that it is not, and there is often a prominent lingual cingulum running around the edge of the hypocone. The M^3 is slightly larger than M^1 but very much smaller than M^2, but the distal cusps are nearly always reduced in size. The molars are relatively broad. In none of these features is there any marked resemblance to modern gibbons, unlike the case of the lower molars. The strong ridge development, the relatively large size of the trigon and the relative breadth of the molars distinguishes these teeth from the contemporary dryopithecines.

Lower molars. Lower molars in modern pongids and hylobatids are almost invariably longer than broad. They have a general pattern of five cusps. Supernumerary cusps are infrequent, occurring most often in the gorilla in the form of an additional buccal cusp(s) next to the hypoconulid. The projection of the cusps above the foveae is greatest in the gorilla and (relatively) in all hylobatids, and is least in the orang-utan. The occlusal ridges are poorly developed, compared with in the Miocene pongids, and are most distinct in the chimpanzee, especially the pygmy chimpanzee, in which both mesial and distal foveae may be sharply delineated. Gorilla lower molars have a characteristic invagination of the buccal border of the crown which isolates all three of the buccal cusps (the hypoconulid being buccal in most cases) and cuts into and reduces the size of the talonid basin. This condition seems to be fairly standard in gorilla lower molars and contrasts with that of chimpanzees and orang-utans where the talonid basin is relatively wider and the buccal edge of the talonid is less cut into. The latter two species often have some degree of occlusal wrinkling, which is greatest in orang-utans.

In the Miocene pongids the lower molars are basically similar to the modern ones. All the Kenya fossil pongids have a strong buccal cingulum, in contrast to both the Eurasian fossil pongids and the modern pongids. Supernumerary cusps are extremely rare, occurring only on M_3 of *P. major*. The occlusal ridges are well developed, although less so than in the hylobatids, and are distinct on *P.* (*R.*) *gordoni* even though this species has a high degree of secondary wrinkling of the occlusal surface. *P. africanus* has a slight amount of occlusal wrinkling, and it is probable that when the lower molars of *P.* (*R.*) *vancouveringi* become known they will be seen to have wrinkling, but the other species lack it altogether. Another distinctive feature of *P.* (*R.*) *gordoni* is the deep invaginations of the buccal border of the lower molars, which makes them very similar in appearance to gorilla lower molars. *Dendropithecus macinnesi* has relatively elongated lower molars, differing in this respect from *Hylobates*. The general cusp patterns are similar, as are the relative dimensions of the trigonid and talonid basins, but both *D. macinnesi* and *Pliopithecus* spp. have very distinct occlusal ridges that distinguish them both from the dryopithecines and the modern hylobatids. The M_3 is still the largest molar, and not as reduced as in *Hylobates*, but it is smaller relative to M_1 than in the dryopithecines (Table 23, no. 35).

Breadth/length indices of modern pongids are not very variable. All the species of pongid have similar ratios, the one for M_2 being greatest and the one for M_3 least. One difference is the increase in index from M_1 to M_3 in chimpanzees, indicating less elongation or narrowing of teeth. Hylobatids have lower values than pongids (see Table 23). Some vestiges of buccal cingulum on the lower molars are fairly frequent in modern pongids. It is most strongly developed in the gorilla, in which it may run the length of the buccal border of the molar crown, divided into three by the buccal grooves running between the cusps. In chimpanzees, a buccal cingulum is less common and, where present, is confined to the protoconid. In orang-utans the cingulum is reportedly only rarely developed (Frisch 1965). Hylobatid lower molars in general do not have buccal cingula except in *Hylobates concolor* where it may be frequent.

The lower molars in the African dryopithecines are relatively much more elongated than in modern pongids (Table 23, no. 34). This is despite the fact that they have the strong buccal cingulum. In fact there seems to be an inverse correlation between cingulum development and relative breadth of the crown, for the Eurasian dryopithecines, in which the cingulum is poorly developed, are relatively broader than African ones, and the modern pongids, which only rarely have a small cingulum, are broader still. It is possible that the buccal cingulum in *P.* (*Proconsul*) and *P.* (*Rangwapithecus*) may not be a primitive retention, as has been suggested (Clark & Leakey 1951), but may be a progressive feature by which the crown widths, and therefore the total occlusal area, are being expanded. Frisch (1965) claims evidence for a trend in pongids towards reduction and loss of molar cingula. This would apparently be true as a general trend from the Miocene to the present, but before that the trend was going the other way. From *Oligopithecus* to *Aegyptopithecus* to *Proconsul* the molar cingula increased in size, and there is no evidence when this tendency to increase was reversed. If the cingulum is adaptive in increasing molar area, then it seems reasonable to suppose that it would start to be reduced only when the molar occlusal area had increased either at the expense of or incorporating the original cingulum.

The relative sizes of M_3 with respect to M_1 are shown in Table 23, no. 35. In modern pongids, the most common size relationship between the lower molars is an increase in size from M_1 to M_3, but there are several variations on this: in both chimpanzee and orang-utan the M_2 is often the largest, and sometimes even the M_1 (Schuman & Brace 1954); in gibbons the M_2 is often the largest. Frisch (1965: table XV) shows that in terms of mesiodistal length the M_3 is usually shorter than M_1 in all species of gibbon, but since the buccolingual breadth is usually greater the overall size is the same or greater. Molar size increases from M_1 to M_3 in all the African dryopithecines to a greater extent than in modern pongids or Eurasian dryopithecines (Table 23, no. 35; Figs

Table 23 Comparative morphology of fossil and modern apes.

		Dendropithecus macinnesi	*Proconsul (Rangwapithecus) vancouveringi*	*Proconsul (Rangwapithecus) gordoni*	*Limnopithecus legetet*	*Proconsul africanus*	*Proconsul nyanzae*	*Proconsul major*
Maxilla								
index naso-alv. ht/M^1–M^3	(1)	24	–	35	–	42	–	46
maxillary sinus floor	(2)	extensive	extensive	v. extensive	small	v. small	small	small
index pal B at M^3/L × 100	(3)	44	–	41	–	52	49	43
B at C/B at M^3	(4)	97	–	97	–	81	96	109
Symphysis								
robusticity	(5)	moderate	–	gracile/robust	moderate	moderate	moderate	v. robust
index t/d × 100		46	–	56	43	45	47	56
Mandibular body at M_3								
robusticity	(6)	moderate	–	gracile/robust	gracile	robust	moderate	robust
index t/d × 100		50	–	56	48	57	53	55
index M_3d/symph. d × 100	(7)	78	–	77	83	78	75	75
Mandibular breadth								
ant. breadth of mand.	(8)	prob. narrow	–	narrow	narrow	narrow	narrow	broad
index C–C/M_3–M_3		–	–	–	51	47	52	62
Incisors								
length of crown (md)	(9)	v. narrow	–	mod. narrow	broad	broad	broad	broad
I^1 index bl/md × 100		86	–	74	78	75	76	79
I_1 index bl/md × 100		137	–	101	119	126	115	125
height of crown (buc)	(10)	v. high	–	mod. high	moderate	moderate	moderate	moderate
I^1 index md/ht × 100		73	–	78	90	90	85	87
I_1 index md/ht × 100		53	–	51	60	43	55	46
shape of I^1	(11)	narrow blade	–	narrow spatulate	spatulate	spatulate	spatulate	spatulate
index I^1md/I^2md × 100	(12)	131	–	122	139	151	151	136
Canines								
bilateral compression	(13)	v. great	–	moderate	little	little	little	little
C^1 index b/l × 100		72	–	71	79	78	80	82
C_1 index b/l × 100		65	–	70	70	72	75	70
height of crown (buc)	(14)	mod. high	–	v. low	moderate	moderate	moderate	moderate
C^1 index l/ht × 100		70	–	99	73	81	76	77
C^1 mesial groove	(15)	double prominent	–	one v. prominent	one shallow	one shallow	one shallow	one shallow
C_1 mesial ridge	(16)	short	–	long	v. short	short	long	v. long
index mes. ridge/ht × 100		69	–	82	61	73	81	92
C_1/M_1 (area) min ♀	(17)	95	–	132	75	85	124	119
max ♂		123	–		115	124	183	153
Lower P3								
sectoriality	(18)	sectorial	–	sectorial	not	not	moderate	not
bilateral compression	(19)	v. great	–	v. great	little	little	moderate	great
index b/l × 100		60	–	58	65	65	63	61
ext enamel mes root	(20)	great	–	moderate	little	little	great	little
index dist. ht/mes. ht × 100		72	–	82	77	76	70	78
height of crown (mes. buc)	(21)	v. high	–	low	low	low	low	low
index l/ht × 100		87	–	111	104	101	105	101
Lower P4								
mesiodistal length	(22)	elongated	–	elongated	elongated	broad	broad	broad
index bl/md × 100		91	–	92	84	108	104	110
buccal cingulum	(23)	weak	–	weak	weak	weak	weak	weak
Upper P3								
buccolingual breadth	(24)	v. broad	narrow	moderate	moderate	broad	broad	broad
index bl/md × 100		168	127	143	148	163	163	149
buccal cusp projection	(25)	v. great	little	moderate	moderate	great	great	great
index buc. ht/ling. ht × 100		170	108	134	141	163	157	161
lingual cingulum	(26)	none	strong	strong	none	none	none	none
Upper P4								
size rel. to P^3	(27)	same	larger	larger	smaller	smaller	smaller	smaller
lingual cingulum	(28)	strong	v. strong	v. strong	strong	none	moderate	weak
Upper M1								
buccolingual breadth	(29)	broad	v. narrow	v. narrow	moderate	moderate	moderate	moderate
index bl/md × 100		127	97	98	121	118	115	116
I^1/M^1 × 100 (module)	(30)	71	–	78	78	79	77	83
lingual cingulum	(31)	v. strong	v. strong	v. strong	strong	strong	strong	strong
Upper M3								
buccolingual breadth	(32)	broad	v. narrow	v. narrow	broad	broad	broad	broad
index bl/md × 100		122	99	99	124	129	119	121
size rel. to M^1 (module)	(33)	sl. larger	much larger	much larger	sl. larger	larger	much larger	larger
index M^3/M^1 (module)		105	118	127	103	110	122	112
Lower M3								
mesiodistal length	(34)	moderate	–	elongated	moderate	moderate	moderate	moderate
index bl/md × 100		80 a	–	73	82	79	81	78
size rel. to M_1 (module)	(35)	sl. larger	–	much larger	sl. larger	larger	larger	much larger
index M_3/M_1 × 100		124	–	140	118	130	137	158
buccal cingulum	(36)	weak	–	strong	strong	strong	strong	strong

Aegyptopithecus zeuxis	*Pliopithecus* spp.	*Dryopithecus fontani*	*Sivapithecus sivalensis*	*Sivapithecus indicus*	*Hylobates* spp.	*Pan troglodytes paniscus*	*Pan troglodytes troglodytes*	*Pan gorilla*	
36	40	–	–	–	48	–	95	66	(1)
–	–	–	small	small	moderate	extensive	extensive	extensive	(2)
37	36	–	–	–	44	–	60	52	(3)
73	77	–	–	–	92	–	118	117	(4)
gracile	moderate	robust	moderate	moderate	gracile	gracile	gracile	moderate	(5)
37	41	50	43	40	35	42	38	43	
gracile	moderate	gracile	robust	robust	gracile	gracile	moderate	moderate	(6)
46	53	49	59	58	49	47	53	53	
75	75	77	74	74	62	88	65	51	(7)
v. narrow	v. narrow	–	–	–	broad	broad	v. broad	broad	(8)
36	43	–	–	–	63	67	75	65	
prob. narrow	v. narrow	–	broad	broad	broad	v. broad	v. broad	broad	(9)
–	97	–	78	77	79	77	80	80	
–	126	–	–	–	106	95	109	117	
high	low	–	mod. high	moderate	v. low	v. low	v. low	v. low	(10)
(74)	89	–	77	89	98	102	103	105	
(57)	50	–	–	–	73	81	74	72	
uncertain	narrow blade	–	v. spatulate	spatulate	narrow spatulate	spatulate	spatulate	spatulate	(11)
–	139	–	128	–	138	138	130	139	(12)
great	moderate	moderate	moderate	moderate	moderate	little	little	little	(13)
74	79	–	78	72	72	79	77	76	
69	68	70	79	78	74	76	80	82	
v. high	v. high	v. high (C_1)	moderate	moderate	ext. high	moderate	moderate	moderate	(14)
68	68	–	82	75	40	78	73	76	
one prominent	one prominent	–	one v. prominent	one prominent	one prominent	one shallow	one shallow	one shallow	(15)
(long ?)	short	moderate	–	moderate	moderate	moderate	long	long	(16)
(79)	66	74	–	76	78	68	80	76	
–	87	101	95	108	90	66	97	75	(17)
–	101			116	114	86	147	132	
prob. sectorial	sectorial	moderate	not	not	sectorial	not	not	not	(18)
great	little	moderate	moderate	great	great	little	little	little	(19)
62	68	64	64	60	61	71	70	69	
–	moderate	great	little	little	great	v. little	little	little	(20)
–	75	70	83	78	70	91	83	82	
–	v. high	low	low	low	low	low	v. low	low	(21)
–	86	105	115	110	114	102	128	115	
broad	sl. elongated	broad	broad	broad	elongated	broad	broad	broad	(22)
105	98	102	113	122	84	104	115	116	
–	weak	none	none	none	none	none	none	none	(23)
v. broad	broad	–	narrow	narrow	v. narrow	narrow	mod. narrow	mod. narrow	(24)
175	164	–	127	122	104	125	131	133	
great	great	–	great	great	v. great	moderate	great	great	(25)
153	150	–	159	189	214	130	150	153	
none	none	–	none	none	none	none	none	none	(26)
smaller	smaller	–	smaller	smaller	smaller	smaller	smaller	smaller	(27)
strong	strong	–	none	none	none	none	none	none	(28)
v. broad	broad	moderate	moderate	moderate	moderate	moderate	moderate	narrow	(29)
137	129	117	114	111	115	111	113	106	
–	69	–	88	86	77	96	96	83	(30)
v. strong	strong	none	none	none	none–weak	none–moderate	none–weak	none	(31)
v. broad	broad	broad	intermediate	narrow	intermediate	intermediate	broad	narrow	(32)
145	127	130	112	108	113	116	120	106	
larger	sl. larger	–	sl. larger	sl. larger	smaller	smaller	smaller	smaller	(33)
113	103	–	103	108	99	93	93	103	
elongated	elongated	short	short	short	short	short	short	short	(34)
77	74	84	85	85	87	94	98	88	
larger	sl. larger	sl. larger	sl. larger	sl. larger	same size	smaller	same size	sl. larger	(35)
131	116	115	123	124	101	93	102	111	
v. strong	weak	weak–moderate	none	none	none–weak	none	none–weak	none–weak	(36)

22–24). The M_3 is an elongated and triangular-shaped tooth very characteristic of the African dryopithecines. The triangular shape must be seen as a reduction in crown area, the distal end of the crown being much abbreviated. Crown elongation is effected by the large heel-like hypoconulid, but the function of this cusp on M_3 is not known, for it does not appear to occlude with any part of the upper dentition. The triangular form is most strongly developed in *P. major* and *P. africanus* and to a lesser extent in *L. legetet* and *P.* (*R.*) *gordoni*. By contrast the M_3 of *P. nyanzae* is rectangular, with the distal end hardly reduced at all.

Wear patterns in modern pongids show great individual variations, but they follow the same general pattern for all living species of pongids and hylobatids. Wear starts at the tips of the buccal cusps and the hypoconulid, exposing dentine at the tips of the cusps. Later, dentine patches are also exposed on the lingual side, by which time the buccal patches are very large and are expanding lingually to meet the lingual ones. Eventually, all the patches unite so that dentine is exposed over the whole crown. The last stage is usually only reached in gorillas, and even well-worn gibbon teeth may have completely separate wear patches on the tips of the cusps. Chimpanzees are intermediate. Orang-utans, having nearly flat occlusal surfaces to begin with, have a less localized pattern of wear so that the rate of change of wear is much slower.

Wear patterns in the African dryopithecines fall into two categories, neither exactly like those of modern pongids. The three species of *P.* (*Proconsul*) and *L. legetet* show few specimens in which wear has exposed large areas of dentine, and the degree of wear is only slightly greater in the M_1 than in the M_3. This pattern is seen most strikingly in *P. africanus*; in *L. legetet* and *P. major*, the smallest and largest species respectively, rather larger areas of dentine are exposed, but not to the same extent as in the Eurasian dryopithecines and modern pongids. The most heavy wear occurs in *P. nyanzae*, and this species also has the steepest wear gradient in the subgenus. The other category of wear is seen in the two species of *P.* (*Rangwapithecus*): in these there appears to be a very steep wear gradient such that there may be extensive areas of dentine exposed on M_1 at a time when M_3 is still almost unworn. This pattern is evident on the type specimens of both *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi* (KNM-SO 700 and RU 2058).

The shape of the cusps of *Limnopithecus* has been described by Hopwood (1933 : 439) as low, blunt and rounded, and wearing at the tip to expose the dentine. Clark & Leakey (1951 : 68) refer to the cusps as

> . . . rounded conical tubercles. The summits of the tubercles are raised into attentuated points thinly covered by enamel, so that quite early in the wear of the tooth the dentine is exposed here and thus becomes evident as a pattern of small dots on the occlusal surface of the crown. Further, the cusps are somewhat small relatively to the size of the crown as a whole, and are arranged round the margins of a talonid basin which forms rather a broad shallow cup-like excavation in the centre. In these respects (as well as in size), the lower molars have a striking resemblance to those of the small modern gibbons. They differ, however, in that the conical cusps are more individualized, being clearly demarcated from each other by relatively deep intervening sulci. In *Hylobates*, they tend to be united at the periphery of the talonid basin by interconnecting crests. The enamel in *Limnopithecus* is singularly free from secondary foldings.

In most respects this is a good description of *Dendropithecus* [formerly *Limnopithecus*] *macinnesi* except that new material emphasizes what after all was clearly visible on the type specimen, that the conical cusps are united along the periphery of the talonid by well-developed ridges. The description does not fit the other species that Clark & Leakey (1951) included in *Limnopithecus*, *L. legetet*, except that, in common with all other pongids, the tips of the cusps do become worn first and dentine is exposed.

Size variation in fossil and modern apes

The African Miocene pongids fall into three size groups. The *Proconsul* group consists of three species increasing in size from the smallest, *P. africanus*, to the largest, *P. major*. Paralleling this is the *Rangwapithecus* group, the smaller species, *P.* (*R.*) *vancouveringi*, being smaller than *P. africanus* and the other, *P.* (*R.*) *gordoni*, being larger. Finally, *Limnopithecus legetet* is on its own as by far the smallest species of Miocene pongid. The hylobatid *Dendropithecus macinnesi* is also on its own, approximating in size to *P.* (*R.*) *vancouveringi.*

The absolute variability in size for each species is shown in the bivariate plots presented in the statistical section (Figs 7–24). There is little overlap in species ranges for the mandibular dimensions (Figs 7–8), and in particular *P. africanus* is widely separated from *P. nyanzae*. The incisor ranges are nearly continuous for each species except for the *P. africanus/nyanzae* ranges in the I^1 which are quite distinct (Fig. 9). *P. nyanzae* and *P. major* are difficult to tell apart on incisor size. The small size and relatively greater breadth of the upper incisors of *L. legetet* make this sample distinctive.

The canine ranges are not consistent between uppers and lowers (Figs 11 and 19). In the upper canine the three species of *P.* (*Proconsul*) have relatively large ranges of variation, particularly *P. africanus* which exceeds even *P. major* in this respect, and there is scarcely any overlap between them. In the lower canines, *P. nyanzae* has the largest range and completely overlaps the limited *P. major* range. *L. legetet* also has a much greater range than in the upper C, and *P. africanus* has a smaller range. These vagaries of sample variation are presumably a result of incomplete or biased samples, and where the ranges of variation are so different for two closely allied teeth it would seem reasonable to take the larger of the two ranges as that typical of the species. For instance, the degree of variability for the upper canine of *P. africanus* can be applied to the actual variability of the lower canine to estimate its probable variation, given a more complete sample.

The ranges of variation of the upper premolars (Figs 12–13) have extensive areas of overlap between all species except in P^4 of *Rangwapithecus*. The two species of this subgenus are not very different in size in P^4 dimensions, but both are distinct from the other Miocene species because of their narrow breadth relative to length. The lower premolars also have extensive areas of overlap between the species (Figs 20–21). In the case of P_3 the samples appear to be unusually variable, and this is confirmed by the comparison with modern ape ranges. The chimpanzee range overlaps but is less than that of *P. nyanzae*, and the gorilla range overlaps but is less than that of *P. major*. Since the other fossil species appear no less variable than these two, making due allowance for size decrease, it would seem that the P_3 was more variable in the Miocene than at present.

The ranges of the upper molars (Figs 14–16) show a clear distinction between the species of *P.* (*Rangwapithecus*) and the others. These two species are also quite distinct from each other, even in M^1, and in M^3 their ranges are far apart. *P. nyanzae* overlaps with *P. africanus* in M^1–M^2 but not in M^3, because in the larger species the M^3 is less reduced, widening the gap between them. The M^3 is poorly known for *P. major*, but in the other two molars it appears substantially bigger than in *P. nyanzae* although there is still extensive overlap.

The lower molars have similar patterns to the upper molars (Figs 22–24). There is a slightly greater degree of overlap between *P. africanus* and *P. nyanzae* due to the presence of the two female mandibles of the latter, KNM-RU 1674 and 2087. As has already been seen this overlap is not matched in the mandibular dimensions of these specimens, nor in the C–P_3 dimension, and neither is it in the upper dentition which is associated with RU 1674. Thus although it is tempting to view these two specimens as the wanted male mandibular specimens of *P. africanus*, in most respects they are more similar to *P. nyanzae* (cf. Greenfield 1972).

It can be concluded from this discussion that the ranges of the larger fossil species are comparable with those of the more variable of the modern great apes. In particular, the differences in the ranges of variation of *P. nyanzae* and *P. major* are strikingly like the differences between the chimpanzee and gorilla and this lends support to the validity of these species.

One of the problems in comparing the sample variation in different-sized species is that the species with a larger overall size will have a similarly larger range of variation. The statistic devised to overcome this drawback, the coefficient of variation, has problems of usage itself, especially the lack of precision of the coefficient value. For instance, in small samples of up to ten the standard error of V will be nearly a quarter the value of V and assigning 95% limits will give V a probable range as big as itself. This is an argument against using small samples, but unfortunately small samples are often all that are available in the study of fossils. In this study standard deviations and coefficients of variation have been calculated for samples greater than ten, and in a few cases for smaller samples, but in many of these the probable (0·95) range of the coefficient of variation is so high as to make it useless. An index that I have devised parallels the effect of the coefficient of variation but, since it takes account of sample size, it allows a probability to be assigned to it; this is arrived at by dividing the range of the 95% confidence limits by the mean rather than the standard deviation by the mean, thus:

$$\frac{t_{0\cdot95}^{N_a}\times 2s_a}{\bar{X}_a}$$

where

N_a = sample size for variable a
s_a = standard deviation of variable a
$\bar{X}_a$ = mean of variable a

The results of using this index are shown in Table 24. The relatively high degree of variability of *D. macinnesi* is emphasized. *P.* (*R.*) *gordoni* is less variable except for the M_3 which is an enlarged tooth in this species. The upper dentition of *P. africanus* is conspicuously more variable than the lower dentition, and this raises the question already commented on, that there do not appear to be any large (male) mandibles of this species in the collection.

An attempt has been made to illustrate this variation in Figs 26–27. These show the mean and 95% confidence limits for dimensions of M^1 and M^3. In certain cases the samples were considered too small to calculate the standard deviation, and in these cases the total range of the sample is shown by dashed lines instead of the 95% confidence limits.

Dendropithecus macinnesi is shown to have high ranges of variation, higher than *Hylobates* and the joint sample of *Pliopithecus*: *P. antiquus* and *P. vindobonensis*. *D. macinnesi* has a lower absolute variation than the chimpanzee, but this is to be expected in a smaller animal, and the M^1 is nearly as variable as in *Papio ursinus* (Freedman 1957).

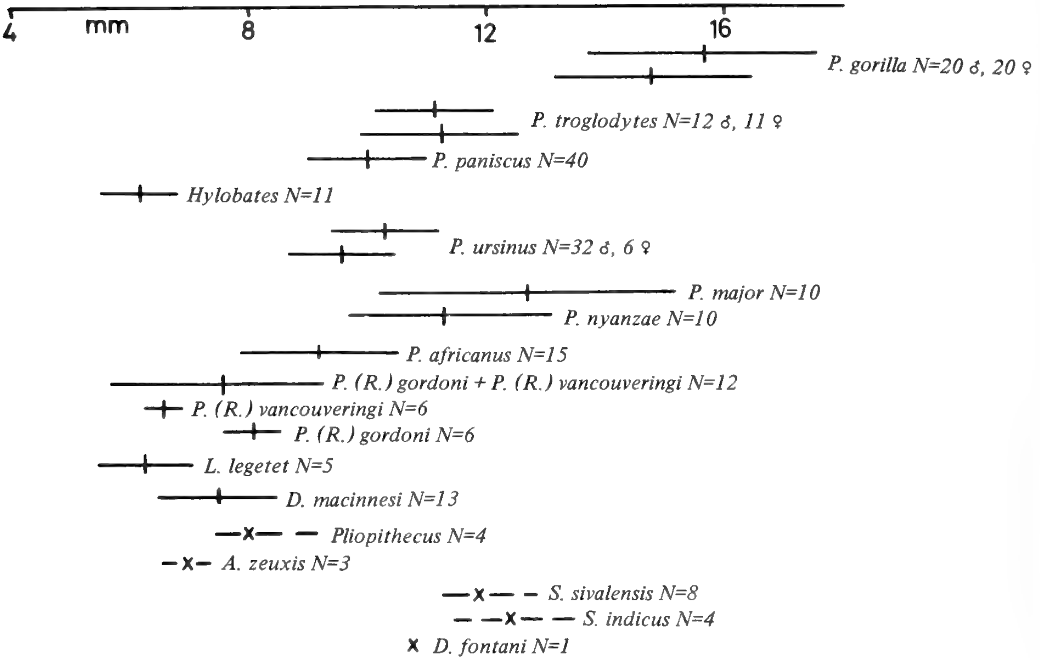

Fig. 26 Variation in M^1 buccolingual breadth (bl): 95% confidence limits.

Table 24 Standardized variation of dental mesiodistal lengths.

md	*D. macinnesi*	*P. (R.) gordoni*	*P. (R.) vancouveringi*	*L. legetet*	*P. africanus*	*P. nyanzae*	*P. major*
$\underline{C}$	61	35	–	38	52	39	30
M^1	24	15	21	20	26	39	45
M^2	32	–	–	22	35	–	–
M^3	44	–	–	30	36	41	–
$\overline{C}$	53	–	–	47	31	32	–
M_1	24	24	–	21	20	23	30
M_2	21	17	–	22	21	36	–
M_3	38	47	–	32	31	44	–

Limnopithecus legetet is much less variable than *D. macinnesi* and is on a similar level with the comparable-sized *Hylobates*. It is quite distinct from *P. africanus* and *P. (R.) gordoni* with no points of overlap in range. The latter two species are similar in size, but since they are distinguished entirely by morphological differences this similarity is not significant. More important is the overlap between *P. africanus* and *P. nyanzae*, and between *P. nyanzae* and *P. major*. There are a number of morphological features distinguishing the first pair, but it is difficult to separate the latter two morphologically. However, the range for M^1 of *P. major* exceeds that of the gorilla and that of *P. nyanzae* approximates to that of the chimpanzee (including the pygmy chimpanzee), and a *t*-test on the statistical difference between the samples gives a probability of 0·02 that they represent

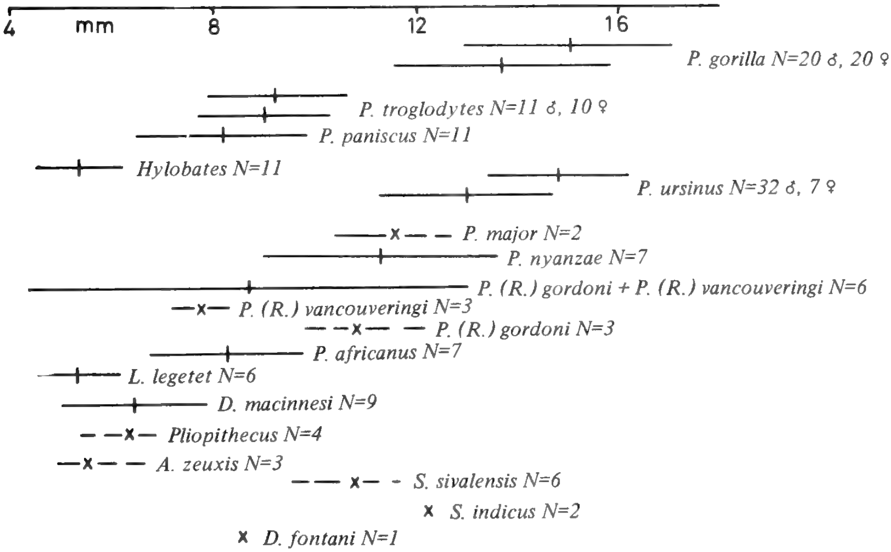

Fig. 27 Variation in M^3 buccolingual breadth (bl): 95% confidence limits.

a single population. On this evidence, therefore, it is unlikely that *P. nyanzae* and *P. major* belong to the same species.

A similar problem was faced with the two *Rangwapithecus* species, *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi*, although in this case there is no overlap in size ranges. Experimental combined sample ranges of these two species were calculated for Figs 26 and 27. In the case of M^1 this combined range equals that of the chimpanzee and is less than that of the gorilla, both much larger animals, while for M^3 their combined range is nearly twice that of the gorilla. A *t*-test on the differences between the means of the two samples of M^1 gives a probability of much less than 0·001 that they could come from one population. This is strong evidence for some degree of separation between the two groups, and is considered sufficient here to justify specific separation.

A final attempt to quantify the variation in the samples of Miocene apes was by means of multivariate analysis. The results are presented here of an untransformed cos θ analysis (Andrews 1973; Andrews & Williams 1973) based on the incisor and canine dimensions together with those of the symphysis and premaxilla. This method has removed the primary effects of size, but it has failed to distinguish between size-related shape changes (allometric) and structural changes in morphology. Similar analyses of the 'sectorial' dentition (Cs, P_3, P^3, symphysis and anterior mandible and maxilla dimensions) and the posterior dentition (upper and lower P4–M3, posterior mandible and maxilla dimensions) gave similar results, but transformed or unnormalized analyses were so heavily weighted by size differences that they provided no new information.

The removal of size as the dominant influence in the multivariate analysis can be seen in the distribution of individuals in Fig. 28. The basic division seems to be between species with relatively high-crowned canines and small symphyseal areas on the left, particularly the modern hylobatids, and species with lower-crowned but more massive canines, large incisors, and more robust symphyses on the right. This is consistent with morphological evidence, the gibbon having the most exaggeratedly high-crowned canines; this feature is shared, though to a lesser degree, by *Aegyptopithecus*, *Pliopithecus*, and *Dendropithecus macinnesi*. *Limnopithecus legetet* with its large incisors, small canines and small symphseal area is predictably midway between the chimpanzee and *P. africanus*, and these form a group with *P.* (*R.*) *gordoni* at the opposite end of the scale from the hylobatids. The slight divergence of *P. major* and the gorilla and orang-utan may be significant, but it is difficult to be certain on the available evidence.

The multivariate analysis was not as informative as was hoped, but some interesting points have emerged. The analysis of the anterior tooth measurements, as shown in Fig. 28 and four other sets of calculations not shown here, points to a high degree of correlation between canine cross-sectional area, incisor heights, and symphysis cross-sectional area. Canine heights are negatively correlated with these in the multivariate function. Discriminating principally by these factors, the analyses distinguish the hylobatids, with their high-crowned canines and small symphyses, from the pongids with relatively low-crowned canines and large symphyses. Linked with the modern hylobatids are *A. zeuxis*, *Pliopithecus* spp., and *D. macinnesi*; with the modern pongids are linked all the dryopithecines including *L. legetet*.

The analysis of the sectorial tooth measurements points to a positive correlation between upper and lower canine heights. The heights of the main cusp in both upper and lower P3 were negatively correlated with canine heights in the multivariate function but generally positively correlated with P4 size. This is puzzling and indicates that the multivariate function, while discriminating mainly on the degree of sectorial development of the dentition, is not entirely limited to this functional complex. The results show that, while the modern hylobatids have a higher degree of sectoriality than fossil hylobatids, the modern pongids have a lower degree of sectorality than the fossil pongids. It does not seem possible to generalize further than this, and it is unlikely that individuals at the smaller end of the size-range can be compared directly with those at the larger end.

The analysis of the posterior tooth measurements points to a negative correlation between anterior mandibular widths (and symphyseal area) and tooth row lengths. This served to distinguish the modern pongids from all the rest on the basis of their deep symphyses and great anterior widths of the mandible. At the opposite extreme was *A. zeuxis* with its posteriorly-diverging tooth rows.

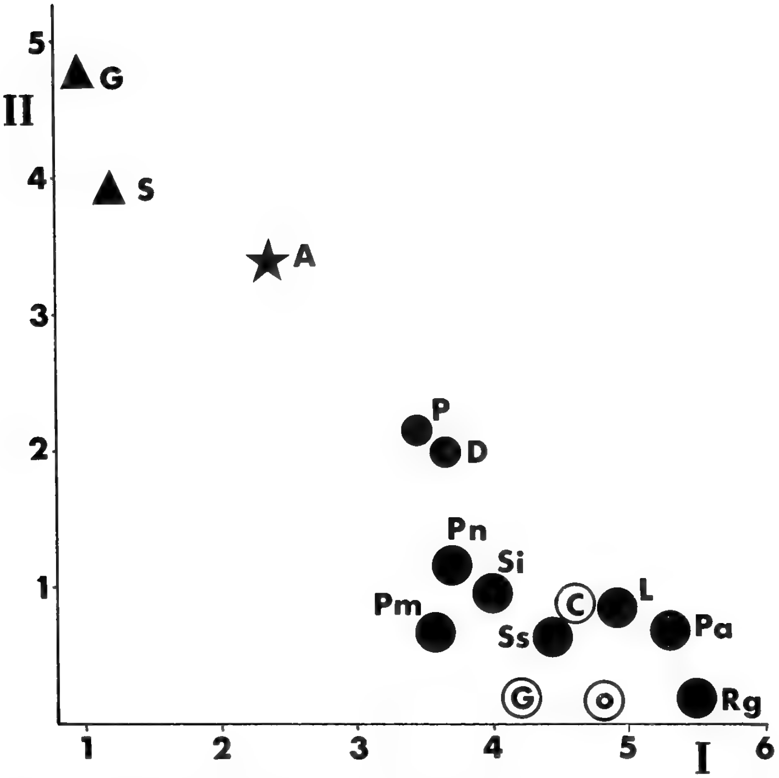

Fig. 28 Principal components analysis of the anterior dentition, principal components I and II. Key: G Gibbon, S Siamang, C Chimpanzee, G Gorilla, O Orang-utan; Pa *Proconsul africanus*, Rg *Proconsul* (*Rangwapithecus*) *gordoni*, Si *Sivapithecus indicus*, Pm *P. major*, Pn *P. nyanzae*, Ss *S. sivalensis*; D *Dendropithecus macinnesi*; L *Limnopithecus legetet*; P *Pliopithecus* species; A *Aegyptopithecus zeuxis*.

Ecology of the African Miocene Hominoidea

It has recently been shown (Andrews 1973, pt. II; Andrews & Van Couvering 1975) that the Miocene apes of Africa probably inhabited forest environments. In the early Miocene the continental divide separating the western equatorial forests from the eastern arid zone was, in the absence of the East African highlands, along the edge of the present eastern rift valley (see Fig. 1). As a result, the western part of East Africa, where most of the Miocene sites are located (see Fig. 1), was probably geographically and climatically part of what is now the Congo basin, so that the equatorial lowland forests, at present limited by the wall of the western rift (Keay 1959), covered most of this region. Forest-adapted land gastropods (Verdcourt 1963) and small mammals in the fossil faunas, and forest trees in the floras (Chesters 1957; Andrews & Van Couvering 1975), correlate with this in suggesting that these sites were sampling forest environments.

A number of fossil ape species have been found in direct association with forest faunas. Association here means at the same level in an excavation, so that probably only one depositional event is represented. (There is no guarantee, of course, that all the bones deposited together come from animals living at the same time in the same place.) *Dendropithecus macinnesi* and *Proconsul africanus* are known from two excavations each on Rusinga Island in association with faunas with strong forest affinities (Clark & Thomas 1951; Whitworth 1953; Verdcourt 1963, 1972; Andrews 1973; Andrews & Van Couvering 1975). Similarly, *Limnopithecus legetet*, *P. major*, and *P.* (*R.*) *gordoni* are each known from two excavations at Songhor in association with similar

Table 25 Distribution of Miocene pongids and hylobatids in Africa (numbers of individuals).

Rusinga	*P. africanus*	*P. nyanzae*	*P. major*	*P. (R.) gordoni*	*P. (R.) vancouveringi*	*L. legetet*	*D. macinnesi*
R1	3	8	–	–	–	1	9
R3	6	3	–	–	–	1	11
Kamugeri	–	–	–	–	–	–	1
Hiwegi general	1	2	–	–	–	–	2
Hiwegi total	10	13	–	–	–	2	23
R100–105	3	1	–	–	–	1	3
R106	6	6	–	–	2	1	4
R107–112	1	4	–	–	–	–	1
Kiahera Hill	–	3	–	–	–	1	1
Kiahera total	10	14	–	–	2	3	9
Kaswanga	13	13	–	–	1	1	12
Sienga	2	–	–	–	–	–	–
Wanyama	–	1	–	–	–	–	–
R114	1	–	–	–	–	–	–
Gumba	1	–	–	–	–	1	–
R2	1	2	–	–	–	1	4
R4	–	1	–	–	–	–	1
Wakondu	–	–	–	–	–	–	1
Kulu total	1	3	–	–	–	1	6
R113 (Kamasengere)	3	3	–	–	–	–	4
R73 (Kalim)	–	1	–	–	–	–	–
Locality unknown	–	3	1	1	–	–	6
Rusinga total	41	51	1	1	3	8	60
Mfwangano	5	3	–	1	1	–	5
Karungu	–	2	–	–	–	–	1
Songhor	5	–	15	17	3	19	12
Koru	3	–	3	–	–	6	2
Losidok	–	–	2	–	–	–	–
Maboko	?	3	–	–	3	2	–
Fort Ternan	2	3	–	–	–	4	–
Ombo	–	–	–	–	–	1	–
Kirimon	–	–	1	–	–	–	–
Moroto	–	–	1	–	–	–	–
Napak	–	–	8	–	–	10	–

faunas. *P.* (*R.*) *vancouveringi* is too little known for any conclusions to be drawn, and the remaining species, *P. nyanzae*, is the only one found in associations suggesting non-forest conditions.

It has previously been pointed out (Andrews 1973; Andrews & Van Couvering 1975) that in the African Miocene the apes may have occupied the ecological niches now fully taken over by the cercopithecoid monkeys. The Miocene apes were in general smaller than those of the present day, the range of estimated sizes being from that of a small *Cercopithecus* monkey, e.g. *C. aethiops*, to about the size of a female gorilla. The study of the limb bones, not yet completed, suggests that the species of *Proconsul* had a more generalized monkey-like arboreal form of locomotion than do the modern apes (Clark & Leakey 1951; Clark 1952; Napier & Davis 1959). At the same time, there is little evidence of the presence of monkeys in the early Miocene environments (Pilbeam & Walker 1968; Simons 1969; Delson 1973), which, being similar in structure to present-day forests, must have provided suitable niches for monkey-like primates. It is logical to assume that the relatively monkey-like dryopithecines occupied part at least of this habitat.

It can be seen that up to five species of dryopithecines can occur in the same deposits (Table 25). Two or three of the species may be very common and the others less so. In addition, the single species of *Dendropithecus* also occurs, making a total of six species for at least two localities: see Table 25. This number of species, while unlike the distribution of modern apes, is very like that of the forest monkey distributions, where there can be three to five species of *Cercopithecus*, one species of the more arboreal *Colobus*, sometimes a species of *Cercocebus*, and one species of the more terrestrial *Papio* all in the same patch of forest (Booth 1956, 1957, 1958; Rahm 1965; Dorst & Dandelot 1970; Kingdon 1971; Preuschoft 1973; Groves, Andrews & Horne 1974; Andrews, Groves & Horne 1975; Morbeck 1975). The proliferation of Miocene ape species, from being unlikely when compared with modern ape distributions, becomes more acceptable if they were ecological equivalents of monkeys.

The comparison of the Miocene apes with the Recent cercopithecines can be carried a stage further. Just as the Recent species of *Cercopithecus*, *Erythrocebus*, *Miopithecus*, *Cercocebus* and *Papio* seem to be representatives of a late Neogene radiation of cercopithecine monkeys, so the Miocene ape populations also seem to be representatives of an earlier Neogene radiation. At least two sets of species were so similar to each other as to make their distinction merely one of size, namely *P. nyanzae/major*, and *P.* (*R.*) *gordoni/vancouveringi*; the other two dryopithecines, while more distinct, were still very similar to the others and to each other. In addition, *Dendropithecus macinnesi* is divided into two distinct geographical forms. The site differences between these pairs suggests either temporal or geographical speciation, or perhaps a mixture of both (see Table 25).

Phylogeny of the Miocene Hominoidea

The Hominoidea are divided into at least three families, the Pongidae, Hylobatidae, and Hominidae. The taxonomic position of controversial forms such as *Ramapithecus* and *Oreopithecus* are beyond the scope of this paper, and only those species that can with a fair degree of certainty be placed in the Pongidae or Hylobatidae are considered here. The main phylogenetic conclusions are presented in Fig. 29.

Dendropithecus macinnesi is included in the Hylobatidae. Not enough is known to say whether it may have been ancestral to modern gibbons, but there is nothing in its morphology that excludes the possibility. There are even some indications that it may have been near the main line of hylobatid evolution, particularly in the limb bone morphology and in the sectorial function of the canines and third premolars (Andrews 1973; Andrews, Simons & Pilbeam 1977). The latter, however, are probably primitive retentions from the ancestral hominoid stock (Delson & Andrews 1975) and therefore cannot be considered as evidence of phylogenetic relationship, except in so far as the contemporary dryopithecine species, like their descendant pongine species, lack these characters. Similarly, the great degree of similarity between *Dendropithecus macinnesi* and *Aegyptopithecus zeuxis* (see Andrews 1970) is based mainly on retention of presumed primitive hominoid characters in both, notably the deep symphysis and body of the mandible, the high-crowned narrow incisors and canines, the sectorial specialization of P_3, and the buccolingual

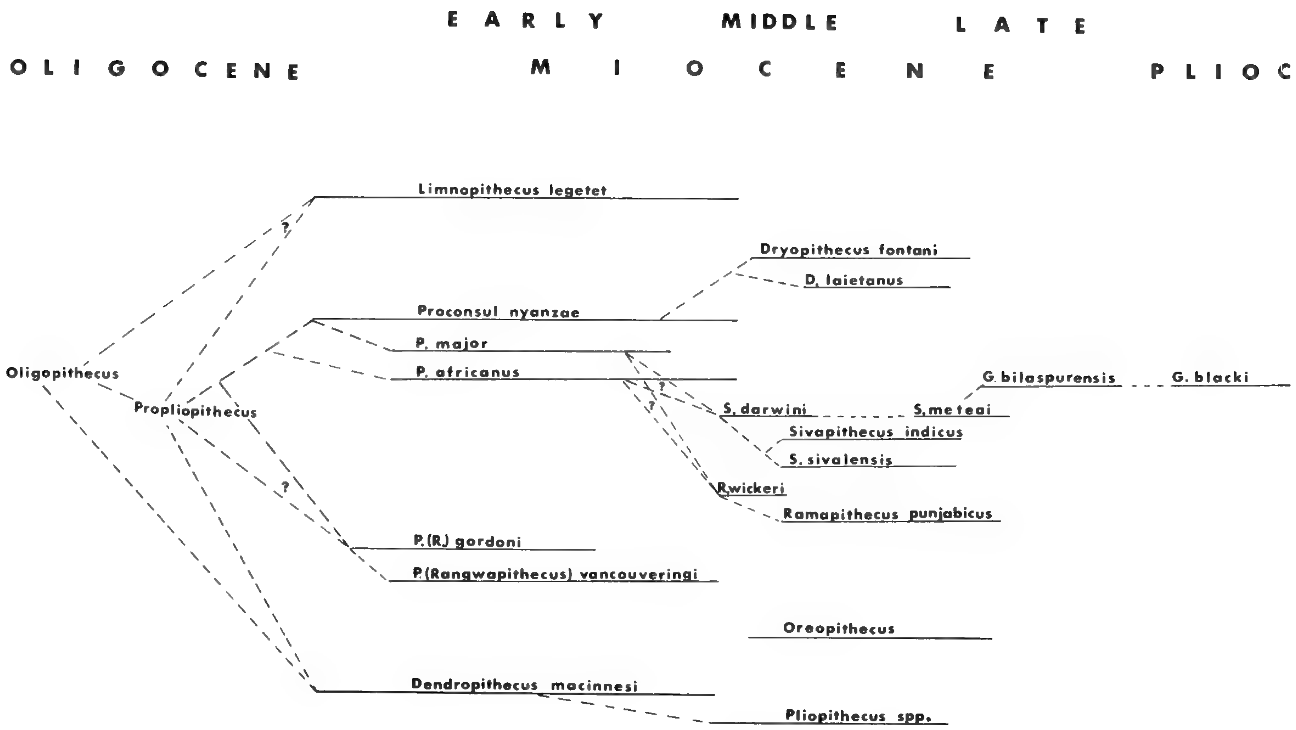

Fig. 29 Phylogeny of the Miocene Hominoidea. Solid lines indicate the life of the species as known at present from the fossil record, and dashed lines indicate possible relationships. If more than one phylogenetic possibility is shown the lines are separated by a '?'. For the purpose of this diagram the Oligocene/Miocene boundary is taken at 23 m.y. and the Miocene-Pliocene boundary at 5 m.y. ago.

expansion and cingulum development of the upper premolars and molars (Delson & Andrews 1975). Since both species have a few presumed derived characters not present in the other, for instance the elongated triangular M_3 and broad ascending ramus in *A. zeuxis*, and the reduced lower molar cingula and large talonid basins of *D. macinnesi*, it makes a direct link between them less plausible.

This matter cannot rest here, however, for there is still dispute over the identification of some of the specimens from the Egyptian Fayum. *Aegyptopithecus zeuxis* was first described by Simons (1965) on the basis of three mandibular specimens. He later added three more mandibular specimens to this species (Simons 1967a : fig. 2; 1971 : fig. 7; Simons & Pilbeam 1972 : pl. 2-1), all from Quarry I of the Fayum (Simons 1967), and a nearly complete skull from Quarry M (Simons 1967). Of these the skull (YPM 23975) and one mandible (CGM 29135) clearly belong with the three specimens of *A. zeuxis* originally described in 1965, but the others, an immature mandible (YPM 23804) and an adult mandible (YPM 23944) are much more similar to the type and only specimen of *Propliopithecus haeckeli* (Schlosser 1911). *P. haeckeli* is very similar to *A. zeuxis*, differing in being slightly smaller and in lacking the specializations of mandible, molar cusp and cingulum morphology, and M_3 enlargement, that characterize *A. zeuxis*. This is the same suite of presumed derived characters that distinguishes between *A. zeuxis* and *D. macinnesi*, and their absence in *P. haeckeli* raises the possibility that it is directly related to *D. macinnesi*. There is, however, too little material of *P. haeckeli* available for such a relationship to be established, and also there is too big a time gap separating the Oligocene from the early Miocene forms.

Propliopithecus is known both from Quarry G and from Quarry I in the Fayum deposits, thought by Simons to be at least 28–30 million years old (Simons 1967). This compares with *D. macinnesi* which is known from the deposits, more than 22 m.y. old, at Karungu (Bishop, Miller & Fitch 1969), and the slightly later deposits at Songhor and Rusinga Island. There is probably thus a time gap of at least 5–6 m.y. between the latest occurrence of *Propliopithecus* and the earliest appearance of *D. macinnesi*, which will need to be filled before it is possible to make any positive statement on the relationships between them.

Simons (1965) suggested that *Aegyptopithecus zeuxis* is similar to later dryopithecines, particularly *P. africanus*. This was based mainly on the lower molar and mandibular morphology. All of the *Aegyptopithecus* specimens known come from the highest levels of the Fayum, Quarry I and M, so that there must again have been a time gap of at least 5 m.y. between these and the earliest known dryopithecine from Kenya.

It has been mentioned earlier that *D. macinnesi* is extremely similar dentally to the European species of *Pliopithecus*. *Pliopithecus* is known in Europe from slightly earlier than 15 m.y. ago to slightly earlier than 12 m.y. After this nothing is known of fossil gibbons until a comparatively recent date, so that on the one hand there is a gap of about 4 m.y. separating *Dendropithecus* and *Pliopithecus*, and about 12 m.y. separating the latter from modern apes. The reason for distinguishing *Dendropithecus* from *Pliopithecus* lies in the post-cranial morphology of the two taxa. In both cases partial skeletons are known associated with cranial and dental remains, and while the limb bones have many points of similarity, those of *D. macinnesi* are more elongated and gibbon-like than those of *Pliopithecus*. This alone is sufficient to suggest that the former was closer to the main line of gibbon evolution than the latter, but there are also some other features of *Pliopithecus* that corroborate this, such as the lack of development of an external auditory meatus, the presence of an entepicondylar foramen on the distal extremity of the humerus (Zapfe 1960), and the absence of laterally placed meniscus markings on the ulnar styloid process (Lewis 1970, 1971). These are primitive features, and their presence does not, therefore, rule out the possibility of *Pliopithecus* being a hylobatid, but it does make it unlikely that it was directly ancestral to any of the living gibbons since in at least one feature the much earlier *Dendropithecus macinnesi* has the derived gibbon morphology in addition to more advanced limb bones.

The relationships of the species of *Proconsul* to the European and Asian species of *Dryopithecus* are still highly conjectural. The earliest dryopithecine known in Eurasia occurs in somewhat later deposits than those of *Pliopithecus*, so that there is a gap in the fossil record of at least 5 m.y. The presence of three of the African early Miocene dryopithecine species at Fort Ternan, more or less contemporary with the occurrence of the earliest Eurasian dryopithecines, does not help to fill the gap, as the specimens assigned to *Proconsul africanus*, *P. nyanzae* and *Limnopithecus legetet* appear quite typical of the early Miocene forms of these species and show no signs of evolution towards the Eurasian forms.

There is, however, an increasing body of evidence that the Eurasian dryopithecines did evolve from one or other of the African species. *D. fontani* is extremely similar to *P. nyanzae*, particularly in its lower dentition, but differs in having less elaborated upper molars, which lack lingual cingula, and in having an inferior transverse torus of the symphysis as compared with the superior torus of *P. nyanzae*. Similarly, *S. indicus* is similar to *P. major*, but in this case there are some known morphological intermediates. These are found in a recent collection of about 65 isolated teeth made by Professor H. Tobien at Pasalar in Turkey. The teeth, representing the nearly complete dentition of a large dryopithecine, are from early Middle Miocene deposits as old as the oldest *Pliopithecus* specimens from Europe (Andrews & Tobien 1977). They are thus earlier in time than any known specimen of *S. indicus*, and, although they resemble that species, they have a number of differences which must exclude them from it. The lower molars have retained the buccal cingula and narrow trigonid present in *Proconsul*, while the incisors and premolars are intermediate between *Proconsul* and *S. indicus*. The upper molars are entirely typical of the latter species.

Unfortunately the mandibular and maxillary structure of *Sivapithecus darwini* from Pasalar is unknown. The structure of the mandible is particularly important because the early Miocene *Proconsul–Limnopithecus* group has a highly specialized mandibular morphology. The primitive condition in the anthropoid mandibular symphysis appears to have included an inferior torus (Delson & Andrews 1975), as is present in *Aegyptopithecus*, and the presence in *Proconsul* and *Limnopithecus legetet* of a superior torus, with no inferior torus, is therefore a derived or specialized condition. The later Eurasian dryopithecines, however, all have an inferior torus rather than a superior one, and the possibility must be considered that they evolved from an early Miocene form that similarly retained the inferior torus. *Proconsul* and *Limnopithecus* are excluded from this because of their superior torus, and there is no established alternative.

Arising out of the possibility that *Proconsul* may not have been ancestral to later dryopithecines, special mention must be made of '*Sivapithecus africanus*'. This taxon, first described by Clark & Leakey (1951), and reassigned by Simons & Pilbeam (1965) to *Dryopithecus* (*Sivapithecus*) *sivalensis*, is only known from one specimen, and because of this it is included here with *Proconsul nyanzae* on the basis of size. It is difficult to do otherwise considering the fragmentary nature of the specimen (maxilla with P^3–M^1), but it has a number of distinctive characters that would be important if supported by additional material, characters such as the greatly enlarged premolars, the thick enamel and reduction of lingual cingula, and the buttressing of the alveolar process of the maxilla. It could be that '*Sivapithecus africanus*' will prove to be closer to the line of descent of later Miocene dryopithecines than is *Proconsul* when additional material is recovered.

The most recently-occurring dryopithecine species are known from material from Greece and Turkey. These are late Miocene in age and similar to *Sivapithecus indicus* except that they are much larger. '*Ankarapithecus meteai*', first described for a single mandibular specimen (Ozansoy 1955, 1957), is now known from other specimens (Andrews & Tekkaya, in prep.). It was synonymized with *Dryopithecus indicus* by Simons & Pilbeam (1965), but the additional material makes it look quite different, so that it should stand as a valid species, albeit of *Sivapithecus*, not '*Ankarapithecus*'. Very similar to it, but probably not belonging to the same species, is a more recently described specimen from similar-aged deposits in Greece, *Dryopithecus macedoniensis* (de Bonis *et al.* 1974). These new specimens from Greece and Turkey differ from *S. indicus* in a few characters, but the main difference is that they are very much larger, approaching *Gigantopithecus* in size and suggesting a close relationship with the *Gigantopithecus* lineage.

There is too big a time gap between the Miocene and the present to attempt to say anything on possible phyletic relations between the dryopithecines and living pongids. There are a number of features which suggest strongly that the African dryopithecines as a whole were ancestral to the living great apes. For instance, the articulation of the wrist joint with the ulnar styloid process is very characteristic in all living apes, and something like this condition was present in *P. africanus*, more advanced than in modern hylobatids but less so than in the great apes (Lewis 1970, 1972).

It would appear from this that *P. africanus* was a part of the pongid lineage after the hylobatids had already become differentiated, a conclusion entirely consistent with the evidence presented here.

Another feature linking fossil and modern apes is the presence of a frontal sinus in *P. major*. This is a feature shared only by *Pan* in living pongids and by hominids. It would seem to preclude *P. major* from being in any way ancestral to the orang-utan, and if it is found that the other Kenya dryopithecines also have frontal sinuses it would suggest that the orang-utan also had become differentiated at this time.

A third set of characters in the post-cranial morphology of *P. africanus* suggest that it was developing towards the condition seen in modern species of *Pan*. The distal extremity of the humerus in particular, and the dimensions of the deltoid crest and the size and robusticity of the radius all foreshadow the condition in *Pan* and are distinct from other species of primate. This is not to say that *P. africanus* was a knuckle-walker, but it does indicate that its morphology, and therefore perhaps its method of locomotion, had some of the prerequisites for developing knuckle-walking locomotion. Also in the post-cranial morphology, *D. macinnesi* has many features that might be expected in a gibbon ancestor. Particularly the long slender limb bones, the general lack of development of the muscular markings on the limb bones, and the rounded nature of the distal articular surface of the humerus, which lacks any prominent heels, all contribute to the gibbon-like appearance of the limb bones.

Pilbeam (1969) has concluded that because of the similarities between *P. major* and the gorilla they are on the same lineage, with the fossil ape directly ancestral to the gorilla. These similarities are listed by Pilbeam (1969 : 124) – marked sexual size dimorphism, males having large projecting canines and relatively prognathous faces, and trends towards the more lophodont and hypsodont molar of the male gorilla. These points of similarity are valid, but they are all size-related features, and it is likely that any large ape would have similar morphology. *Gigantopithecus* has some of these features but not others. In view of the time separating *P. major* from the present-day gorilla, these size-dependent features are poor evidence for substantiating an ancestor–descendant relationship between them. This is also true of the hypotheses put forward to link *P. africanus* with the chimpanzee.

It may be concluded, however, that the Kenya dryopithecines as a whole may have given rise to some of the living pongids, especially the African ones. There is no evidence other than that of size to connect any of the fossil species with any one of the living ones. Similarly the single hylobatid species *D. macinnesi* may have been ancestral to modern hylobatids as a whole.

Appendix I

Summary of exploration of East African Miocene Sites

Year	*Worker*	*Site*	*Description of material*
1909	R. Chesnaye, (C. W. Hobley), D. B. Pigott	Muhoroni, Koru and Karungu	Andrews 1911
1911	F. Oswald	Karungu	Oswald 1914, Andrews 1914
1926	H. L. Gordon	Koru	hominoid maxilla
1927	(E. J. Wayland)	Koru	2 hominoid incisors
1931	A. T. Hopwood	Koru	9 further hominoid specimens all described, Hopwood 1933a
1931–32	L. S. B. Leakey	Rusinga Island	several hominoids
	D. MacInnes	Songhor	2 hominoids, Keith 1932
1932	E. Nielsson	Koru	hominoid mandible

Year	*Worker*	*Site*	*Description of material*
1933	W. E. Owen	Ombo, Maboko, Mariwa, Majiwa, Uyoma	
	C. Arambourg	Losidok	Arambourg 1933
1934	V. E. Fuchs, D. MacInnes	Losidok	
	D. MacInnes	Maboko excavations	hominoid limb bones
		Songhor	more hominoid fossils
1934–35	L. S. B. Leakey, P. E. Kent	Rusinga Island	more hominoid fossils Kent 1944
1938	D. MacInnes	Songhor	more hominoid fossils
1940	L. S. B. Leakey	Rusinga Island	more hominoid fossils
1942	L. S. B. Leakey	Rusinga Island	more hominoid fossils Leakey 1943, MacInnes 1943
1944	R. M. Shackleton	Maralal	Shackleton 1946
	F. Dixey	Loperot	Dixey 1944
1947	K. P. Oakley, D. M. A. Bate, J. Waechter, L. S. B. Leakey	Rusinga Island, Mfwangano Island	'further important Miocene fossils were found'; Clark & Leakey 1951 : 2
1947	British–Kenya Miocene Expedition	Rusinga Is.; visits to Mfwangano, Karungu, Koru, Uyoma	64 specimens of hominoids; Clark & Leakey 1951, and 6 not described
	R. M. Shackleton	Mtete Valley (Songhor)	
	D. MacInnes	Tambach, Maboko	1 specimen of hominoid
1948	University of California Expedition	Losidok, Moruorot	3 specimens of hominoid; Madden 1972
	British–Kenya Miocene Expedition	Rusinga Island	57 specimens of hominoid
		Songhor	48 specimens of hominoid; Clark & Leakey 1951, Clark & Thomas 1951
	L. S. B. Leakey	Loperot, new site at Koru	2 specimens of hominoid
1949	British–Kenya Miocene Expedition	Rusinga Island	21 specimens of hominoid
		Mfwangano Island	2 specimens of hominoid
		Songhor	31 specimens of hominoid
	L. S. B. Leakey	Kirimon	Clark & Leakey 1951
		Mbgathi	Clark 1952
	D. G. MacInnes	Maboko	
1950	British–Kenya Miocene Expedition	Rusinga Island	69 specimens of hominoid
		Karungu	3 specimens of hominoid
		Koru	4 specimens of hominoid
		Mfwangano	4 specimens of hominoid
		Songhor	6 specimens of hominoid; Clark 1952
1951	T. Whitworth	Rusinga Island at Gumba	Dryopithecine forelimb; Napier & Davis 1959
	British–Kenya Miocene Expedition	Rusinga Island	60 specimens of hominoid
		Mfwangano	2 specimens of hominoid; Whitworth 1953, Clark 1952
	L. S. B. Leakey, D. G. MacInnes	Moruorot, Losidok	3 specimens of hominoid

Year	*Worker*	*Site*	*Description of material*
1952	L. S. B. Leakey	Rusinga Island Mfwangano	12 specimens of hominoid 5 specimens of hominoid
1955	L. S. B. Leakey	Rusinga Island	2 specimens of hominoid
	T. Whitworth, R. J. G. Savage	Mfwangano	10 specimens of hominoid; Whitworth 1961
1956	Rosalie Osborn	Rusinga Island	33 specimens of hominoid
1958	L. S. B. Leakey	Rusinga Island	4 specimens of hominoid
1961	W. W. Bishop	Songhor	1 specimen of hominoid
1962	L. S. B. Leakey	Songhor	34 specimens of hominoid
1966	L. S. B. Leakey	Songhor	130 specimens of hominoid; Andrews 1970, 1974
1967	J. A. Van Couvering	Rusinga Island	4 specimens of hominoid; Leakey 1968
1968	J. A. Van Couvering	Rusinga Island	2 specimens of hominoid; Van Couvering & Miller 1969, Andrews 1974
1970	P. J. Andrews	Songhor	27 specimens of hominoid
1971	P. J. Andrews, J. A. Van Couvering	Rusinga Island	18 specimens of hominoid; Andrews & Van Couvering 1975
1972	P. J. Andrews	Songhor	30 specimens of hominoid
1973	D. R. Pilbeam, P. J. Andrews, J. A. Van Couvering	Maboko	10 specimens of hominoid
	P. J. Andrews	Karungu	

Appendix II

Summary of specimens available for study

	described	undescribed	Totals
D. macinnesi	49	111	160
P. (R.) gordoni	27	52	79
P. (R.) vancouveringi	1	9	10
L. legetet[1]	41	75	116
P. africanus[2]	73	45	118
P. nyanzae[3]	65	38	103
P. major[4]	19	34	53
Pongidae indet.	1	4	5
Totals	276	368	644

Detailed lists giving brief descriptions of the specimens assigned to each species, with their Museum collection numbers and published references, are deposited in the Palaeontology Library of the British Museum (Natural History).

[1] 57 additional specimens referred to this species, 20 from Fort Ternan and Maboko Island and 37 from Napak, Uganda.

[2] 2 additional specimens referred to this species from Fort Ternan.

[3] 6 additional specimens referred to this species from Fort Ternan.

[4] 28 additional specimens referred to this species, 24 from Napak and Moroto, Uganda, and 4 from Losidok, Moruorot and Kirimon.

Appendix III

List of specimen field numbers used by earlier workers with the equivalent permanent accession number used in this work. In addition to the field numbers, Pilbeam (1969) used a further set of numbers which put the field numbers roughly into numerical order. These are given in the first column. Examples of Pilbeam's numbering system are 1, CMH 1 and 271, 55.

Numerical order	Field no.	Permanent accession no.
1	CMH 1	KNM-RU 1674
	CMH 2	BM(NH) M 16647
5	CMH 3	KNM-RU 1677
4	CMH 4	KNM-RU 1676
6	CMH 5	KNM-RU 1678
	CMH 6	BM(NH) M 16649
7	CMH 7	KNM-RU 1679
8	CMH 8	KNM-RU 1680
	CMH 9	KNM-RU 1681
	CMH 10	KNM-RU 1685
	CMH 11	KNM-MB 104
	CMH 12	KNM-RU 1682
	CMH 13	KNM-RU 1684
	CMH 14	KNM-SO 373
	CMH 15	KNM-RU 1685
	CMH 16	KNM-RU 1686
	CMH 17	KNM-RU 1687
	CMH 18	KNM-RU 1688
	CMH 19	not primate
	CMH 20	lost
	CMH 21	KNM-RU 1690
	CMH 23	KNM-RU 1691
95	CMH 24	KNM-SO 375
	CMH 26	KNM-SO 942
	CMH 26	KNM-MB 107
	CMH 27	KNM-RU 1692
	CMH 28	KNM-RU 1747
	CMH 29	KNM-MB 108
23	CMH 30	KNM-RU 1694
24	CMH 31	KNM-RU 1695
25	CMH 32	KNM-RU 1696
	CMH 33	KNM-RU 1697
101	CMH 34	KNM-SO 381
102	CMH 35	KNM-SO 382
	CMH 36	KNM-SO 1086
	CMH 39	KNM-MB 125
	CMH 40	KNM-RU 1698
	CMH 41	KNM-RU 1699
	CMH 42	KNM-RU 1700
	CMH 43	KNM-RU 1701
	CMH 44	KNM-RU 1702
	CMH 45	KNM-RU 1749
	CMH 46	KNM-RU 1704
	CMH 47	KNM-SO 383
	CMH 48	lost
34	CMH 101	KNM-RU 1705
35	CMH 102	KNM-RU 1706
	CMH 103	KNM-RU 1707
	CMH 104	KNM-SO 385
	CMH 105	KNM-SO 386
	CMH 106	KNM-SO 387
	CMH 107	KNM-SO 388
	CMH 108	KNM-RU 1708
38	CMH 109	KNM-RU 1709
39	CMH 110	KNM-RU 1710
	CMH 111	KNM-RU 1711
41	CMH 112	KNM-RU 1712
	CMH 113	KNM-RU 1713
	CMH 114	lost
44	CMH 115	KNM-RU 1714
	CMH 116	KNM-RU 1715
	CMH 117	KNM-RU 1716
	CMH 118	KNM-RU 1717

Numerical order	Field no.	Permanent accession no.
	CMH 119	KNM-RU 1718
	CMH 120	KNM-RU 1719
50	CMH 121	KNM-RU 1720
	CMH 122	KNM-RU 1721
	CMH 123	KNM-RU 1722
	CMH 124	KNM-RU 1723
	CMH 125	KNM-RU 1724
	CMH 126	KNM-RU 1725
	CMH 127	KNM-RU 1726
	CMH 128	KNM-RU 1727
58	CMH 129	KNM-RU 1728
	CMH 130	not primate
	CMH 131	KNM-RU 1730
	CMH 132	KNM-RU 1731
	CMH 133	KNM-RU 1732
	CMH 134	KNM-RU 1733
64	CMH 135	KNM-RU 1734
65	CMH 136	KNM-RU 1735
	CMH 137	KNM-RU 1736
	CMH 138	KNM-RU 1737
	CMH 139	KNM-RU 1738
	CMH 140	KNM-RU 1739
	CMH 142	KNM-RU 1740
	CMH 143	KNM-RU 1741
	CMH 144	KNM-RU 1742
	CMH 147	KNM-RU 1743
	Rs C8	KNM-RU 1693
	72-41	KNM-RU 1758
113	F 3104	KNM-SO 391
	SH	KNM-SO 380
90	SD 4	KNM-SO 371
	S 5	KNM-SO 376
	S 5	KNM-SO 395
	S 13	KNM-SO 378
	S 15	KNM-SO 375
	S 17	KNM-SO 370
	S 19	KNM-SO 373
94	S 21	KNM-SO 374
	S 44	KNM-SO 384
	S 54	lost
91	S 9′38	KNM-SO 372
		KNM-SO 377
	1947 – Rusinga	
	60	KNM-RU 1762
	142	KNM-RU 1763
125	143	KNM-RU 1764
	144	KNM-RU 1765
129	257	KNM-RU 1767
	258	KNM-RU 1768
131	342	KNM-RU 1769
	503	KNM-RU 1773
	545	KNM-RU 1774
	546	KNM-RU 1775
	546	KNM-RU 1776
	593	KNM-RU 1778
	593	KNM-RU 2018
140	599	KNM-RU 1728
141	600	KNM-RU 1780
	602	KNM-RU 1781
144	603	KNM-RU 1782
	604	not primate

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
147	645	KNM-RU 1785
	663	KNM-RU 1787
	667	KNM-RU 1788
151	683	KNM-RU 1789
	735	KNM-RU 1790
	684	KNM-RU 1791
	693	KNM-RU 1792
	710	BM(NH) M 16650
155	712	KNM-RU 1674
	746	KNM-RU 1795
	814	KNM-RU 1796
	843	KNM-RU 1797
	847	KNM-RU 1798
	908	KNM-RU 1799
	924	KNM-RU 1801
166	993	KNM-RU 1803
	994	KNM-RU 1804
	1011–1022	KNM-RU 1806
181	1043	KNM-RU 1818
	1047	KNM-RU 1806
183	1097	KNM-RU 1820
	1178	KNM-RU 1821
185	1228	KNM-RU 1822
186	1229	KNM-RU 1823
	1230	KNM-RU 1824
	1947 – Songhor	
190	1	KNM-SO 396
191	2	KNM-SO 397
	3	KNM-SO 398
	4	KNM-SO 399
	15	KNM-SO 401
196	16	KNM-SO 402
	17	KNM-SO 403
198	28	KNM-SO 404
	29	KNM-SO 405
	45	not primate
	80	BM(NH) M 16648
	105	KNM-SO 411
	1947 – Maboko	
	39	KNM-MB 109
	1948 – Rusinga	
	8	KNM-RU 1825
	27	KNM-RU 1826
1948	50	BM(NH) M 32363
	79	KNM-RU 1830
216, 48	80	KNM-RU 1831
218	103	KNM-RU 1833
220	138	KNM-RU 1835
	200	KNM-RU 1836
	205	KNM-RU 1837
	270	KNM-RU 1839
	276	KNM-RU 1840
	280	KNM-RU 1842
	334	KNM-RU 1667
	374 A	KNM-RU 1844
	B	KNM-RU 1850
	C	KNM-RU 1850
	D	KNM-RU 1847
	E	KNM-RU 1849
	F	KNM-RU 1849
	G	KNM-RU 1850
	G1	KNM-RU 1850
	G2	KNM-RU 1850
	374 H	KNM-RU 1849
	I	KNM-RU 1849
	J	KNM-RU 1849
	375	KNM-RU 1855
	394	not primate
	443	KNM-RU 1857
	444	KNM-RU 1858
	445	not primate
	446	KNM-RU 1860
	447	KNM-RU 1861
	571	KNM-RU 1862
262	635	KNM-RU 1864
	636	KNM-RU 1865
	637	KNM-RU 1664
	638	KNM-RU 1866
268	893	KNM-RU 1868
	893	KNM-RU 1869
	1948 – Songhor	
	1	KNM-SO 413
	7	KNM-SO 414
	52	KNM-SO 418
	53	KNM-SO 419
	54	lost
271	55	KNM-SO 415
272	56	KNM-SO 416
	57	KNM-SO 417
277	58	KNM-SO 420
	59	KNM-SO 421
	60	KNM-SO 422
	61	KNM-SO 423
	62	KNM-SO 424
	63	KNM-SO 425
	64	KNM-SO 426
	87	KNM-SO 428
	88	KNM-SO 429
	89	KNM-SO 430
	99	KNM-SO 434
	100	KNM-SO 435
	101	KNM-SO 436
	111	KNM-SO 441
301	112	KNM-SO 442
	120	KNM-SO 443
	121	KNM-SO 444
	122	KNM-SO 445
	123	KNM-SO 396
	404	KNM-SO 449
334	405	KNM-SO 450
	406	KNM-SO 451
	407	KNM-SO 462
	409	KNM-SO 452
	410	lost
	411	KNM-SO 453
	412	KNM-SO 454
	413	KNM-SO 455
	415	KNM-SO 457
	416	KNM-SO 458
	417	KNM-SO 459
	418	KNM-SO 460
	419	KNM-SO 461
	441	KNM-SO 462
	Sgr. '48	KNM-SO 561
	1948 – Koru	
	1	KNM-KO 6
	2	KNM-KO 7

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
	1949 – Rusinga	
	73	KNM-RU 1870
	148	KNM-RU 1871
	155	KNM-RU 1872
	156	KNM-RU 1873
	278	KNM-RU 1874
	300	KNM-RU 1875
	516	KNM-RU 1876
	518	KNM-RU 1878
	519	KNM-RU 1650
	520	KNM-RU 1649
	541	KNM-RU 1880
	542	KNM-RU 1881
	605	KNM-RU 1882
	606	KNM-RU 1883
	649	KNM-RU 1887
374	692	KNM-RU 1889
	767	not primate
	769	KNM-RU 1666
	1949 – Mfwangano	
	64	KNM-MW 39
	65	KNM-MW 60
	1949 – Songhor	
380	1	KNM-SO 463
381	2	KNM-SO 464
382	3	KNM-SO 465
383	4	KNM-SO 466
384	5	KNM-SO 467
	6	KNM-SO 962
	7	KNM-SO 412
	11	KNM-SO 470
	12	KNM-SO 472
	13	KNM-SO 473
	14	KNM-SO 474
	15	KNM-SO 475
	16	KNM-SO 476
	245	KNM-SO 512
	246	KNM-SO 513
	247	KNM-SO 514
	307	KNM-SO 481
	308	KNM-SO 482
	309	KNM-SO 483
405	381	KNM-SO 485
406	382	KNM-SO 486
	384	KNM-SO 487
409	385	KNM-SO 488
	387	KNM-SO 489
	388	KNM-SO 490
	639	KNM-SO 506
	640	KNM-SO 507
	1950 – Rusinga	
	92	KNM-RU 1893
	93	KNM-RU 1894
507	94	KNM-RU 1895
	234	KNM-RU 1896
	280	KNM-RU 1897
	281	KNM-RU 1901
	282	KNM-RU 1899
	283–295	KNM-RU 1901
531	286	KNM-RU 1904
	296	KNM-RU 1914
	297	KNM-RU 1915
	298	KNM-RU 1916
	301	KNM-RU 1919
	302	KNM-RU 1920
	303	not primate
	448	KNM-RU 1922
538	486	KNM-RU 1923
539	487	KNM-RU 1924
	548	KNM-RU 1925
	582	KNM-RU 1926
542	583	KNM-RU 1927
	614	KNM-RU 1929
545	628	KNM-RU 1931
	669	KNM-RU 1932
547	670	KNM-RU 1933
	671	KNM-RU 1934
	748	KNM-RU 1935
550	777	KNM-RU 1936
	844	KNM-RU 1937
	878	KNM-RU 1928
	924	KNM-RU 1939
557	1040	KNM-RU 1942
560	1056	KNM-RU 1945
	1111	KNM-RU 1946
562	1145	KNM-RU 1947
	1185	KNM-RU 1948
	1335	KNM-RU 1949
566	1342	KNM-RU 1951
	1365	KNM-RU 1952
	1396	KNM-RU 1953
569	1403	KNM-RU 1954
570	1404	KNM-RU 1979
	1405	KNM-RU 1980
	1406	KNM-RU 1981
573	1558	KNM-RU 1955
	1559	KNM-RU 1956
	1592	KNM-RU 1957
	1681	KNM-RU 1671
	1756	KNM-RU 1958
578	1775	KNM-RU 1959
	1798	KNM-RU 1960
	1814	KNM-RU 1962
	1815	KNM-RU 1963
	1816	KNM-RU 1964
	1817	KNM-RU 1965
	1854	KNM-RU 1966
	1900	KNM-RU 1968
	1901	KNM-RU 1969
	1915	KNM-RU 1970
	1985	KNM-RU 1971
	1986	KNM-RU 1972
	1987	KNM-RU 1973
593	1988	KNM-RU 1974
594	1989	KNM-RU 1975
	1991	KNM-RU 1977
	2003	KNM-RU 1857
	1950 – Songhor	
	2	KNM-SO 927
	3	KNM-SO 928
	4	KNM-SO 929
	70	KNM-SO 516
	71	KNM-SO 517
	1950 – Mfwangano	
	3	KNM-MW 40
	4	KNM-MW 41
	5	KNM-MW 42
	2	KNM-MW 61

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
	1950 – Karungu	
	21	KNM-KA 5
	24	KNM-KA 6
	25	KNM-KA 7
	1950 – Koru	
	1	KNM-KO 8
618	2	KNM-KO 9
	1 A	KNM-KO 11
	1951 – Rusinga	
620	1	KNM-RU 1982
	77	KNM-RU 1984
	111	KNM-RU 1985
	112	KNM-RU 1986
	176	KNM-RU 1988
	177	KNM-RU 1989
	178	KNM-RU 1990
	179	KNM-RU 1991
	180	KNM-RU 1992
	181	KNM-RU 1993
	182	KNM-RU 1994
	183	KNM-RU 1995
	184	KNM-RU 1996
	259	KNM-RU 1998
637	260	KNM-RU 1999
	346	KNM-RU 2000
	409	KNM-RU 2001
	417	KNM-RU 2002
	493	KNM-RU 2003
	505	KNM-RU 2004
	538	KNM-RU 2005
	539	KNM-RU 2007
	543	KNM-RU 2008
	560	KNM-RU 2009
	590	KNM-RU 2010
	591	KNM-RU 2011
	592	KNM-RU 2012
	593	KNM-RU 2013
	636	KNM-RU 2015
	706	KNM-RU 2016
	707	KNM-RU 2017
	708	KNM-RU 2018
	709	KNM-RU 2019
	711	KNM-RU 2020
	716	KNM-RU 2021
	725	KNM-RU 2023
	738	KNM-RU 2024
	749	KNM-RU 2025
	774	KNM-RU 2026
	807	KNM-RU 2027
	808	KNM-RU 2028
	809	KNM-RU 2028
	1087	KNM-RU 2030
	1100	KNM-RU 2038
	1158	KNM-RU 2037
	1243	KNM-RU 2031
	1244	KNM-RU 2032
	1245	KNM-RU 2033
	1376	KNM-RU 2034
	1435	KNM-RU 2035
51	1499	KNM-RU 2036
	1951 – Losidok	
	5	KNM-LS 1

After 1951, specimens described by Pilbeam (1969) for the first time.

R 686,313	KNM-RU 2041	Sgr. 1′62	KNM-SO 396
R 688,315	KNM-RU 2043 (lost)	Sgr. 139′62	KNM-SO 521
R 690,317	KNM-RU 2045	Sgr. 143′62	KNM-SO 522
R 694,2542	KNM-RU 2049	Sgr. 144′62	KNM-SO 523
R 715,156	KNM-RU 2051	Sgr. 145′62	KNM-SO 524
R 722,550	KNM-RU 2061	Sgr. 8′62	KNM-SO 528

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Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales

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Synopsis

The early Arenig stratigraphy of the Carmarthen district is described. It is shown that the previously accepted succession in the area is upside down. The Ogof Hên Formation, first recognized on Ramsey Island, has been identified, and is divided into the Allt Cystanog Member succeeded by the Bolahaul Member. The overlying Carmarthen Formation is divided into three, the Pibwr, Cwmffrŵd and Cwm yr Abbey Members in ascending order. From the Bolahaul Member upwards a succession of trilobite faunas allows biostratigraphic subdivision. The increasing depth of the ocean floor during the Arenig resulted in changing ecological conditions to which particular trilobites were adapted; these are generalized into informal communities, the Neseuretus (inshore), Raphiophorid (intermediate, muddy substrate) and Olenid (deoxygenated, deeper water) respectively. The endemicity of the associated trilobites decreases with depth.

The new asaphid genus *Merlinia* (type species *M. rhyakos* sp. nov.) is erected to include the controversial species *M. murchisoniae* (Murchison), *M. selwynii* (Salter) and *M. major* (Salter). Other new species are *Bienvillia praecalva*, *Hypermecaspis venerabilis* and *Ampyx cetsarum*. Graptolites are described for the first time from the early Arenig of the Carmarthen district.

Introduction and acknowledgements

The outcrop of Arenig rocks in Dyfed, SW Wales, extends discontinuously for some 70 miles (112 km) from Ramsey Island to near Llanarthney. Exposure is on the whole poor; the structure is complex and fossils are not usually abundant; thus these rocks have received only scant attention since the Geological Survey mapped large parts of their outcrop about 70 years ago.

Where their base is seen, these Arenig strata rest disconformably upon the Tremadoc. Strata erroneously assigned to this series in the St David's region by Hicks (1873) and in the Carmarthen region by Crosfield & Skeat (1896) have subsequently been identified as being of Arenig age. In the latter area they contain a small but well-preserved trilobite fauna, and have become known as the '*Peltura punctata* Beds'. They have hitherto been regarded as the oldest sediments in the Carmarthen region (e.g. Strahan *et al.* 1907, 1909). One of us (Fortey 1974b : 72) noted the close similarity of *P. punctata* to olenids of Arenig age from Spitsbergen; with this apparent tie to a well-documented succession, and because of the abundance and good preservation of the fauna, we decided to investigate the *Peltura punctata* Beds and adjacent strata in the neighbourhood of Carmarthen to see if it was possible to map and work out the succession in greater detail than has been attempted before. We spent two field seasons in the area during 1974 and 1975, and intensive collecting and logging of the sections has greatly enlarged the faunas and has enabled us to revise and refine the stratigraphy.

Detailed mapping has not proved possible except in a few localities, and all of the better and more complete sections are to be found in stream exposures. We have, however, been able to revise the old Geological Survey maps, and to present new generalized maps of parts of the area between Carmarthen and Llanarthney.

We thank Dr A. W. A. Rushton, Institute of Geological Sciences, London, Dr R. B. Rickards, Sedgwick Museum, Cambridge and Dr G. Thorbecke, Geologisch-Paläontologisches Institut, Freiburg-im-Briesgau, Germany, for loan of material in their care. Mr F. Cross, Department of Geology, University College, Swansea, kindly made available specimens he had collected from a temporary exposure. Dr J. K. Ingham and Dr C. P. Hughes kindly commented on the trinucleid trilobites. For help in the field we thank Mr S. F. Morris, Dr N. J. Morris, Miss J. Francis and Colonel G. Chaldicott; Dr D. L. Bruton generously allowed us to use his field notes. Mrs D. G. Evans drafted most of the illustrations and Dr D. A. Bassett kindly read the first draft of the manuscript.

Historical survey

Fossils have long been known from the Carmarthen district. Arenig trilobites from Pensarn and Mount Pleasant (now Penbryn) were sufficiently conspicuous to be associated with old local legends concerning the magician Merlin, and pygidia were said to represent 'petrified butterflies' (Symonds 1872 : 79). The earliest scientific descriptions of the Arenig rocks and fossils were by Murchison (1839) in his *Silurian System*; here trilobites and brachiopods from Pensarn were described and figured, and the area is included on the geological map (the first to depict this area) and on one of the sections (pl. 34, fig. 9). Strata now known to be Arenig were represented as Caradoc, Llandeilo and 'Upper Cambrian (beds of passage)', the latter described (1839 : 361) as quarried at Gallicistaniog (i.e. Allt Cystanog).

The first Geological Survey maps of the area (one-inch sheet 41 SW), based on the original survey of de la Beche, were published in 1845; additional lines in the Lower Palaeozoic, mapped by Aveline in 1855–56, were incorporated on the 1857 edition. On these maps the area was coloured as Lower Silurian Llandeilo flags, limestones and conglomerates. At about this time Salter (1864a) and Davidson (1869) refigured Murchison's species of trilobites and brachiopods from Pensarn in their Palaeontographical Society monographs. In 1896 Crosfield & Skeat published the first detailed account of the area immediately around Carmarthen, and described further fossils – the first from outside the Pensarn–Mount Pleasant area. They considered a group of dark mudstones with an abundant trilobite fauna to be of Tremadoc age – mainly because they believed (1896: 532) that the common olenid trilobites were 'typical Cambrian genera'; the less common asaphids (referred to '*Ogygia*') were believed to be 'characteristically Ordovician'. They concluded: 'This mixture of Cambrian and Ordovician forms indicates the position of these beds in the stratigraphical succession, and enables us to correlate them with the Tremadoc Series of North Wales and with the Shineton Shales of Shropshire.' They further suggested correlation with Stage 3a (*Ceratopyge* Series, Tremadoc) of southern Norway. They correctly assigned the strata they considered to overlie these mudstones to the Arenig (the first identification of Arenig rocks in the area) and, based on misidentification of the brachiopods and trilobites, believed that the grits and subordinate shales of the Bolahaul–Allt Cystanog anticlinal area were of 'Bala' age.

At the turn of the century, the entire area was remapped on a scale of six inches to the mile by the Geological Survey, with the resultant six and one inch sheets published by 1909; memoirs descriptive of the Ammanford (230) and Carmarthen (229) one-inch sheets were published (Strahan *et al.*) in 1907 and 1909 respectively. The term '*Peltura punctata* Beds' was first employed for Crosfield & Skeat's 'Tremadoc Slates' in the Ammanford memoir (Thomas *in* Strahan *et al.* 1907 : 6); they were still included in the Tremadoc and were said to form 'a more or less perfect passage into the overlying Arenig rocks'. In the same memoir he also introduced the term '*Ogygia marginata* Beds' for the Arenig strata; however, in a footnote (1907 : 7) he stated that specimens of *O. marginata* had been submitted to Lake who considered that this species was a synonym of *O. selwynii*. It is presumably for this reason that Cantrill & Thomas (*in* Strahan *et al.* 1909) did not use the name in the Carmarthen memoir, where the entire Arenig is grouped in the Tetragraptus Shales. The name '*Ogygia marginata* Beds' was resuscitated by Stubblefield (*in* Smith 1933 : 374), and is used in the Geological Society of London Ordovician correlation chart (Williams *et al.* 1972).

Stubblefield (*in* Smith 1933 : 374), having re-examined the fauna of the '*Peltura punctata* Beds', concluded that they were of Arenig age, rather than Tremadoc; following earlier workers, he believed them to be the oldest strata at Carmarthen.

The stratigraphical term 'Allt Cystanog Grits' was introduced somewhat cryptically by Jones (1938 : lxxiii) in the statement '. . . between Carmarthen and Llandeilo, the Allt Cystanog Grits are typical greywackes alternating with dark shales'. There has since been no reference to these beds save a brief mention by Bassett (1963 : 47).

In the present century, several of the Arenig trilobites have been redescribed or referred to in a number of works – e.g. Lake (1913, 1919), Stubblefield *in* Smith (1933), Henningsmoen (1957), Whittard (1964), Whittington (1966), Bates (1969b) and Fortey (1974b). In addition, Bates (1969b) has refigured some of the brachiopods.

<table>
<tr><th>CROSFIELD & SKEAT
1896</th><th>CANTRILL & THOMAS
1907</th><th colspan="2">CANTRILL & THOMAS
1909</th><th colspan="2">FORTEY & OWENS
(this paper)</th></tr>
<tr><td>Llanvirn</td><td>Llanvirn</td><td colspan="2">Llanvirn</td><td colspan="2">Llanvirn</td></tr>
<tr><td rowspan="4">Arenig
Beds</td><td rowspan="4"><i>Ogygia marginata</i>
Beds</td><td rowspan="4">TETRAGRAPTUS BEDS</td><td><i>Didymograptus hirundo</i> Beds</td><td colspan="2">TETRAGRAPTUS BEDS</td></tr>
<tr><td rowspan="3"><i>Didymograptus extensus</i> Beds
(with trilobite mudstones developed in the east)</td><td rowspan="3">CARMARTHEN FORMATION</td><td>Cwm yr Abbey Member
(=<i>Peltura punctata</i> Beds pars)</td></tr>
<tr><td>Cwmffrŵd Member
(=<i>Peltura punctata</i> Beds pars)</td></tr>
<tr><td>Pibwr Member
(=<i>Ogygia marginata</i> Beds)</td></tr>
<tr><td rowspan="3">Tremadoc Slates</td><td rowspan="3"><i>Peltura punctata</i>
Beds (Tremadoc)</td><td colspan="2" rowspan="3"><i>Peltura punctata</i>
Beds (Tremadoc)</td><td rowspan="2">OGOF HÊN Fm</td><td>Bolahaul Member</td></tr>
<tr><td>Allt Cystanog Member</td></tr>
<tr><td colspan="2">Tremadoc</td></tr>
</table>

Fig. 1. The main interpretations of the early Ordovician (Arenig) succession in the Carmarthen district.

Stratigraphy

The succession in the early Ordovician of the Carmarthen district is completely revised in this work. Fig. 1 shows the views of the succession around Carmarthen adopted by the various authors concerned with the Arenig of the area since the end of the last century. The '*Peltura punctata* Beds' were supposedly followed by the Tetragraptus Beds, including at least in their lower part the '*Ogygia marginata* Beds'. Thomas *in* Strahan *et al.* (1909 : 5) emphasized that there was a continuous passage between the supposedly Tremadoc '*Peltura punctata* Beds' and the Arenig, and Crosfield & Skeat (1896 : 526) further noted that their Arenig Beds could be found to 'pass under the older Tremadoc Beds', that is the '*Ogygia marginata* Beds' could be found underlying the '*Peltura punctata* Beds' which they attributed to inversion of the succession.

Our interpretation is that the succession is regionally normal, and that the previously accepted

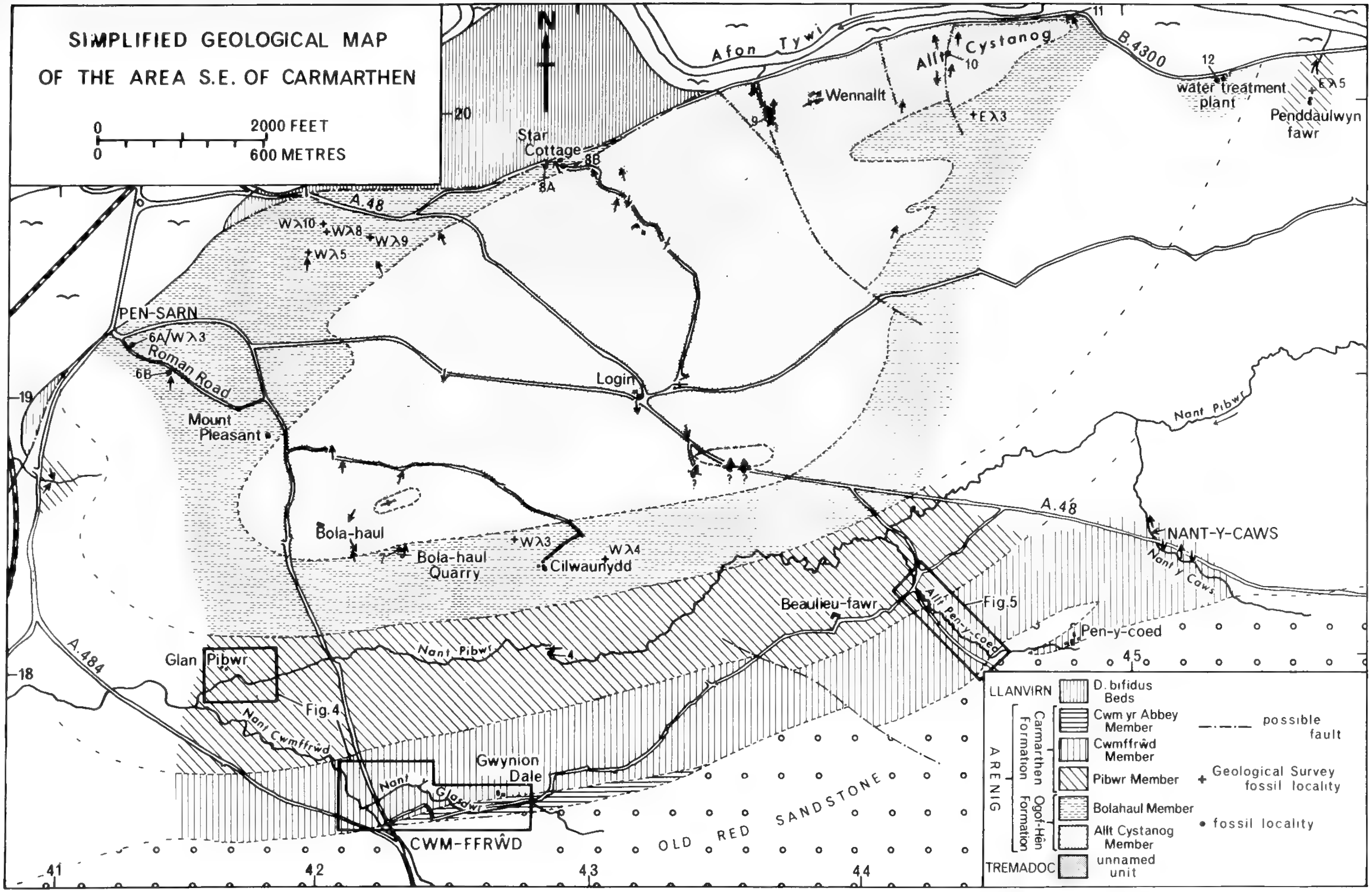

Fig. 2. Generalized map of the region SE of Carmarthen, showing the approximate areas of outcrop of Arenig formations and members described in this paper.

view of the succession is upside down. The '*Peltura punctata* Beds' are the youngest deposits dealt with in the present work, and pass upwards without a break into the Tetragraptus Beds; the '*Ogygia marginata* Beds' everywhere underlie the shales bearing olenid trilobites. The oldest Arenig rocks in the area are lithologically and faunally comparable with the basal Arenig rocks of Ramsey Island (Bates 1969b), and are given the same formation name. They overlie Tremadoc rocks in the Bolahaul–Allt Cystanog anticline. The contact of the Arenig with the Tremadoc is nowhere exposed, but there is nothing to suggest angular unconformity, and the younger strata probably lie disconformably upon the Tremadoc.

The proposed order of the succession is consistent with the development of the Arenig elsewhere in south Wales where exposure is more complete, and with the structural framework of the area. The main outlines of the structure were deduced by the Geological Survey: the early Arenig rocks are brought to the surface in the cores of anticlines trending approximately east–west and arranged *en echelon*, the most important of which are those to the east of Carmarthen in the Bolahaul–Allt Cystanog area (Fig. 2). A second minor anticline may be present at Capel Dewi, and there is a third to the east of the Polin (New Lodge Inn) which includes in its core the best exposure of the Cwm yr Abbey Member (Fig. 3). The northern limb of the Bolahaul–Allt Cystanog anticlinal area is faulted with the down-throw to the north, the southern limb slightly overturned; major dip faults have associated baryte and galena mineralization. The true complexity of the folding is only shown on stream sections (Figs 4, 5), and is on too fine a scale to be represented on the generalized large maps. Independent evidence of the facing direction of individual sections is provided by grading in the turbidite units in the middle part of the Carmarthen Formation (Cwmffrŵd Member) and within the Tetragraptus Beds. Grading in the former is well shown in Nant Cwmffrŵd and in Allt Pen-y-Coed dingle, in the latter in Cwm yr Abbey; in all cases the way up of the beds is in agreement with the present view of the succession. The sequence of trilobites supports the same interpretation, the only important change being the acceptance of the olenid fauna of the former '*Peltura punctata* Beds' as being younger than the early Arenig. Since diverse olenid faunas are now known from Spitsbergen (Fortey 1974b) through much of the Arenig, the interpretation of the '*P. punctata* Beds' as of Arenig age seems more probable today than it would have done to Crosfield & Skeat.

Division of the Carmarthen rocks described here into formal lithostratigraphic units is necessary for mapping their outcrop and accurately localizing the fossils. These divisions are as follows:

Carmarthen Formation	3. Cwm yr Abbey Member ('*Peltura punctata* Beds' *pars*)
	2. Cwmffrŵd Member ('*Peltura punctata* Beds' *pars*)
	1. Pibwr Member ('*Ogygia marginata* Beds')
Ogof Hên Formation	2. Bolahaul Member
	1. Allt Cystanog Member

Of these, all but the Ogof Hên Formation are new, and their lithological characters are described below. The underlying Tremadoc rocks are only well exposed adjacent to the main Carmarthen–Swansea (A48) road south-east of Login School; there they consist of at least 60 m of fine micaceous sandstones and siltstones with interbedded green shales and occasional conglomeratic beds, with sporadic *Lingulella* on some bedding surfaces. The more resistant beds of the Tremadoc probably crop out elsewhere over the Bolahaul–Allt Cystanog anticline area, but exposure here is generally so poor that they cannot be distinguished with confidence from the lower part of the Allt Cystanog Member of the Ogof Hên Formation.

The upper limit of this study is taken at the base of the Tetragraptus Beds. These beds are grey, highly fissile graptolitic shales identical to their type development on the coast near St David's. They can be seen to pass downwards into the Cwm yr Abbey Member ('*Peltura punctata* Beds') at several sections, notably in Cwm yr Abbey, and in the stream west of the Polin, south of Nantgaredig. The Tetragraptus Beds will be the subject of a future paper.

A summary follows of the lithostratigraphic subdivisions employed in this paper, proceeding from the local base of the Ordovician upwards. Because of the intense folding that affects many of the shale and mudstone units, sections of these parts of the succession are composite, and the thicknesses given inevitably minima.

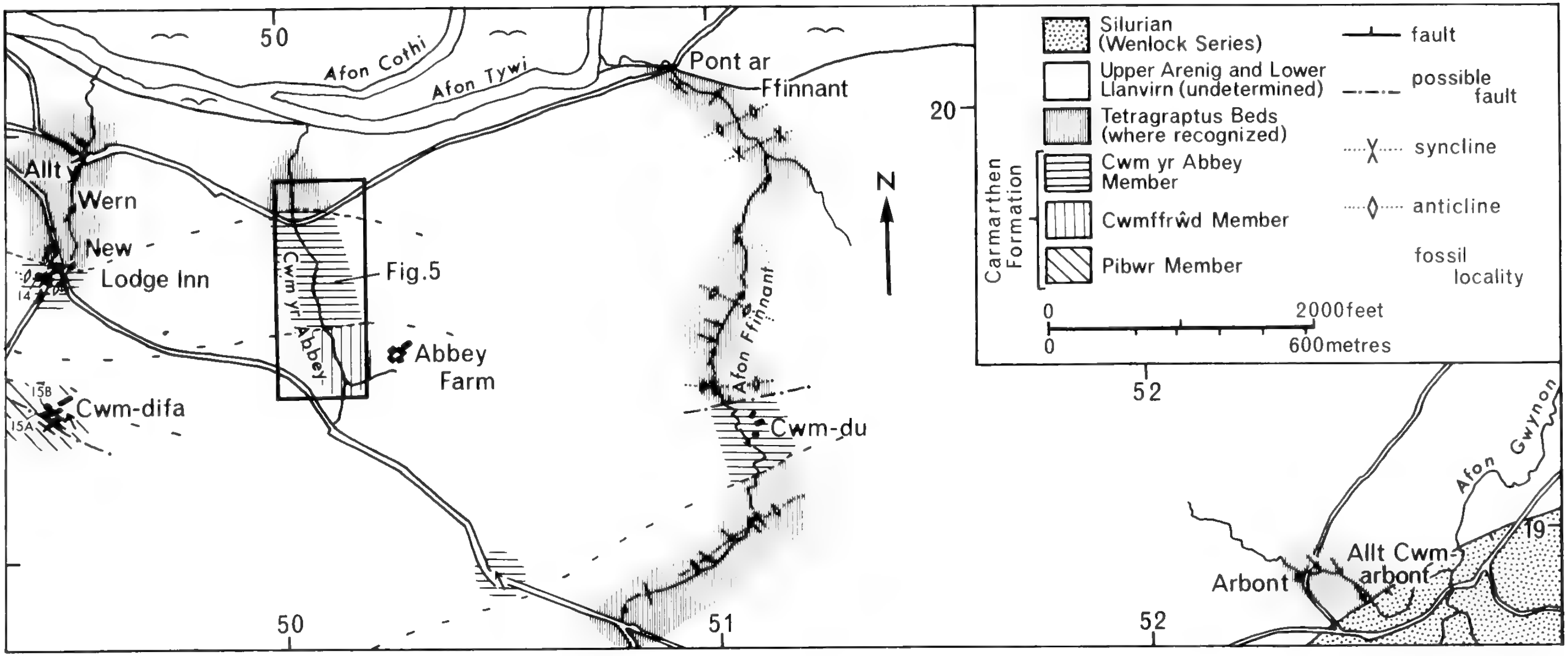

Fig. 3. Generalized map of the area between Nantgaredig and Llanarthney, showing approximate areas of outcrop of Arenig formations and members described in this paper.

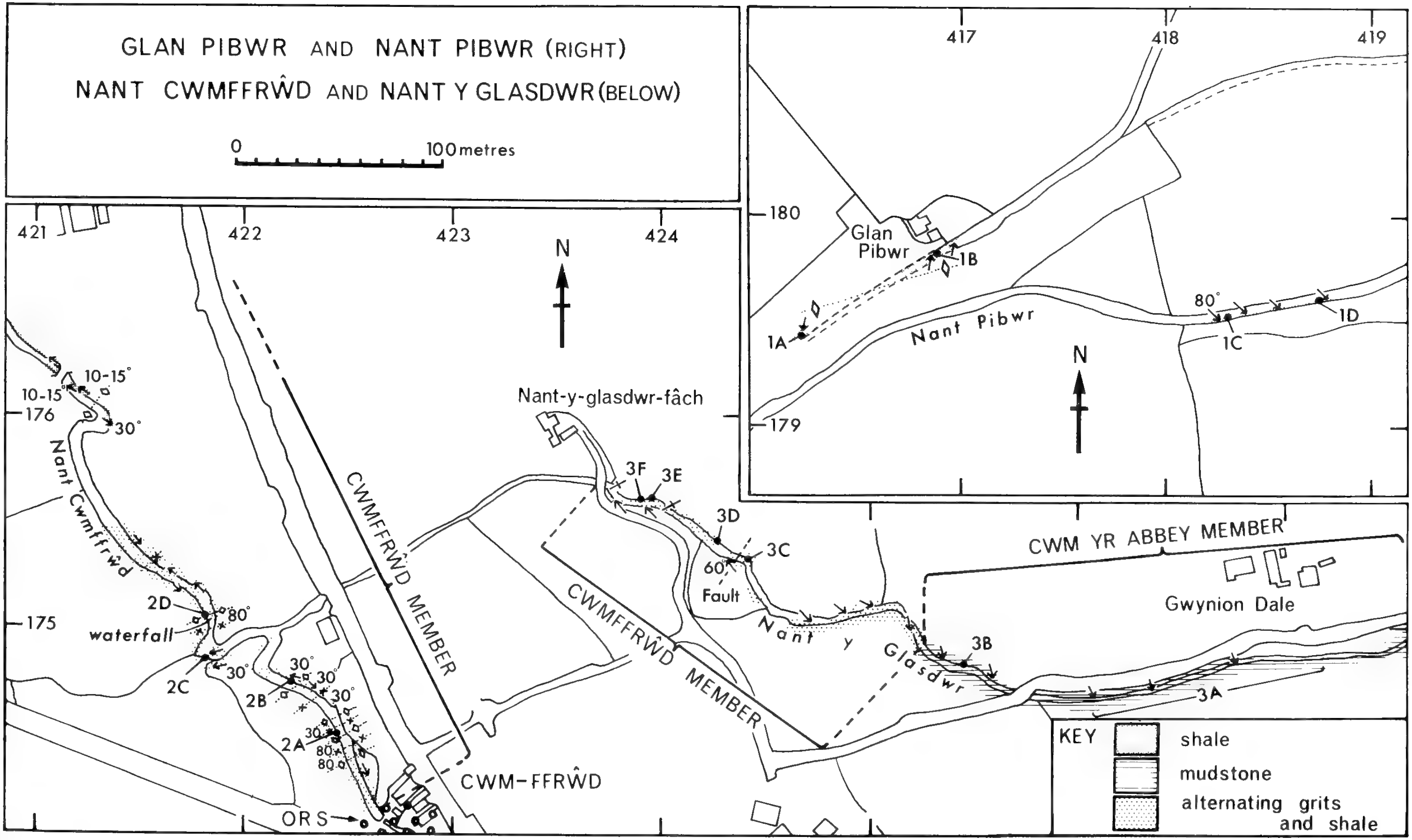

Fig. 4. Outcrops of Arenig rocks in Nant Cwmffrŵd, Nant y Glasdwr and at Glan Pibwr.

Ogof Hên Formation

The term Ogof Hên Formation was proposed by Bates (1969b : 4) for the lowest Arenig as developed on Ramsey Island, including therein the Porth Gain Beds and Abercastle Beds of earlier authors. The basal beds in the Carmarthen region compare closely with those to the west, and there is no reason to employ a different formational name.

1. *Allt Cystanog Member*

The term Allt Cystanog Member is introduced here for the unfossiliferous conglomerates, sandstones and siltstones at the base of the Ordovician succession. It is a modification of 'Allt Cystanog Grits' employed by Jones (1938 : lxxiii) to describe coarse Arenig clastic deposits exposed SE of Carmarthen, and it is an appropriate name as the beds in question are exposed in many places in the Bolahaul–Allt Cystanog anticlinal region. The contact with the Tremadoc is nowhere exposed, although Tremadoc and Arenig rocks cannot be separated by more than a few tens of metres near Login. The fullest exposure of the Allt Cystanog Member and an appropriate type section is on the western side of a disused quarry immediately south of the Carmarthen–Swansea (A48) road, 100 m east of its junction with the Carmarthen–Llandeilo road. 25 m of strata are exposed here, the lower 10 m massive conglomerates (in units greater than 1 m) with rounded quartz clasts in a siliceous matrix, interbedded with 10–15 cm units of finely bedded, yellow silty shales. Isolated outcrops similar to the massive beds are frequent in the fields in the Bolahaul–Allt Cystanog area, but from the varied attitudes of the beds it is likely that the sequence is repeated. The grits become progressively finer upwards, the finer-bedded silty units increasing at the expense of the coarser beds. The characteristic rock type of the upper 10 m is a fine micaceous sandstone 1–5 cm thick, with crowded ripple drift laminations a few millimetres apart at most, outlined by dark argillaceous films. The lithology resembles no other in the Arenig above or the Tremadoc below, and is widely traceable. These beds are exposed in several places on the small scarp running eastwards behind Star Cottage on the northern limb of the Bolahaul–Allt Cystanog anticline, on the southern limb in the hillsides behind Bolahaul Farm, south of the Carmarthen–Swansea road at Login crossroads, and in small quarries over the crest of the anticline.

Similar lithologies are present in the lower part of the Ogof Hên Formation at its type locality (Bates 1969b : fig. 1; pl. 1), and as at that locality there are no fossils except for numerous straight or sinuous 'worm' tracks on some bedding planes. The uppermost 2–3 m of the Member become progressively argillaceous, transitional in character with the Bolahaul Member.

2. *Bolahaul Member*

The term Bolahaul Member is introduced here for the series of micaceous mudstones and shales succeeding the Allt Cystanog Member. The base of the Member is well exposed in the quarry east of Bolahaul (loc. 7, Fig. 2), where the succession is just inverted on the southern limb of the Bolahaul–Allt Cystanog anticline, and is taken at the first mudstone horizon. The contact is also exposed on the northern limb behind Star Cottage (where the beds are normal) and at the eastern limit of the anticline adjacent to the Carmarthen–Llandeilo road. At Bolahaul quarry some 10 m of micaceous, slightly cleaved mudstones are exposed, which at about 3 m from their base yield the first fossils – echinoderm fragments, strongly ribbed brachiopods including *Lenorthis alata* (Sowerby), and the inarticulate brachiopod *Monobolina plumbea* (Salter), which has recently been redescribed by Williams (1974). A few obscure fragments of asaphid trilobites also occur, but trilobites are more numerous in the higher beds, which become progressively more shaly and are in places highly cleaved. These higher shales are not well exposed but can be seen in the lane behind Star Cottage (loc. 8), where they were originally identified by Murchison (1839); the Survey had additional localities, now built upon, about 500 m to the northeast of Pensarn (Fig. 2). The trilobites *Merlinia murchisoniae* (Murchison) and *Neseuretus parvifrons* (M'Coy) are common, the latter confined to this Member, together with gastropods and rare bivalves (? *Lyrodesma* sp.). The thickness of the shaly part of the Member is not known, but exceeds 50 m, exposed on the Roman Road section. The fauna of this Member, as noted by Bates

(1969b : 8), is identical to that of the upper part of the Ogof Hên Formation, and their correlation is not in doubt.

Carmarthen Formation

The term Carmarthen Formation is proposed to include the distinctive early Arenig mudstones and shales overlying the Ogof Hên Formation, and including the '*Ogygia marginata* Beds' and '*Peltura punctata* Beds' of earlier authors. It is widely exposed in the neighbourhood of Carmarthen, but is generally much folded and faulted, and the exposure, particularly of the Pibwr Member, is therefore incomplete. The Formation falls naturally into three lithological divisions, here called Members, the younger two of which are equivalent to the '*Peltura punctata* Beds' of earlier authors. These beds are succeeded by grey shales of the Tetragraptus Beds. The Carmarthen Formation is absent, or has not yet been recognized, to the west at Whitland and beyond. As discussed below, the facies development of the Carmarthen Formation is not known elsewhere in the Arenig of Wales, and it seems possible, as indicated by Cantrill & Thomas *in* Strahan *et al.* (1909 : 10), that it represents a facies equivalent of the Tetragraptus Beds to the west. This carries with it the implication that the Tetragraptus Beds in the Carmarthen region are equivalent only to the upper part of that unit to the west.

1. *Pibwr Member*

The base of the Pibwr Member is drawn at the lowest beds exposed in the lane leading past Glan Pibwr Cottage (loc. 1B). The beds at this locality, and others now mapped as the Pibwr Member, have been termed '*Ogygia marginata* Beds' by previous authors. The Member occupies the broad, low-lying tract of land flanking the Pibwr Valley, and its exposure is correspondingly incomplete. Being relatively incompetent and lacking grit beds the Pibwr Member has been repeatedly folded. The lack of exposure is unfortunate as the Member contains particularly well preserved fossils at some localities. Only the lowest 5–6 m are shales transitional in character with the upper part of the Bolahaul Member below; they have yielded *Myttonia* cf. *fearnsidesi* Whittington and *Phyllograptus densus* Törnquist, neither of which has been recovered elsewhere in the section. Above lie a monotonous series of mudstones, black, well-bedded (5–15 cm) and remarkably reluctant to split when fresh, weathering to show an iridescent dark purplish or umber surface film. These mudstones are characterized by an abundance of asaphid trilobites (dominant *Merlinia selwynii* with subordinate *M. murchisoniae*) and bivalves ('*Actinodonta*' aff. *naranjoana* and nuculoids), locally numerous raphiophorids (*Ampyx cetsarum* sp. nov.) and occasional 'ghosts' of trinucleids. At a few localities the trilobites and bivalves are preserved in relief, but flattening is the rule. Although the Pibwr Member is exposed at a number of localities it is not possible to measure more than a few tens of metres without repetition, so the total thickness is not known; it probably greatly exceeds our minimum estimate of 80 m. The upper part of the Member is well exposed on the lower reaches of Allt Pen-y-Coed dingle where the asaphids are accompanied by rare olenid trilobites (*Bienvillia praecalva* sp. nov.) for the first time, and bivalves become progressively rarer as the Cwmffrŵd Member is approached. It should be noted here that several of the localities mapped or recorded by the Survey as exposing '*Ogygia marginata* Beds' yield a different asaphid and are younger than the Carmarthen Formation: these include outcrops adjacent to the Carmarthen–Llandeilo (B4300) road on Cwm yr Abbey, and in Cwm Ffinnant to the east.

2. *Cwmffrŵd Member*

The term Cwmffrŵd Member is proposed here for the thick turbidite/shale sequence overlying the Pibwr Member. The base of the member is taken at the first turbidite unit exposed in Allt Pen-y-Coed (Fig. 5). The beds here assigned to it have been previously regarded as part of the '*Peltura punctata* Beds', based on the erroneous identification of *Bienvillia praecalva* sp. nov. with *P. punctata*. Faunally the Cwmffrŵd Member grades into the upper part of the Pibwr Member, but bivalves are very rare, and the olenids outnumber asaphids (*Merlinia rhyakos* gen. et sp. nov.). The most complete section is in Allt Pen-y-Coed, but the Member is more accessible in Nant Cwmffrŵd, where it is displayed in a series of gentle folds beneath and immediately to the north of the unconformity with the Old Red Sandstone. The turbidite units vary from a few cm thick to

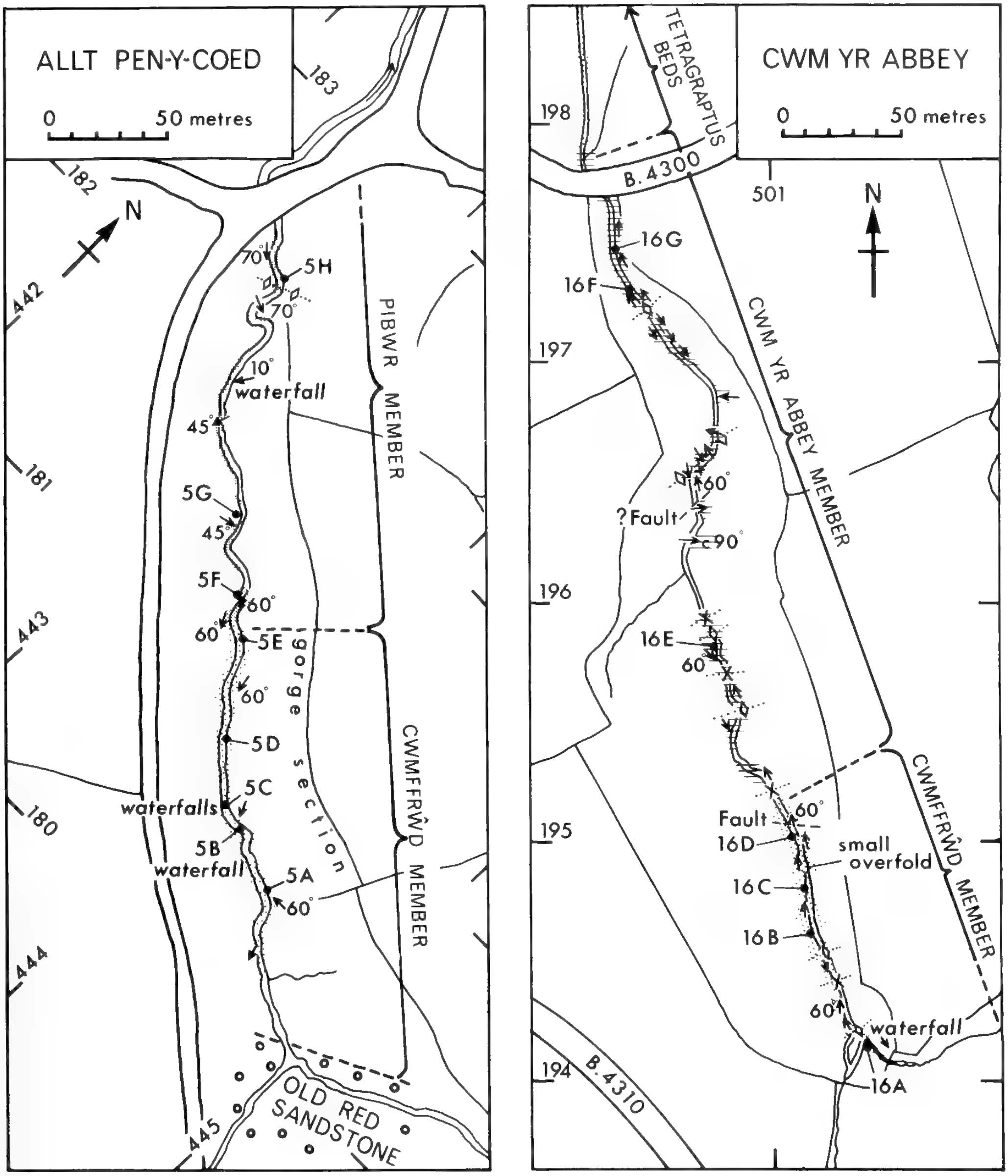

Fig. 5. Outcrops of Arenig rocks in Allt Pen-y-Coed and Cwm yr Abbey.

over 1 m, generally separated by an equal or slightly greater thickness of black mudstones or shales; the Member is about 70 m thick. The turbidites are generally well graded, with quartz and feldspar clasts in a dark siliceous matrix. Towards the mid-part of the Member the turbidites greatly increase in thickness at the expense of the intervening shales; the 2 m thick graded units in this part of the section include feature-forming conglomeratic beds. Fossils are confined to the interbedded argillaceous rocks and are usually flattened. Pyritic 'ghosts' of trilobites are frequent. When poorly preserved, cranidia of *Bienvillia praecalva* sp. nov. are easily confused with those of *Porterfieldia punctata* (Crosfield & Skeat); discovery of the spinose free cheeks of the former supplies a simple method of discriminating the two species in the field. The Cwmffrŵd Member is also exposed on the lower part of the Nant y Glasdwr SW of Nant-y-glasdwr-fâch, and in the upper parts of Cwm yr Abbey. Faunally it grades upwards into the Cwm yr Abbey Member, the first appearance of *P. punctata* being within the upper Cwmffrŵd Member; the division is taken at the last turbidite bed.

3. *Cwm yr Abbey Member*

The term Cwm yr Abbey Member is introduced here for the mudstones overlying the Cwmffrŵd turbidite beds, equivalent to part of the '*Peltura punctata* Beds'. Like the Pibwr Member it is a recessive unit, usually incompletely exposed, and much folded. Its minimum thickness is 45 m. The typical lithology is a grey mudstone, bedded, but poorly so, fracturing irregularly and often as a result splitting through fossils on fresher surfaces. Weathered surfaces are brown to ochreous, generally without the iridescence of the Pibwr Member mudstones. The exposure on Nant y Glasdwr above the bridge opposite the house Gwyniondale – where the stream follows the strike of the beds – is the most accessible for collecting, and it was from here that Crosfield & Skeat (1896) obtained most of their material from the '*Peltura punctata* Beds', but only a few metres are exposed here. A better section is afforded by the stream cutting in Cwm yr Abbey, from which the Member is named, and which is an appropriate type section (Fig. 5). Parts of the section are repeated several times by folding and faulting at this locality. The upper part of the Member is well exposed upstream from the bridge, where the beds are progressively more shaly, conspicuously micaceous, ultimately passing upwards into grey, fissile shales of the Tetragraptus Beds. Throughout the Cwm yr Abbey Member *Porterfieldia punctata* is an abundant and characteristic trilobite, with many articulated exoskeletons, rarely accompanied by *Merlinia rhyakos* gen. et sp. nov. Graptolites (*Callograptus* and *Palaeodictyota*) reappear high in this Member, accompanied by other elements, such as cyclopygid trilobites, typical of the 'open sea' environment developed in the Tetragraptus Beds. A convenient local lithological base for the latter in the Carmarthen district is provided by the reappearance of turbidites in the succession, well-exposed in the lower part of Cwm yr Abbey, and in several localities near the Polin (New Lodge Inn), south of Nantgaredig (loc. 14). *P. punctata* continues into the lower 10 m or so of these 'transition beds', but is soon replaced by a new fauna outside the scope of the present work.

Correlation

The 'basal' Arenig fauna of the Ogof Hên Formation is widespread across Wales and extends into Shropshire. It is a transgressive fauna (Bates 1969a : 155), and some of the species appear to have long stratigraphic ranges (*Neseuretus parvifrons*, for example, is found throughout the Mytton Flags in Shropshire – Whittard 1966 : 300), in which circumstances exact contemporaneity is difficult to establish. In view of the faunal and lithological similarity of the Ogof Hên Formation in Pembrokeshire and in the Carmarthen region age equivalence is likely (Bates 1969b : 8). Whittard has demonstrated that the trinucleid trilobites have more restricted stratigraphic ranges than some other groups in the Mytton Flags (Dean 1967 : 308). It is significant therefore that *Myttonia* cf. *fearnsidesi* is found at the base of the Pibwr Member. This species is found in the Henllan Ash at Arenig (Whittington 1966), where it is associated with *Merlinia murchisoniae* and *Neseuretus* spp. The Henllan Ash might therefore correlate with the Bolahaul or the lower part of the Pibwr Member, or both.

We discuss below the facies development of the Carmarthen Formation; here it is noted that the fauna differs from all other Arenig faunas in Wales in the dominance of Olenidae in the Cwmffrŵd and Cwm yr Abbey Members. For this reason the fauna of that part of the succession compares most closely with the Arenig of Spitsbergen (Fortey 1974b), where the olenid environment is also well developed in post-Tremadocian strata. The fact that *Porterfieldia punctata* succeeds *Bienvillia praecalva* is of biostratigraphic importance within the Carmarthen Formation. So is the succession of *Merlinia* species, as follows:

Cwm yr Abbey Member	*M. rhyakos* sp. nov.
Cwmffrŵd Member	*M. rhyakos* sp. nov. and *M. selwynii* (Salter) – ('late' forms)

Pibwr Member	*M. selwynii* (Salter) – upper *M. murchisoniae* (Murchison) and *M. selwynii* – lower
Bolahaul Member (Ogof Hên Formation)	*M. murchisoniae* (Murchison)

The olenid and asaphid trilobites of the early Arenig of the Carmarthen district thus show a minimum of three successive faunas. A fourth fauna remains to be described from the overlying Tetragraptus Beds. According to the Survey (Thomas *in* Strahan *et al.* 1909 : 16) the *hirundo* Zone as recognized by Elles (1904 : 210) occurs in the graptolitic Tetragraptus Beds assuredly overlying the Carmarthen Formation, so the Carmarthen and Ogof Hên Formations are together included within the old *extensus* Zone of Elles & Wood (1895). As indicated above (p. 234) graptolitic equivalents of the Carmarthen Formation probably occur to the west. Skevington (1969 : 168) states that the Llyfnant Flags underlying the Henllan Ash in Arenig belong to the *deflexus* (sub)zone, which is therefore the probable age of the Bolahaul Member.

Biostratigraphical subdivision of the Arenig rocks of south Wales on the basis of shelly faunas will no doubt prove a possibility, of which the sequence of species in the Carmarthen area is a first indication. The redescription of the Tetragraptus Beds, and their palaeontological subdivision, are a necessary prerequisite to the definition of any formal biostratigraphic units.

Environmental interpretation of the early Arenig of the Carmarthen district

The base of the Ogof Hên Formation is transgressive, terminating the period of uplift that

Formation	OGOF HÊN		CARMARTHEN			Lower part of TETRAGRAPTUS BEDS
Member	Allt Cystanog	Bolahaul	Pibwr	Cwmffrŵd	Cwm yr Abbey	
Merlinia murchisoniae		●	●			
Merlinia selwynii			● ●	'late forms'		
Merlinia rhyakos				●	● ●	
Microparia grandis					●	
Porterfieldia punctata					● ●	●
Bienvillia praecalva			●	● ●		
Hypermecaspis venerabilis				●	● ●	
Myttonia cf. fearnsidesi			●			
Ampyx cetsarum		●	●			
Neseuretus parvifrons		●				

Fig. 6. Summary of stratigraphic distribution of trilobites in the early Arenig of the Carmarthen district.

accounts for absence of Tremadoc rocks in the extreme SW of Wales. The subsequent Arenig history is one of progressive deepening of the geosyncline, and it is a response to this deepening which produces the faunal changes recorded in this paper.

The Allt Cystanog Member shows a change from coarse conglomerates at its base to fine sandstones and siltstones showing fine-scale slumping and ripple drift lamination, which indicate that it was deposited in an intertidal environment. Although body fossils are not present, 'worm' burrows are numerous on certain bedding planes, and these are the only trace fossils found in the Arenig of the area. The Allt Cystanog Member passes up into the progressively more shaly Bolahaul Member and with the passage the shelly fauna appears, at first only the coarse-ribbed brachiopod *Lenorthis alata* and echinoderm fragments. These are joined in higher beds by a *Neseuretus–Merlinia* trilobite assemblage. It has long been recognized that this fauna represents a shallow-water, inshore community accompanying the invading Arenig seas (Stubblefield 1939 : 52; Bates 1969b : 155). We here term it the Neseuretus Community after its most characteristic trilobite.

With upward passage into the Pibwr Member of the Carmarthen Formation, *Neseuretus* disappears, and the asaphid *Merlinia selwynii* (Salter) dominates the fauna, but the deeper water also allows the appearance of numerous raphiophorids (*Ampyx cetsarum*) and rare trinucleids (*Myttonia* cf. *fearnsidesi*). The bivalve '*Actinodonta*' is a characteristic new addition to the fauna; articulate brachiopods are absent, and inarticulates rare except for occasional larvae. The bivalve is an infaunal form (N. J. Morris, personal comm.), and its general occurrence through the black mudstones of the Pibwr Member indicates that the sediment was originally soft, this feature presumably accounting for the absence of surface-living sessile benthos such as articulate brachiopods and echinoids of Ogof Hên type, which require a firm substrate. The trilobites are generally of low convexity with a high ventral surface area/volume ratio (*Merlinia*), or with long genal spines (*Ampyx*), or both genal spines and a well-developed peripherally flattened fringe (*Myttonia*), all of which may be regarded as adaptations for support on soft sediment surfaces. There is no doubt that this assemblage of species represents a once-living community, because of the large number of articulated specimens, some representing moulted arrangements of parts, and the presence of early asaphid growth stages (Fortey 1975a). It is appropriately named the Raphiophorid Community, as members of that family are confined to it.

Towards the top of the Pibwr Member the first olenids (*Bienvillia praecalva* sp. nov.) appear, though rarely, with the Raphiophorid Community, but upwards into the Cwmffrŵd Member they become dominant, raphiophorids and trinucleids disappear, and asaphids (*Merlinia rhyakos*) comprise a smaller proportion of the fauna, until in the Cwm yr Abbey Member they are generally rare. Throughout the Cwmffrŵd and Cwm yr Abbey Members the fauna is an autochthonous Olenid Community. The conditions under which olenids abounded has been extensively discussed by Henningsmoen (1957 : 61–65) for the Upper Cambrian and Tremadoc and by Fortey (1975a : 338) for the Ordovician (Arenig–Llanvirn). Olenids were specially adapted to oxygen-impoverished environments, their dominance being associated with virtual disappearance of all other benthic animals (the infaunal bivalves so plentiful in the Pibwr Member are absent higher in the succession). Fortey (1975a : 338) indicated that in the Ordovician the olenid environment was also a relatively deep-water one, perhaps corresponding to the oxygen-minimum layer in present oceans, but the evidence for depth is indirect. In the Carmarthen succession the indirect evidence of a relatively deep-water site for the deoxygenated olenid environment is as follows:

(i) The olenid fauna is never found adjacent to the shallow-water Neseuretus Community either stratigraphically or palaeogeographically; the Neseuretus–Raphiophorid–Olenid Communities form an intergrading series in that order. In the transgressive context an environmental gradient induced by increasing depth is both the simplest and most plausible explanation for the faunal changes. It is interesting to note that we have a single example of a *Lenorthis* from the Cwm yr Abbey Member, probably an allochthonous specimen transported downslope, but no contrary examples of olenids in the Neseuretus Community.

(ii) The Cwmffrŵd Member has turbiditic horizons, providing positive evidence for the existence of a palaeoslope. While the depth at which turbidites may be emplaced is variable, it is significant that they are not found in rocks containing either the Raphiophorid or Neseuretus communities, but that they are characteristic of the graptolitic latest Arenig and Llanvirn sediments succeeding the Carmarthen Formation.

We disagree with Bergström's (1973 : 45–46) contention that olenids were pelagic. A pelagic habit is unlikely because of the strict facies dependence of the Olenidae, indicating that their life habits were closely tied to bottom or near-bottom conditions. Also they exhibit a mutually exclusive relationship with the benthic trilobites of the Raphiophorid and Neseuretus Communities, as well as the Nileid and Illaenid–Cheirurid Communities in Spitsbergen (Fortey 1975a : 336). A pelagic trilobite is independent of benthic assemblage types (vide *Carolinites* Fortey 1975a : 343; *Opipeuter* Fortey 1974a : 123; *Microparia* this paper, p. 256). Furthermore, the morphology of the large flattened olenid *Hypermecaspis venerabilis* sp. nov. is surely typical of a benthic animal. Both this morphological type and the more convex, *Bienvillia*-type of morphology may be interpreted as adaptations to cope with life on muddy sediments deoxygenated at, or just below, the sediment surface (Fortey 1974b : 11). Finally, Childress (1971) has shown that the Recent mysid *Gnathophausia ingens* can cope with minimum oxygen conditions because of an increase in the surface area of its oxygen-absorbing surfaces. Many Olenidae, such as *Hypermecaspis* herein, and a number of other forms of other families convergent with Olenidae (Fortey & Owens 1975 : 237), have wide (trans.) thoracic pleurae and a large number of thoracic segments, which is consistent with both lateral extension and multiplication of gill lamellae, and hence more efficient oxygen absorption. In short both morphology and occurrence of Ordovician olenids suggest benthic habits, and much of the same evidence can be applied to the Cambrian representatives of the family. However, there are a few Cambrian olenid genera, especially *Sphaerophthalmus* (Rushton 1968 : text-fig. 2), which differ radically in organization from the typical olenid, and it is among these that pelagic species may exist.

Palaeogeographic reconstruction

A palaeogeographic model which accounts for the distribution of the trilobite community types described here is presented in Fig. 7. Their occurrence is related to a continent-edge profile, extending from the shallow water Neseuretus Community through the Raphiophorid Community to the oxygen-deficient, and, by inference, deeper water Olenid Community. A broadly similar

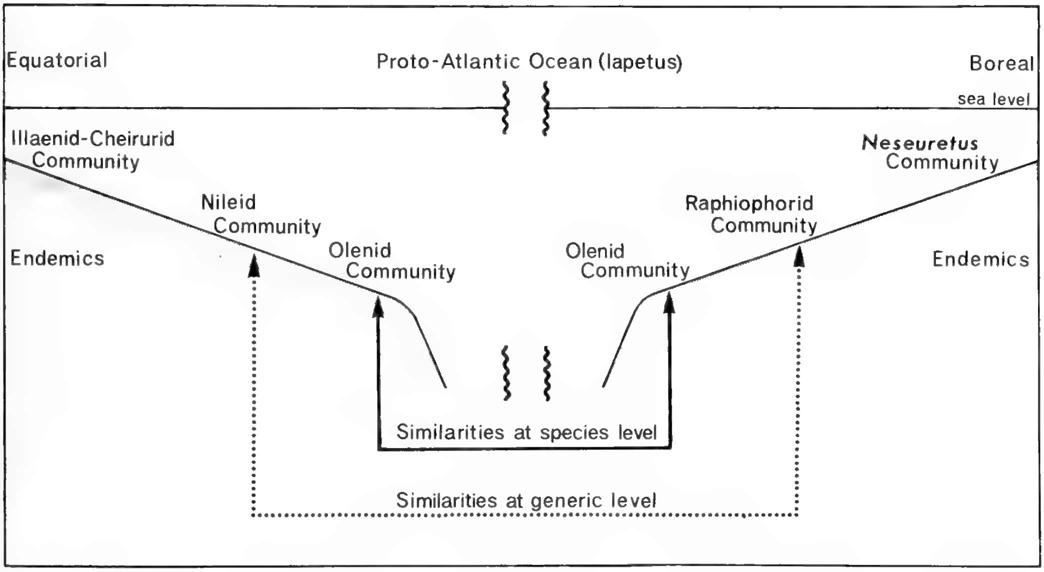

Fig. 7. Hypothetical section across Arenig continental margins, showing relation of community types to dispersal of species.

interpretation for the younger Ordovician was presented by Elles (1940). There is an obvious analogy to the profile proposed within the Bathyurid province by Fortey (1975a : 340) based on a succession of similar age in Spitsbergen. World maps for the early Ordovician (Smith, Briden & Drewry 1973; Whittington & Hughes 1972) indicate an equatorial position for Spitsbergen and the Bathyurid province, and a subpolar position for Wales (as part of the Selenopeltis province). Separation of the two areas by the Iapetus ocean (formerly referred to as the proto-Atlantic), with the corresponding shift in latitude, induced separate speciation, reflected eventually in different generic or even familial composition of trilobite faunas (Whittington & Hughes 1972 : 236). Fortey (1975a : 348) showed that this distribution pattern may be modified by the influence of the ecological circumstances producing different natural assemblages of trilobites – community types in a limited sense. In particular, genera inhabiting deeper water were proposed to be more or less independent of the surface temperature conditions and to include a larger number of province-independent forms.

In the Arenig of the Carmarthen district it is interesting to note that of the Olenidae, *Hypermecaspis* is now recorded from Spitsbergen, Nevada and Newfoundland (Bathyurid province), Bolivia and Argentina (Asaphopsis province) and Wales (Selenopeltis province); a closely related genus (*Tropidopyge*) is found in Norway (Asaphid province). That is, the Carmarthen Arenig shows connections with all four of the faunal provinces of the early Ordovician. *Bienvillia*, as understood here (p. 249), is similarly widespread. *Porterfieldia* occurs in Argentina (Asaphopsis province), Wales (Selenopeltis province) and North America (Bathyurid province). This provides strong support for the notion that the distribution of the olenid environment and the trilobites adapted to it as independent of provincial differences.

By contrast the genera *Neseuretus* and *Merlinia* are not present in either the Bathyurid or Asaphid provinces, although both extend into the Asaphopsis province (Harrington & Leanza 1957). The species of *Merlinia* in the Olenid Community is closest to that from slightly younger beds in South America. Of the genera of the Raphiophorid Community, *Ampyx* occurs in the early Ordovician of the Bathyurid and Asaphid provinces, as well as being widespread in the Selenopeltis province. *Myttonia* is confined to the Selenopeltis province. The evidence is limited, because only a few genera are present in the faunas of Carmarthenshire, but is consistent with the proposition of decreasing endemicity with depth.

Fossil localities

The following list is of localities referred to in the text and on the maps (Figs 2–5).

1. **Glan Pibwr** (Pibwr Member)
    - 1A. 77 m at 229° from Glan Pibwr Cottage (SN 4162 1794).
    - 1B. 18 m at 160° from Glan Pibwr Cottage (SN 4169 1798).
    - 1C. 156 m at 117° from Glan Pibwr Cottage (SN 4183 1795).
    - 1D. 197 m at 101° from Glan Pibwr Cottage (SN 4187 1795).
2. **Nant Cwmffrŵd** (Cwmffrŵd Member)
    - 2A. 100 m at 314° from bridge at S end of Cwmffrŵd (SN 4224 1745).
    - 2B. 130 m at 315° from bridge at S end of Cwmffrŵd (SN 4222 1747).
    - 2C. 167 m at 308° from bridge at S end of Cwmffrŵd (SN 4218 1748).
    - 2D. 183 m at 313° from bridge at S end of Cwmffrŵd (SN 4218 1750).
3. **Nant y Glasdwr** (Cwm yr Abbey and Cwmffrŵd Members)
    - 3A. Strike section, 326–360 m at 74° from bridge at S end of Cwmffrŵd (SN 4263 1746 – SN 4266 1747).
    - 3B. 254 m at 66° from bridge at S end of Cwmffrŵd (SN 4254 1748).
    - 3C. 197 m at 39° from bridge at S end of Cwmffrŵd (SN 4244 1753).
    - 3D. 195 m at 34° from bridge at S end of Cwmffrŵd (SN 4242 1754).
    - 3E. 198 m at 23° from bridge at S end of Cwmffrŵd (SN 4239 1756).
    - 3F. 197 m at 22° from bridge at S end of Cwmffrŵd (SN 4238 1756).
4. **Pibwr weir** (Pibwr Member)
    - 4. 300 m at 174° from Cilwaunydd (SN 4289 1805).

5. Allt Pen-y-Coed (upper part of Pibwr Member and Cwmffrŵd Member)
  - 5A. 530 m at 165° from Pont Pibwr (SN 4444 1805).
  - 5B. 525 m at 166° from Pont Pibwr (SN 4443 1805).
  - 5C. 520 m at 167° from Pont Pibwr (SN 4442 1806).
  - 5D. 500 m at 171° from Pont Pibwr (SN 4438 1808).
  - 5E. 455 m at 172° from Pont Pibwr (SN 4436 1812).
  - 5F. 442 m at 177° from Pont Pibwr (SN 4435 1813).
  - 5G. 430 m at 177° from Pont Pibwr (SN 4433 1815).
  - 5H. 350 m at 188° from Pont Pibwr (SN 4426 1823).

6. Roman Road, Pensarn (Bolahaul Member)
  - 6A. Exposure opposite cottage, N side of road, 45 m at 112° from chapel at Pensarn (SN 4133 1918).
  - 6B. S side of road, 75 m at 126° from chapel at Pensarn (SN 4136 1915).

7. Bolahaul Quarry (Bolahaul Member)
  - 7. 245 m at 88° from E end of Bolahaul Farm (SN 4235 1844).

8. Star Cottage (Bolahaul Member)
  - 8A. E side of road, immediately behind Star Cottage (SN 4293 1982).
  - 8B. E side of road, 20 m S of Star Cottage (SN 4294 1981).

9. Wenallt (Bolahaul Member)
  - 9. 185 m at 253° from Wenallt (tipped material) (SN 4369 2000).

10. Allt Cystanog (Bolahaul Member)
  - 10. Tips from old mines, 72 m at 203° from Penlan Villa (SN 4436 2025).

11. E end of Allt Cystanog (Bolahaul Member)
  - 11. Road cutting, S side of B4300, 140 m at 52° from Penlan Villa (SN 4482 2032).

12. Water treatment plant, Penddaulwyn fawr (upper part of Bolahaul Member)
  - 12. Temporary exposure 312 m at 289° from Penddaulwyn fawr, S of B4300 (SN 4538 2008).

13. Capel-Dewi stream section (? Cwmffrŵd Member)
  - 13. 100 m at 276° from chapel at Capel Dewi (SN 4745 2022).

14. Stream section opposite Polin (Cwm yr Abbey Member).
  - 14. 35 m at 226° from Polin (SN 4944 1968).

15. Cwm-difa (Pibwr Member)
  - 15A. 40 m at 223° from Cwm-difa Farm (SN 4944 1934).
  - 15B. 24 m at 244° from Cwm-difa Farm (SN 4945 1935).

16. Cwm yr Abbey (Cwm yr Abbey and Cwmffrŵd Members).
  - 16A. 126 m at 246° from Abbey Farm (SN 5014 1941).
  - 16B. 140 m at 268° from Abbey Farm (SN 5011 1946).
  - 16C. 144 m at 276° from Abbey Farm (SN 5011 1948).
  - 16D. 153 m at 285° from Abbey Farm (SN 5011 1950).
  - 16E. 216 m at 303° from Abbey Farm (SN 5008 1958).
  - 16F. 344 m at 322° from Abbey Farm (SN 5004 1973).
  - 16G. 358 m at 323° from Abbey Farm (SN 5003 1975).

Geological Survey localities

The map number (e.g. 39 NE) refers to the Geological Survey six-inch sheet on which the locality is situated. A complete list of these localities is given in the Carmarthen (sheet 229) memoir (Strahan *et al.* 1909).

Carm. 39 NE Wλ5. 250 m at 72° from Cablehill Farm (SN 4201 1949) (Bolahaul Member).

Carm. 39 NE Wλ7. 25 m at 44° from chapel at Pensarn, on S side of road (SN 4131 1918) (Bolahaul Member).

Carm. 39 NE Wλ3. 150 m at 312° from Cilwaunydd (SN 4274 1845) (Bolahaul Member).

Carm. 39 NE Eλ5. 75 m at 29° from Penddaulwyn fawr (SN 4570 2040) (Pibwr Member).

Carm. 40 NW Wλ8. Head of dingle, 970 m at 65° from bridge at Nant y Caws (SN 4601 1879) (Pibwr Member).

Systematic descriptions

A. Trilobites

Terminology. Descriptive terms used here follow the *Treatise*, Part O (Harrington *et al.* in Moore 1959 : O117–126), with the following exceptions:

(i) angular measurements on Raphiophoridae follow Fortey (1975a);
(ii) the glabella is here considered to include the occipital ring;
(iii) the course of the facial sutures in Asaphidae is described using the angular notation of R. & E. Richter (see Owens 1973 : 4, fig. 1A).

Preservation. There are particular problems in trilobite taxonomy when the variability in the initial population is allied with variability in the state of preservation. Welsh Arenig trilobites, and particularly the asaphids, have suffered from exceptional taxonomic confusion. Approaches to these animals have oscillated between two extremes: in the last century most new localities yielded 'new' species, whereas in the latter half of this century all Arenig asaphid species have been subsumed beneath one or two specific names. In the present work we have tried to strike a balance between the two approaches, by discovering material with little or no distortion and comparing it with the types of previously-named species, and by trying to find specific characters that are as little affected by distortion as possible.

It is usual for some flattening to have occurred even where a specimen has escaped distortion; often this results in 'composite surfaces' where the dorsal and ventral surface sculptures, for example, are impressed upon a single preserved surface (Pl. 5, fig. 1). With distortion (compression, and concomitant extension in a second dimension, accompanied by varying degrees of shearing and crushing) absolute measurements suffer grossly compared with relative proportions. We have tried to describe proportional characters in a way which will be consistent regardless of distortion; sculptural characters are also used and where they occur seem to be consistent within a species, usually surviving the hazards of preservation.

Sadly, type specimens are often distorted (Bates 1969a : pl. 6, fig. 3) and we have been tempted to restrict the species name to the type specimen in such cases in order to make a 'clean start'. However, so many of the names (*Ogygia selwynii* for example) are familiar and established in the literature that a conservative approach was eventually used in all cases, the old names reappearing here for what is probably not the last time.

Synonymy. We have used here the symbols proposed by Richter (1948) and explained by Matthews (1973 : 713) to amplify the information included in the synonymy lists.

Figured material. Figured material is in the British Museum (Natural History) (BM(NH)), National Museum of Wales (NMW), Institute of Geological Sciences, London (GSM) and Sedgwick Museum, Cambridge (SM).

Family **OLENIDAE** Burmeister 1843

Subfamily **TRIARTHRINAE** Ulrich 1930

Genus ***PORTERFIELDIA*** Cooper 1953

DIAGNOSIS. Triarthrine trilobites resembling *Triarthrus* but with sutural ridges prominent in adult. Eyes small, anteriorly placed, eye ridges present. Preglabellar field short to absent. Free cheeks lacking genal spines. Thorax with 11 (?) to 13 thoracic segments (where known); pleurae narrower (trans.) than axis. Pygidium small, with few axial rings.

TYPE SPECIES. *Triarthrus caecigenus* Raymond 1920, from the Athens shale (middle Ordovician) of Virginia, U.S.A.

DISCUSSION. Whittard (1961 : text-fig. 7) has reillustrated the type species of *Porterfieldia*. In diagnosing the genus Cooper (1953 : 8) described it as blind, but this was disputed by Whittington (1957 : 943) who believed that *Porterfieldia* had narrow free cheeks, eye lobes and sutures much like those of *Triarthrus*, and was therefore a junior synonym of that genus. Cooper's assumption of blindness was based on the identification of an apparent lateral cephalic border, but Fortey (1974b : 72) suggested that this 'border' was really a well-developed sutural ridge on the cranidium. *P. punctata* (Crosfield & Skeat), redescribed here, shows well the combination of a *Triarthrus*-like free cheek with a *Porterfieldia*-like cranidium with prominent sutural ridge.

The presence of this well-defined sutural ridge in the adult cranidium is here regarded as the defining character of *Porterfieldia*. Such a sutural ridge is common on small growth stages of a variety of olenids (Fortey 1974b : 41), but does not persist as a strong feature in the adult, although it is present in modified form as the post-palpebral furrow of *Cloacaspis ekphymosa* Fortey 1974. *Porterfieldia* is closely related to *Triarthrus*, and was probably derived neotenously from an early *Triarthrus* or late *Bienvillia* species.

A number of species show the distinct sutural ridge in the adult, and may be included within the revised concept of *Porterfieldia*. Besides the type species and *P. punctata* there are: *P. jachalensis* Harrington & Leanza 1957, from the Caradoc of Argentina, and '*Triarthrus*' *convergens* Whittard 1961 from the Hope Shales (Llanvirn) of Salop. Whittard (1961 : 190) interpreted the sutural ridge of the latter species as the lateral cephalic border, and regarded the facial suture as proparian. In view of the cephalic morphology of *P. punctata* (Pl. 1, fig. 2) and the position of the sutural ridge in olenids as a whole, it seems more probable that '*T.*' *convergens* had an opisthoparian suture and a free cheek of *Triarthrus* type. Whittard (1961 : 189) further commented that the material identified with *P. caecigena* by Cooper (1953 : 8–9; pl. 2, figs 7–10) differed significantly from the type material of that species. Thus *Porterfieldia* may include as many as five species, ranging in age from Arenig to Caradoc, and, like other olenids (see p. 240), with a biogeography independent of the Ordovician faunal provinces. They appear to form a morphologically discrete group, distinguishable from *Triarthrus* of *eatoni* type. The type species of *Triarthrus*, *T. beckii* Green 1832, needs redescription before the limits of *Porterfieldia* and *Triarthrus* can be finally defined.

It is noted that the earliest species of *Porterfieldia*, *P. punctata* (Crosfield & Skeat 1896), has a short preglabellar field; later species do not. This may indicate a derivation of *Porterfieldia* from a *Bienvillia* species like *B. praecalva* sp. nov., the cranidium of which shows many similarities to that of *P. punctata*.

Porterfieldia punctata (Crosfield & Skeat 1896)
(Pl. 1, figs 1–8; Pl. 2, figs 1–4, 7)

v*.1896 *Peltura punctata* Crosfield & Skeat : 535; pl. 26, figs 1–10.
.1908 *Triarthrus punctatus* (Crosfield & Skeat) Raw : 512.
v.1919 *Peltura punctata* Crosfield & Skeat; Lake : 99–100; pl. 11, fig. 13; pl. 12, figs 1–3.
v.1957 *Triarthrus punctatus* (Crosfield & Skeat); Henningsmoen : 148, 149–150.

DIAGNOSIS. *Porterfieldia* species with narrow (sag., exsag.) preglabellar field and pitted anterior border furrow. Glabellar and axial furrows subdued. Hypostoma as wide as long, with prominent maculae, posterior margin truncate. Pygidium with three axial rings, carrying sculpture of fine terrace lines.

LECTOTYPE. SM A3099, dorsal exoskeleton lacking free cheeks, original of Crosfield & Skeat 1896 : pl. 26, fig. 3; Lake 1919 : pl. 12, fig. 1 (Pl. 1, fig. 1 herein). Selected by Henningsmoen 1957 : 149.

TYPE LOCALITY AND HORIZON. The specimens originally figured by Crosfield & Skeat (1896) all came from Nant y Glasdwr, and the lithology and preservation further suggests that they are from our locality 3A.

OTHER OCCURRENCES. Crosfield & Skeat listed the species from Nant Cwmffrŵd and Cwrt-hir farm. Thomas (*in* Strahan 1907: 6–7; 1909: 5–8) further extended the list of occurrences around the Carmarthen district to virtually every outcrop of the '*Peltura punctata* Beds'. An extended list also appears in Lake (1919 : 100). Most of these additional records are spurious, presumably based on the misidentification of *Bienvillia praecalva* sp. nov. We have identified *P. punctata* from the type locality and lower down in Nant y Glasdwr (locs 3B, 3C), Cwm yr Abbey (locs 16D–G) and at the head of Cwm Ffinnant at Cwm-du (Geological Survey loc. Wλ1). It ranges from the top of the Cwmffrŵd Member to the lowest part of the Tetragraptus Beds.

DESCRIPTION. A good general account of this species was given by Lake (1919) and the following remarks amplify his description. New collections include a few specimens preserving the original convexity and with a minimum of distortion (Pl. 2, fig. 4). These show that the cephalic furrow effacement is an original feature, and not due to flattening or tectonic deformation. The glabella is scarcely elevated above the fixed cheeks, the whole cranidium having a broadly arcuate outline in anterior view. Axial and preglabellar furrows are uniformly shallow except where deepened at the anterolateral corners of the glabella. The two pairs of glabellar furrows are gently arcuate and extend to just over one-third the width of glabella. They are very shallow, but crushing may exaggerate the depth of both glabellar and axial furrows (Pl. 1, fig. 3). Outer parts of the occipital furrow curve backwards but the median part is bowed forwards. A minute occipital tubercle is visible on most specimens, but mid-thoracic tubercles are only visible on small specimens, particularly those that have been crushed.

The fixed cheeks are widest at the posterior margin; their maximum transverse width varies between 0·33 and 0·41 maximum transverse width of glabella, the lower values being obtained from uncrushed material. Internal moulds of some specimens are strongly caecate. Posterior border furrow a little deeper than furrows outlining glabella, and continued along posterolateral margin of cranidium as a well-defined furrow outlining the sutural ridge. Sutural ridge about half as wide as the posterior border. Furrow outlining the sutural ridge continues forward into the furrow delimiting the palpebral lobe, and then outlines the posterior margin of the short eye ridge. The palpebral lobes are placed in a forward position, posterior limit opposite 2P glabellar furrow on larger cranidia, a little behind this furrow on smaller cranidia. The lobes are small, of length between 0·16 and 0·23 sag. length of glabella. The preglabellar field is short, on uncrushed material continuing the downward slope of the anterior part of the glabella, but on crushed specimens opened outwards to a near-horizontal position; even on the most crushed specimens the preglabellar field is less than one-tenth sag. length of glabella (Pl. 1, fig. 6). Caeca are doubtfully present – corrugations on the preglabellar field are on a similar scale to those induced by crushing elsewhere on the exoskeleton. Border furrow deep on uncrushed material, with about 25–30 small pits, which are indistinct on poorly preserved specimens. Anterior border of width (sag.) equal to, or slightly less than, that of preglabellar field, gently rounded about mid-line, on badly preserved specimens having a pointed outline due to crushing (Pl. 1, fig. 6). Facial sutures subparallel in front of palpebral lobes, diverging outwards behind the lobes at about 20° – 30° to sagittal line, and posteriorly curving adaxially to become parallel, or almost so, to sagittal line at posterior margin. Dorsal surface of cranidium minutely punctate.

Hypostoma (Pl. 2, figs 1, 2) with maximum width across anterior wings, this equal to or slightly exceeding sag. length, gently backward-tapering. Middle body elliptical, divided in two lobes by transverse middle furrow. Anterior lobe posteriorly slightly pointed, and probably originally of considerable convexity, judged on the extensive cracking of the flattened material. Large maculae on posterolateral flanks of anterior lobe, internal surfaces covered with a fine grille of raised lines. Posterior lobe of middle body takes up about one-fifth (sag.) its length, and is

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Plate 1

Porterfieldia punctata (Crosfield & Skeat 1896). Early Arenig, Carmarthen Formation, Cwm yr Abbey Member.

Fig. 1. **Lectotype** (selected Henningsmoen 1957), almost entire dorsal shield lacking free cheeks. **Original** of Crosfield & Skeat 1896 : pl. 26, fig. 3. Nant y Glasdwr, loc. 3A. SM A3099. × 4.

Fig. 2. Latex cast of external mould of small, well-preserved dorsal exoskeleton without free cheeks. Sutural ridges well shown. Locality as Fig. 1. It 14000. × 8.

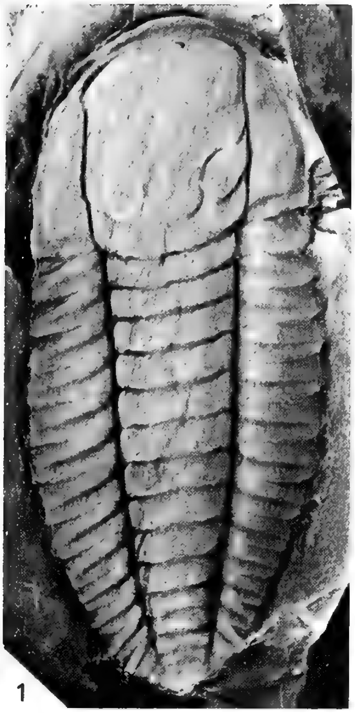
Fig. 3. Latex cast of small, flattened dorsal exoskeleton, to show exaggeration of cephalic furrows. Note presence of mid-thoracic tubercles. From the upper part of the stratigraphic range of the species. Cwm yr Abbey, loc. 16D. It 14001. × 8.

Fig. 4. Large cranidium, partially flattened and slightly extended (sag.). Locality as lectotype, Fig. 1. It 14002. × 6.

Fig. 5. External mould of dorsal exoskeleton lying ventral surface uppermost, preserving hypostoma in life position (cf. Henningsmoen 1957 : 92). Cwm yr Abbey, loc. 16G. It 14003. × 3.

Fig. 6. Almost completely flattened large cranidium, showing extension of preglabellar field and pointed appearance of anterior margin, pits in border furrow. Locality as Fig. 1. It 14004. × 6.

Figs 7, 8. Latex cast of external mould of 4 thoracic segments and pygidium to show surface sculpture (Fig. 7) and upward arch in pygidial margin (Fig. 8). Locality as Fig. 1. It 14005. × 10.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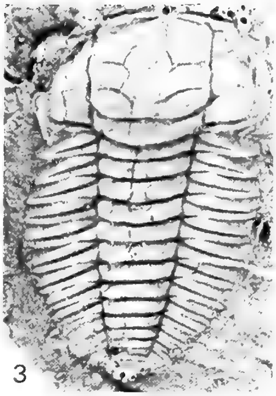
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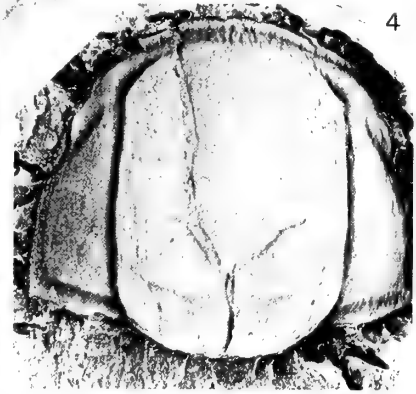
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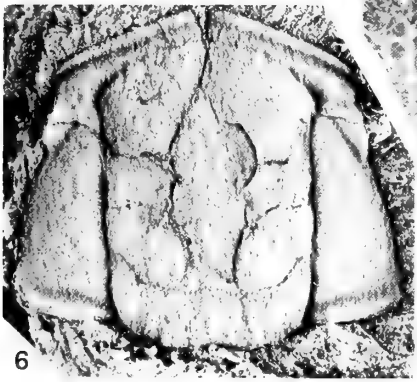
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narrowest medially, continuing upward slope of posterior part of anterior lobe. Lateral borders gently converge backwards, steep adjacent to middle body, depressed posterolaterally. Posterior border meets lateral borders abruptly at an obtuse angle (about 110°), runs transversely or very slightly pointed medially. Border furrows shallow except anteriorly. Surface of hypostoma is punctate, but punctation is coarser and more scattered than that of dorsal surface of exoskeleton.

Narrow free cheeks with maximum width just behind eye, this being less than that of the fixed cheeks. One specimen (Pl. 2, fig. 3) shows the narrow strip of ventral doublure connecting the free cheeks, lacking both median and connective sutures. Small elevated nodes on the upper surfaces of the doublure correspond to the pits in the border furrow, so that the border of *P. punctata* has a strutted structure similar to that of *Balnibarbi* species (Fortey 1974b: fig. 4C). Free cheeks show faint genal caeca, which do not pass onto the convex lateral border.

Thorax with 12 segments, expanding in width to fourth and fifth segments, tapering gently posteriorly such that the width (trans.) of the twelfth segment is half that of the fifth. The (exsag.) length of the thoracic segments is similar on the second to fifth segments, decreasing progressively thereafter posteriorly. Axis similarly tapers over the last seven segments, exceeding the transverse width of the thoracic pleurae, more markedly so on larger specimens. Of the pleurae themselves the first two pairs are more pointed, those posterior blunter-tipped. Articulating fulcra close to the axis; triangular facets abaxial to fulcra are relatively broader (exsag.) on the first two thoracic segments. Pleural furrows straight or slightly concave-forwards anteriorly, running almost to tip of pleurae.

Pygidium of width more than twice length, posterior margin rounded and upward-arched about mid-line. Axis with three axial rings of similar width (sag.), the third incompletely defined by shallow ring furrow. Terminal piece short and wide, not clearly defined from postaxial field. Three pairs of pleural furrows, which slope progressively more steeply backwards posteriorly, and one pair of interpleural furrows delimiting anterior segment only. Posterior border narrow, especially adaxially.

Discussion. The discovery of the hypostoma of this species helps to clarify some problems of homology of hypostomal structures in other Olenidae. The primitive olenid hypostoma, as exemplified by *Olenus* (Westergård 1922: pl. 4, figs 4, 9) has a large middle body transected

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Plate 2

Porterfieldia punctata (Crosfield & Skeat 1896). Early Arenig, Carmarthen Formation, Cwm yr Abbey Member.

Fig. 1. Hypostoma, ventral view. Cwm yr Abbey Member, Nant y Glasdwr, locality 3B. It 14006. × 10.

Fig. 2. Detail of hypostoma to show punctate sculpture and grooved maculae. Locality as previous specimen. It 14007. × 15.

Fig. 3. External mould of free cheek, with doublure connecting second cheek lacking median or connective sutures. Same bed as Fig. 1. It 14008. × 10.

Figs 4, 7. Almost undistorted cranidium in dorsal and anterior views. Same bed as Fig. 1. It 14009. × 10.

Bienvillia praecalva sp. nov. Early Arenig, Carmarthen Formation, Cwmffrŵd Member.

Fig. 5. Slightly crushed cranidium, front part of glabella crushed over preglabellar field. Nant Cwmffrŵd, loc. 2A. It 14010. × 10.

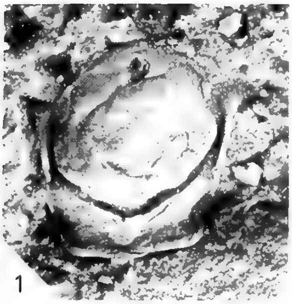
Figs 6, 9. Almost undistorted cranidium in lateral and dorsal views. Locality as previous specimen. It 14011. × 6.

Fig. 8. Cranidium, only slightly crushed, and showing median effacement of preglabellar furrow. Locality as previous specimens. It 14012. × 6.

Fig. 10. Pair of fused free cheeks, showing narrow connecting doublure lacking sutures. Nant y Glasdwr, loc. 3F. It 14013. × 6.

Fig. 11. **Holotype**, large, flattened cranidium. Preglabellar field slightly extended, but median effacement of preglabellar furrow characteristic of species, and pits in border furrow well displayed. Nant Cwmffrŵd, loc. 2A. It 14014. × 6.

Fig. 12. Right free cheek. Locality as holotype. It 14015. × 6.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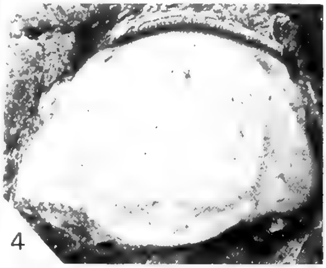
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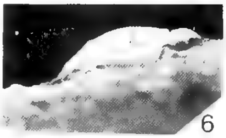
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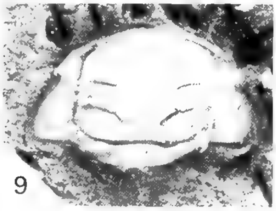
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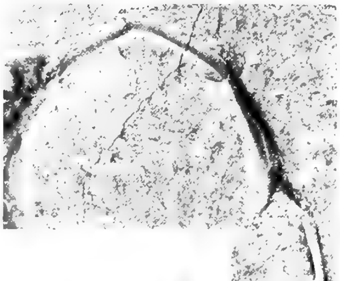
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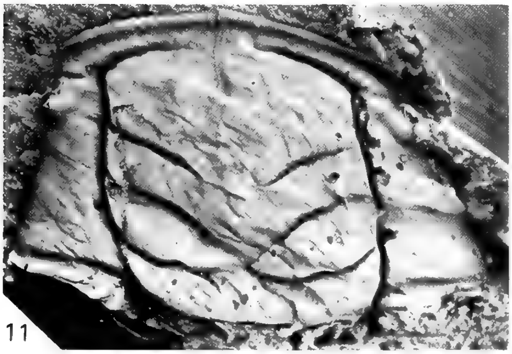
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posteriorly by a deep middle furrow, the whole surrounded by narrow borders. With the differentiation of the olenid subfamilies in the Upper Cambrian the hypostoma underwent various modifications which tended to remain conservative within a given subfamily. In *Parabolinella* (Henningsmoen 1957 : pl. 12, fig. 5), Balnibarbiinae (Fortey 1974b : pl. 1, figs 5–7) and *Hypermecaspis* (Fortey 1974b : pl. 14, figs 1, 6) the middle body is large and with narrow borders as in the primitive condition; in the Balnibarbiinae and *Hypermecaspis* there are in addition prominent maculae. These latter occur immediately in front of the middle furrows. On *Porterfieldia punctata* maculae are also prominent, and these occur immediately in front of a prominent furrow passing completely between the borders (Pl. 2, fig. 1). It is probable that this furrow is homologous with the middle furrows of other olenids, thereby dividing the middle body into an inflated anterior and a depressed posterior lobe, the latter superficially appearing to belong to the border. A similar situation seems to pertain in some pelturines, for example in *Peltura transiens* (Brøgger) (Henningsmoen 1957 : pl. 26, fig. 12) and other *Peltura* species the apparent 'middle body' is inflated and terminates with a pair of posterolateral raised areas, which are probably maculae. The true middle body includes in addition a narrow (sag.), crescentic posterior lobe which lies immediately in front of the posterior border; the boundary between the anterior, inflated and posterior, depressed parts of the middle body is the homologue of the middle furrow in the primitive condition.

The hypostoma of *P. punctata* has more in common with those of the pelturines listed above, and also that of the type species of *Psilocara*, *P. comma* (Fortey 1974b : pl. 19, figs 14, 18), than with any triarthrine for which the hypostoma is known. In *Bienvillia tetragonalis broeggeri* the middle body is undivided (Henningsmoen 1957 : pl. 11, fig. 7), similarly in *Triarthrus thor* (Fortey 1974b : pl. 23, fig. 21), while in *Parabolinella limitis* there is a short pair of middle furrows (Henningsmoen 1957 : pl. 12, fig. 5). This might suggest that the affinities of *P. punctata* lie with the Pelturinae rather than the Triarthrinae, a view favoured by Lake (1919). Henningsmoen (1957 : 150) also noted similarities to pelturines, especially *Peltocare*, in the form of the free cheek and the twelve thoracic segments (like *Peltura*, *Protopeltura*, *Saltaspis* and *Beltella*), but favoured an assignment to *Triarthrus* on the grounds that cranidial features of *P. punctata* were closer to that genus. The evidence of the new material from south Wales rather favours this interpretation. The likely close relationship of *P. punctata* to *Bienvillia praecalva* will be mentioned (p. 249). *B. praecalva* is assuredly triarthrine; it is possible that the distinctive hypostoma of these species is a derived character linking the *Porterfieldia* species group. More knowledge of Ordovician triarthrine hypostomata is needed before this can be established.

Genus ***BIENVILLIA*** Clark 1924

Bienvillia praecalva sp. nov.

(Pl. 2, figs 5, 6, 8–12; Pl. 3, figs 2–7)

Diagnosis. A *Bienvillia* species with moderately narrow (trans.) fixed cheeks for the genus. Palpebral lobes very small, less than one-fifth glabellar length, and in front of 2P glabellar furrows. Preglabellar furrow effaced medially; preglabellar field about one-tenth length of glabella. Posterior border of free cheeks curving forward strongly to genal spines, which are long and stout, slightly outwardly-directed proximally.

Name. Latin, *praecalvus*, 'balding in front' referring to the median effacement of the preglabellar furrow.

Holotype. BM(NH) It 14014, flattened cranidium.

Type Locality and Horizon. Material figured here is from black shales of the Cwmffrŵd Member, loc. 2A, Nant Cwmffrŵd.

Other occurrences. *B. praecalva* has been recorded from loc. 2B, Nant Cwmffrŵd, and loc. 3F, Nant y Glasdwr, both from the Cwmffrŵd Member. In Allt Pen-y-Coed poorly-preserved specimens of *B. praecalva* occur in the upper part of the Pibwr Member (locs 5F, 5H) and in the Cwmffrŵd Member higher in the dingle (locs 5B, 5C, 5E). Poorly-preserved specimens probably referable to this species have been found in the Cwmffrŵd Member exposed in Cwm yr Abbey (locs 16B, 16C).

Description. Cranidium with maximum width at posterior margin, this about one and a half times sagittal length. Fixed cheeks originally sloped downwards, so that in plan view on the flattened material they appear wider than they are on uncrushed material in dorsal view. Their maximum width is just under half the maximum width of glabella, the latter equal to, or slightly less than, sagittal glabellar length. Glabella expands forwards to maximum width at 1P lobe, thereafter tapering gently forwards, but becoming parallel-sided at anterior lobe. Axial furrows deep, as are the lateral parts of the preglabellar furrow, but this furrow is effaced medially so that the frontal lobe of the glabella is continuous there with the preglabellar field. Two pairs of glabellar furrows extend more than one-third across glabella, deeply incised and sloping backwards at about 40°–50° to sagittal line at inner ends. Outer parts of occipital furrow slope backwards, median part horizontal or slightly bowed forwards, so that the median part of the occipital ring is wider (sag.) than lateral parts (exsag.). Occipital tubercle more prominent on smaller specimens. Posterior border furrow deep, outlining posterior border of less than half width (exsag.) of occipital ring. Sutural ridges absent on larger cranidia, faint and very narrow on smaller cranidia. Preglabellar field narrow, about one-tenth length of glabella, probably originally downward-sloping, although flattened out on crushed material. Some specimens (Pl. 2, fig. 5) are flattened so that the preglabellar field is crushed beneath the frontal lobe of the glabella. Border furrow moderately impressed, with 25–30 small pits visible on well-preserved cranidia. Gently convex anterior border half the width (sag., exsag.) of preglabellar field. Palpebral lobes small and far forward, posterior limit opposite outer end of glabellar furrow 2P, between 0·12 and 0·17 of glabellar length. Palpebral furrows shallow, continued anteriorly into furrow outlining posterior limit of short, faint eye-ridge. Short, anterior sections of facial sutures subparallel in front of palpebral lobes, but flattening may produce a slight divergence; posterior sections straight or slightly bowed outwards, diverging at about 20°–30° to sagittal line, and cutting the posterior margin at an acute angle approaching 90 degrees.

Free cheeks yoked together as a single unit, connected by a narrow strip of doublure (Pl. 2, fig. 10), which comes to a point medially. Anterior band of doublure depressed and carrying terrace lines, posterior part elevated dorsally, with minute nodes which are presumed to have been ventrally correspondent with the pits in the anterior border furrow. Lateral and posterior borders narrow, with fine terrace lines parallel to margins of cheeks. Posterior border curves sharply forward to genal spine, subtending an angle to the spine of about 60°. Spine curves outwards initially, almost in line with lateral margin of cheek and slightly inflected, posteriorly curving to become parallel to sagittal line and extending to more than 1·5 cephalic length.

There are more than 10 thoracic segments (Pl. 3, fig. 3) but there are no perfectly-preserved specimens displaying the full thoracic complement. On one fragment the eighth segment bears a long medial spine (Pl. 3, fig. 2), but it is not certain that this spine arose from the eighth segment on the entire animal, or one posterior to it.

Pygidium small, and strongly upward-arched posteriorly, only two axial rings clearly defined, axis (?) extending to posterior margin. Pleural fields carrying two pairs and a third faint pair of interpleural furrows; surface sculpture of fine terrace lines. Small growth stages of this species are known from Nant Cwmffrŵd, indicating that the olenid assemblage there is truly autochthonous (Pl. 3, figs 4, 5). They are not well preserved, but conform to the description of triarthine growth stages given by Whittington (1957) and Fortey (1974b : 73). Probable degree 2 meraspis (Pl. 3, fig. 4) clearly shows the forward-expanding glabella and the strongly furrowed, posteriorly truncate pygidium common to small *Triarthrus* and related genera.

Discussion. The arbitrariness of the division between *Triarthrus* and *Bienvillia* has been recently discussed by Fortey (1974b : 65–66). The species described above is particularly difficult as it lies halfway between typical members of each genus. The presence of a preglabellar field, albeit a narrow one, together with fixed cheeks of moderate width, comparable with those of *B. tetragonalis broeggeri* (Henningsmoen 1957 : pl. 11, figs 1, 2, 4) and *B. stikta* (Fortey 1974b : pl. 22, figs 9, 11), makes us favour an assignment to *Bienvillia*. It must be emphasized, however, that several species assigned to *Triarthrus*, such as those of Harrington & Leanza (1957), are similar to *B. praecalva* and must be considered in the discussion.

The type species, *B. corax* (Billings), figured by Rasetti (1954 : pl. 61, fig. 15), has both wider fixed cheeks and preglabellar field than those of *B. praecalva*, and longer, straighter glabellar furrows. The very small, advanced palpebral lobes of *B. praecalva* and the forward position of its genal spines distinguish it from *B. stikta* Fortey (1974b : 66–69; pl. 22, figs 1–15; pl. 24, figs 5–7), the only other Arenig species of the genus, and *B. shinetonensis* (Raw) (Lake 1913 : 70; pl. 7, figs 13–16; Harrington & Leanza 1957: 115; fig. 42, 9–12; Henningsmoen 1957; pl. 1, fig. 7), *B. tetragonalis broeggeri* (Henningsmoen 1957 : 145–146; pl. 11, figs 1–7), *B. tetragonalis tetragonalis* (Harrington) (Harrington & Leanza 1957 : 113–115; fig. 42, 1–6; assigned by them to *Triarthrus*) and *B. grandis* Robison & Pantoja-Alor (1968 : 788; pl. 100, figs 16–18). A distinctive feature found on *B. praecalva* and no other *Bienvillia* is the median effacement of the preglabellar furrow. In other species the front of the glabella is frequently indented by the preglabellar furrow in the same area. Similar features distinguish *B. praecalva* from '*Triarthrus*' from Argentina – '*T.*' *parchaensis* Harrington & Leanza (1957 : 117, 119; fig. 43, 1a–h; fig. 44, 1a–e) and '*T.*' *rectifrons* (Harrington) (Harrington & Leanza 1957 : 115; fig. 43, 2a–g). All the species here compared with *B. praecalva*, except the type, have long genal spines, where the free cheeks are known, a feature uncommon among middle Ordovician *Triarthrus*. Since they also have other features in common, such as a short preglabellar field and fixed cheeks about half the width of the glabella, this might suggest that they could be accommodated within a new genus forming a 'bridge' between Tremadoc *Bienvillia* on the one hand and Middle Ordovician *Triarthrus* on the other. However, this would simply double the number of boundary problems, as there are already species known with intermediate character states – for example, *Triarthrus papulosus* Fortey (1974b : 70; pl. 23, figs 1–11) has long genal spines, but lacks a preglabellar field like typical *Triarthrus*.

Subfamily **HYPERMECASPIDINAE** Harrington & Leanza 1957

Genus ***HYPERMECASPIS*** Harrington & Leanza 1957

DIAGNOSIS. The diagnosis given by Harrington & Leanza (1957 : 121) is accepted here.

TYPE SPECIES. *Hypermecaspis inermis* Harrington & Leanza 1957 (by original designation).

Hypermecaspis venerabilis sp. nov.

(Pl. 3, figs 1, 8–10)

v.1896 *Olenus* (*Parabolinella*) sp. nov. Crosfield & Skeat : pl. 26, figs 11, 12.

Plate 3

Bienvillia praecalva sp. nov. Early Arenig, Carmarthen Formation, Cwmffrŵd Member.

Fig. 2. Eight thoracic segments, showing median spine on eighth. Nant Cwmffrŵd, loc. 2A. It 14016. × 10.

Fig. 3. Small, incomplete dorsal exoskeleton, showing 10 (? 11) thoracic segments. Allt Pen-y-Coed, loc. 5F. It 14017. × 4.

Fig. 4. Degree 2 meraspis. Nant Cwmffrŵd, loc. 2A. It 14018. × 15.

Fig. 5. Meraspis of at least degree 5. Nant Cwmffrŵd, loc. 2A. It 14019. × 8.

Fig. 6. Poorly preserved hypostoma. Nant Cwmffrŵd, loc. 2A. It 14020. × 10.

Fig. 7. Incomplete pygidium. Nant y Glasdwr, loc. 3F. It 14021. × 15.

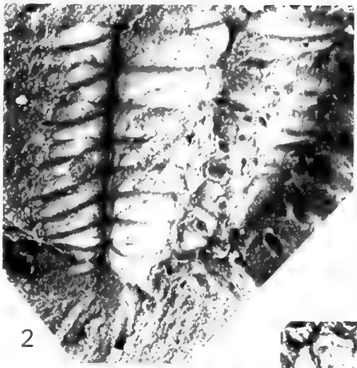
Hypermecaspis venerabilis sp. nov. Early Arenig, Carmarthen Formation, Cwmffrŵd and Cwm yr Abbey Members.

Figs 1, 8. Eighteen thoracic segments and pygidium, incomplete on right side. Fig. 8, plan view, × 3; Fig. 1, detail of pygidium to show terrace lines, × 6. Cwmffrŵd Member, Allt Pen-y-Coed, loc. 5D (Eλ5). GSM JP4700.

Fig. 9. Cranidium with preglabellar area largely missing, but showing anterior branch of facial suture on right. Original of Crosfield & Skeat 1896 : pl. 26, fig. 11. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. SM A550a. × 3.

Fig. 10. **Holotype**, almost complete cranidium. Cwmffrŵd Member, Allt Pen-y-Coed, loc. 5D (Eλ5). GSM 26062. × 4.


1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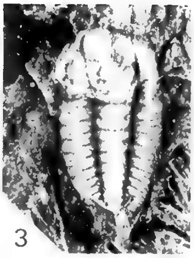
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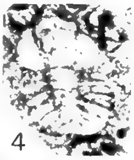
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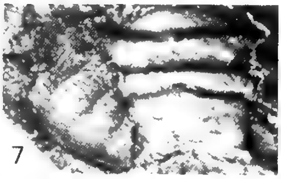
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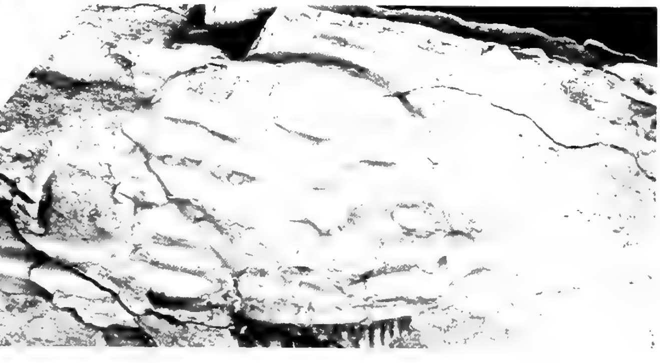
10

v.1909 *Parabolinella rugosa* Brögger; Thomas *in* Strahan *et al.*: 5, 7.
v.1909 *Dikelocephalus serratus* Boeck; Thomas *in* Strahan *et al.*: 5, 7.
v.1909 *Parabolinella* sp. nov. Thomas *in* Strahan *et al.*: 7.
v.1913 *Parabolinella rugosa* Brögger var.; Lake: 67; pl. 7, fig. 3.
v.1957 ? *Parabolinella rugosa* Brögger; Henningsmoen: 137–138.

DIAGNOSIS. A *Hypermecaspis* species with a short preglabellar field which is not caecate. Anterior border not clearly defined on cranidium. Preocular facial sutures slightly divergent. Pygidium with three axial rings and terminal piece.

NAME. Latin, *venerabilis*, 'venerable', referring to wrinkled appearance of cranidium.

HOLOTYPE. GSM 26062 (Pl. 3, fig. 10), almost complete cranidium preserving preglabellar field.

TYPE LOCALITY AND HORIZON. Cwmffrŵd Member, Allt Pen-y-Coed, loc. 5D (Survey loc. Eλ5). The thorax and pygidium figured here (Pl. 3, fig. 8) are from the same locality.

OTHER OCCURRENCES. The specimen figured by Crosfield & Skeat (1896) is from the lower part of the Cwm yr Abbey Member, loc. 3A, Nant y Glasdwr. The species thus ranges through the Cwmffrŵd Member and the lower part at least of the Cwm yr Abbey Member. Isolated thoracic segments probably attributable to this species have also been obtained from the Cwm yr Abbey Member, loc. 16D, Cwm yr Abbey.

DESCRIPTION. Although the available material of this species is flattened, enough features are preserved to be sure of its specific distinction. Relief *Hypermecaspis* species from the Arenig of Spitsbergen (Fortey 1974b: 44–51) are all of low convexity, and it is unlikely that the species described here was very different in this respect. However, it is probable that the preglabellar field originally sloped downwards, and that flattening caused it to be horizontally disposed around the front of the glabella (cf. Fortey 1974b: pl. 14, figs 7, 9). The glabella tapers gently forwards, front margin somewhat truncate, gently rounded about midline. Occipital and glabellar furrows typical of *Hypermecaspis*: the short 1P furrow is bifurcate at its inner end; 2P, 3P and 4P extend more than one-third across glabella, inner ends deflected backwards. Outer end of 4P almost at anterolateral corner of glabella. One specimen (Pl. 3, fig. 9) shows exsagittal effacement of part of the 2P furrow, so that the outer and inner parts of the furrow are separated by a smooth area. Occipital ring divided into three lobes: median, forward-bowed part of occipital furrow continued backwards to isolate triangular lateral occipital lobes between lateral, backward-sloping parts of occipital furrow. Palpebral lobes large, anterior limits opposite 4P where they almost touch the glabella, posterior limits opposite 1P and not so close to glabella. Palpebral rims broad. The narrow (exsag.), strap-like postocular fixed cheek is bisected by the posterior border furrow, which curves outwards and forwards from where it meets the axial furrow almost at the posterior cephalic margin, in the process becoming shallower and ill-defined. Posterior border widening abaxially, with depressed posterior band. Anterior border not distinguishable from preglabellar field, both together about one-sixth (sag.) glabellar length. The holotype shows little trace of caeca and on the second specimen they are faint on the fragment of the preglabellar field preserved. Anterior branches of facial sutures diverge at about 20° to sagittal line in front of the palpebral lobes; posterior branches swing out to run transversely, distally curving sharply posteriorly to cut the posterior cranidial margin at a right angle.

Free cheek and hypostoma not known.

Thorax shows 18 segments but is probably incomplete in known specimens. (The complete specimens of *H. inermis* and *H. armata* from the Arenig of Argentina both have 19 segments.) The long, pointed-tipped thoracic pleurae are of similar transverse length along the thorax, but slope progressively more backwards posteriorly. The long pleural furrows extend almost to the tips of the pleurae.

Pygidium fan-shaped, maximum width near posterior margin slightly exceeding sagittal length. Short, gently tapering axis occupying under half pygidial length (sag.), with three axial rings of equal width (sag.) and a short terminal piece which is rounded posteriorly. The postaxial ridge which is seen on other species of the genus is not visible, but this may be due to the flattening of the only specimen. Three pairs of pleural furrows were probably present, not reaching the posterior margin, and a single pair of interpleural furrows. Dorsal surface shows fine terrace lines, densely crowded about posterior margin, more widely spaced near the axis.

DISCUSSION. *H. venerabilis* differs from the type species, *H. inermis* Harrington & Leanza (1957 : 123–125; figs 45, 46, 48 : 6) from the Arenig of Salta, Argentina, in having a wider (sag., exsag.) preglabellar field and a longer pygidium with only three axial rings. The other Arenig species from Argentina, *H. armata* (Harrington & Leanza 1957 : 125; figs 47, 48 : 3–5) has a preglabellar field of similar width to that of *H. venerabilis*, but convergent anterior sections of the facial sutures and a distinctly-defined anterior cranidial border; the pygidium of the Argentine species is small. Of the three species of *Hypermecaspis* from the Arenig Olenidsletta Member of the Valhallfonna Formation, Spitsbergen, only one, *H. brevifrons* Fortey (1974b : 48–49; pl. 14, figs 1–9; pl. 24, fig. 9), has a preglabellar field as narrow as that of *H. venerabilis*, but this is strongly caecate, even when flattened, although the anterior border furrow is effaced on some specimens as on the Welsh material. The pygidium of the Spitsbergen species has four axial rings and a terminal piece. The resemblance between the Spitsbergen (Bathyurid province), Welsh (Selenopeltis province) and Argentine (Asaphopsis province) species is such that a close relationship is undoubted and lends credence to the theory that distribution of olenid trilobites was independent of provincial barriers in the early Ordovician (see p. 240).

Family **RAPHIOPHORIDAE** Angelin 1854
Subfamily **RAPHIOPHORINAE** Angelin 1854
Genus ***AMPYX*** Dalman 1827

TYPE SPECIES. *Ampyx nasutus* Dalman 1827.

DIAGNOSIS. Raphiophorine trilobites with 6 thoracic segments, subisopygous. Glabella with long anterior spine with circular cross-section. Glabella expanding forwards, overhanging anterior border, muscle impressions variously incised, three pairs visible on most species. Pygidium with only one pair of pleural furrows clearly visible; pygidial axis shows more than 5 segments indicated by muscle impressions on internal moulds. Surface sculpture combinations of raised lines, incised grooves and pitting.

REMARKS. This diagnosis is based on a *sensu lato* concept of *Ampyx*. As noted by Fortey (1975a : 65–66) *Ampyx* as at present conceived is likely to include a number of species only distantly related to the type species, *A. nasutus* Dalman, and may eventually be divisible into several genera. The characters germane to such a division are not yet clearly identified, but will include the degree of impression and arrangement of glabellar muscle impressions, the shape and extent of the posterior border furrow and occipital ring, and the outline of the facial sutures. The new species described below differs from the type in having facial sutures with convex-forward outline, and in the straight, incomplete pygidial pleural furrows. These differences are shared by some other Arenig *Ampyx* species such as *A. spongiosus* Fortey 1975 and *A. volborthi* Schmidt 1894.

Ampyx cetsarum sp. nov.
(Pl. 4, figs 1–4, 6, 7)

v.1966 *Ampyx* aff. *salteri* Hicks; Whittington : pl. 2, figs 1–3, 6; ? 4, 5.

DIAGNOSIS. An *Ampyx* species with surface sculpture of fine raised lines on forward parts of cheeks and glabella. Muscle impressions not incised. Posterior borders and occipital ring form a continuous band, gently forward-sloping. Outline of facial sutures convex forwards. Pygidial axis weakly defined, with about 5 pairs of muscle impressions. One pair of shallow pygidial pleural furrows not extending as far as axis.

NAME. After Crosfield & Skeat, the original (1896) discoverers of the Carmarthen faunas; a contraction of 'C. et S'.

HOLOTYPE. BM(NH) It 14022, slightly crushed cranidium preserving exoskeleton anteriorly.

TYPE LOCALITY AND HORIZON. Glan Pibwr (loc. 1A), the specimens collected from the highest beds exposed there, but still quite low in the Pibwr Member.

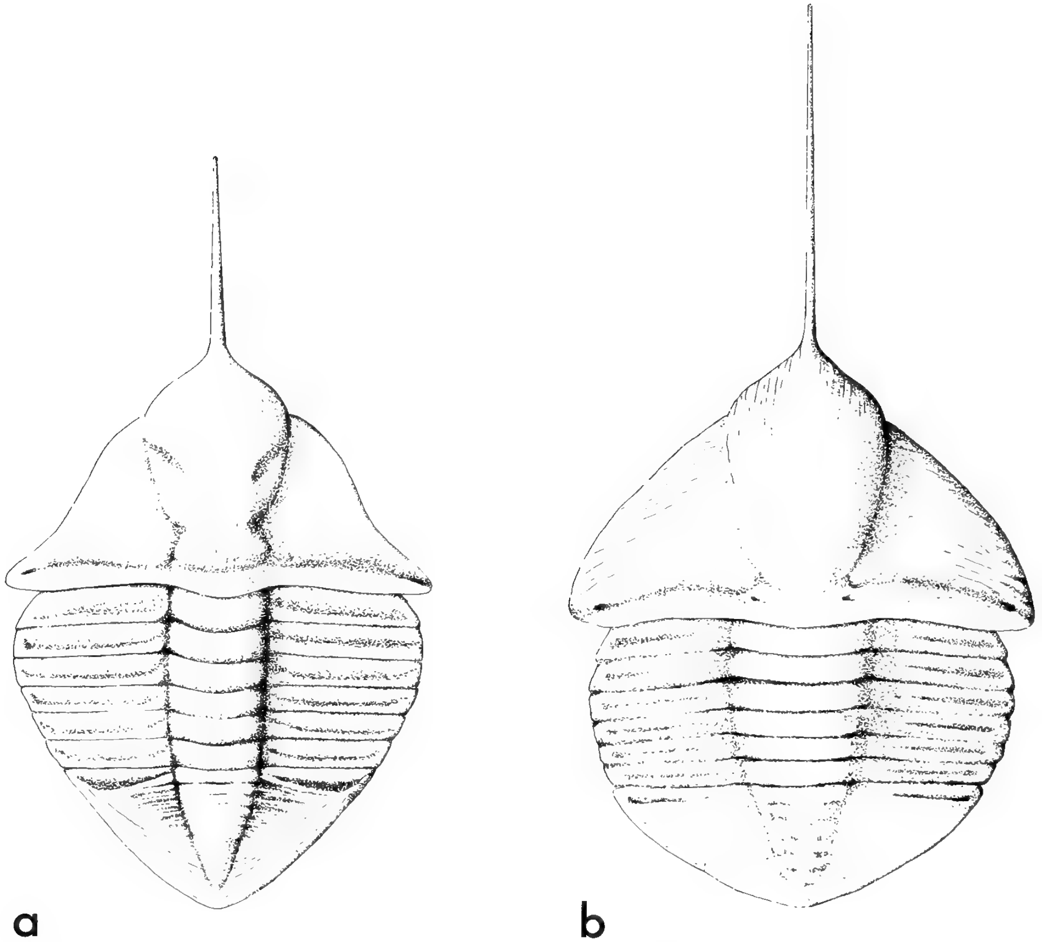

Fig. 8. Reconstructions of dorsal exoskeletons (lacking free cheeks) of: a, *Ampyx salteri* Hicks and b, *Ampyx cetsarum* sp. nov., to summarize diagnostic differences. (Both approx. × 3½.)

Other occurrences. The species is represented by numerous specimens from the temporary exposure of the uppermost part of the Bolahaul Member at the water processing plant west of Capel Dewi (loc. 12).

Description. Although much of the material of this species is crushed, enough parts are known in an undistorted state to enable a nearly complete reconstruction to be made (Fig. 8b), and sufficient details are known of the dorsal cuticle surface to be certain of the characteristic surface sculpture. Length of exoskeleton (excluding frontal spine) slightly exceeding width across mid-part of thorax; sagittal length of thorax about equal to that of pygidium, both exceeded by length of glabella.

Cranidium with almost semicircular outline, glabella not greatly elevated above genal areas compared with many *Ampyx* species. Glabella expands rather uniformly forward from occipital ring (θ in the range 30°–45°), preoccipital width being about half maximum width across antero-lateral corners. Degree of forward protrusion of glabella relatively slight, although most specimens are not well preserved in this region (ω approximately a right angle). Stout anterior spine exceeding length of glabella. Muscle impressions not visible upon glabella when it is hardly distorted, and lack of distinctly impressed muscle attachment sites is considered to be an original feature. Axial furrows shallow, not continued posteriorly to define occipital ring. Posterior border and occipital ring form a continuous band, which slopes gently forwards. Posterior border furrow is bowed slightly forwards, deep laterally, shallowing and broadening adaxially. Posterolateral fossulae well developed. There is a pair of pits, clearly visible on internal moulds (Pl. 4, fig. 2), at the posterior ends of the axial furrows at the anterior edge of the occipital region, representing small, ventrally-directed apodemes. Outline of facial sutures convex forwards, even on flattened material. Presumably these sutures ran almost marginally to the cephalon; unfortunately, specimens with free cheeks are lacking.

Surface sculpture on cheeks of fine, only rarely bifurcating raised lines which run subparallel to the anterior cranidial margin. They do not extend on to the posterior, adaxial parts of the fixed cheeks. Similar raised lines, directed more or less sagittaly, are present on the flanks of the anterior part of the glabella. The terrace lines are weakly reflected on internal moulds, where some specimens (Pl. 4, fig. 1) show a genal ridge, directed obliquely backwards, but not reaching posterolateral corner of cranidium.

Thorax with maximum width at third segment, where transverse width of pleurae equals or slightly exceeds axial width. Axial furrows shallow; furrows between axial rings deep. Exfoliated specimen (Pl. 4, fig. 6) shows that the half rings are only about one-third length (sag.) of axial ring. Pleural furrows straight and transverse, nearer posterior than anterior margin of segment, deep laterally, where they extend almost to the tips of the segments, progressively narrower and shallower adaxially, not extending to meet axial furrows. First segment not conspicuously macropleural.

Pygidium triangular, width 2·5–3·0 times sagittal length. Axis ill-defined, on the one undistorted specimen (Pl. 4, fig. 6) extending almost to posterior border. The same specimen shows 5 pairs of lateral muscle impressions. Pleural fields are unfurrowed except for the anterior pair of pleural furrows, which are narrow, transverse and extend little more than halfway across the pleural fields towards the axis. Posterior border steeply downturned, deepest exsagittally, and slightly upward-arched on mid-line. The border carries terrace lines similar to those on the cephalon, and at least a few of these are continued onto the posterior parts of the pleural fields. The available pygidia are stripped of their cuticle, so further sculptural details are not known.

DISCUSSION. Welsh Arenig *Ampyx* have been assigned to *A. salteri* Hicks, the type material of which is from the 'middle' Arenig rocks north of Whitesand Bay, St David's. Whittard (1955 : 15–18; pl. 1, fig. 15) redescribed *A. salteri*, and identified with that species some relatively complete material from the Mytton Flags in the Shelve inlier. Surprisingly, the species under discussion is very different from *A. salteri*, notably in lacking incised muscle insertion areas on the glabella, in having an almost continuous pleuroccipital band, a longer frontal spine, faint pygidial axis and an incomplete pair of pygidial pleural furrows. *A. salteri* from the type locality shows no sign of the raised lines on the cranidium seen on *A. cetsarum*; since they are visible on internal moulds of the new species, it seems probable that some trace of them would have survived the flattening of the St David's species if they were originally there.

Ampyx aff. *salteri* (Whittington 1966, especially pl. 2, figs 1–3, 6), from the Henllan Ash, Gwynedd, shows similar terrace lines to those of *A. cetsarum*, has adaxially incomplete pygidial pleural furrows, and subdued axial and border furrows; it is referred here to *A. cetsarum*.

Salient differences from the type species, *A. nasutus*, have been mentioned above (p. 253). Of Arenig species from the Valhallfonna Formation, northern Spitsbergen, *A. cetsarum* resembles *A. spongiosus* (Fortey 1975a : pl. 22, figs 1–10; pl. 23, figs 1, 3, 4, 5) in the general proportions of cranidium and pygidium, in having the facial sutures convex forwards and in the broad posterior border furrows of the cranidium, but differs in its low transverse occipital convexity, single (not paired) genal ridge, lack of cuticular pitting and in having few segments in the pygidial axis. *A. priscus* Thoral 1946 (redescribed by Dean 1966 : 279–281; pl. 3, figs 1–9; pl. 4, figs 1–6), from the early Arenig of the Montagne Noire, southwestern France, is similar to *A. cetsarum* in this latter respect. It differs from the Welsh species in most other details, however, of which its considerable occipital convexity (trans.), complete (trans.) pygidial pleural furrows and scarcely upward-arched pygidial posterior border are the most obvious. Finally, the Swedish species *Ampyx pater*

Holm 1882 (redescribed by Tjernvik 1956 : 270; pl. 11, figs 13, 14) resembles *A. cetsarum* in the outline of the facial sutures, lack of scars of glabellar muscles and in having five pygidial axial rings, but differs in the narrowness of the cranidial posterior border and the distinct occipital ring, lack of reflexion of sculpture on the internal mould and completeness of pygidial pleural furrows.

Family **CYCLOPYGIDAE** Raymond 1925
Genus ***MICROPARIA*** Hawle & Corda 1847

DIAGNOSIS. That of Richter & Richter (*in* Moore 1959 : O362) is followed here, with the exception that species with six thoracic segments may be included in *Microparia*, a modification introduced by Whittard (1961 : 177).

TYPE SPECIES. *Microparia speciosa* Hawle & Corda 1847, from the Králův Dvůr Formation (Ashgill), Czechoslovakia.

REMARKS. The type species of *Microparia* has been redescribed by Marek (1961 : 37–38; pl. 3, figs 5–10; text-fig. 11). The species from south Wales is the earliest yet described, with the possible exception of *M. broeggeri* (Holub 1912) from the Arenig Klabava Formation of Czechoslovakia, the type (and only) specimen of which is missing. In common with *M. nuda* Whittard, *M. grandis* (Salter) has 6 thoracic segments – later species have 5 – but this character alone is not considered of generic importance. *M. grandis* also has a medially-expanded, forward-tapering glabella, in this respect more closely resembling *Pricyclopyge*, especially *P. binodosa* (Salter). Possibly this glabellar shape is a plesiomorphic character shared by early cyclopygids which are already on separate evolutionary lines. Certainly the pygidium of *M. grandis* is typical of *Microparia*, and does not have the distinct border and triangular outline of *Pricyclopyge* pygidia.

Microparia grandis (Salter)
(Fig. 9; Pl. 4, figs 5, 8, 9)

v*.1859	*Aeglina grandis* Salter *in* Murchison : 53, fig. 6.
v.1864b	*Aeglina grandis* Salter : 3–4; pl. 4, figs 7 [*non* fig. 8, = ? *Pricyclopyge* sp.].
v.1873	*Aeglina grandis* Salter : 23.

Plate 4

Ampyx cetsarum sp. nov. Early Arenig, Ogof Hên Formation, upper part of Bolahaul Member and Carmarthen Formation, Pibwr Member.

Fig. 1. Cranidium, with patches of thin cuticle adhering. Upper part of Bolahaul Member, temporary section at water treatment plant, Penddaulwyn Fawr, loc. 12. NMW 76.3G.1. × 3.

Figs 2, 7. **Holotype**, cranidium, part (Fig. 2) and latex cast of counterpart (Fig. 7) of little-crushed specimen, showing surface sculpture on cheeks. Glan Pibwr, loc. 1A. It 14022. Fig. 2, × 6; Fig. 7, × 5.

Fig 3. Dorsal exoskeleton; crushed cranidium, but with thorax and pygidium retaining almost their original outlines. Same horizon and locality as Fig. 1. NMW 76.3G.2. × 4.

Fig. 4. Counterpart of Fig. 1, preserving frontal spine and showing surface sculpture. × 4.

Fig. 6. Thorax and pygidium, the latter almost without distortion. Same horizon and locality as Fig. 1. NMW 76.3G.3. × 7.

Microparia grandis (Salter 1859). ? Early Arenig, Tetragraptus Beds, south side of St David's Head, Dyfed.

Fig. 5. Nearly complete external mould of exoskeleton identified with *M. grandis* by Salter (1873), showing well the outline of the facial suture and anteriorly developed palpebral rims (compare Fig. 9). SM A44335. × 3.

Fig. 8. **Holotype**, poorly-preserved but almost complete dorsal exoskeleton, showing similar thorax and pygidium to that of previous specimen. GSM 35276. × 2.

Microparia grandis (Salter 1859). Early Arenig, Carmarthen Formation, Cwm yr Abbey Member.

Fig. 9. Well-preserved cephalon and 4 thoracic segments. Nant y Glasdwr, loc. 3A. It 14023. × 3.


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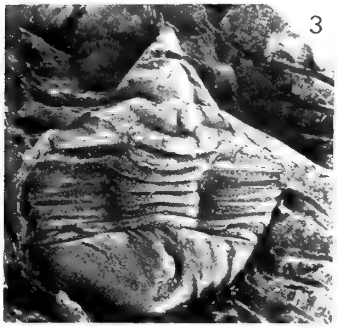
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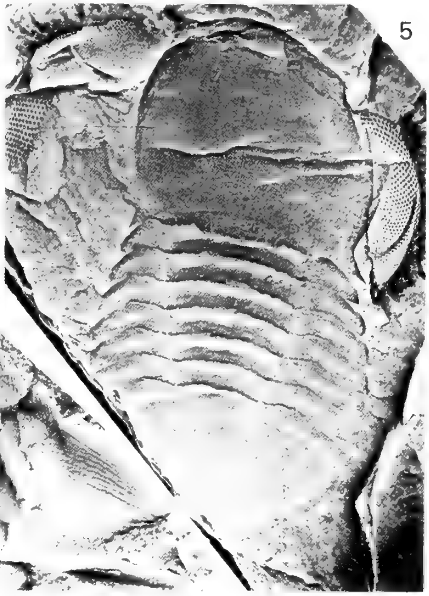
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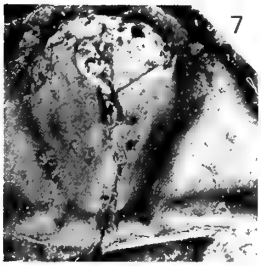
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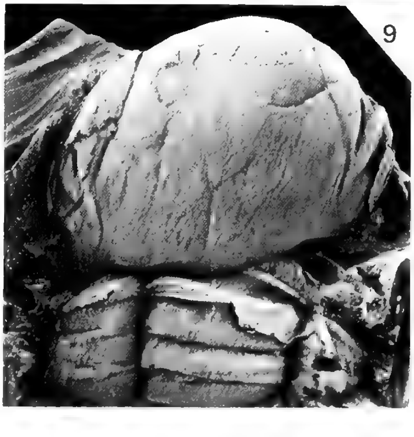
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v.1961 *Cyclopyge grandis* (Salter) Whittard : 182.
? 1961 Cyclopygid C Whittard : 184; pl. 24, fig. 14.

DIAGNOSIS. A *Microparia* species with six thoracic segments, eyes widely separated at anterior margin. Glabella expanding in width to about one-third cephalic length, tapering anteriorly; narrow (trans.) eyes, with correspondingly curved inner margins. Palpebral rims narrow, effaced posteriorly. Semicircular pygidium with short, narrow axis, with single axial ring clearly defined; border faint, especially postaxially.

HOLOTYPE. GSM 35275, by monotypy. Imperfectly preserved and flattened dorsal shield, front part of cephalon not present. This specimen is that figured by Salter (*in* Murchison 1859 : 53).

TYPE LOCALITY AND HORIZON. Salter (1864b) recorded *M. grandis* from the 'south side of St David's Head' in Dyfed, that is, from within the broad outcrop of Tetragraptus Beds exposed there. He subsequently (1873) recorded specimens he regarded as conspecific from the 'middle Arenig' of Whitesand Bay, a designation equivalent to the south side of St David's Head, and equally imprecise. It is not possible to refine the locality until the St David's area is redescribed, but it is worth noting that we have collected cyclopygid eyes similar to those of *M. grandis* from Pwlluog, just north of Trwynhwrddyn, Whitesand Bay.

OTHER OCCURRENCE. From the Carmarthen area a single specimen has been found in the Cwm yr Abbey Member in Nant y Glasdwr (loc. 3A). It is here associated with *Porterfieldia punctata* (type locality) and *Merlinia rhyakos* sp. nov. It is of pre-*hirundo* Zone age.

DESCRIPTION. Length of cephalon exceeding that of thorax, which is about same length as pygidium. Maximum transverse width of cephalon about 1·4 times sagittal length, less than one-third of width occupied by dorsal aspect of eyes in least-distorted specimens (Pl. 4, fig. 9), although flattening tends to lay out visual surfaces horizontally, which therefore appear wider. Glabella expands in width forwards, maximum at about one-third glabellar length, tapering forwards thereafter, axial furrows enclosing an angle of 30°–40°. Front margin of cephalon downturned, gently rounded about mid-line, transverse width about two-thirds maximum glabellar width. There are no impressions of muscle insertion areas on the glabella, which is completely smooth except for a few terrace lines around anterior margin. Palpebral rims narrow, defined by distinct palpebral furrows, but only adjacent to anterior, tapering part of glabella. Posteriorly palpebral lobes are incorporated into median cephalic area. Postocular fixed cheeks minute, triangular. Facial sutures cut posterior margin of cephalon at an acute angle, anteriorly closely following outline of glabella. Along front margin of glabella sutural outline is not well preserved, and line of separation from cephalic doublure not visible on the one specimen with cheeks not disturbed. Doublure shows no indication of median or connective sutures. Free cheeks when in life orientation probably had a large part of their visual surfaces directed dorsally and laterally – this observation is based on the specimen in Pl. 4, fig. 9, which has the eyes attached, although both are slightly crushed. Eyes with curved inner margins, relatively narrow for a cyclopygid, length about four times transverse width, and widely separated at anterior margin of cephalon. Number of files of lenses (counted laterally across the visual surface) about fifteen to twenty. Cheek borders narrow, progressively so anteriorly.

Thorax with six segments, expanding in width backwards, axis tapering posteriorly, gently at first but more so on last three segments, such that axial furrows enclose an angle of about 30°–40°. Pleurae correspondingly wider backwards, those of sixth segment twice as wide as those of first. Anterior pleurae pointed, and particularly the first segment has a large, downturned facet. Posterior pleurae truncated and without obvious facets, which suggests that much of the dorso-ventral movement in this species was confined to the cephalic region. Articulating half-ring of first thoracic segment (Pl. 4, fig. 9) is correspondingly broad (sag.), with a deep and wide defining furrow and a convex, upturned anterior rim, those on posterior segments are much narrower (sag.). Pleural furrows narrow, oblique, extending almost to tips of pleurae.

Pygidium about two-thirds as long as wide with an evenly curved posterior margin. Convexity and fine details cannot be described owing to the poor preservation of available material. Almost pointed axis extends to about half pygidial length and continues posterior taper of thorax. Only one axial ring is distinctly defined; there are faint indications of a second. Similarly, there is a single pair of anterior pygidial pleural furrows, which continue into the posterior border furrows. These are deepest laterally, becoming shallower posteriorly, and hardly continued behind the axis, thereby defining narrow posterolateral pygidial borders. Doublure and surface sculptural details not known.

DISCUSSION. It is difficult to compare the Carmarthen specimen directly with Salter's type material because of their difference in preservation. Specimens that Salter identified with *M. grandis*, and which agree in preservation, pygidial morphology and locality with the type, can be compared more directly with the Carmarthen specimen. The specimen shown in Pl. 4, fig. 5 shows well the diagnostic cranidial outline and the curved form of the eyes; furthermore, the posteriorly incomplete palpebral furrows (present on the left side of the Carmarthen specimen) are clear on both sides of the cranidium. There is a second species associated with *M. grandis* in the St David's Arenig rocks; Salter (1864b : pl. 4, fig. 8) figured the pygidium of this species as a variety of *M. grandis*, but the border is deeper and more clearly defined than in *M. grandis*, and it is more likely to belong to a *Pricyclopyge* species.

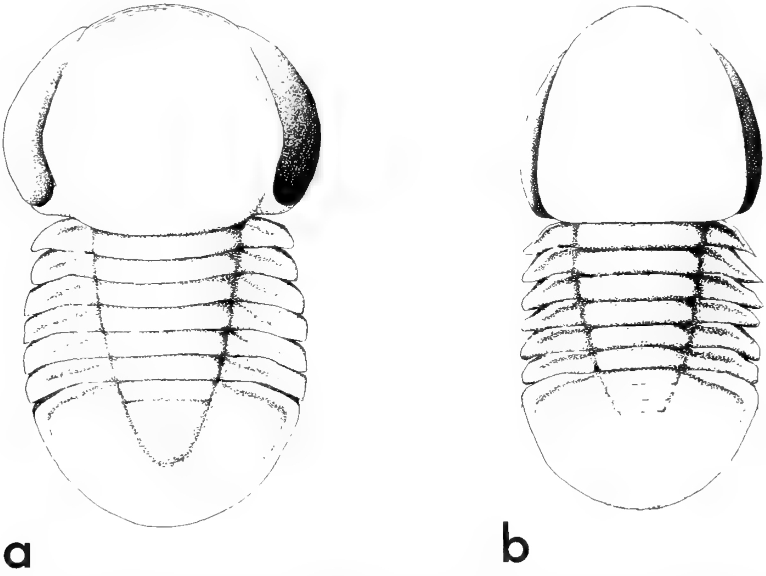

Fig. 9. Reconstruction of dorsal exoskeletons of: a, *Microparia grandis* (Salter) and b, *Microparia nuda* Whittard, to summarize diagnostic differences. (Both approx. ×2½.)

M. grandis differs from the type species, *M. speciosa* (Marek 1961 : pl. 3, figs 5, 6, 11) in its outward-bowed cranidium, number of thoracic segments and narrow pygidial axis, but agrees in the wide anterior separation of the eyes. A similar separation is also shown by *M. nuda* (Whittard 1961 : 180–182; pl. 24, figs 5–10) from the Llanvirn of the Shelve district, Shropshire, and like *M. grandis* this species has 6 thoracic segments (fig. 9); it differs from *M. grandis* in having a parallel-sided or gently forward-tapering cranidium, and a pygidium with longer, gently tapering axis. Whittard (1961 : 181, 182) indicated that *M. grandis* might be conspecific with his species *M. nuda*; present evidence shows that they are distinct. *M. broeggeri* (Holub 1912 : 7; pl. 1, fig. 8; Marek 1961 : 45; pl. 3, fig. 16), from the Arenig Klabava Formation of Bohemia, is known from a single specimen which is now lost. Holub's original illustration shows that this species has a pygidium similar to that of *M. grandis*, but apparently only 5 thoracic segments, and so conspecificity is unlikely.

Whittard (1961 : 184; pl. 24, fig. 14) described a pygidium (which he termed Cyclopygid C) preserved in relief from the Mytton Flags; it may be conspecific with *M. grandis*. It shows a single axial ring, and the rather narrow, short axis that distinguishes pygidia of *M. grandis* from those of other *Microparia* species.

Family **ASAPHIDAE** Burmeister 1843

Generic assignment of the Asaphids

The systematics of asaphids is a persistent problem which has been tackled, though far from solved, by several authors over the past 20 years, in particular by Harrington & Leanza (1957), Jaanusson (*in* Moore 1959), Whittard (1964) and Hughes (1973). Arenig asaphids from Wales and the Borderland have been grouped in several ways. Whittard (1964 : 232, 238) placed them in *Ogygiocaris* Angelin 1854, with the species *O. selwynii* (Salter *in* Murchison 1859), *O. marginata* (Crosfield & Skeat 1896) and *O. murchisoniae* (Murchison 1839). Whittington (1966 : 496) placed *selwynii* in *Ogygiocaris* with much reservation, while Bates (1969b : 17) synonymized *selwynii* and *marginata* with *murchisoniae*, which he assigned with question to *Megalaspidella* Kobayashi 1937. Some or all of these authors considered other putatively related genera such as *Ogyginus* Raymond 1912, *Ogygiocarella* Harrington & Leanza 1957 and *Hoekaspis* Kobayashi 1937. Thus, in attempting to assign the asaphids to a genus, it is necessary first to consider a group of early to middle Ordovician genera to which they show a greater or lesser degree of resemblance.

Ogygiocaris

There has been some discussion as to how this genus should be defined. Henningsmoen (1960 : 211; pl. 1, figs 1–6) redescribed the type species, *Trilobus dilatatus* Brünnich 1781, together with a number of other species from the Ogygiocaris Series, Stage 4aα (Llanvirn–Llandeilo) of the Oslo district, Norway. He noted (1960 : 214) that these had in common a scalloped inner margin to the pygidial doublure and a similarly scalloped paradoublural line on the dorsal surface of the pygidium, and suggested that the genus be restricted to species possessing this character.

Whittard (1964 : 231) did not consider this criterion to be of generic rank, and thus included *selwynii*, which has an entire pygidial doublural margin, as well as *seavilli* Whittard 1964, which has a scalloped one, in *Ogygiocaris*. He also noted that the scalloping was developed in *Ogygiocarella debuchii* (Brongniart 1822), but followed the convention in classifying asaphids on the basis of position of the facial suture in front of the glabella. Thus he perpetuated the separation of *Ogygiocaris* from *Ogygiocarella* Harrington & Leanza (1957 : 161) based on the position of the suture, intramarginal in the former, marginal in the latter.

All *Ogygiocaris* species with a scalloped pygidial doublure are of Llanvirn or Llandeilo age, and despite the fact that Whittard (1964 : 244) claimed that *O. seavilli* (from the Lower Llanvirn) was 'stratigraphically much older' than the Scandinavian species, the range of the latter extend at least as far back as the Upper Llanvirn (cf. Strand & Henningsmoen 1960 : 140, 141; Pl. 7 and Henningsmoen 1960 : 215, fig. 3; 221), so that the possible age difference at the most cannot be great. Fortey (1975b : 23) described an Arenig species, *Gog catillus*, which has a scalloped pygidial doublure and suggested it might be ancestral to *Ogygiocaris*. The species and subspecies *O. dilatata*, *O. sarsi sarsi* Angelin 1878, *O. sarsi* Angelin 1878 *regina* Henningsmoen 1960, *O. sarsi* Angelin *delicata* Henningsmoen 1960, *O. striolata striolata* Henningsmoen 1960, *O. striolata corrugata* Henningsmoen 1960 and *O. seavilli* all have a combination of similar cephalic and pygidial characters; *Ogygiocarella debuchii* is also very close to some of these, in particular *O. seavilli*, *O. sarsi sarsi* and *O. sarsi regina*. Within this group, there is variation in the expansion of the frontal lobe of the glabella (cf. Harrington & Leanza 1957 : 161 and Whittard 1964 : 231), as well as in the presence or absence or strength of pygidial interpleural furrows (despite Jaanusson's (*in* Moore 1959 : O352) observation that the pygidial pleural ribs are unfurrowed in *Ogygiocaris*). While precise details of the stratigraphical occurrence of some Scandinavian species are unknown, Henningsmoen (1960 : 216) has been able to make some general observations and to postulate the probable order of appearance. The species listed above do seem to form a natural phyletic group, and one unifying character is the scalloped pygidial doublure. Although Whittard

(1964 : 231) dismissed this as a generic character (for no obvious reason) it is here considered to be significant in that it is one of the only 'presence or absence' characters to be found in these trilobites; other characters are highly variable. It is absent in all the other early to middle Ordovician asaphids, and thus serves to define and to identify easily the close-knit group of species discussed above; there is one exception, and that is *O. debuchii*, excluded from *Ogygiocaris* only on the basis of its supposed marginal suture. It is highly doubtful if this character really is of generic rank, because, as Whittard has stated (1964 : 232), a very slight shift in suture position would convert one genus to the other. This makes the definition of *Ogygiocarella* arbitrary. There is, however, no good reason to assign the Arenig asaphids from south Wales to *Ogygiocaris*, nor to consider them closely related to that genus.

Ogyginus

This genus, type species *Asaphus corndensis* Murchison 1839, occurs in the Llanvirn and Llandeilo of Wales and the Borderland. The species *O. corndensis*, *O. intermedius* Elles 1940, *O. porcatus* Whittard 1964 and *O. grandis* Whittard 1964 have been described. The genus is similar to *Ogygiocaris* in its intramarginal suture; Whittard (1964 : 245) claimed that the suture was marginal but Hughes (1973 : 15) has shown that earlier interpretations that it is intramarginal are correct. It differs, however, in the flask-shaped glabella, typically with a well-expanded frontal lobe and in having an entire pygidial doublural margin. The pygidial pleural ribs are commonly unfurrowed and reach close to the pygidial margin; the pleural furrows are deep. The pygidium is proportionately longer and more parabolic than that of *Ogygiocaris*. All the above species depart little from the basic pattern of the genus, which forms an easily recognizable unit.

Hoekaspis

The type species, *Megalaspis matacensis* Hoek *in* Steinmann & Hoek 1912, is from the middle Ordovician of Bolivia and is based on very incomplete material. Kobayashi (1937 : 496), however, used it to found his genus *Hoekaspis*. He also assigned a second species to it, which, like the type, is based on similarly incomplete and badly preserved material.

Ross 1965 (pl. 8, figs 8, 9, 12, 13, 16, 19) has figured topotype material of the type species of *Hoekaspis*, and we have examined the only surviving specimen (a pygidium) of Hoek's original collection. Bates' (1969b : 21) comparison of Welsh Arenig asaphids with *Hoekaspis* was presumably based on the *Hoekaspis* species figured in the *Treatise* (Moore 1959 : O346), *H. megacantha* (Leanza 1941) from the Llanvirn of Argentina. The type species, *H. matacensis*, differs from both the Welsh material and *H. megacantha* in its wide pygidium with almost unfurrowed, convex pleural fields, and with a strongly furrowed and deeply defined axis, and a very narrow cranidial anterior border sharply defined from the steeply sloping frontal lobe of the glabella. *H. megacantha* is probably best excluded from *Hoekaspis* and included with the Welsh species in the same genus (below).

Megalaspidella

The type species, *Megalaspidella kayseri* Kobayashi 1937, is from the Arenig of Argentina (see Harrington & Leanza 1957 : 162–164, fig. 73). Its pygidial characters are similar to those of the Welsh species from the Arenig, but the pleural furrows are not as deep as in *Ogyginus*. The principal distinguishing features of *Megalaspidella* are the parallel preocular facial sutures, the glabella hardly encroaching onto the anterior border. The glabellar surface is practically smooth, with hardly any indication of muscle impressions.

It is difficult to place the British Arenig species into any of the above; if *Ogygiocaris* is to be restricted as suggested, then they can clearly be excluded from that genus; this would broadly follow Whittington (1966) and Bates (1969b). The species currently assigned to *Ogyginus* form a close-knit group of Llanvirn and Llandeilo species; the Arenig species are very similar to them in cephalic characters, but differ in pygidial ones, especially in lacking the characteristic deep pleural furrows. *Hoekaspis, sensu stricto*, is not related. *Megalaspidella* differs particularly in its parallel preocular sutures and glabella hardly encroaching onto the anterior border.

Within the genera discussed above, there are two major groups – one comprising *Ogygiocaris* and *Ogygiocarella* (if the latter is to be regarded as being distinct) and the other comprising *Ogyginus* and *Megalaspidella*. The Welsh Arenig asaphids are closer to the latter than the former. Without an understanding of their phyletic relationships, it is difficult to know how to define them realistically; indeed it is only possible at present to group together similar morphotypes which might be plausible phyletic units. Within the asaphids, as with many other trilobite groups, there appears to have been a pool of characters which recur repeatedly in various combinations within the group; rapid adaptation at different times to similar environments led to a succession of similar-looking genera appearing from different asaphid stocks. There are few good 'presence or absence' characters available – the scalloped pygidial doublure appears to be one of the few.

Two alternatives are open with regard to the British Arenig asaphids. One is to follow the example of Whittington and Bates and to assign species questionably to the closest available genus. This often 'fogs' the true relationship of the species, and results in paraphyletic taxa. The second alternative is to propose a new genus. Both Whittington and Bates declined to do this, a conservative view in accordance with the distorted material available to them. We have now good additional material of old and new species, from which it is possible to identify a combination of common characters which preclude their inclusion in any of the above genera. Thus we feel justified in erecting a new genus to accommodate them; its validity can only be tested when the phylogeny of this complex group is better understood, but we feel that to take this step is the best compromise in the present state of knowledge.

Subfamily **OGYGIOCARIDINAE** Raymond 1937

[*nom. correct.* Jaanusson 1959 *ex* Ogygiocarinae Raymond 1937]

REMARKS. The new Arenig asaphid genus described below is considered to be closely related to *Ogyginus* and *Megalaspidella*. While the former was placed in the Ogygiocaridinae by Jaanusson (*in* Moore 1959 : O352) the latter was placed by the same author (*in* Moore 1959 : O346–347) in the subfamily Isotelinae 'Group B'. Since these genera may be closely related, they might be better included in one subfamily. However, since asaphid phylogeny is still poorly understood, rearrangement at subfamily level at this stage is premature, and for the moment they are placed, somewhat arbitrarily, in the Ogygiocaridinae.

Genus ***MERLINIA*** nov.

DIAGNOSIS. Suture intramarginal; preocular sections divergent; glabella encroaches onto anterior border, and is flask-shaped and forward-expanding or nearly parallel-sided in mature specimens, parallel-sided in immature; no occipital ring defined, but muscle areas commonly present; cephalic border flat, cephalic border furrow typically crosses preocular cheek to terminate in hypostomal pit close to axial furrow; hypostoma with entire posterior margin which is acuminate; thoracic segments with pleurae distally pointed; pygidium with doublure with entire inner margin; pleural furrows weak, not reaching margin; interpleural furrows commonly absent; pygidial border weakly defined. Panderian organs apparently lacking.

NAME. From Merlin, the legendary Arthurian magician, from whose name Carmarthen is derived, and with whose legends this asaphid is associated. Feminine.

TYPE SPECIES. *Merlinia rhyakos* gen. et sp. nov.

DISCUSSION. The defining characters of genera related to *Merlinia* have been discussed above, pp. 260–261. *Merlinia* includes five species (Arenig–Llanvirn): *M. rhyakos* sp. nov., *M. selwynii* (Salter), *M. major* (Salter), *M. murchisoniae* (Murchison) and *M. megacantha* (Leanza). *M. murchisoniae* (Murchison) is the oldest of these, and is furthest morphologically from the type species, having only a short, cranidial section of the anterior border furrow, and generally broader borders than the other species. It is possible that *M. murchisoniae* was derived from an *Asaphellus*-like ancestor in the late Tremadoc, being similar to that genus in its hypostoma and broad cephalic and pygidial borders. The evolution of the genus in the Arenig was accompanied by a forward migration of the anterior border furrow – and hence an increasing definition of its

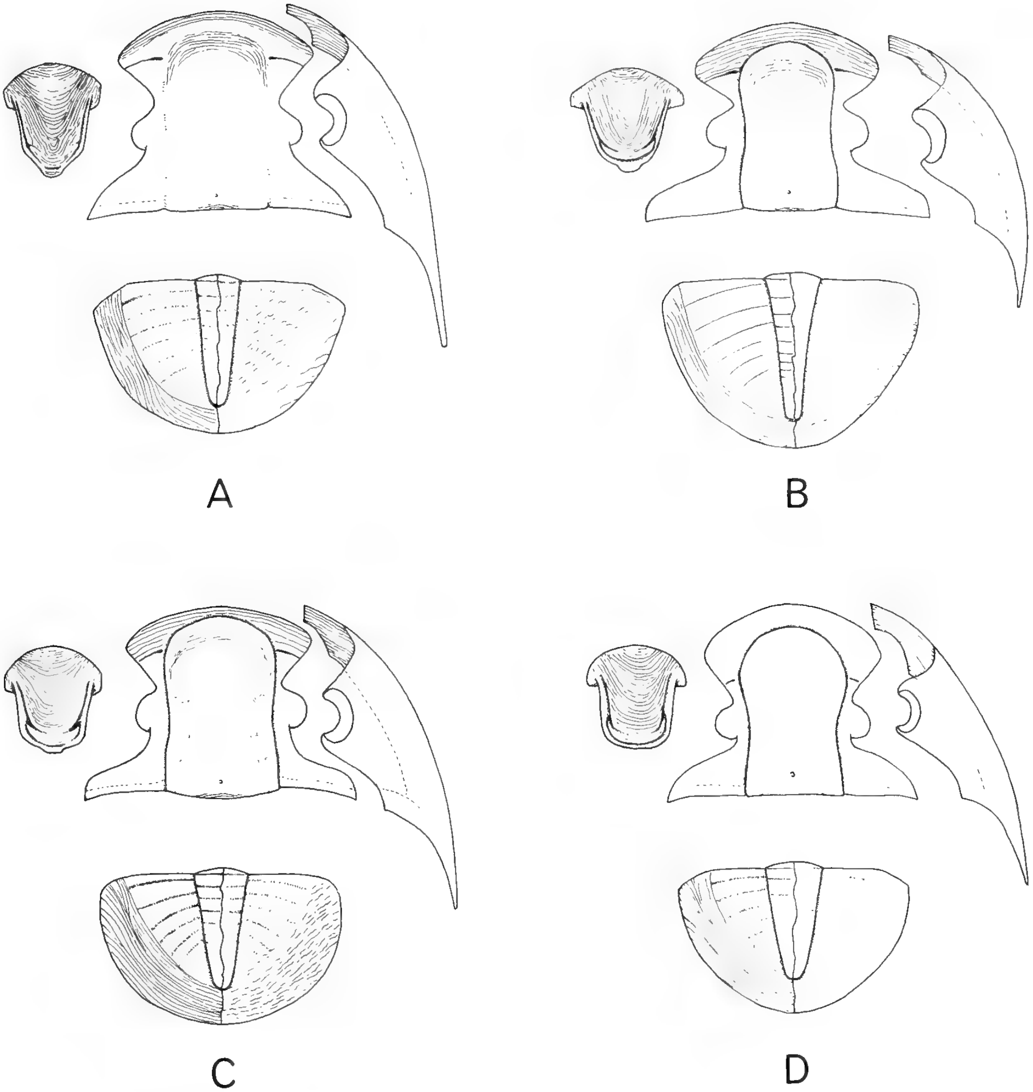

Fig. 10. Diagram summarizing salient points of difference between *Merlinia* species from the Arenig of Wales and the Welsh Borderland. A, *M. rhyakos* sp. nov. B, *M. selwynii* (Salter). C, *M. major* (Salter). D, *M. murchisoniae* (Murchison).

cranidial section. This distinct furrow is a characteristic feature of *Merlinia*, which is absent from *Ogyginus* and *Megalaspidella*.

Merlinia rhyakos gen. et sp. nov.

(Figs 10–11; Pl. 5, figs 1–6; Pl. 6, figs 1–5)

v.1896 *Ogygia marginata* Crosfield & Skeat *pars*: 538; pl. 26, fig. 14 [*non* figs 13, 15–18, 20–25, =*M. selwynii* (Salter); *nec* figs 19, 26, =*M. murchisoniae* (Murchison)].

Diagnosis. Cephalic axial furrows shallow, preglabellar furrow almost effaced; frontal glabellar lobe hardly inflated, with dense prominent terrace lines; inner section of lateral border furrow and hypostomal pit shallow; line ϵ/ζ–ϵ/ζ at 0·33–0·37 of sagittal cranidial length; hypostoma with prominent terrace lines and long posterior acumination; pygidial doublure narrow, short, wavy terrace lines on dorsal pygidial surface, extending onto adaxial parts of pleural fields.

Name. Genitive of Greek *ῥύαξ*, a mountain stream or torrent swollen by rains.

Holotype. BM(NH) It 14024 (Pl. 5, fig. 1), a nearly complete internal mould, lacking the cranidium, but exposing the hypostoma.

Type Locality and Horizon. High Cwmffrŵd Member, from Cwm yr Abbey, loc. 16D.

Other occurrences. *M. rhyakos* has been found in the Cwmffrŵd Member in Cwm yr Abbey, at the type locality, in Nant Cwmffrŵd loc. 2A, and Allt Pen-y-Coed locs 5A, 5B, 5C, 5E; it has been found in the Cwm yr Abbey Member in Cwm yr Abbey locs 16E, 16F and in Nant y Glasdwr locs 3A, 3B.

Description. Cranidium depressed, and with exception of lateral border furrow lacking any deep furrows. Glabella parallel-sided, width about $\frac{4}{7}$ length, defined by very shallow axial furrows which merge anteriorly with nearly effaced preglabellar furrow, which is discernible only as a slight change in slope. Glabella encroaches upon anterior border to reduce its width by half sagittally. Muscle impressions hardly apparent except as very weak depressions on dorsal surface. 1P runs from slight lateral constriction of glabella (this is a short distance behind level of palpebral lobe) running backwards and towards, but not reaching, the posterior margin at about 45° in a weak, adaxially convex curve. 2P opposite ϵ/ζ, nearly transverse. 3P opposite γ or just behind, slightly forwardly directed. Frontal lobe with 15–20 dense, anastomosing terrace lines, of which the more posterior ones are shallower, extending backwards laterally as far as 3P, and about half this distance sagitally. Extreme anterior part of frontal lobe, where it impinges upon anterior border, is smooth.

Occipital ring not defined, although very weak trace of occipital furrow is to be seen on some specimens a short distance in front of posterior margin. Median tubercle fainter than on other species of the genus, far back, not visible on several specimens. Three or four terrace lines occur close to posterior margin sagittally.

Anterior border with 3–4 rather weak terrace lines on its anterior part; posterior part smooth. Shallow, narrow, lateral border furrow deepens into hypostomal pit where it meets axial furrow, the section on cranidium forming a weakly forward-convex arc. Whole lateral border almost flat.

Preocular facial suture divergent at 30°–40° from an exsagittal line through γ. Postocular suture defines broad, triangular postocular fixed cheek; backward divergence less than that of *M. selwynii*. Palpebral lobe away from axial furrow, ϵ/ζ further from it than γ. Eye small, crescentic, separated by width of lateral border from lateral border furrow at its closest. Field of free cheek broad, weakly convex. Lateral border and doublure narrow, of more or less constant width, the latter widening conspicuously, with its inner margin mirroring dorsal lateral border furrow close to hypostoma. Genal spine narrow-based, with no panderian opening on the doublure near its

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Plate 5

Merlinia rhyakos gen. et sp. nov. Early Arenig, Carmarthen Formation, Cwmffrŵd and Cwm yr Abbey Members.

Fig. 1. **Holotype,** almost complete dorsal exoskeleton, lacking cranidium, but showing hypostoma *in situ*. Note sculpture on free cheek and pygidium. Cwmffrŵd Member, Cwm yr Abbey, loc. 16D. It 14024. × 1½.

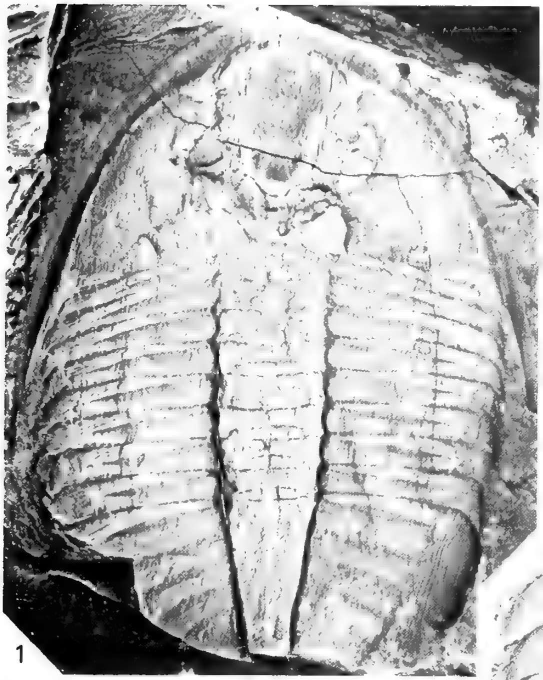
Fig. 2. Hypostoma, counterpart of Fig. 1. Note maculae and distribution of terrace lines. × 3.

Fig. 3. Cranidium, showing terrace lines on frontal lobe of glabella and extension of lateral border furrow onto fixed cheek. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. It 14025. × 2½.

Fig. 4. Latex cast of parts of five thoracic segments, showing fine details of dorsal surface sculpture. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. It 14026. × 2½.

Fig. 5. Cranidium. Note fine terrace lines close to posterior margin of glabella. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. It 14027. × 3.

Fig. 6. Thorax and pygidium. Original of Crosfield & Skeat 1896: pl. 26, fig. 14. Cwmffrŵd Member, Nant Cwmffrŵd, probably from close to our loc. 2A. SM A3107. × 1½.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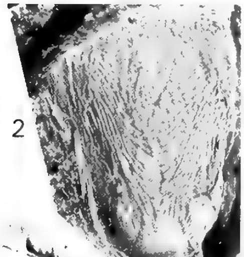
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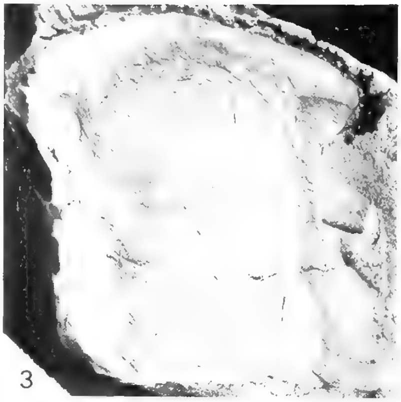
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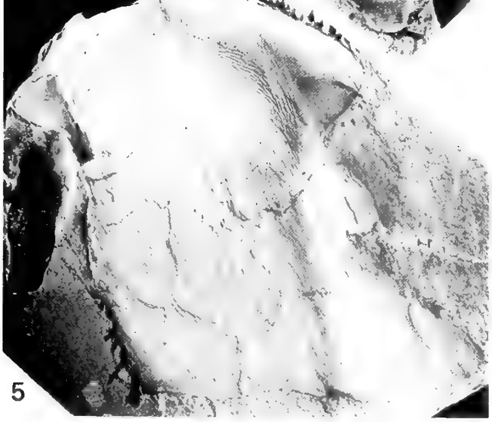
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base, extending backwards as far as sixth thoracic segment. Posterior border furrow very shallow, hardly apparent.

Hypostoma $\frac{7}{8}$ as wide across anterior wings as long (sag.). Tapers fairly strongly backwards, posterior margin acuminate. Anterior wings broad, anterior margin quite strongly forwardly convex. Lateral border narrow, widest at its mid-length and separated from median body by broad, shallow furrow. Narrows markedly where it meets posterior border, which is short and lip-like. Pair of prominent maculae about $\frac{3}{4}$ way back on lateral parts of median body, opposite widest part of lateral border. Whole of median body covered with prominent terrace lines; anterior ones weakly convex backwards, but towards posterior become increasingly more so on median body, so as to form deep Us in region of maculae. Sagittally, terrace lines widely spaced as far back as maculae, where they become more crowded, and are similarly crowded laterally. Both lateral and posterior margins with terrace lines, and weak ones also developed in lateral and posterior border furrows.

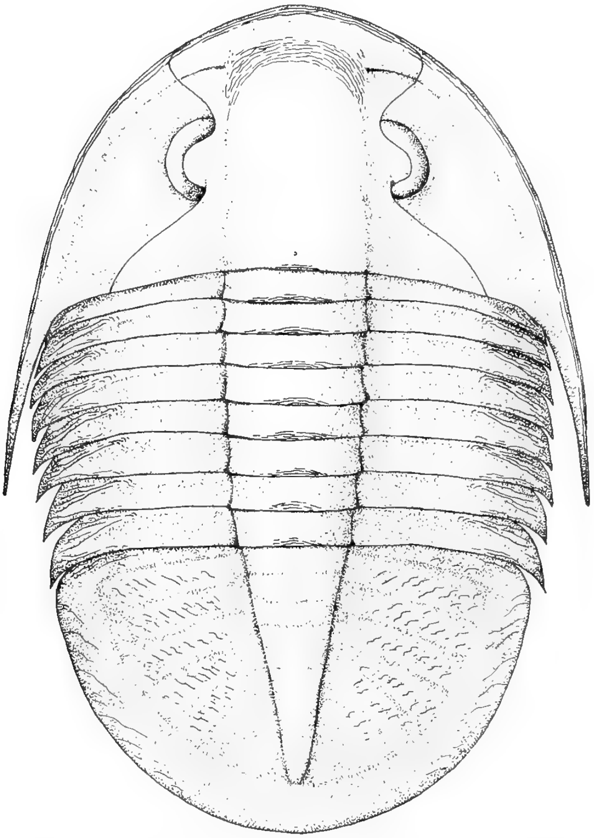


Fig. 11. Reconstruction of dorsal exoskeleton of *Merlinia rhyakos* gen. et sp. nov., × 1½ approx.

Thorax of 8 segments, which decreases in width (trans.) backwards only slightly. Axis less than pleural width, weakly convex; axial furrows zigzag. Articulating furrow narrow and deep, weakly backwardly convex; articulating half-ring approximately half length (sag.) of annulus, its margin weakly convex forwards. Pleura with deep, oblique pleural furrow of about equal depth all along, beginning close to anterior margin adaxially and diverging from it slowly abaxially, to about half way across pleura (exsag.) where it dies out, about $\frac{5}{7}$ distance towards end of pleura. Anterolateral corner of pleura rounded, posterolateral drawn out into a short spine. Inner edge of doublure forms an inward-facing V with its apex at end of pleural furrow: posterior shorter than anterior part which has coarse terrace lines running parallel to its inner margin. No panderian opening has been observed. Finer terrace lines run transversely on dorsal surface of end of pleura, and these are commonly impressed onto the internal mould by compression.

Pygidium parabolic, on undistorted specimens of length/width ratio about 0·6, with narrow, flat border of constant width. Axis narrow, defined by rather shallow axial furrows which are weakly adaxially bowed. Eleven or twelve rings weakly defined, ring furrows commonly hardly apparent on dorsal surface, but more obvious on internal moulds. Posterior tip of axis reaches close to or touches inner edge of border. Pleural fields (inside paradoublural line) anteriorly broader (trans.) than both axis and doublure, with 7–8 pairs of pleural ribs. Pleural furrows almost straight or weakly curved, very shallow on dorsal surface, posterior ones more or less effaced; more conspicuous on internal moulds, and may be accentuated on compressed material. Interpleural furrows not seen on dorsal surface, although weak ones can be observed on some internal moulds. Doublure as wide as border, nearly flat, with about 9–10 strong terrace lines which laterally run subparallel to and more exsagittal than its margins. Dorsal surface carries fine, scalloped terrace lines which extend onto the adaxial parts of the pleural fields.

Discussion. This species is distinguished from *M. selwynii* principally by its lack of glabellar inflation, short preglabellar border, shallow axial and preglabellar furrows, the strong development of terrace lines on the frontal lobe of the glabella and the presence of terrace lines on the adaxial parts of the pygidial pleural fields, and the outline and terrace line pattern on the hypostoma. It is most similar in its cranidial characters to specimens from the Mytton Flags, described and figured by Whittard (1964 : 232; pl. 35, figs 1–3; pl. 34, fig. 7) as *Ogygiocaris selwynii*. One of these specimens (1964 : pl. 35, fig. 3) is a syntype of Salter's (1866b : pl. 9, fig. 5) '*O. selwynii* var. *major*'. All these cranidia, as well as the other Mytton Flags '*selwynii*', are clearly distinct from *selwynii* as understood herein (see below), and we here resuscitate Salter's variety as a distinct species of *Merlinia* to accommodate the Mytton Flags material. The glabellar shape is like that of *M. rhyakos*, but the axial and preglabellar furrows are better defined, as are the muscle areas; the terrace lines on the frontal lobe are much finer, and the lateral border furrow and hypostomal pit are conspicuously deeper. The cephalic and pygidial doublures are also much broader, and the pygidial pleural furrows deeper.

The cranidium from the Henllan Ash figured by Whittington (1966 : pl. 3, fig. 6) as *Ogygiocaris* ? cf. *selwyni* is like *M. rhyakos* in the strength and distribution of terrace lines on the frontal glabellar lobe, but the anterior border is somewhat more convex, and the anterior border furrow and hypostomal pits deeper – in these respects it is like *M. major*. This single specimen is difficult to place, but on balance would seem closer to *M. major* than to *M. rhyakos*.

Symmetrically elongated specimens (Pl. 6, fig. 4) can present a spurious appearance of a distinct species. However, they show the same dorsal surface sculpture of *M. rhyakos*, and the sagittal extension on the thorax (about 1·2 times sag.) of these specimens, compared with the undistorted holotype, is matched by a comparable pygidial extension.

Hoekaspis megacantha (Leanza), from the early Llanvirn of Argentina (Harrington & Leanza 1957 : 179–180; figs 88, 89), is here attributed to *Merlinia* (p. 262), resembling as it does *M. rhyakos* more than other species herein in the width of the cranidial border, the forward position of the eye and the pygidial surface sculpture (1957 : fig. 89; 2, 4). The main points of difference are the more forward position of the eyes such that ϵ/ζ–ϵ/ζ is at about 0·4 of the sagittal length of cranidium, the inflated glabellar frontal lobe, apparently smooth, and the short cranidial section of the anterior border furrow. It is interesting to note that *M. selwynii*, *M. rhyakos* and *M. megacantha* form a morphological series characterized by a progressive forward shift of the eyes. It is significant that the *M. rhyakos* is found in the olenid community with postulated increased independence of faunal provinces, in which a subsequent migration to South America is more easily understood.

Merlinia selwynii (Salter *in* Murchison 1859)

(Fig. 10B; Pl. 6, figs 6–8; Pl. 7, figs 1–9; Pl. 8, figs 1–7)

.1853 *Asaphus Selwynii* Salter : 57 [*nom. nud.*].
.1854 *Asaphus Selwynii* Salter; Morris : 100 [*nom. nud.*].

v*.1859 *Ogygia Selwynii* Salter *in* Murchison: 53, fig. 8.

v.1866a *Ogygia Selwynii* (Salter); Salter *pars*: 136; pl. 17, fig. 3 [*non* figs 1, 2, 4–7, =*Merlinia major* (Salter)].

v.1866b *Ogygia Selwynii* (Salter); Salter *pars*: 255, 313; pl. 9, figs 2–4, 4a [*non* pl. 11B, figs 5, 5a, =*M. major* (Salter)].

non .1869 *Ogygia Selwynii* (Salter); Morton: 15 [=*M. major* (Salter)].

.1873 *Ogygia Selwynii* (Salter); Salter *pars*: 23 [*pars* = *M. major* (Salter)].

v.1881 *Ogygia Selwynii* (Salter); Salter & Etheridge *pars*: 375, 380, 509; pl. 9, figs 2–4, 4a [*non* pl. 11B, figs 5, 5a, =*M. major* (Salter)].

v.1896 *Ogygia marginata* Crosfield & Skeat *pars*: 538; pl. 26, figs 13, 15–18, 20–25 [*non* fig. 14, =*M. rhyakos* sp. nov.; *nec* figs 19, 26, =*M. murchisoniae* (Murchison)].

.1931 *Ogyginus marginatus* (Crosfield & Skeat) Reed: 461.

.1931 *Niobella selwyni* (Salter) Reed: 463.

non .1952 *Ogygia selwyni* (Salter); Jackson: 40 [=*M. major* (Salter)].

v.1964 *Ogygiocaris selwynii* (Salter) Whittard *pars*: 232; pl. 37, fig. 1 [*non* pl. 34, figs 7–13; pl. 35, figs 1–4, 6–9; pl. 36, figs 1–7; pl. 37, figs 2–11, =*M. major* (Salter); *nec* pl. 35, fig. 5, ?≐*M. murchisoniae* (Murchison); *nec* pl. 35, fig. 10, =‘*Asaphus*’ *hybridus* Salter].

v.1964 *Ogygiocaris marginata* (Crosfield & Skeat); Whittard: 237; pl. 36, figs 8–10.

v.1966 *Ogygiocaris*? cf. *selwyni* (Salter); Whittington *pars*: 496; pl. 2, figs 9, 11–12; pl. 3, figs 1, 5, 7–9; pl. 4, fig. 16 [*non* pl. 2, figs 7, 10; pl. 3, figs 2, 10–11, =*Merlinia murchisoniae* (Murchison); *nec* pl. 3, fig. 6, ? =*M. major* (Salter)].

non .1968 *Ogygiocaris selwynii* (Salter); Bates: 179; pl. 12, figs 1–2, 5–6 [=*Merlinia* sp.].

v.1969b *Megalaspidella* (?) *murchisoniae* (Murchison); Bates *pars*: 17 [*non* pl. 6, figs 1–6; pl. 7, figs 1–9; pl. 8, figs 1, 2, 5, =*Merlinia murchisoniae* (Murchison)].

(Note: Besides those of Whittard's (1964) synonymy entries which refer to *M. major* (see below), we have excluded some references to faunal lists since we cannot judge whether these refer to *M. selwynii*, *M. major* or to another species.)

DIAGNOSIS. Differs from *M. rhyakos* in having deep axial and preglabellar furrows, inflated frontal glabellar lobe with very fine terrace lines, deep inner section of lateral border furrow and hypostomal pit, line ϵ/ζ–ϵ/ζ at 0·27–0·32 of sagittal cranidial length; hypostoma with fine terrace lines, and bluntly acuminate posteriorly; very fine terrace lines on pygidial pleural fields.

HOLOTYPE. SM A44425 (by monotypy), immature pygidium collected by Salter and Sedgwick, 1844.

TYPE LOCALITY AND HORIZON. Arenig Series, Basement Group, Hengwrt Uchaf near Dolgellau, Gwynedd (see also Whittard 1964: 236–237).

Plate 6

Merlinia rhyakos gen. et sp. nov. Early Arenig, Carmarthen Formation, Cwmffrŵd and Cwm yr Abbey Members.

Fig. 1. Pygidium with dorsal surface preserved. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. It 14028. ×2½.

Figs 2, 3. Free cheek, internal mould. Cwm yr Abbey Member, Nant y Glasdwr, loc. 3A. It 14029. ×3½; Fig. 3 eye ×10.

Fig. 4. Silicone rubber cast of tectonically-elongated specimen. Compare details of sculpture with Figs 1, 5 and Pl. 5, figs 1, 4. Cwm yr Abbey Member, Cwm yr Abbey, loc. 16E. It 14030. ×1½.

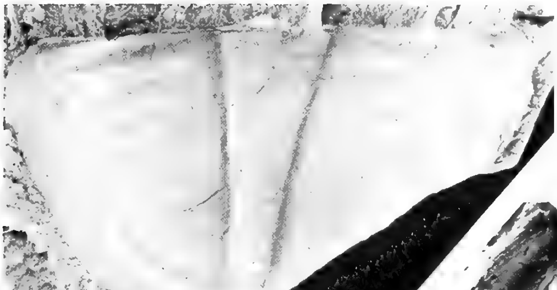
Fig. 5. Pygidium. Compression has impressed terrace lines of doublure onto dorsal surface, and accentuated depth of pleural furrows. Compare with Fig. 1. Cwmffrŵd Member, Allt Pen-y-Coed, loc. 5D (Eλ5). GSM JP4696. ×1½.

Merlinia selwynii (Salter 1859). Early Arenig, Carmarthen Formation, Pibwr Member.

Fig. 6. Ventral side of cephalon, with hypostoma *in situ*. Glan Pibwr, loc. 1A. It 14031. ×3.

Fig. 7. Hypostoma. Note arrangement of fine terrace lines. Glan Pibwr, loc. 1A. It 14032. ×4.

Fig. 8. Moult, with inverted cephalon and hypostoma partially underlying thorax. Glan Pibwr, loc. 1C. It 14033. ×2½.



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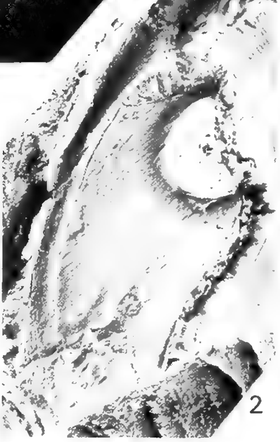

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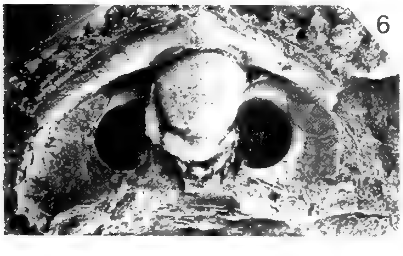

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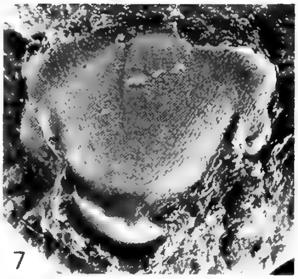

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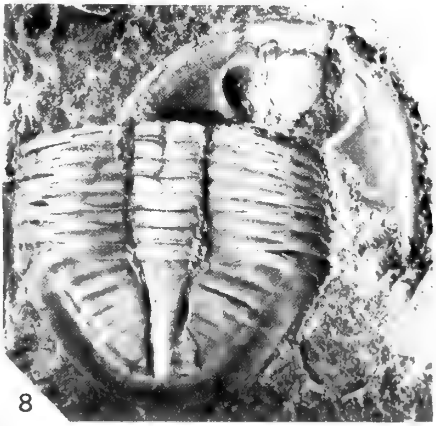

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OTHER OCCURRENCES. *M. selwynii, forma typica*, occurs in the Pibwr Member: it is particularly common at Glan Pibwr (locs 1A–D), and also occurs at Pibwr Weir (loc. 4), Cwm-difa (locs 15A, B), dingle 970 m at 65° from Nant y Caws (Survey locality Wλ8) and Penddaulwyn fawr (Survey locality Eλ5). Stratigraphically high forms occur in the high Pibwr Member at Allt Pen-y-Coed (locs 5F–H) and in the Cwmffrŵd Member at Nant Cwmffrŵd (loc. 2A).

DESCRIPTION. Cranidium with posterior width about two-thirds width across anterior border. Glabella elongate, more or less parallel-sided, frontal lobe weakly expanded and slightly inflated in some large specimens. Basal width 0·4 (in smaller) to 0·5 (in larger specimens) times sagittal length. Defined by shallow, narrow axial furrows, which are shallower in the palpebral region and merge anteriorly with shallower preglabellar furrow, which in larger specimens is comparatively ill-defined and broader. Glabella encroaches slightly onto anterior border to reduce its width by between $\frac{1}{4}$ and $\frac{1}{3}$. Muscle impressions weak and hardly apparent on some small specimens (Pl. 7, fig. 6), but fairly conspicuous on larger ones (Pl. 7, fig. 1). 1P opposite mid-point of an exsagittal line from ϵ/ζ to posterior margin, and is short, shallow and nearly transverse. 2P opposite ϵ/ζ, backwardly oblique at about 45°; between it and 1P is a small, triangular raised area. 3P a broad, triangular area, directed a little less strongly backwards than 2P, its antero-lateral angle opposite γ. There is an ovoid, raised area between 2P and 3P. On some less crushed specimens muscle impressions and intervening raised areas are almost effaced. They are thus accentuated by slight compression. Frontal lobe has extremely fine terrace lines, their disposition like that of *M. rhyakos*.

Occipital band defined by very weak, forwardly-arched furrow, which meets posterior border at axial furrows, thereby defining a very narrow, lozenge-shaped depressed area. Median tubercle present a short distance in front of crescent-like impression of doublure, more prominent than is the rule on *M. rhyakos*.

Anterior and lateral borders rather narrow, weakly convex, with 5–7 weak terrace lines concentrated on outer two-thirds. Shallow lateral border furrow deepens and narrows on cranidium where it deepens into hypostomal pit at axial furrow, the cranidial section forming a forward convex, gentle arc. Preocular facial suture divergent at an average 50° (compared with 30°–40° in *M. rhyakos*) to an exsagittal line through γ, which is close to axial furrow. Postocular suture defines broad, triangular postocular fixed cheek. Palpebral lobe fairly close in to axial furrow, γ closer than ϵ/ζ. Eye of moderate size, crescentic, anteriorly separated from lateral border by a width exceeding that of the border. Field of free cheek broad, weakly convex. Doublure rather narrow, weakly convex ventrally, its inner edge reaching as far as inner edge of lateral border furrow. Genal spine narrow, narrow-based, with no panderian opening on doublure near its base. Posterior border furrow shallow and fairly narrow adaxially, broadening markedly on free cheek.

Hypostoma gibbose in outline, as wide (trans.) as long. Tapers rather strongly backwards to bluntly acuminate posterior margin. Anterior wing broad, anterior margin forwardly convex.

Plate 7

Merlinia selwynii (Salter 1859). Early Arenig, Carmarthen Formation, Pibwr Member.

Fig. 1. Cranidium. Note fine terrace lines on frontal lobe of glabella. Glan Pibwr, loc. 1D. It 14034. ×2.

Fig. 2. Cranidium. Note weak lateral glabellar furrows. Glan Pibwr, loc. 1C. It 14035. ×5.

Fig. 3. Free cheek, with part of hypostoma *in situ*. Internal mould. Glan Pibwr, loc. 1A. It 14036. ×3.

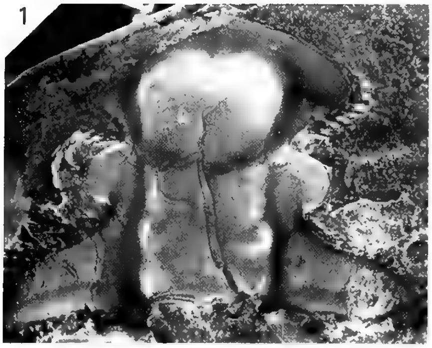
Figs 4, 5. Small cranidium in dorsal and anterior view. Compare elongated, parallel-sided glabella with those of large specimens (Figs 1, 7). Glan Pibwr, loc. 1A (Wλ1). GSM HT71. ×4.

Fig. 6. Small cranidium. Note ill-defined frontal lobe of glabella, with fine terrace lines. Glan Pibwr, loc. 1B. It 14037. ×$3\frac{1}{2}$.

Fig. 7. Large, incomplete cranidium. Note fine terrace lines on frontal lobe. Original of Whittard 1964: pl. 36, fig. 9. Glan Pibwr. SM A44350. ×3.

Fig. 8. Small pygidium. Glan Pibwr, loc. 1C. It 14038. ×5.

Fig. 9. Large pygidium. Note doublural terrace lines superimposed onto dorsal surface by compression, and weak terrace lines on posterior parts of pleural fields. Glan Pibwr, loc. 1D. It 14039. ×$3\frac{1}{2}$.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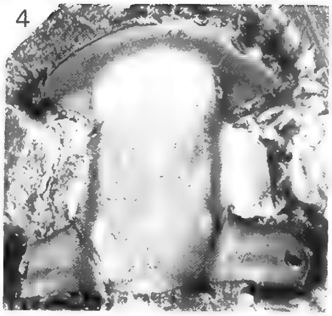
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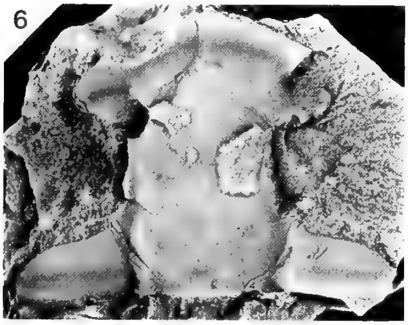
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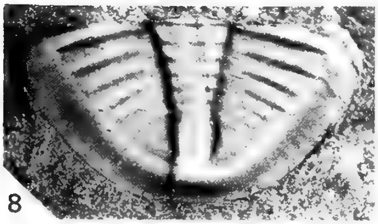
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Lateral border narrow, nearly flat, separated from median body by broad, shallow lateral border furrow. Posterior border similar to lateral. Pair of prominent, transversely elongate maculae about $\frac{7}{8}$ way back on lateral parts of median body. Entire median body covered with very fine terrace lines, disposed in a pattern similar to that of *M. rhyakos*.

No completely articulated specimens known, but a moult (Pl. 6, fig. 8) has 8 articulated thoracic segments joined to a pygidium, with the inverted cephalon lying nearby. Details of the thorax are essentially the same as *M. rhyakos*, although the posterolateral points of the pleurae are shorter, and the terrace lines on the pleural doublure finer.

Pygidial length ranging from 0·5 to 0·7 of anterior width with increase in size and allowing for distortion; narrow, weakly concave border on small specimens is proportionately wider on larger ones, is of more or less constant width, but narrows very slightly forwards. Axis narrow, defined by deep, narrow axial furrows which are weakly bowed adaxially. Ten to twelve rings (exact number difficult to estimate, since more posterior ones are almost effaced), defined by shallow, nearly transverse ring furrows which become progressively shallower, and finally obsolete posteriorly. Some specimens (Pl. 7, fig. 9) have suggestions of paired muscle impressions and a very narrow, weak sagittal linear feature on axial rings. Posterior tip of axis reaches close to or just touches inner edge of border. Pleural fields inside paradoublural line anteriorly broader (trans.) than both axis and doublure, with 6–7 pairs of pleural ribs. Pleural furrows broad, shallow, nearly straight, posterior ones nearly effaced. They tend to be accentuated by compression. Interpleural furrows, running parallel with pleural, are seen only on some smaller specimens (Pl. 7, fig. 8). Doublure as wide as border, weakly ventrally convex and parallel with dorsal surface. Fine terrace lines run parallel with margin. Dorsal terrace lines, which run transversely, oblique to doublure terrace lines, are commonly impressed onto doublure by compression (Pl. 7, fig. 9), and do not extend onto adaxial part of pleural fields.

DISCUSSION. It is unfortunate that the holotype of this well-known and much-quoted species is a poorly-preserved, immature pygidium. This has undoubtedly been a major contributory factor to the confusion and varied interpretations associated with it in the past. The abundant and well-preserved asaphid material from Carmarthen has enabled us to gain a clearer understanding both of morphology and stratigraphical occurrence of *selwynii* and related species.

In the Geological Museum, Institute of Geological Sciences, there are two topotype pygidia (GSM 12874–5) of *selwynii*, both larger and better-preserved than the holotype. Despite the fact

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Plate 8

Merlinia selwynii (Salter 1859). Early Arenig, Carmarthen Formation, Pibwr Member.

Fig. 1. Thorax and pygidium. Lectotype of *Ogygia marginata* Crosfield & Skeat 1896: pl. 26, fig. 13. Refigured Whittard 1964: pl. 36, fig. 8. Nant Pwntan. SM A3106. ×2.

Fig. 2. Large pygidium. Glan Pibwr. GSM HT66. ×1½.

Fig. 3. Pygidium. Note fine terrace lines on pleural fields. Lane near Glan Pibwr Cottage. SM A67995. ×4.

Fig. 4. Small pygidium. Compare proportions with larger specimens, and with holotype of *M. selwynii* (Whittard 1964: pl. 37, fig. 1). Glan Pibwr, loc. 1A. It 14040. ×4.

Fig. 5. Pygidium. Glan Pibwr, loc. 1A. It 14041. ×5.

Fig. 6. Smallest pygidium. Glan Pibwr, loc. 1A. It 14042. ×10.

Merlinia selwynii (Salter 1859). Early Arenig, Basement Group.

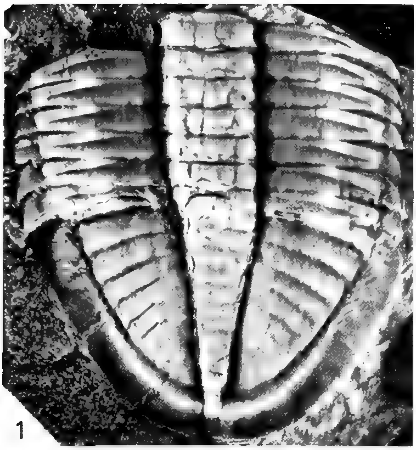
Fig. 7. Topotype pygidium. Hengwrt Uchaf, SW of Drws-y-nant station, near Dolgellau, Gwynedd. GSM 12874. ×3.

Merlinia selwynii (Salter 1859), 'late forms'. Early Arenig, Carmarthen Formation, upper part of Pibwr Member.

Fig. 8. Incomplete cephalon. Allt Pen-y-Coed, loc. 5H. It 14043. ×3.

Fig. 9. Hypostoma. Compare with that of *M. selwynii, forma typica* (Pl. 6, fig. 7). Allt Pen-y-Coed, loc. 5G. It 14044. ×4.

Fig. 10. Cranidium. Allt Pen-y-Coed, loc. Eλ8. GSM JP4708. ×3.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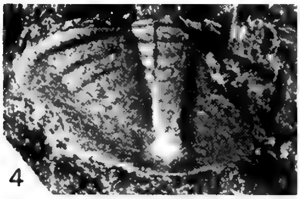
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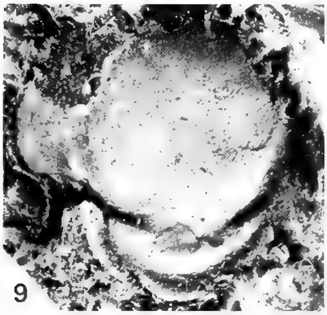
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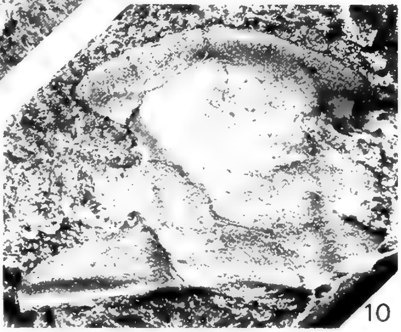
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that they are proportionately longer than the holotype (the latter has suffered some distortion, and Carmarthen specimens show a proportionate length increase with size increase), all three specimens have a narrow axis, narrow doublure of constant width and pleural fields broader than axis or doublure. In these respects they can immediately be distinguished from the Mytton Flags '*selwynii*' (see p. 267 and below) as well as from *M. murchisoniae* (see p. 280). They differ from similarly-sized *M. rhyakos* in having a convex axis, deeper axial furrows and more distinct pleural furrows. In these same respects they agree with type and topotype specimens of *Ogygia marginata* Crosfield & Skeat, as well as with certain of the specimens from the Henllan Ash figured by Whittington (1966 : pl. 3, figs 5, 7, 8 for example) as *Ogygiocaris* ? cf. *selwyni*, and with specimens from western Lleyn in the collections of the National Museum of Wales (e.g. NMW 27.110.G258 from Benallt Mine, Rhiw, near Aberdaron). We consider all these occurrences to represent a single species, for which the name *selwynii* has priority.

Whittard (1964 : 232) described and figured a large suite of specimens from the Mytton Flags of the Shelve district as *Ogygiocaris selwynii.* Specimens from this area have long been considered to be 'typical' *selwynii*, and comparison has commonly been made with such specimens in considering this species, rather than those from the type locality. The Mytton Flags specimens differ from *selwynii* as here defined principally in having a consistently broader pygidial doublure, stronger pleural furrows and the pleural field inside the paradoublural line anteriorly no wider than the doublure (e.g. Whittard 1964 : pl. 37, figs 6, 7). The cranidium differs in having shallower axial furrows, the glabella encroaching further onto the preglabellar field and the eye closer to the lateral border furrow. In cranidial characters, the Mytton Flags '*selwynii*' are quite similar to *M. rhyakos* (see above). We here consider the Mytton Flags specimens to represent a third species, *M. major* (see above), which is diagnosed below.

Bates (1968 : 179) figured cranidia and pygidia from the Arenig Carmel Formation, Anglesey, as *Ogygiocaris selwynii.* These specimens have a flat anterior border, the cranidial section of the lateral border furrow is short and the pygidial axis is relatively broad and of low relief. These characters preclude inclusion in *M. selwynii* as here defined, but instead indicate affinities with *M. murchisoniae.*

Merlinia selwynii, as characterized in the description above, has been found in the lower part of the Pibwr Member. Specimens from the upper part of the Pibwr Member from Allt Pen-y-Coed, and from the Cwmffrŵd Member on Nant Cwmffrŵd are here figured (Pl. 8, figs 8–10; Pl. 9, figs 1–7) as 'stratigraphically high *M. selwynii*'. They show features intermediate with the succeeding species *M. rhyakos.* For example, the position of the palpebral lobes is almost exactly midway between that (forward) of *M. rhyakos* and (rearward) *M. selwynii, forma typica*, so that

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Plate 9

Merlinia selwynii (Salter 1859), 'late forms'. Early Arenig, Carmarthen Formation, Pibwr and Cwmffrŵd Members.

Fig. 1. Incomplete cephalon. Note well-defined frontal glabellar lobe. Cwmffrŵd Member, Nant Cwmffrŵd, loc. 2A. It 14045. × 2.

Fig. 2. Cranidium. Note nearly parallel-sided glabella. Upper part of Pibwr Member. Allt Pen-y-Coed, loc. 5H. It 14046. × 4.

Fig. 3. Pygidium. Compare with *M. selwynii, forma typica* (e.g. Pl. 8, fig. 5). Upper part of Pibwr Member, Allt Pen-y-Coed, loc. 5H. It 14047. × 4.

Fig. 4. Small pygidium. Pibwr Member, Nant Pwntan. It 14048. × 5.

Fig. 5. Pygidium with parts of four attached thoracic segments. Upper part of Pibwr Member, Allt Pen-y-Coed, loc. 5H. It 14049. × 2.

Fig. 6. Small cranidium. Cwmffrŵd Member, Nant Cwmffrŵd, loc. 2A. It 14050. × 5.

Fig. 7. Large cranidium. Cwmffrŵd Member, Nant Cwmffrŵd, loc. 2A. It 14051. × 2½.

Merlinia murchisoniae (Murchison 1839). Early Arenig, Ogof Hên Formation, upper part of Bolahaul Member.

Fig. 8. Silicone rubber cast of external mould of cranidium. Temporary section at water treatment plant, Penddaulwyn Fawr, loc. 12. NMW 76.3G.4. × 2.

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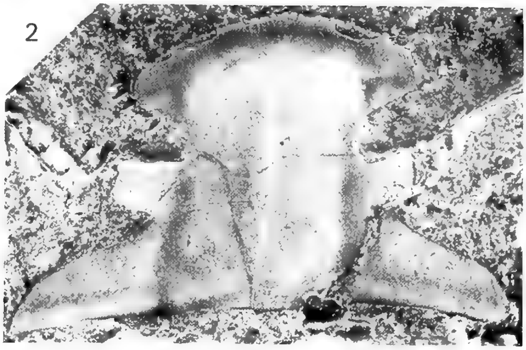

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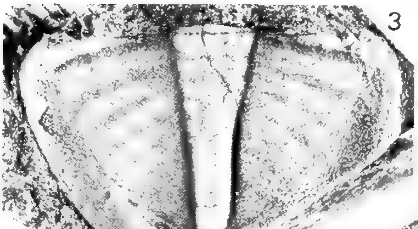

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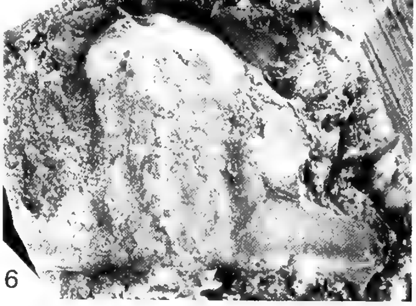

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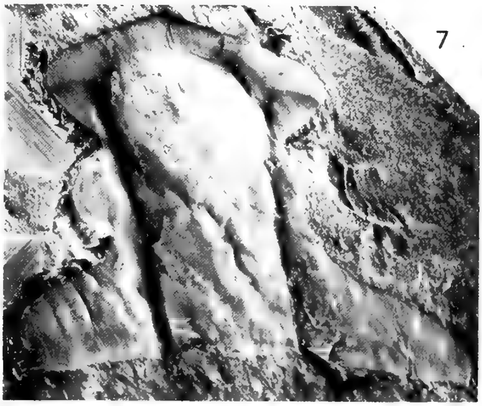

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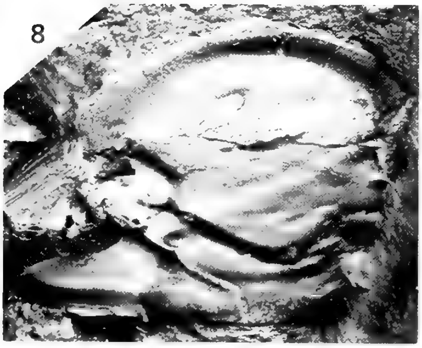

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the transverse line connecting ϵ/ζ–ϵ/ζ is at 0·3–0·35 sag. length (mean 0·33), compared with the mean values of 0·35 for *M. rhyakos* and 0·31 for *M. selwynii* from the Pibwr Member. We have examples (Pl. 8, fig. 10) of cranidia of stratigraphically high *M. selwynii* with terrace lines on the frontal lobe of the glabella approaching *M. rhyakos* in prominence. So there is apparently complete intergradation between the two species. We do not name a third species for stratigraphically high *M. selwynii* partly because of the difficulties of framing a diagnosis for such an intermediate, and because it is not possible to specify where, on such a spectrum, the holotype of *M. selwynii* from north Wales lies.

Merlinia major (Salter 1866)

v.1866a *Ogygia Selwynii* (Salter); Salter *pars*: 136; pl. 17, figs 1, 2, 4, 7 [*non* fig. 3, =*Merlinia selwynii*].
v.1866b *Ogygia Selwynii* (Salter); Salter *pars*: 255, 313; pl. 11B, figs 5, 5a [*non* pl. 9, figs 2–4, 4a, =*M. selwynii*].
v*.1866b *Ogygia Selwynii* var. *major* Salter: 314; pl. 9, figs 5, 6.
.1869 *Ogygia Selwynii* (Salter); Morton: 15.
.1873 *Ogygia Selwynii* (Salter); Salter *pars*: 23 [*pars*=*M. selwynii*].
v.1881 *Ogygia Selwynii* (Salter); Salter & Etheridge *pars*: 375, 380, 509; pl. 11B, figs 5, 5a [*non* pl. 9, figs 2–4, 4a, =*M. selwynii*].
v.1881 *Ogygia Selwynii* var. *major* Salter; Salter & Etheridge: 510; pl. 9, figs 5, 6.
.1884 *Ogygia Selwynii* (Salter); La Touche: 56; pl. 1, fig. 21.
.1931 *Ogygia* (*Niobella*) *selwyni* (Salter); Whittard *pars*: 326 [*non* ref. on 237, =*Megalaspidella whittardi* Bates].
.1952 *Ogygia selwyni* (Salter); Jackson: 40.
v.1964 *Ogygiocaris selwynii* (Salter); Whittard *pars*: 232; pl. 34, figs 7–13; pl. 35, figs 1–4, 6–9; pl. 36, figs 1–7; pl. 37, figs 2–11 [*non* pl. 37, fig. 1, =*M. selwynii*; *nec* pl. 35, fig. 5, ?=*Merlinia murchisoniae*; *nec* pl. 35, fig. 10, ='*Asaphus*' *hybridus* Salter].
? .1966 *Ogygiocaris* ? cf. *selwyni* (Salter); Whittington *pars*: 496; pl. 3, fig. 6 (*non* pl. 2, figs 9, 11–12; pl. 3, figs 1, 5, 7–9; pl. 4, fig. 16, =*M. selwynii*; *nec* pl. 2, figs 7, 10; pl. 3, figs 2, 10–11, =*M. murchisoniae*].
v.1969b *Megalaspidella* (?) *murchisoniae* (Murchison); Bates *pars*: 17 [*non* pl. 6, figs 1–6; pl. 7, figs 1–9; pl. 8, figs 1, 2, 5, =*M. murchisoniae*].

DIAGNOSIS. Closely similar to *M. selwynii* except that cephalic doublure is broader, so that front end of eye is closer to paradoublural line; pygidial doublure wider, inner margin not parallel to pygidial margin, so that doublure has its greatest width exsag.

LECTOTYPE. GSM 59425, herein selected. Whittard (1964: pl. 34, fig. 3) figured one known syntype of *Ogygia selwynii* var. *major* as well as an additional 'possible syntype' (1964: pl. 34, fig. 4). We here select the former, an internal mould of an incomplete cranidium with partial right hand free cheek, from Mytton Flags, Whitegrit Mine, Shelve, Shropshire, as the lectotype of *Merlinia major*.

OCCURRENCE. This species is common in the Mytton Flags of the Shelve district (see Whittard (1964) for details). It has not yet been positively identified outside this area, but the cranidium figured by Whittington (1966: pl. 3, fig. 6) from the Henllan Ash might belong to this species (see also above, under *M. rhyakos*).

DISCUSSION. For comparative remarks, see under *M. rhyakos*, *M. selwynii* and *M. murchisoniae*.

Merlinia murchisoniae (Murchison 1839)

(Fig. 10D; Pl. 9, fig. 8; Pl. 10, figs 1–10; Pl. 11, fig. 1)

v*.1839 *Ogygia Murchisoniae* Murchison: 664; pl. 25, figs 3a–b.
v.1854 *Stygina* (*Ogygia*) *Murchisoniae* (Murchison) Murchison: pl. 4, fig. 1.
.1854 *Stygina Murchisoniae* (Murchison); Morris: 115.
.1859 *Stygina* (*Ogygia*) *Murchisoniae* (Murchison); Murchison: 55; Fossils (10), fig. 4; pl. 4, fig. 1.
.1864b *Stygina Murchisoniae* (Murchison); Salter: 3.
v.1866a *Stygina Murchisoniae* (Murchison); Salter: 173; pl. 18, fig. 11.
.1866a *Asaphus*, sp. undetermined; Salter: pl. 25, fig. 4.

v.1872 *Stygina Murchisoniae* (Murchison); Murchison : 51; Fossils (11), fig. 4; pl. 4, fig. 1.
.1873 *Asaphus Menapiae* Hicks; Salter : 23 [*nom. nud.*].
.1873 *Asaphus solvensis* Hicks; Salter : 23 [*nom. nud.*].
.1873 *Niobe menapiensis* Hicks : 46; pl. 4, figs 1–9.
.1873 *Niobe solvensis* Hicks : 47; pl. 4, figs 10–16.
1886 *Asaphellus menapiensis* (Hicks) Brøgger : 61–62.
non 1887 *Stygina Murchisoniae* (Murchison); Nicholson & Marr : 342, 343 [='gen. et sp. indet.' Dean 1963 : 58; pl. 4, figs 2, 7].
1891 *Niobe menapiensis* Hicks; Woods : 148.
1891 *Niobe solvensis* Hicks; Woods : 148.
non 1895 *Stygina Murchisoniae* (Murchison); Elles & Wood : 247, 248 [='gen. et sp. indet.' Dean 1963 : 58; pl. 4, figs 2, 7].
1896 *Asaphellus Menapiensis* (Hicks); Brøgger : 206, 210, 218.
1896 *Asaphellus Solvensis* (Hicks) Brøgger : 206, 210.
v.*1896* *Stygina Murchisoniae* (Murchison); Crosfield & Skeat : 531, 535.
v.1896 *Ogygia marginata* Crosfield & Skeat *pars*: 538; pl. 26, figs 19, 26 [*non* figs 13, 15–18, 20–25, =*M. selwynii* (Salter); *nec* fig. 14, =*M. rhyakos* sp. nov.].
1900 *Niobe menapiensis* Hicks; Reed : pl. 12, fig. 7.
v.*1909* *Stygina Murchisoniae* (Murchison); Thomas *in* Strahan *et al.* : 15.
1910 *Niobe* (*Hemigyraspis*) *menapiensis* Hicks; Raymond : 41.
1910 *Niobe* (*Hemigyraspis*) *solvensis* Hicks; Raymond : 41.
1930 *Niobe menapiensis* Hicks; Reed : 314.
1930 *Niobe solvensis* Hicks; Reed : 314–5.
1931 *Ogyginus* ? *menapiensis* (Hicks) Reed : 461–2.
1931 *Niobe* ? *solvensis* Hicks; Reed : 461, 471.
.*1949* *Niobe menapiensis* Hicks; Edmonds : 61.
.*1949* *Niobe solvensis* Hicks; Edmonds : 61.
.*1952* *Ogygia selwyni* Salter; Jackson : 40.
v.1964 *Ogygiocaris murchisoniae* (Murchison) Whittard *pars* : 238; pl. 38, figs 5–11, ? pl. 35, fig. 5 [*non* pl. 37, figs 12, 13, *nec* pl. 38, figs 1–4, =*Megalaspidella whittardi* Bates].
v.1966 *Ogygiocaris* ? cf. *selwyni* (Salter); Whittington *pars* : 496; pl. 2, figs 7, 10; pl. 3, figs 2, 10–11 [*non* pl. 2, figs 9, 11–12; pl. 3, figs 1, 5, 7–9; pl. 4, fig. 16, =*Merlinia selwynii*; *nec* pl. 3, fig. 6, ?=*M. major* (Salter)].
v.1969b *Megalaspidella* (?) *murchisoniae* (Murchison) Bates : 17; pl. 6, figs 1–6; pl. 7, figs 1–9; pl. 8, figs 1, 2, 5.

DIAGNOSIS. Cephalic doublure and eye position like *M. major*; glabella apparently lacking terrace lines on frontal lobe, which is more expanded than in other species; cranidial section of lateral border furrow very short; palpebral lobes shortest in genus; hypostoma with fine terrace lines, sparser and less backwardly-bowed than on other species, posterior margin non-acuminate; pygidial doublure broad, with inner margin parallel to posterior pygidial margin.

HOLOTYPE. GSM 18988 A, B (by monotypy), counterpart internal and external moulds of crushed cephalon with parts of 5 thoracic segments and associated pygidium (figd Whittard 1964 : pl. 38, figs 5, 6; Bates 1969b : pl. 6, fig. 3).

TYPE LOCALITY AND HORIZON. Early Arenig, Bolahaul Member of the Ogof Hên Formation, old quarry on the Roman Road, Pensarn, Carmarthen.

OTHER OCCURRENCES. In the Bolahaul Member, this species has been recorded from Roman Road, Pensarn (locs 6A, 6B, Survey loc. Wλ7), tip-heaps at Wenallt (loc. 9) and Allt Cystanog (Survey loc. Eλ3), water treatment plant excavations, Penddaulwyn fawr (loc. 12), Cilwaunydd (Survey loc. Wλ3) and Cablehill Farm (Survey loc. Wλ5).

DESCRIPTION. Glabella typically with frontal lobe weakly laterally expanded, only nearly parallel-sided on smaller and distorted specimens; defined by weak axial and preglabellar furrows, former shallowing in region opposite palpebral lobe, but on compressed and distorted internal moulds (e.g. Bates 1969b : pl. 17, figs 1, 5) appears deep. Preglabellar furrow shallow but distinct. Glabella encroaches upon anterior border to reduce its width by about half. Poor preservation precludes description of muscle impressions, but probably similar to those of *M. rhyakos* and *M. selwynii.* Occipital ring narrow (sag.), lozenge-shaped, defined by shallow, weak occipital furrow.

Anterior and lateral borders broad, flat, weakly concave, maintaining constant width with exception of preglabellar section. Lateral border furrow shallow, broad, indicated by an abrupt change of slope rather than a furrow. Cranidial section very short, terminating in a shallow hypostomal pit not far in front of eye. Preocular facial suture divergent at 35°–55° (estimated) to an exsagittal line through γ, which lies very close to axial furrow. Postocular suture defines broad, triangular postocular fixed cheek. Palpebral lobe $\frac{1}{6}$ length of cranidium (compared with $\frac{1}{4}$ on other *Merlinia* species) and close to axial furrow in a forward position, γ and ϵ/ζ close to axial furrow, former closer than latter. Eye crescentic, its anterior part close to lateral border furrow. Field of free cheek as broad as lateral border, weakly convex. Genal spine broad-based, tapering rather rapidly backwards and extending as far as sixth or seventh thoracic segment. Posterior border furrow very shallow on free cheek, deeper on cranidium, its depth commonly accentuated by crushing (e.g. Bates 1969b : pl. 7, fig. 8). Doublure as broad as lateral border, narrowing in front of hypostoma, and weakly ventrally convex, with fine parallel terrace lines.

Hypostoma slightly longer than wide, suboval. Posterior margin transverse to weakly backwardly convex; anterior margin forwardly convex. Lateral border broad, widening gradually to a position opposite maculae. Lateral border furrow deepens slightly and widens backwards, where it meets broad, deep posterior border furrow. Lateral and posterior border furrows together form a rather flat-based U around median body. Maculae transversely elongated, close to posterior end of median body, opposite widest part of lateral border. Whole median body covered with fine, widely-spaced terrace lines, which all have a more or less constant backward convexity.

Thoracic axis possibly comparatively broader than in *M. rhyakos* and *M. selwynii.* Details are like those of these species, although the terrace lines on the distal parts of pleurae are much finer than in *M. rhyakos.*

Pygidial length approximately 0·6 of anterior width. Axis moderately broad and of low convexity, defined by shallow, straight axial furrows, tapering fairly strongly backwards, axial furrows enclosing an angle of about 20°–25°. Ring furrows weak on dorsal surface, 10–12 rings indicated. Posterior tip of axis reaches close to or touches inner edge of border. Pleural fields anteriorly as wide, or marginally narrower or wider than border, with 6–8 pairs of ribs distinguishable. Pleural furrows moderately deep and broad; interpleural boundaries marked by faint

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Plate 10

Merlinia murchisoniae (Murchison 1839). Early Arenig, Ogof Hên Formation, upper part of Bolahaul Member.

Fig. 1. Thorax and pygidium, internal mould. Roman Road section, Pensarn. In 49536. ×2.

Fig. 2. Pygidium, internal mould. Temporary section at water treatment plant, Penddaulwyn Fawr, loc. 12. NMW 76.3G.5. ×4.

Fig. 5. Large pygidium, internal mould. Roman Road section, Pensarn, loc. 6B (Wλ2). GSM HT275. ×1½.

Fig. 6. Small, complete internal mould. Roman Road section, Pensarn, loc. 6A (Wλ3). GSM HT254. ×2½.

Fig. 7. Incomplete thorax and pygidium, internal mould, showing well the broad doublure with terrace lines. Spoil from mine shaft, Allt Cystanog, loc. Eλ3. GSM HT233. ×2.

Fig. 8. Hypostoma. Note distribution of terrace lines (compare Fig. 10). S of Ty-gwyn, 90 m N of loc. Wλ9. GSM HT277. ×3.

Fig. 9. Free cheek, internal mould. Note wide doublure and hypostomal suture. S of A48, near Ty-gwyn. In 49520. ×2½.

Fig. 10. Hypostoma *in situ* on incomplete cephalon. Note pattern of terrace lines (compare Fig. 8). Roman Road section, Pensarn. In 49533. ×4.

Merlinia murchisoniae (Murchison 1839). Early Arenig, Carmarthen Formation, Pibwr Member.

Figs 3, 4. Small, incomplete pygidium in dorsal and lateral view. Note fine terrace lines on dorsal surface. Glan Pibwr, loc. 1A. It 14052. ×5.


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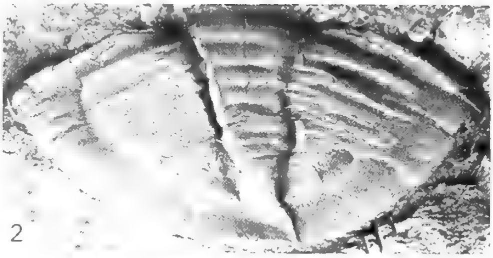
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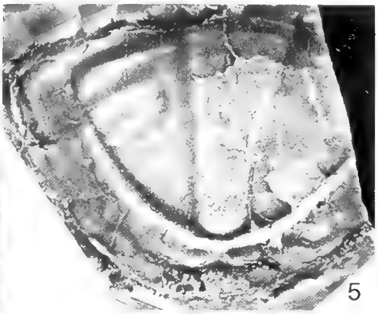
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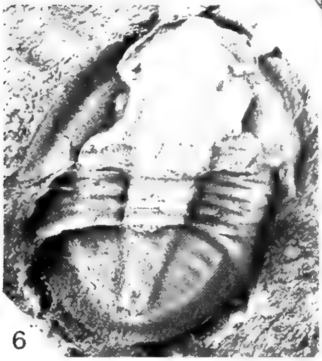
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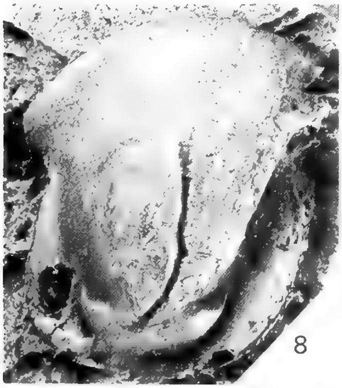
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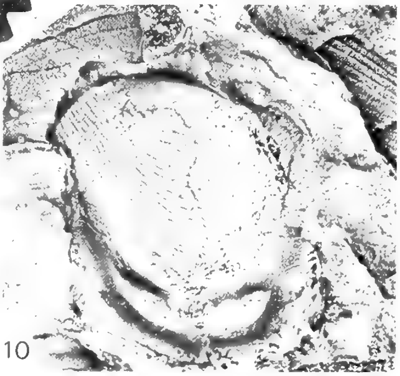
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raised lines on specimens retaining cuticle. Border broad, weakly concave. Doublure as wide as border, its inner edge parallel or subparallel to margin. About 15 fine terrace lines are present.

Much of the material of *M. murchisoniae* is too badly preserved to show details of surface sculpture, but the dorsal surface of cephalon and pygidium is apparently without terrace lines.

DISCUSSION. Whittard (1964 : 238) restricted this species to specimens from Pensarn, Ramsey Island and Shelve. Bates (1969b : 20) remarked that specimens from the last-named locality differed significantly from *M. murchisoniae* from the other localities, and referred them to a new species, *Megalaspidella* (?) *whittardi* Bates 1969. They are from the Upper Arenig, *hirundo* Zone, Tankerville Flags, stratigraphically higher than any of the others. We agree with Bates that a different species is represented at Shelve. The parallel preocular facial sutures (Whittard 1964 : pl. 37, fig. 12; pl. 38, figs 1, 3), are like those of *Megalaspidella kayseri* Kobayashi 1937 (see Harrington & Leanza 1957 : 163; fig. 75 1, 3, 9) and *Plesiomegalaspis* [=*Megalaspidella*] *graffi* (Thoral 1946 : pl. 8, fig. 1), and we feel that *whittardi* can be placed in *Megalaspidella.* It is not known whether *M. kayseri* and *M. graffi* have panderian openings and protuberances on the thoracic pleurae like *M. whittardi* (Whittard 1964 : pl. 38, fig. 4). They are absent in *Merlinia* species.

Bates (1969b) included in *M. murchisoniae* specimens which we have placed in *M. selwynii.* More and better-preserved material than that available to Bates shows that two species can be distinguished, with different stratigraphic ranges (Figs 6, p. 237, 10, p. 263). *M. murchisoniae* is distinguished from *M. selwynii* principally by its broader doublure, shorter cranidial section of the anterior border furrow and posteriorly rounded hypostoma with sparser terrace lines. Specimens figured by Bates (1968 : pl. 12, figs 1, 2, 5, 6) from the Arenig Carmel Formation, Llanerchymedd, Anglesey, as *Ogygiocaris selwynii,* and later (1969b : 17) placed by him in the synonymy of *M.* (?) *murchisoniae,* do not appear to belong to either of these species, and the combination of cranidial (glabellar outline, preglabellar furrow, anterior border) and pygidial (axial furrows, border) characters is at variance with those of both species as here defined. It is likely that a different species is present in the Arenig of Anglesey, but the extant material is insufficient to draw up its diagnostic characters.

Family **TRINUCLEIDAE** Hawle & Corda 1847
Subfamily **HANCHUNGOLITHINAE** Lu 1963
Genus ***MYTTONIA*** Whittard 1955
Myttonia cf. ***fearnsidesi*** Whittington 1966
(Pl. 11, figs 2–8)

MATERIAL. Five specimens (NMW 75.45G.1–3, GSM JP4655–58), including two fairly complete cranidia from low in the Pibwr Member at Glan Pibwr (loc. 1B), and one specimen (NMW 75. 45G.4) from Pibwr Member, Allt Pen-y-Coed (loc. 5G). 'Ghosts' of trinucleids, possibly referable to *Myttonia,* have been found rarely in the Pibwr Member at Pibwr weir (loc. 21) and in Allt Pen-y-Coed (locs 5G, 5H).

DESCRIPTION. Glabella simple, pyriform, showing beginnings of pseudofrontal lobe. On the larger cranidium (Pl. 11, fig. 2) it is swollen anteriorly and slightly overhangs the fringe. The smaller cranidium (Pl. 11, figs 6, 8) shows a small, remnant preglabellar field. Occipital furrow shallow, differentiating narrow occipital ring from remainder of glabella. Occipital ring badly preserved on our material, but appears to be backwardly pointed. Axial furrow broad posteriorly. Baculae present at its posterior end, and the larger specimen (Pl. 11, fig. 2) has a prominent lateral glabellar lobe. Cheek swollen, on smaller specimen with trace of eye ridge. Cheek and glabella of the larger specimen have a distinct reticulate sculpture, and on the smaller specimen the cheek is pitted, the pits becoming finer towards the fringe. There is a small posterior fossula immediately adaxial to the narrow ridge joining the posterolateral corner of the cheek with the posterior border.

Fringe rather narrow, sloping gently downwards and widening slightly towards the genal angle. Girder marginal. On the upper lamella I_1 and I_2 pits are situated in radial sulci. On the larger specimen these extend laterally close to the genal angle, while on the smaller one they are not evident except close to the sagittal region. On a lower lamella (Pl. 11, figs 4, 6) I_1 and I_2 can be seen in radial sulci as far as R_{19}. Pits on the inner part of the fringe on both upper and lower lamellae have an irregular arrangement.

Discussion. The Carmarthen specimens closely resemble *M. fearnsidesi* Whittington 1966 from the Arenig Henllan Ash, Arenig area, Gwynedd (see Whittington 1966 : 494; pl. 1, figs 1–6; Hughes, Ingham & Addison 1975 : pl. 1, figs 11, 12) in the number and arrangement of pits on the fringe. The cheek of *M. fearnsidesi*, although not well preserved, shows obscure traces of reticulation (Whittington 1966 : pl. 1, fig. 4; Hughes, Ingham & Addison 1975 : pl. 1, figs 11, 12). With the small amount of material from the Henllan Ash and from the Pibwr member at our disposal, we are unable to be certain whether it is conspecific, since we lack sufficient well-preserved specimens, and thus designate the Carmarthen specimens *M.* cf. *fearnsidesi.*

M. confusa (the type species) (Whittard 1955 : 29; pl. 13, figs 5–6; *non* fig. 7, = *Anebolithus simplicior* (Whittard 1966) – see Whittard 1966 : 271, 276 and Hughes & Wright 1970 : 688 ; pl. 127, figs 7, 10) and *M. multiplex* Whittard (1966 : 272; pl. 46, figs 8, 9; pl. 47, figs 2, 3) from the Arenig Mytton Flags of the Shelve district are both similar to *M.* cf. *fearnsidesi* and *M. fearnsidesi*, but have larger numbers of smaller, irregular pits on the inner parts of the fringe. Other parts of the exoskeleton of these species are unknown.

Dr J. K. Ingham (verbal communication, December 1975) regards *M. fearnsidesi* and *M.* cf. *fearnsidesi* as advanced members of the Hanchungolithinae, with the glabella shape, the simplification of the fringe and the beginnings of the development of radial arcs tendencies towards early trinucleines such as *Anebolithus* and *Incaia* (cf. Hughes, Ingham & Addison 1975 : 555).

B. Graptolites

With the exception of *Phyllograptus* spp. from the Pibwr Member, all the graptolites in the Carmarthen Formation are dendroids, and all occur in the Cwm yr Abbey Member. Even here they are rare, confined to particular bedding planes, and probably for this reason they have been overlooked from the early Arenig succession of Carmarthen. Bulman (*in* Teichert 1970 : 36) has emphasized that most of the genera of Dendroidea are 'form genera' based on gross rhabdosomal shape, and, while more details of thecal morphology are becoming known which might be the basis of a more refined taxonomy, these cannot be applied to the majority of species which are known from flattened or poorly-preserved material. A few details can be discerned on the Carmarthen species, but they are not sufficient to do more than assign them to established genera.

Family **DENDROGRAPTIDAE** Roemer *in* Frech 1897
Genus ***CALLOGRAPTUS*** Hall 1865
Subgenus ***CALLOGRAPTUS*** Hall 1865

Type species. *Callograptus elegans* Hall from the Levis Shale, Quebec, Canada.

Diagnosis. See Bulman (*in* Teichert 1970 : 38) and the differential discussion of Skevington (1963 : 12–13).

Callograptus (Callograptus) cf. ***tenuis*** Bulman 1934
(Fig. 12C)

Diagnosis and Type data. Type material is from the Tankerville Flags (Arenig: Zone of *Didymograptus hirundo*) of the Shelve Inlier. The diagnosis of Bulman (1934 : 90) is followed here.

Occurrence. In the Carmarthen Formation material of this species has been recovered from one locality in the Cwm yr Abbey Member on Cwm yr Abbey (loc. 16F).

Material. Three partially complete rhabdosomes, BM(NH) Q5049–51, of which one, BM(NH) Q5049, is figured here.

Description. Rhabdosome delicate, available material suggesting that it could be either flabelliform or conical. Our material is preserved in a soft mudstone in partial relief, with the dorsal surface of the stipes uppermost, maximum axial length of available material 2·5 cm, although all material is incomplete. The stipes are 0·2 mm broad, a width that remains consistent over the whole rhabdosome, and are generally parallel, separated for the most part by a distance greater than the stipe width itself, occasionally approaching more closely, lying side by side or even crossing over. One specimen (Fig. 12C) shows a rapid, near-proximal zone of branching, otherwise bifurcation is somewhat irregular, 2 mm or more apart, and not necessarily simultaneous in adjacent stipes. The dorsal aspect of the preservation of individual stipes presents an appearance closely similar to that figured by Bulman (1934 : text-fig. 43a), with the proximal parts of the autothecae and bithecae parallel to the stipe direction, with the stolothecal canal occupying a gently undulating course between. The preservation does not permit a description of the disposition of the thecal apertures, although in dorsal aspect their spacing is similar to that of the type specimen. Dissepiments are apparently lacking.

DISCUSSION. The material from the Carmarthen Formation agrees closely with the type (and only) specimen of *C. tenuis*, but because details of thecal apertures cannot be discerned the identification must be tentative. The thin stipes, with only one series of thecae adjacent at any one point indicate the assignment to *Callograptus* (*Callograptus*) rather than *Callograptus* (*Pseudocallograptus*).

Subgenus ***PSEUDOCALLOGRAPTUS*** Skevington 1963

TYPE SPECIES. *Callograptus salteri* Hall, from the 'Quebec group of Gros Maule, Quebec'.

Callograptus* (*Pseudocallograptus*) *salteri Hall 1865
(Fig. 12B; Pl. 11, fig. 9)

DIAGNOSIS AND TYPE DATA. Defining characters and locality data on the type and other British material are fully listed by Bulman (1934 : 84); lectotype of *C. salteri* designated by Bulman (1967 : 94).

OCCURRENCE. A single specimen from the Cwm yr Abbey Member, Carmarthen Formation, in Nant y Glasdwr, loc. 3B.

DESCRIPTION. Rhabdosome incomplete, preserved in a soft shale in three pieces which indicate a total length exceeding 5·5 cm. The incomplete specimen is acutely fan-shaped, but this may be

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Plate 11

Merlinia murchisoniae (Murchison 1839). Early Arenig, Ogof Hên Formation, upper part of Bolahaul Member.

Fig. 1. Pygidium with three attached thoracic segments. Spoil from mine shaft, Allt Cystanog, locality Eλ3. GSM HT230. × 3.

Myttonia cf. ***fearnsidesi*** Whittington 1966. Early Arenig, Carmarthen Formation, Pibwr Member.

Fig. 2. Cranidium with some of dorsal surface preserved, showing reticulate sculpture on cheek and on posterior part of glabella. Note basal glabellar lobe and bacula. Glan Pibwr, loc. 1C (Wλ5). GSM JP4658. × 9.
Fig. 3. Incomplete ventral mould of lower lamella. Allt Pen-y-Coed, loc. 5G. NMW 75.45G.4. × 8.
Fig. 4. Incomplete dorsal mould of lower lamella. Glan Pibwr, loc. 1C (Wλ5). GSM JP4656. × 10.
Fig. 5. Small cranidium, showing pitted surface of cheek and glabella, short eye ridge, bacula and posterior fossula. Glan Pibwr, loc. 1B. NMW 75.45G.1a. × 12.
Fig. 6. Ventral mould of same specimen as Fig. 4. GSM JP4655. × 10.
Fig. 7. Latex cast of external mould of incomplete enrolled specimen. Glan Pibwr, loc. 1B. NMW 75.45G.2b. × 12.
Fig. 8. Latex cast of external mould of same specimen as Fig. 5. NMW 75.45G.1b. × 12.

Callograptus* (*Pseudocallograptus*) *salteri (Hall 1865). Early Arenig, Carmarthen Formation, Cwm yr Abbey Member.

Fig. 9. Fragmentary rhabdosome. Nant y Glasdwr, loc. 3B. Q5048. × 1⅓.

Palaeodictyota sp. Early Arenig, Carmarthen Formation, Cwm yr Abbey Member.

Fig. 10. Incomplete rhabdosome. Nant y Glasdwr, loc. 3B. Q5047. × 2.


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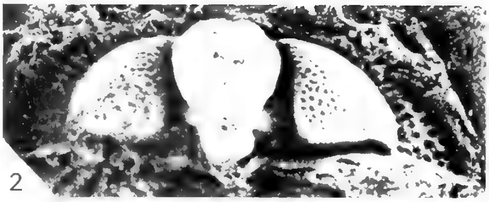
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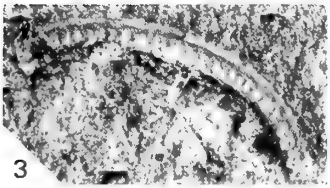
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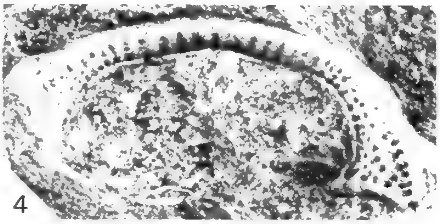
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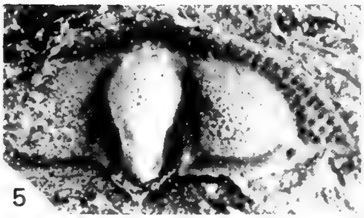
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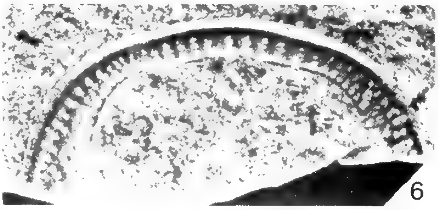
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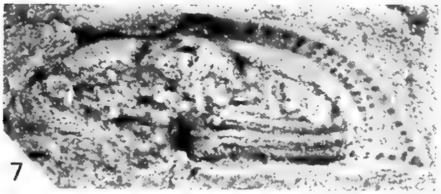
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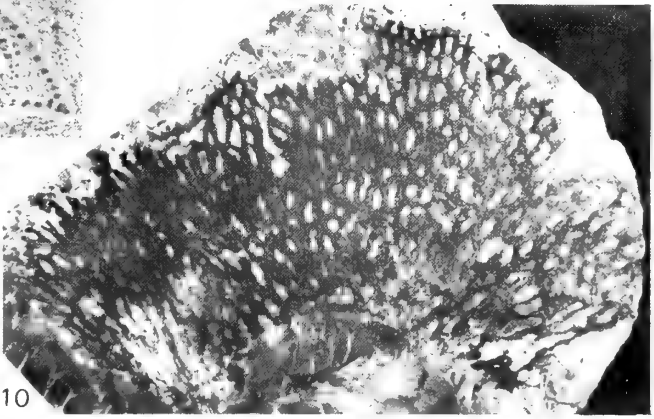
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misleading. The preservation is with the dorsal surface uppermost so that thecal apertures are obscured. It is clear, however, that as many as 6 thecae are present intertwined through any one stipe; these run along the stipe for a considerable distance, so that the thecal system is complex and single stipes are likely to contain more than one set of autothecae and bithecae side by side. Width of individual stipes generally about 0·5 mm, with a maximum of 0·65 mm. Thirteen such stipes occur within 10 mm in the distal part of the rhabdosome, and except distally, width between stipes is less than the stipe width itself.

Stipes run more or less parallel, but are wavy, and this results in their touching one another at frequent intervals. Close examination usually reveals that true anastomosis does not occur at such points of contact, that is there is no interchange of thecae from stipe to stipe, but there are other examples where there is interchange of thecae or even fusion of two stipes. There are also very rare dissepiments in the distal part of the rhabdosome. This species thus has three ways of sharing support of adjacent stipes: by anastomosis, by contact without interchange of thecae, and by dissepiments. Where branching occurs it does so simultaneously, and at least 3 out of 4 adjacent stipes undergo division. Frequency of branching not known proximally; first and second sets separated by about 10 mm, second and third sets by 15 mm. Thecal apertures are only visible along one short section of stipe, but it is not clear there whether apertures of autothecae and bithecae are both present; if one side of the apertural surface of the stipe is present, as seems probable, then the thecae exposed would include autothecae and one series of bithecae. Of the total thecal spacing (27 in 10 mm) two-thirds (i.e. 18 in 10 mm) would be attributable to the autothecae.

DISCUSSION. The specimen from Carmarthen is preserved in a different way from those described by Bulman (1934 : 81–84; pl. 9, figs 1–7; text-figs 39, 40) from the Arenig of Whitesand Bay, St David's, but similarities in proportion of stipes and branching habit are such as to make the assignment of the present specimen to *C. salteri* well-founded. The apparent impression of an acutely conical rhabdosome is misleading as Bulman (1934 : 82) notes, for fragments of complete specimens frequently display this appearance. The undulating appearance of the stipes of the material under discussion is more in accord with Hall's (1865 : 135) original description than with the material from Pembrokeshire. Distal spacing of stipes (13 in 10 mm), width of individual stipes, and the branching habit are closely comparable to the specimens from Whitesand Bay. *C. hopkinsoni* Bulman (1934 : 84; pl. 8, figs 1–5; text-fig. 41), which occurs with *C. salteri* in Whitesand Bay, has broader stipes and correspondingly fewer stipes in 10 mm. Bulman (1934 : 85) mentions that *C. hopkinsoni* shows some specimens intermediate with *Desmograptus cancellatus* Hopkinson. The same applies to the present specimen of *C. salteri*, which includes a number of anastomosing stipes, and even where stipes touch without anastomosis they present a desmograptoid appearance. Bulman (1934 : 40) notes that *Desmograptus* occupies an intermediate position between Dendrograptidae such as *Callograptus*, in which there is no interchange of thecae between stipes, and Acanthograptidae such as *Palaeodictyota*, in which such interchange is the rule. Such species as *C.* (*Pseudocallograptus*) *salteri* indicate the intergradational nature of such 'generic' distinctions. No doubt the desmograptoid condition is one which could be polyphyletically achieved.

Family **ACANTHOGRAPTIDAE** Bulman 1938

Genus ***PALAEODICTYOTA*** Whitfield 1902

TYPE SPECIES. *Inocaulis anastomoticus* Ringueberg 1888.

REMARKS. Whitfield (1902 : 399) described *Inocaulis ramulosus* Spencer 1884 as a species of *Palaeodictyota*. He figured a specimen he identified with *I. ramulosus* showing anastomosing, broad stipes, which might be regarded as typical of *Palaeodictyota* as subsequently understood (Ruedemann 1947 : 269; Bulman *in* Teichert 1970 : 43). Unfortunately, Spencer's original (1884 : pl. 6, fig. 1) specimen is quite different, and might with some justice be assigned to *Inocaulis*. However, Whitfield (1902) did not formally designate *I. ramulosus* Spencer as type species of the genus, and Ruedemann (1908 : 200) was accordingly free to designate *Inocaulis anastomoticus* Ringueberg 1888 as type species. This selection is particularly appropriate because the species figured (mistakenly) by Whitfield as *I. ramulosus* may be more reasonably assigned to *I. anastomoticus* (Ruedemann 1908 : 199–201).

Palaeodictyota sp.

(Fig. 12A; Pl. 11, fig. 10)

OCCURRENCE. Cwm yr Abbey Member of the Carmarthen Formation, Nant y Glasdwr (loc. 3B).

MATERIAL. A single specimen, with counterpart, BM(NH) Q5047a–b.

DESCRIPTION. Fragmentary rhabdosome, almost 6 cm across, broadly flabellate, but possibly representing a segment of a flattened conical species like *Palaeodictyota anastomotica.* Proximal end of rhabdosome not present. Distal stipe width 0·4–0·5 mm; proximally anastomosis is so frequent that transverse stipe width varies rapidly between 0·5 and 1·0 mm over a few millimetres of the stipe. Distally there are 9–13 stipes in 10 mm, with an average of 11. In the proximal, anastomosing part of the rhabdosome width of stipes generally exceeds the width of the interspaces. These are themselves highly variable, ranging from small, circular openings 0·5–0·8 mm diameter, to large, irregular ellipses with long axes parallel to the direction of propagation of the stipes, length exceeding 2 mm, but width invariably less than 1 mm. Seventy per cent of the interspaces fall in the range of length 1·2–1·5 mm, width 0·5–0·6 mm.

The specimen is preserved with dorsal surface uppermost, so that details of thecal apertures are obscured. Such details of thecae that can be seen show that interchange of thecae does occur at the junction between stipes proximally, that individual autothecae have a diameter of about 0·1 mm, and that the stipes are composed of complex bundles of thecae running largely parallel to the direction of growth. One section of the distal part of the rhabdosome (Pl. 11, fig. 10) shows a more regular, reticulate mesh structure reminiscent of *Dictyonema*; the stipes here are less sinuous than those in other parts of the rhabdosome, 0·4–0·5 mm wide, and separated by interspaces of equal or slightly greater width. Furthermore, they appear to be connected by transverse 'dissepiments' at intervals of 1 mm or less. There are indications, however, that these dissepiments are, in fact, thecate, that is they are a special case of the kind of anastomosis that occurs elsewhere on the colony.

DISCUSSION. *Palaeodictyota* is recorded by Bulman (*in* Teichert 1970 : 43) as ranging from the Silurian to Devonian, this presumably excluding from the genus such Ordovician species as *P. raymondi* Ruedemann (1947 : 269; pl. 11, figs 21, 22; pl. 28, figs 10–17) and *P. succulenta* Ruedemann (1947 : 269–270; pl. 29, figs 1–7), the former because its slender stipes and regular anastomosis are more suggestive of *Desmograptus*, the latter because its broad stipes and sparse anastomosis makes its affinities problematic. If the assignment of the species from the Carmarthen Formation to *Palaeodictyota* is correct then it is by far the earliest known occurrence. Certainly it is in close agreement with the type species (Ringueberg 1888 : 131; Whitfield 1902 : 399; pl. 53; Ruedemann 1947 : pl. 29, fig. 16) in the irregular anastomosis of the stipes, although the elliptical interspaces on the type species are on average at least twice as long. The material at hand is not considered sufficient for the formal establishment of a new species. Although the anastomosing habit is comparable with that of *Desmograptus,* we have noted above that the type species of *Desmograptus* was probably derived from a *Callograptus.* The present species shows no indication of a *Callograptus* habit at the distal margin, this part of the rhabdosome either showing irregular bifurcation, or, over a restricted area, a *Dictyonema*-like habit. Derivation of *Palaeodictyota*-like rhabdosome characters is possible from the more robust, rooted species of *Dictyonema.*

Family **DICHOGRAPTIDAE** Lapworth 1897

Genus ***PHYLLOGRAPTUS*** Hall 1858

TYPE SPECIES. *Phyllograptus typus* Hall 1858.

Phyllograptus densus Törnquist 1879

(Fig. 12D)

DIAGNOSIS AND TYPE DATA. The diagnosis of Monsen (1937 : 206) is followed here. The type locality of Törnquist (1879 : 447–448) is the Lower Didymograptus Shales of Skattungbyn,

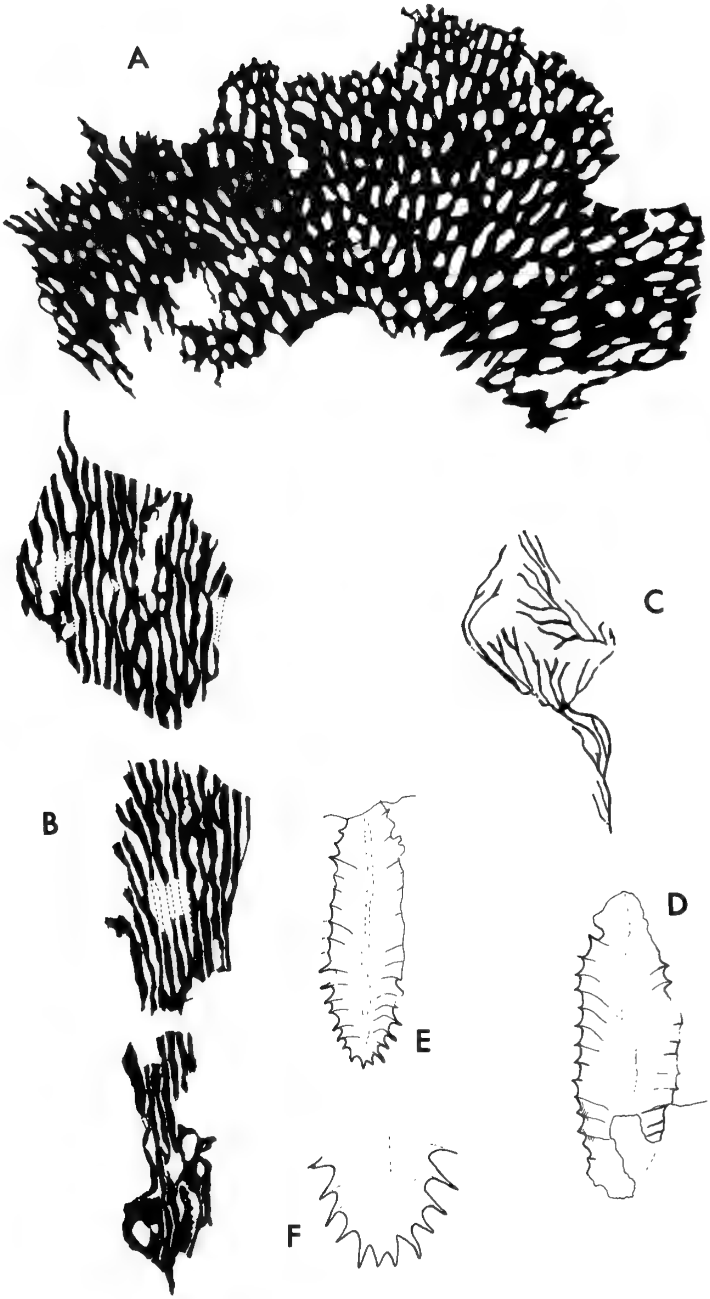

Fig. 12. Graptolites from the Carmarthen Formation. A, *Palaeodictyota* sp. Q5047, Cwm yr Abbey Member, × 2. B, *Callograptus* (*Pseudocallograptus*) *salteri*. Q5048, Cwm yr Abbey Member, × 2. C, *Callograptus* (*Callograptus*) cf. *tenuis*. Q5049, Cwm yr Abbey Member, × 2. D, *Phyllograptus densus*. GSM HT317, Pibwr Member, × 4. E, *Phyllograptus* aff. *angustifolius*. SM A67996, Pibwr Member, × 2. F, detail of previous specimen, proximal end, × 4. Compare size of thecal apertural lips with those of *P. densus* at same scale.

Dalarne, Sweden, but a lectotype has not yet been selected for the species. Material from the Carmarthen Formation is not an adequate basis for attempting revision of the species or its synonymy.

OCCURRENCE. Two specimens, GSM HT317–8, 319, from the lower part of the Pibwr Member at Glan Pibwr (loc. 1B).

DESCRIPTION. The two specimens are not well preserved, but are believed to be undistorted, like other material from the Pibwr locality, and for reasons discussed below. The smaller specimen is the better preserved, with a length of 1 cm, width of about 3·3 mm; the larger specimen has a length of about 2·7 cm, width of about 5·5 mm. The length and width of the whole rhabdosome is scarcely to be regarded as an important character, as both change during growth and the manner in which this happens has not been investigated; Törnquist (1904) states that specimens up to 5 cm long are known. On the larger specimen thecal spacing is 13 in 10 mm; on the smaller 16 corrected for 10 mm distally. Rhabdosomes are fusiform, with maximum width in the mid-region. Few thecal details are visible, except that the thecae are subparallel over the mid-part of the stipe, curved, proximal inclination about 30°–40°. The smaller specimen shows well that the apertures are barely concave and that the denticles are short – consistently 0·2 mm on this specimen.

DISCUSSION. The most complete accounts of this species are by Törnquist (1904 : 11–14) and Monsen (1937 : 206–208). Törnquist emphasized the variability of specimens he included within *P. densus*, and indicated that there was an intergradation with *P. angustifolius* Hall. A population from the type locality (Törnquist 1904 : 13) shows thecal spacing varying from 11 to 16 in 10 mm with 70% having either 14 or 15 per 10 mm. The range 11–13 per 10 mm is given for *P. angustifolius* from Quebec (Ruedemann 1947 : 315), although it is stated that the type horizon of this species at Point Levis, Quebec, is not known. Thus the smaller of the specimens from the Carmarthen Formation lies outside the range of variation (with regard to thecal spacing) of *P. angustifolius* and has the crowded thecae of *P. densus*. The same specimen also shows only slight concavity of the apertural thecal margins and short denticles, both deemed by Törnquist (1904 : 13–14) to be characteristic of the species. Since the second species of *Phyllograptus*, following, from Glan Pibwr, has deeply excavated apertures, it seems unlikely that the apertural appearance of the present specimens is due merely to preservation.

The question whether *P. densus* grades stratigraphically upwards into *P. angustifolius* can only be resolved by studying populations of both species in their type localities and adjacent strata. However, an *angustifolius*-like species occurs as a contemporary of *P. densus* in the Pibwr Member.

***Phyllograptus* aff. *angustifolius* Hall 1858**
(Fig. 12E, F)

DISCUSSION. A single specimen (SMA 67996) from the Pibwr Member (loc. 1B) is discussed here; it is obviously different from *P. densus*, having a thecal spacing of only 9–10 in 10 mm distally (up to 12 corrected for 10 mm proximally). Preservation is good, and there is evidence that distortion is not involved because a second fragmentary specimen lying at right angles to the specimen figured here also shows similar thecal spacing; any tectonic extension of the complete specimen would have resulted in crowding of the thecae of the other specimen.

The proximal end (Fig. 12F) shows a number of details, although flattened. The angle between the sicula and first theca is acute; neither show well-developed denticles. Subsequent thecae on the two series displayed have excavated apertures, and the ventral extension of the thecal apertures into lip-like denticles is unmistakeable; these are 0·5 mm long. Interthecal septa of the first three thecae on each series curve downwards distally; subsequently they curve from a proximal inclination of about 30°–40° to become more or less transverse. At the distal extremity of the rhabdosome the thecae are overall slightly upward-directed.

Both Holm (1895) and Bulman (1936) show the proximal end of *P. angustifolius* with sicula, downward-directed, flanked by th1^1 and th1^2, all three without apertural lips as prominent as those on subsequent thecae, and disposed more or less in line. Our material from the Carmarthen Formation shows evidence of only *two* such apertures at the proximal end, suggesting that its development was different from that of *P. angustifolius*, *sensu* Holm and Bulman. Here it should be noted that the Scandinavian *P. angustifolius* occurs in the high Arenig; the Welsh specimen is from the earlier part of the series. Holm (1895 : 345) gives the thecal spacing as 12–13 in 10 mm, greater than our specimen. In North America specimens identified with *P. angustifolius* are recorded in the early Arenig in several localities (Ruedemann 1947; Berry 1960 : 57). In Texas the species apparently does not extend upwards into beds of *hirundo* Zone age into which its range extends in Europe. Hall's original (1858) definition of *P. angustifolius* as having thecae 'about 24 to the inch', which indicates about 9 in 10 mm, agrees well with our specimen, but the exact horizon of Hall's type material is not yet determined. All this suggests that more than one species is involved in *P. angustifolius* as it has been understood, but the problems cannot be resolved without discussion of the type population. For these reasons we designate the Carmarthen Formation specimen with 'aff.', and recall Bulman's (1936 : 44) caution that *Phyllograptus* may have 'arisen from several different lines of descent'.

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A. H. Rankin

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With photographic contributions by

Frank Greenaway

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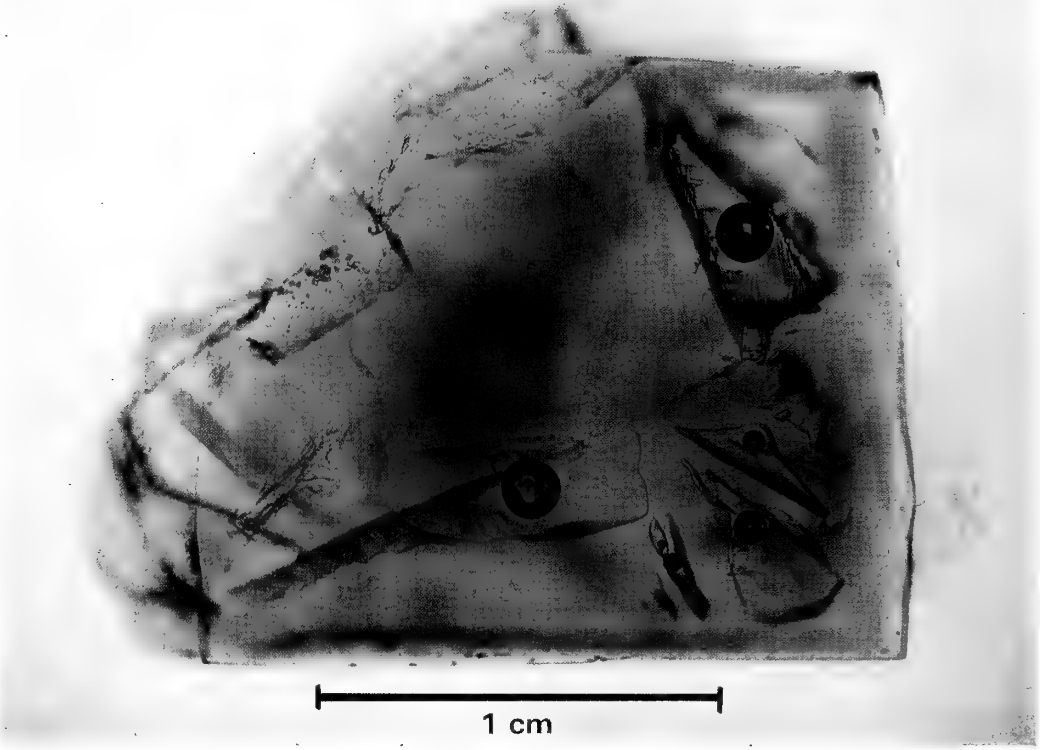

Frontispiece

Weardale fluorite containing a group of two phase (gas/liquid) macroscopic inclusions of fluid. BM 56271.

Macroscopic inclusions of fluid in British fluorites from the mineral collection of the British Museum (Natural History)

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Contents

Synopsis

Exceptionally large (macroscopic) fluid inclusions are present in 21 fluorite specimens from the mineral collection of the B.M.(N.H.). The maximum size of the inclusions, in three dimensions at right angles to one another, range from 1 × 1 × 2 to 24 × 17 × 4 mm. It is estimated that the largest cavity contains between 1 and 1·5 cm^3 of fluid. They are primary in origin, show no visible signs of leakage and, as such, are suitable for further work on the chemical composition of their contained fluids. Macroscopic inclusions (those whose maximum dimensions at right angles to one another exceed 1 mm) are restricted to fluorite from the Weardale area of the North Pennine orefield; they are absent in fluorite from other British localities.

Introduction

Crystal imperfections range from point defects on the atomic scale to gross defects, including twinning, on the macro scale (Bollman, 1970). To the crystal grower these imperfections cause endless obstacles in his efforts to grow near-perfect crystals (Egli & Johnson, 1961), but to the geologist, gross imperfections, in the form of occluded gases, liquids and solids in minerals, can provide a valuable key to his understanding of the physical and chemical conditions prevailing during the growth of rocks and minerals (Roedder, 1967).

For more than 150 years scientists have been intrigued by the existence of fluid-filled cavities (fluid inclusions) in natural crystals, but before the development of suitable high resolution optical microscopes studies were usually restricted to exceptionally large (> 0·5 cm) fluid inclusions in minerals (for example, Boyle, 1672; Davy, 1822; Hidden, 1882). In recent years, however, the

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majority of fluid inclusion studies* have been concerned with the more common microscopic (< 100 μm) cavities, and although these have contributed greatly to the formation of current ideas on the nature and gross composition of ancient mineral-forming fluids (Roedder, 1967 and 1972), they have failed to provide much in the way of useful quantitative information on the chemical composition of individual fluid inclusions. This is perhaps understandable when one considers that a spherical inclusion 100 μm in diameter contains no more than 5×10^{-5} cm^3 of fluid. The problems involved in the extraction and quantitative analysis of such minute quantities of fluid are, at present, almost insurmountable (it is possible, however, with ultra-sensitive, non-destructive, analytical techniques, such as neutron activation analysis, to obtain quantitative data on certain elements present in unopened inclusions, though serious problems of contamination from the host mineral are inherent in these methods).

The most obvious solution to these analytical problems is to sample exceptionally large (macroscopic) fluid inclusions which would provide a larger, more usable volume of fluid. With this object in mind the fluorite crystals in the mineral collection of the B.M.(N.H.) were examined. This paper will provide the results of the first part of this investigation, that is, a description of the size, distribution, abundance and physical characteristics of the most notable macroscopic inclusions. In addition, the origin and significance of such inclusions will be discussed. A second paper, to be published elsewhere, will provide chemical analysis of the fluid contained in certain of the fluorites described.

Before considering these inclusions, it is necessary to consider some of the more important general characteristics of fluid inclusions in minerals.

Fluid inclusions in minerals

Size and abundance

Fluid inclusions rarely exceed 1 mm in size (Roedder, 1967), and those whose contents are clearly visible to the unaided eye are exceptionally rare. Most are smaller than 100 μm and, according to Roedder (1967), could conceivably range in size down to the dimensions of single dislocations (2 Å).

Deicha (1976) refers to fluid inclusions as *macroscopic* if they exceed 1 mm in size, *microscopic* if they fall within the size range 1 mm to 1 μm and *nanoscopic* if they are less than 1 μm. This convention has been adopted in this paper.

The abundance of fluid inclusions depends to a large extent on the physical and chemical conditions prevailing during, and after, the growth of the host crystal, and on the size of the inclusions. To illustrate this latter point, let us assume fluid inclusions occupy 0·1% of the volume of a given crystal, and that these inclusions are cubic in shape. Table 1 shows the maximum number of inclusions of a particular size that can be accommodated per unit volume of a crystal. It is apparent that this number increases dramatically with decrease in inclusion size.

Table 1

Average inclusion size	Maximum number of inclusions per cubic centimetre occupying 0·1% of volume
1 mm	1
100 μm	10^3
10 μm	10^6
1 μm	10^9

Morphology and gross composition

Fluid inclusions exhibit a variety of different shapes. They may be *well-formed* with a regular 'negative crystal', tubular, ovoid or spheroidal morphology, or highly irregular with complex

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* For up-to-date information on the extensive literature on fluid inclusion the reader is referred to the yearly publication of abstracts, Proceedings of COFFI, Fluid inclusion research.

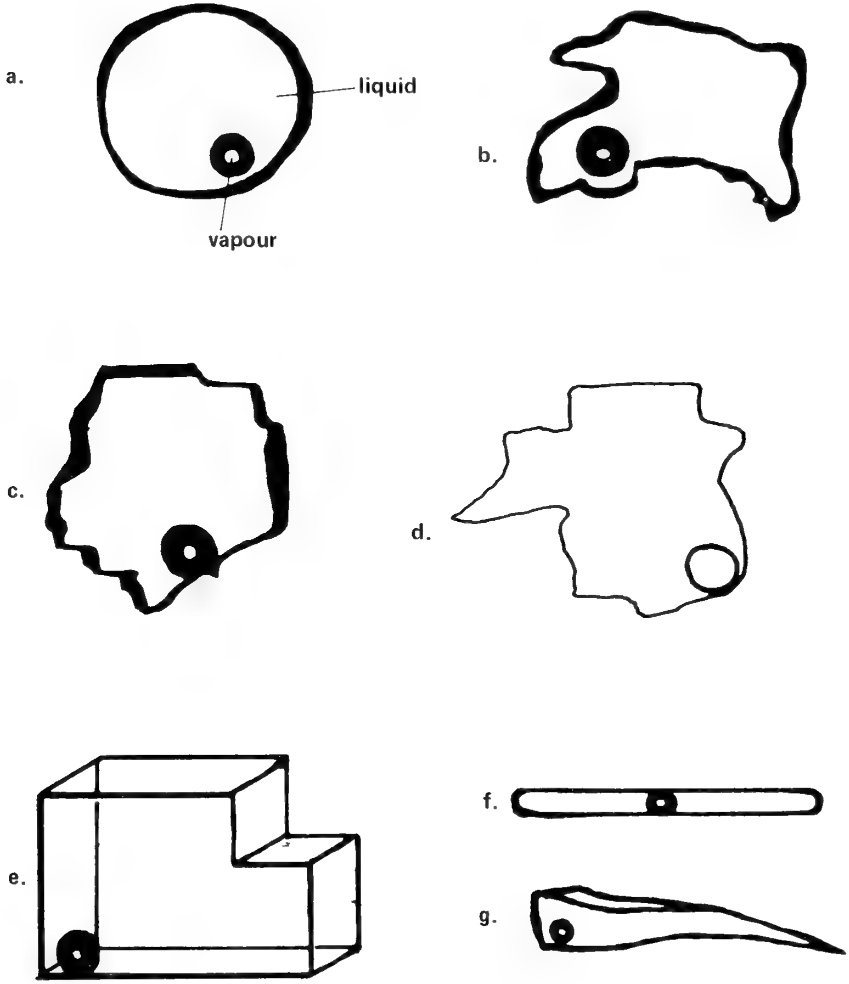

Fig. 1 Some common morphologies of fluid inclusions in fluorite. (a) Spheroidal; (b) irregular; (c) semi-regular, faceted; (d) flattened, irregular; (e) negative crystal (cubic); (f) tubular; (g) tapered. Note all inclusions are two-phase (vapour-liquid). The vapour bubble in (d) is flattened.

shapes. The different fluid inclusion morphologies most commonly encountered in fluorite are illustrated in Fig. 1.

At room temperatures most fluid inclusions in minerals formed by hydrothermal processes in the presence of homogeneous aqueous fluids contain a vapour bubble in addition to an aqueous brine (liquid phase). These bubbles generally owe their origin to the differential shrinkage of the contained fluid and host mineral during cooling from the higher temperature at which they were trapped (Fig. 2a); the coefficient of volumetric thermal expansion of minerals such as quartz and fluorite is exceedingly small in relation to that of the aqueous fluids. H. C. Sorby was one of the earliest mineralogists to recognize the significance of the vapour bubbles. He realized that by reheating the specimen and recording the temperature at which the liquid and vapour phases rehomogenized an estimate of the minimum formation temperature of the host mineral could be obtained. His comprehensive paper on the subject, published in 1858, laid the foundation for the now widely used method of fluid inclusion geothermometry.

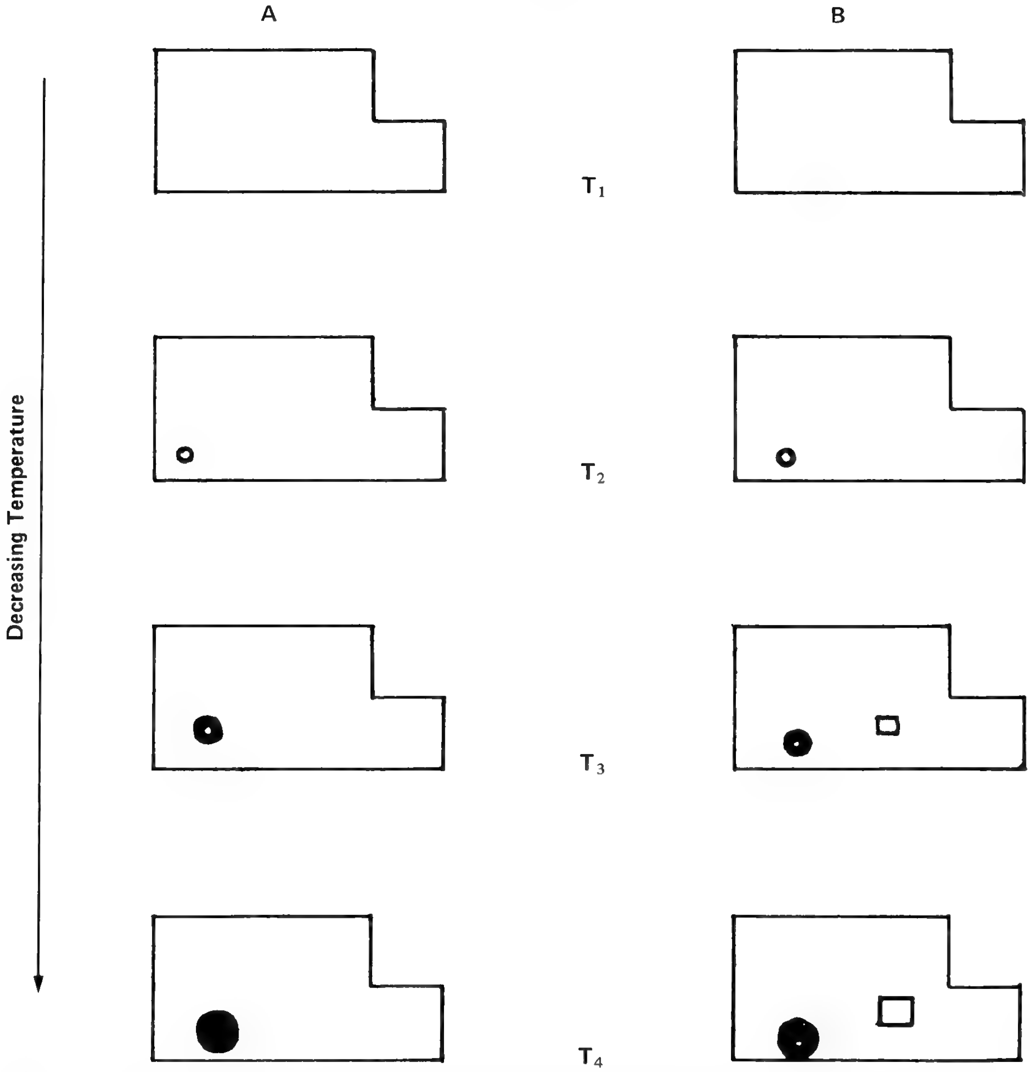

Fig. 2 Development of a contraction vapour bubble and a daughter mineral in fluid inclusions. As the inclusion cools from its temperature of trapping (T_1), a vapour bubble nucleates at temperature T_2 and continues to grow in size on cooling from T_2 to T_4 (room temperature). A small daughter phase also develops on cooling in the more saline brine contained in inclusion B. If inclusions A and B are reheated, their contents re-homogenize at temperatures slightly above T_2. This gives an estimate of the minimum formation temperature of the inclusion, and, if it is primary, of the host mineral, and forms the basis for fluid inclusion geothermometry.

Fluid inclusions trapped from high density, homogeneous, concentrated brines often contain *daughter minerals*. These are observed at room temperatures because the solubility of components in fluid inclusions, such as NaCl and KCl, decreases with temperature. As the trapped fluid cools from the temperature at which the inclusion formed, a point is reached at which the fluid becomes saturated with respect to these components, and crystalline phases begin to precipitate (Fig. 2B).

Some fluid inclusions contain liquid and vapour phases other than, or in addition to, aqueous

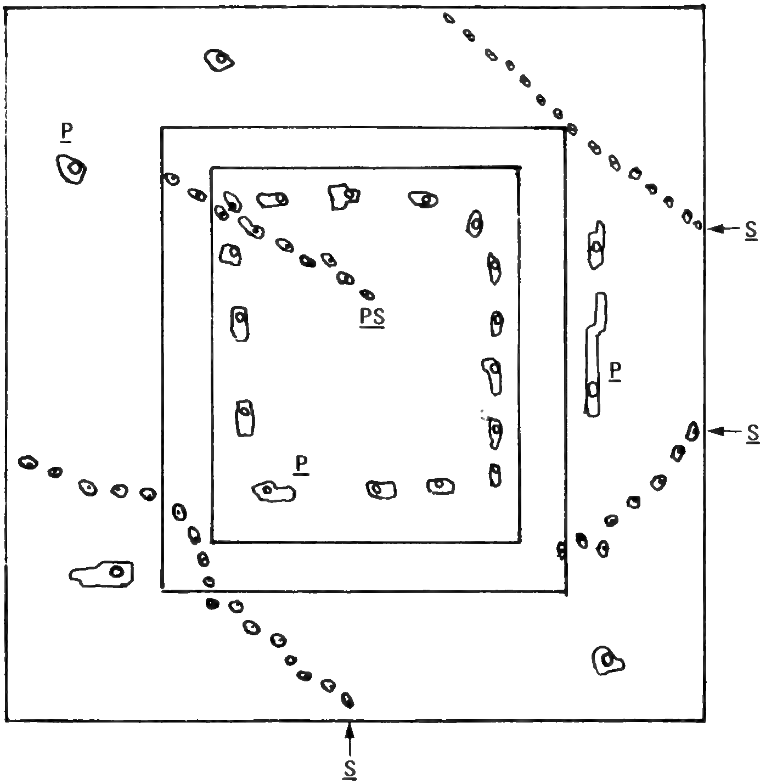

Fig. 3 Diagrammatic representation of the distribution of P, PS and S inclusions in a section through a cubic crystal of fluorite.
Secondary and pseudosecondary (S and PS) inclusions occur in planes which traverse growth zones. Primary (P) inclusions occur either as isolated cavities, unrelated to fractures, or in planes parallel to, and within, growth zones.

brines and water vapour. The most common is carbon dioxide, but hydrocarbons and hydrogen sulphide have also been reported (Roedder, 1972).

Origin

Three different genetic classes of fluid inclusions are generally recognized (Fig. 3). These are termed primary (P), secondary (S) and pseudosecondary (PS). Primary inclusions are those formed during the primary growth of a crystal. Secondary inclusions are formed after growth has terminated, usually as a result of healing of post-depositional fractures within a crystal. Pseudosecondary inclusions are those formed by healing of a fracture before primary growth has terminated. The common distribution of these three classes of inclusions is shown diagrammatically in Fig. 3. Plate 1 shows the cross-cutting relationship of different generations of microscopic inclusions in fluorite from Illinois. When studying samples containing an abundance of micro-inclusions it is often difficult to distinguish between these three different types of inclusions. Fortunately, it has been possible in this present study to classify with confidence all the macroscopic inclusions.

Leakage and 'necking down'

It is generally assumed that the composition of primary fluid inclusions approximates in composition to that of the fluid from which the host mineral crystallized, provided that fluid has not

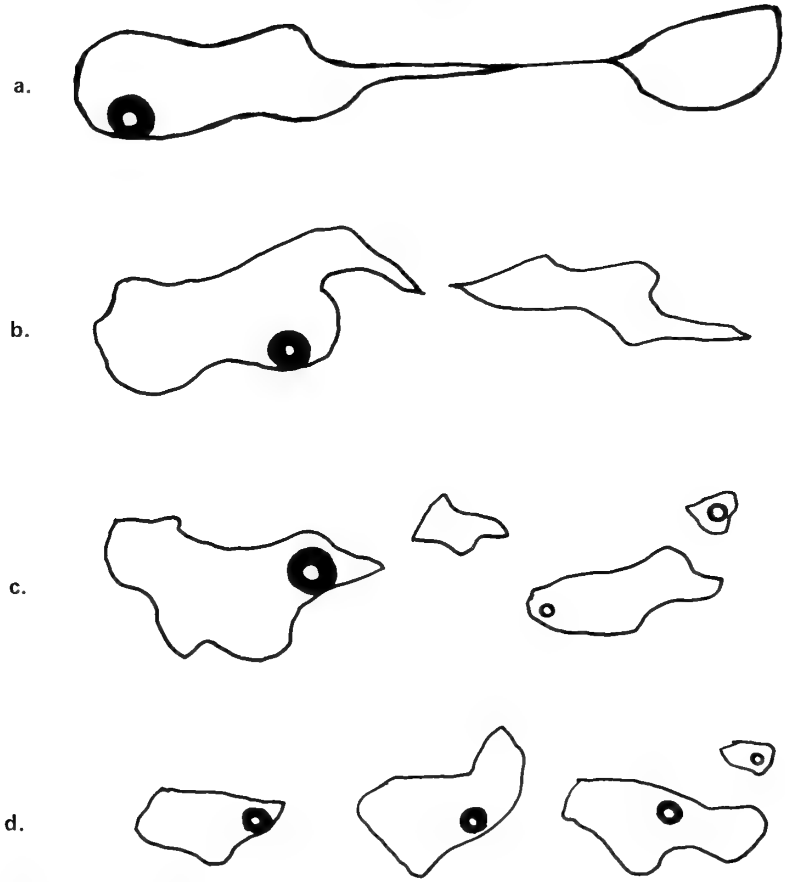

Fig. 4 'Necking down' of fluid inclusions.
(a) Partial 'necking down'. Two portions of the inclusion (one with a vapour bubble) are connected by a thin tube of fluid. (b) Completely necked inclusions. One portion contains a vapour bubble, the other does not (complete necking down has taken place below the temperature of formation of the inclusion). (c) Several 'necked down' inclusions. The vapour bubbles occupy different volumetric proportions of each of the cavities. (Necking down has taken place at different temperatures.) (d) Several 'necked down' inclusions. The vapour bubbles occupy the same volumetric proportion of each of the cavities. (Necking down has taken place at approximately the same temperature.)

subsequently leaked into or out from the inclusion. Roedder (1967) has dealt fully with this subject, and points out that there is indisputable evidence that some inclusions have leaked and that others have remained sealed. It is usually possible to recognize inclusions which have leaked, but difficult to judge whether partial leakage has occurred.

Roedder (1967) has also described the common phenomenon, referred to as 'necking down', whereby larger, irregular inclusions tend to split up into a series of smaller, more regular portions. This, however, makes little difference to the composition of the fluid, but can markedly affect the results of homogenization temperature determinations (Fig. 4).

Macroscopic fluid inclusions in fluorite

All available British fluorite samples in the collection were examined with the naked eye for the presence of macroscopic fluid cavities. Inclusions smaller than 1 mm in less than three directions, at right angles to one another, were not considered. A hand lens and binocular microscope were used to determine the size, shape and contents of the inclusions.

The major deficiency of this procedure is that only clear, light-coloured fluorites could be studied; translucent or deeply coloured specimens could not be examined (at least, without immersing them in a liquid of suitable refractive index, such as kerosene). It is also possible that macroscopic inclusions deep within large crystals were not detected. However, these are likely to be relatively small (1–4 mm). There are also other specimens with fluorite as an accessory mineral. These could not be considered in the time available. Only those specimens catalogued as fluorite were studied.

Macroscopic inclusions were located in 21 fluorite samples. Nine of these specimens are in the Russell collection (Table 2) and 12 in the main collection (Table 3). All of these fluorites are from the North Pennine orefield, more specifically, with the possible exception of specimen BM 88944, Weardale. The significance of this observation will be discussed in the following section.

Table 2 British fluorite specimens from the Russell Collection containing macroscopic fluid inclusions

Sample Number*	Locality given on specimen label	Description (and approximate size of crystal containing the macroinclusions)
1414	Bolt's Burn mine, Weardale	Purple green cube (4–5 cm^3) intergrown with several smaller crystals
1443	Bolt's Burn mine, Weardale	Green, twinned cube (2·5 cm^3) intergrown with several other similarly sized crystals
1534a	Height's mine, Weardale	Green, twinned cube (3·5 cm^3)
1538	Weardale	Green, twinned cube (1·5 cm^3)
1539	White's level, Westgate, Weardale	Green twinned, cube (2·5 cm^3)
1540	White's level, Westgate, Weardale	Green, twinned cube (2 cm^3)
1541	Weardale	Green, twinned cube (1·5 cm^3)
1542	Weardale	Green, twinned cube (1·5 cm^3)
1559	Burtree pasture mine, Weardale	Purple, twinned cube (3·5 cm^3)

* All numbers are prefixed by BM 1964R.

Table 3 British fluorites from the main collection containing macroscopic fluid inclusions

Sample Number	Locality given on specimen label	Description (and approximate size of crystal containing the macroinclusions)
BM 1907, 433	Bolt's Burn mine, Weardale	Purple, twinned cube (3·5 cm^3)
BM 33216	Weardale	Green, twinned cube (3 cm^3)
BM 40238	Weardale	Green, twinned cube (2·5 cm^3)
BM 46482	Weardale	Green, twinned cube (2 cm^3)
BM 56268	Height's mine, Weardale	Green, twinned crystal (2 cm^3) intergrown with several smaller crystals
BM 56269	Weardale	Green, twinned cube (2 cm^3)
BM 56270	Weardale	Green, twinned cube (2 cm^3)
BM 56271	Weardale	Green, twinned cube (2 cm^3)
BM 56313	Weardale	Green, twinned cube (2 cm^3)
BM 69124	Weardale	Pale purple, twinned cube (2 cm^3)
BM 88944[1]	Alston or Weardale	Pale yellow, twinned cube (2 cm^3)
	Height's mine, Weardale[2]	Green, twinned cube (1·5 cm^3)

[1] Locality of the specimen was originally given as Alston, but later changed to Weardale (?).

[2] This specimen is a duplicate and has not been assigned a B.M. number,

The number and size of the inclusions in each of the samples is given in Tables 4 and 5. Size refers to the three maximum dimensions of the cavity, at right angles to one another. The maximum number of macroscopic inclusions seen in any one crystal is seven (BM 56271). Most commonly, however, individual crystals contain only one such inclusion. The largest inclusion (in

Table 4 Number and size of macroscopic fluid inclusions in fluorites from the Russell Collection

Sample Number BM 1964R	Number of inclusions	Approximate dimensions (mm)	Comments
1414	1	7 × 2 × 2	Note 1
1443	1	24 × 17 × 4	Note 2
1534a	2	3 × 2 × 2 3 × 2 × 2	Note 3
1538	1	5 × 2 × 2	Note 4
1539	1	4 × 2 × 1	Note 3
1540	1	7 × 4 × 2	Note 5
1541	1	8 × 3 × 2	Plate 4A
1542	1	10 × 4 × 2	Plate 4B
1559	1	7 × 3 × 2	Plate 5B

Notes
1. Microscopic inclusions have necked-down from this inclusion.
2. Inclusion is flattened parallel to the uppermost cube face of the crystal.
3. Internal fractures are common but do not traverse the inclusion.
4. Inclusion roughly elongate parallel to one of the cube crystal faces.
5. Inclusion walls show stepped growth.

Table 5 Number and size of macroscopic fluid inclusions in fluorite from the main collection

Sample Number BM	Number of inclusions	Approximate dimensions (mm)	Comments
1907,433	1	4 × 3 × 3	Plate 3, note 1
33216	4	(a) 6 × 4 × 2, (b) 4 × 3 × 2 (c) 3 × 1 × 1, (d) 4 × 3 × 3	Note 2
40238	3	(a) 5 × 2 × 1, (b) 2 × 1 × 1 (c) 3 × 3 × 1	Plate 6B
46482	1	(a) 4 × 1 × 1	Plate 6A
56268	5	(a) 5 × 2 × 1, (b) 5 × 1 × 1 (c) 3 × 2 × 1, (d) 3 × 2 × 1 (e) 3 × 1 × 1	Note 3
56269	3	(a) 11 × 6 × 4, (b) 6 × 3 × 2 (c) 4 × 2 × 1	Plate 7
56270	1	14 × 6 × 5	Plate 8
56271	7	(a) 12 × 3 × 2, (b) 6 × 5 × 3 (c) 2 × 2 × 2, (d) 3 × 3 × 1 (e) 4 × 3 × 1, (f) 4 × 2 × 1 (g) 2 × 1 × 1	Plate 9, note 4
56313	2	(a) 8 × 3 × 2, (b) 2 × 1 × 1	Plate 2, note 5
69124	1	13 × 5 × 4	Plate 5B
88944	1	4 × 1 × 0·5	Note 6
Duplicate	1	3 × 2 × 2	Note 7

Notes
1. Dimensions refer to the equant portion only.
2. Inclusions a, b, c occur in the larger of the two cubes comprising the twin. Inclusion d is in the smaller cube.
3. The inclusions occur in a planar grouping parallel to one cube face.
4. Several smaller (0·5 to 1 mm) inclusions are also present.
5. Several other smaller, tubular inclusions are present. Their length is 1 to 2 mm and width less than 0·5 mm.
6. One smaller inclusion has necked down from this larger cavity.
7. Small monophase liquid inclusions have necked from the macroscopic inclusion.

sample 1443, Russell collection) has a maximum dimension of 2·4 cm, and occupies between 5 and 10% of the total volume of the host crystal. It contains between 1 and 1·5 cm^3 of fluid.

Most of the inclusions possess complex, irregular morphologies which can be only be described as amoeboid; many are roughly elongate or flattened parallel to the external cube faces of the crystal. In no instance can the inclusions be described as roughly equant or true negative crystals. In detail, parts of the cavity walls are aligned with distinct crystallographic directions within the crystal; most commonly the cube directions {100}, {010}, {001}, less commonly the octahedral directions, $\{111\}$, $\{11\bar{1}\}$, $\{\bar{1}11\}$, $\{1\bar{1}1\}$. The larger inclusion in sample BM 56271 (Plate 9) exemplifies this tendency towards shapes governed by crystallographic directions.

All the inclusions contain a mobile vapour bubble in addition to the aqueous fluid. This occupies less than about 10% of the total volume of the cavity, but, because of the irregular shape of the inclusions, it is not possible to give a more precise estimate. The diameter of the vapour bubble is 3·5 mm in the largest inclusion (1443, Russell). Whether the bubbles are composed entirely of water vapour is not yet known. Two inclusions from different samples (BM56269 and BM 56270) contain a mass of small, unidentified crystals (Plates 7 & 8). These crystals are probably a captured phase and not true daughter minerals.

Without exception the inclusions are believed to be primary in origin, because:

(i) they are large in relation to the size of the host crystal;
(ii) they are commonly aligned roughly parallel to external faces of the host crystal;
(iii) when coloured growth zones are present the inclusions occur within a particular growth zone and do not extend into other growth zones.

In some samples, microscopic inclusions are closely associated with the macroscopic inclusions. Usually it is possible to demonstrate (Plates 3, 7 & 8) that these represent necked-down portions of the larger cavity.

Obvious signs of leakage of the contents of the macroscopic inclusions, such as an anomalously large vapour bubble, or the presence of small fractures leading from the inclusion to the crystal surface are, with one exception (BM 56270), absent. In this specimen (Plate 8) a fracture, now healed, traverses the inclusion, but, instead of leading to the crystal's surface, terminates abruptly at the outer colour growth zone. Evidently, fracturing took place after growth of the central portion of the crystal containing the inclusion, but before the growth of the outermost portion. Because leakage took place before primary growth had ceased, the inclusion contents are still primary at least with respect to the outer crystal zone.

Discussion

This study has shown that all the macroscopic fluid inclusions are suitable for chemical analysis, because they are primary in origin and do not appear to have leaked. Their characteristics are no different from the more common microscopic inclusions apart from their unusually large size.

With the possible exception of one sample (BM 88944), all the fluorites containing macroscopic inclusions (as defined) are confined to the Weardale area of the Northern Pennine orefield. It might be thought that the vast majority of fluorites in the collection are from this area. It can be seen, however (Table 6), that although just under one half of the Russell collection, and approximately one quarter of the main collection fluorites are from Weardale, a large number of fluorites from other localities, all apparently devoid of macroscopic fluid inclusions, constitute the main part of these collections. Two alternative explanations can be proposed:

1. Because they commonly occur as large (>2 cm) transparent crystals with well-developed crystal faces, Weardale fluorites are more amenable to the methods of study used than less perfect fluorites from other localities. (Considered least likely.)
2. Growth conditions were more favourable to the formation of large inclusions at Weardale than at other localities in the British Isles. (Considered most likely.)

Roedder (1967), and more recently Deicha (1975), have summarized the factors governing the formation of primary fluid inclusions in minerals. These are complex and varied, but perhaps the simplest explanation is that inclusions form when growth rates are relatively fast (in other words, the degree of supersaturation in the mother liquor is high) (Pamplin, 1975). In essence,

Table 6 Geographical distribution of fluorite samples from the British Isles in the Mineral Collection of the B.M.(N.H.)

	Number of samples (figures rounded to the nearest 5)	
Location	Russell collection	Main collection
Northern England*	490	280
(Weardale localities)	(475)	(160)
Rest of England	470	440
Wales	30	5
Scotland	65	5
Ireland	130	5
Total	**1185**	**635**

* The old counties of Westmorland, Northumberland and Cumberland (now Cumbria) and Durham.

the degree of supersaturation of the solution close to the face of a crystal is lower than at the edges. Edges grow faster than the centre which leads to a depression at the face centre. Covering of the surface during a period of slower growth (lower supersaturations), when growth rates decrease below a critical value, will form an inclusion of mother liquor (see, for example, Denbigh & White, 1966; Belyustin & Fridman, 1968; Brooks et al., 1968; Wilcox, 1968; Petrov et al., 1969). If the degree of supersaturation is very high, the growth rate is also very high and the crystals grow as dendrites.

To produce macroscopic inclusions of fluid it is necessary, therefore, to sustain a uniformly higher degree of supersaturation at the edges of a growing crystal than at the centres of its faces for a prolonged period of time. This can be achieved if material is continually being supplied to the growing crystal by mass flow of fluid as opposed to diffusion (see Roedder, 1967, for discussion). Unfortunately, it is not possible to assess whether the degree of supersaturation of fluid was locally maintained at a higher level for a longer period of time in the Weardale area during the formation of fluorite than at any other British fluorite locality, and this contention must remain speculative. It can be said, however, that mass movement of fluid was indeed important in the formation of the North Pennine fluorite deposits (Smith & Phillips, 1975) and that locally the vertical flow velocity was between 0·5 and 1·0 cm s^{-1} (op. cit.).

Acknowledgements

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Appendix

Photographic procedure

The essential requirements of this study were to obtain clarity of image of the fluid inclusions, which were located at various depths within the fluorite crystals, while retaining, in most instances, some indication of the external morphology. In addition, it was important that colour banding (or zonation) and growth zonation should be rendered as accurately as possible.

Following a suggestion by P. G. Embrey, it was decided to immerse the crystals in a liquid of nearly identical refractive index to the fluorite. Odourless kerosene was used for this purpose. This was contained in a specially constructed 'box' made from transparent optical glass flats.

A vertically mounted monorail, 5 × 7 inch format camera, equipped with Leitz 120, 80, 40 and 20 mm lenses, was used to obtain maximum definition (a smaller format could have been used with little loss of detail). The specimen container was held in, or near, the focus of a pair of glass condenser lenses, selected to match the camera lens in use. An aluminized plane mirror was placed below the condensers at 45° to the camera lens axis, and with the light source at 45° to this (normal to the lens axis). Illumination for focusing was provided by a 600 W quartz halogen source, which was part of the 1400 W electronic flash spotlight used to expose the Agfa half-plate transparency film. This source has a fairly high ultraviolet component, but the glass fresnel lens in the spotlight and various glass surfaces interposed between it and the fluorite crystals successfully prevented unwanted fluorescence.

The kerosene immersion liquid rendered even crystals with surface imperfections (crazed and/or overgrown) transparent; indeed, crystals which, in air, were deeply coloured and translucent, became thoroughly transparent. Its use also resulted in a greatly increased depth of field (the depth of focus was controlled by the selection of the required aperture followed by adjustment of the light reaching the film with neutral filters). The enhanced transparency had one disadvantage, in that crystal boundaries tended to merge with the background. In extreme cases this was overcome by using conventional dark field illumination.

Finally, colour fidelity and consistency were achieved by colour matching the background areas of the transparencies and by visual comparison with the immersed specimens. These colours are visually true. However, it will be understood that they are somewhat different from the colours of the crystals, out of the immersion liquid, in air.

Plate 1

A. Cross-cutting planes of secondary inclusions (the two planes are arrowed) in an octahedral cleavage fragment. Individual inclusions are less than 100 µm. (Photograph taken with oblique illumination.) BM 1931,472. Spar Mountain mine, Hardin Co., Illinois, U.S.A.

B. Planes of microscopic primary inclusions, parallel to the purple colour growth band {100}, cut by later generations of secondary and pseudosecondary inclusions (one of these later planes is shown by the arrow). (Photograph taken in oblique illumination.) BM 1931,469. Spar Mountain mine, Hardin Co., Illinois, U.S.A.

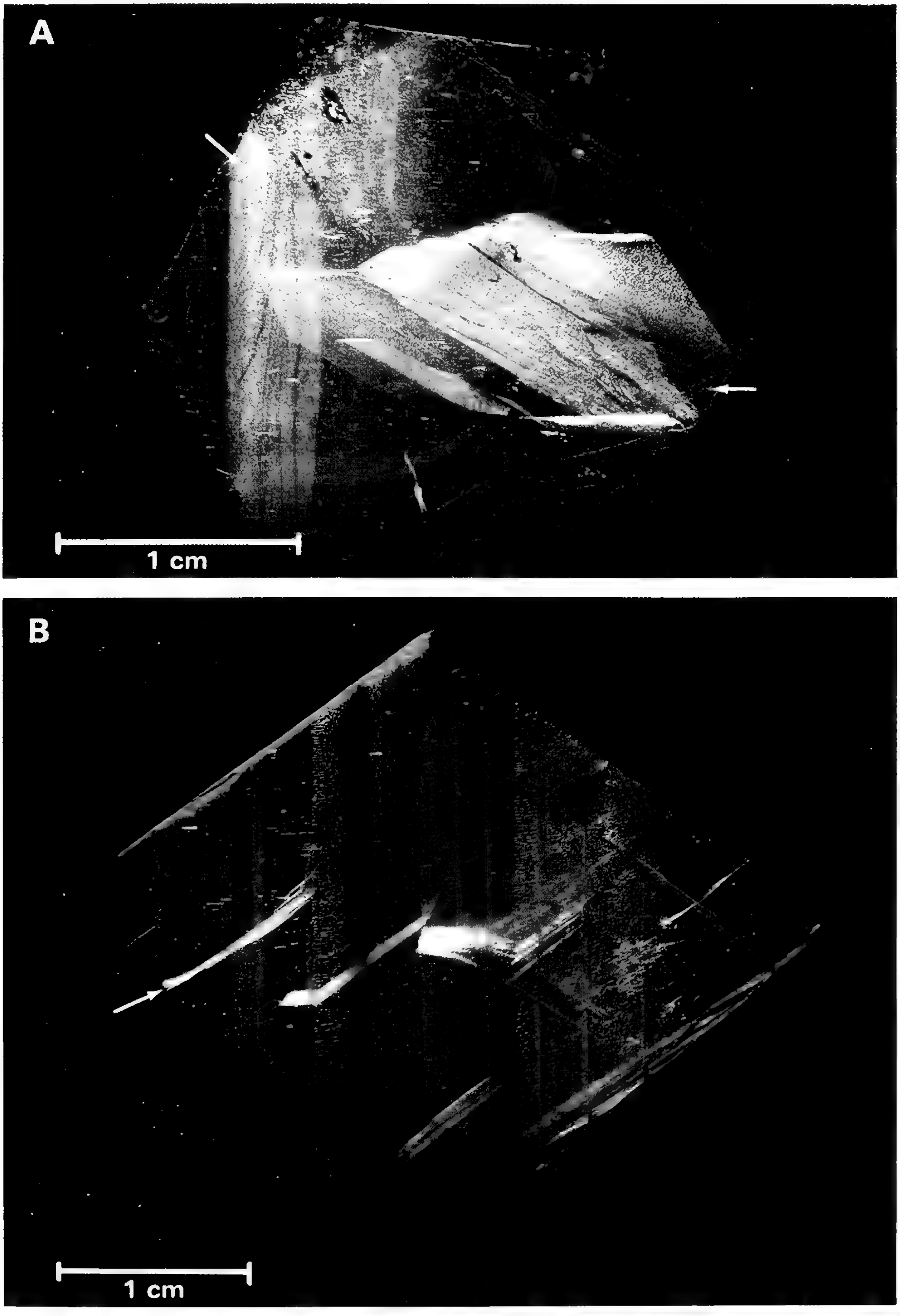


Plate 1

Plate 2

A. BM 56313. Planar group of one large and several smaller inclusions parallel to, and only about 1 mm from, one of the cube faces of the host crystal. (Photograph taken with oblique illumination.)

B. BM 56313. Close-up of a portion of A above showing the main group of inclusions. (Photograph taken with oblique illumination.)

C. BM 56313. As B above, showing details of the inclusions when viewed in a different orientation, and in transmitted light.

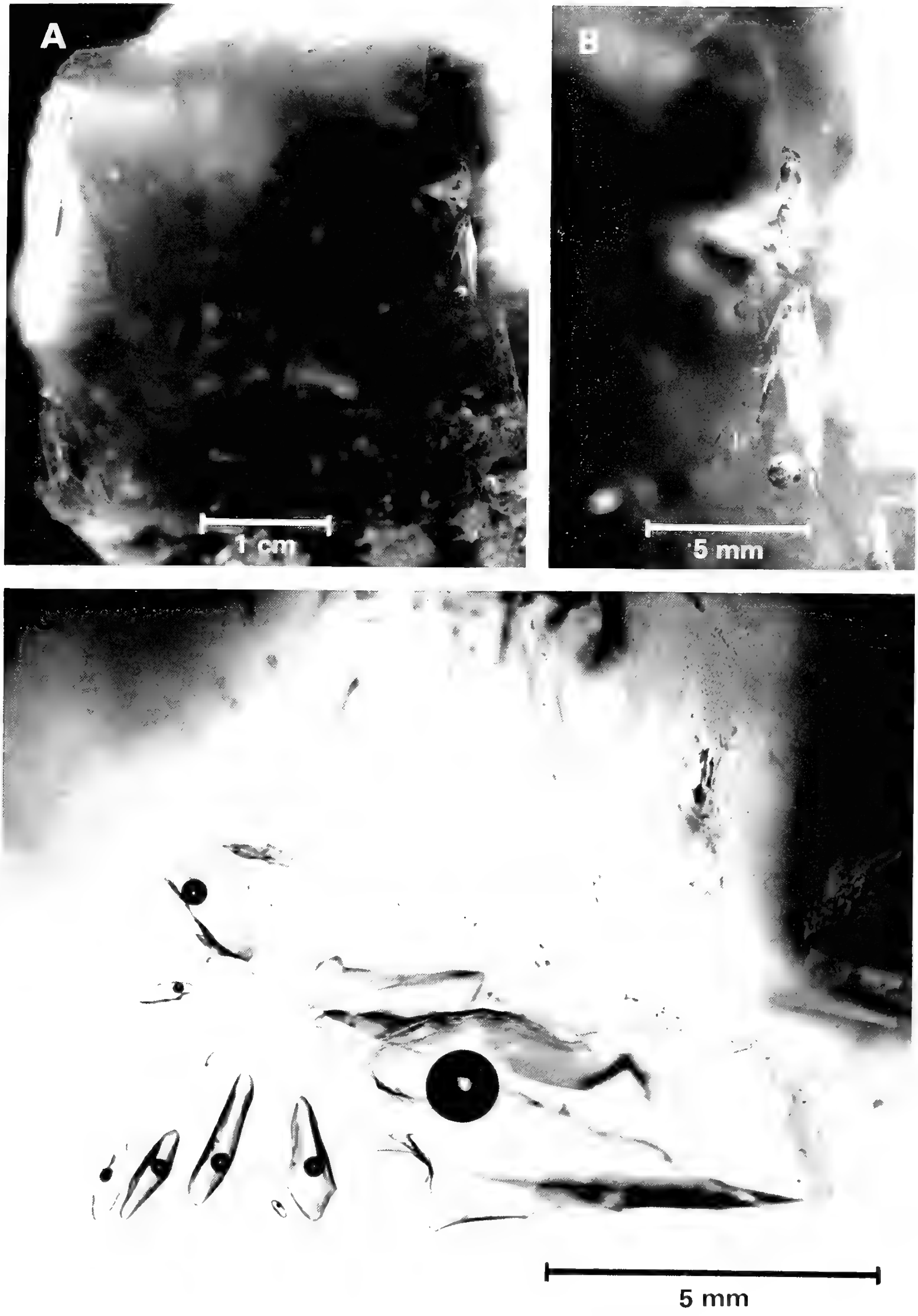


Plate 2

Plate 3

A. BM 1907,433. Complex shaped, two-phase (liquid plus vapour) macroscopic inclusion in well-formed cubic crystal. Although located less than 2 mm from the surface of the crystal, leakage does not appear to have taken place.

B. BM 1907,433. Close-up of A above. The central, well-faceted equant portion of the cavity, which contains the vapour bubble, is connected to a much flatter (0·1 mm in width), more irregular portion. A train of smaller, monophase liquid inclusions (arrowed) have necked down from this larger cavity. Some of the walls of the equant portion of the cavity are parallel to cubic {100} crystallographic directions, others to octahedral {111} directions.

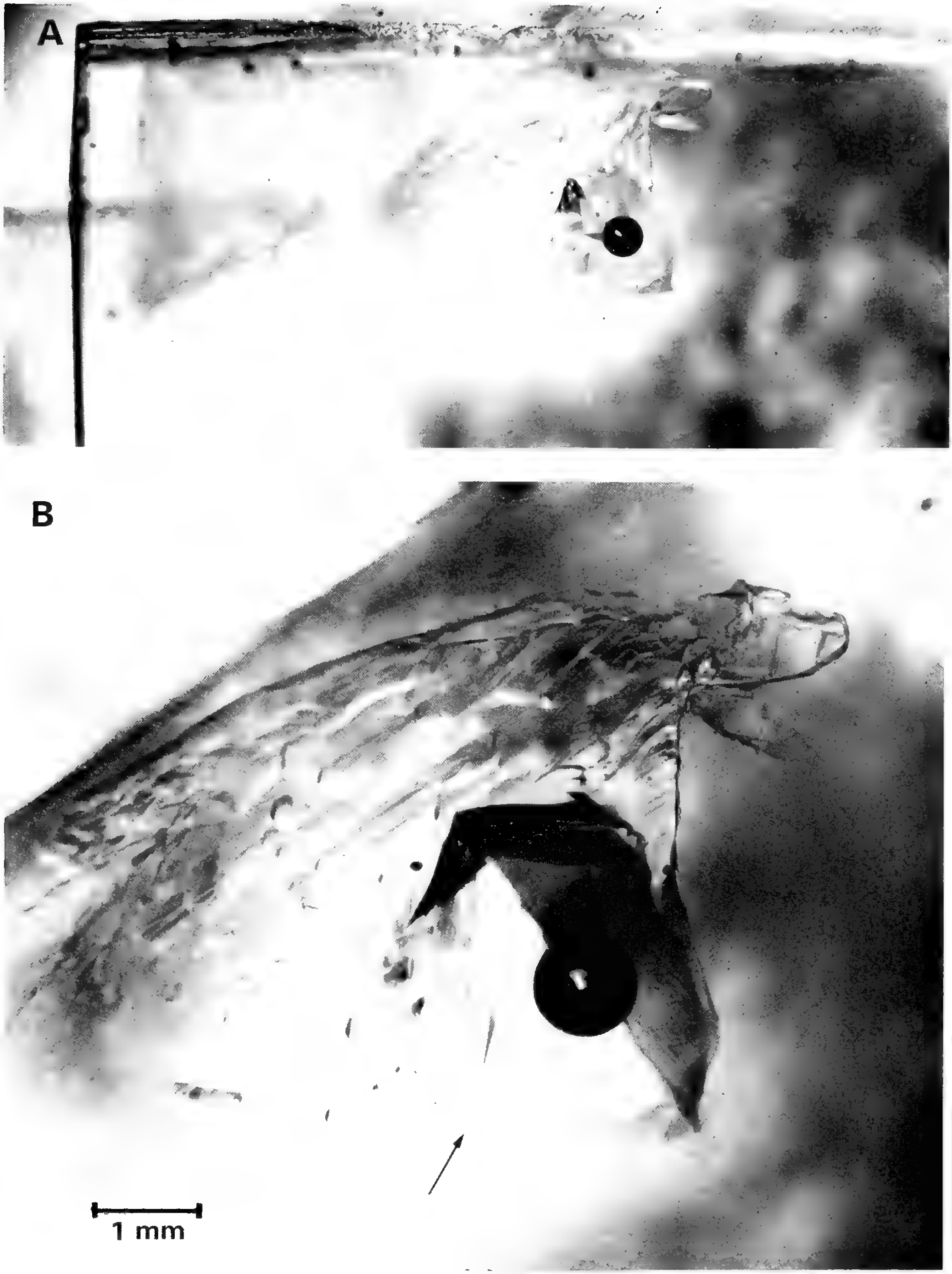


Plate 3

Plate 4

A. BM 1964R,1541. This unusually shaped inclusion is located in the central portion of the zoned crystal. Note how the red-coloured zone 'bends' to accommodate the inclusion. The shape of the cavity is unusual because it is reminiscent of a butterfly with closed wings; the elongate, regularly shaped portion containing the bubble corresponds to the body, and the upper, flat, irregular portion corresponds to the wings.

B. BM 1942,1542. One macroscopic and three smaller inclusions are present. Note the weak colour zonation parallel to the faces of the smaller penetration twin crystal, and the way in which one of the edges of the inclusion is parallel to these growth zones.

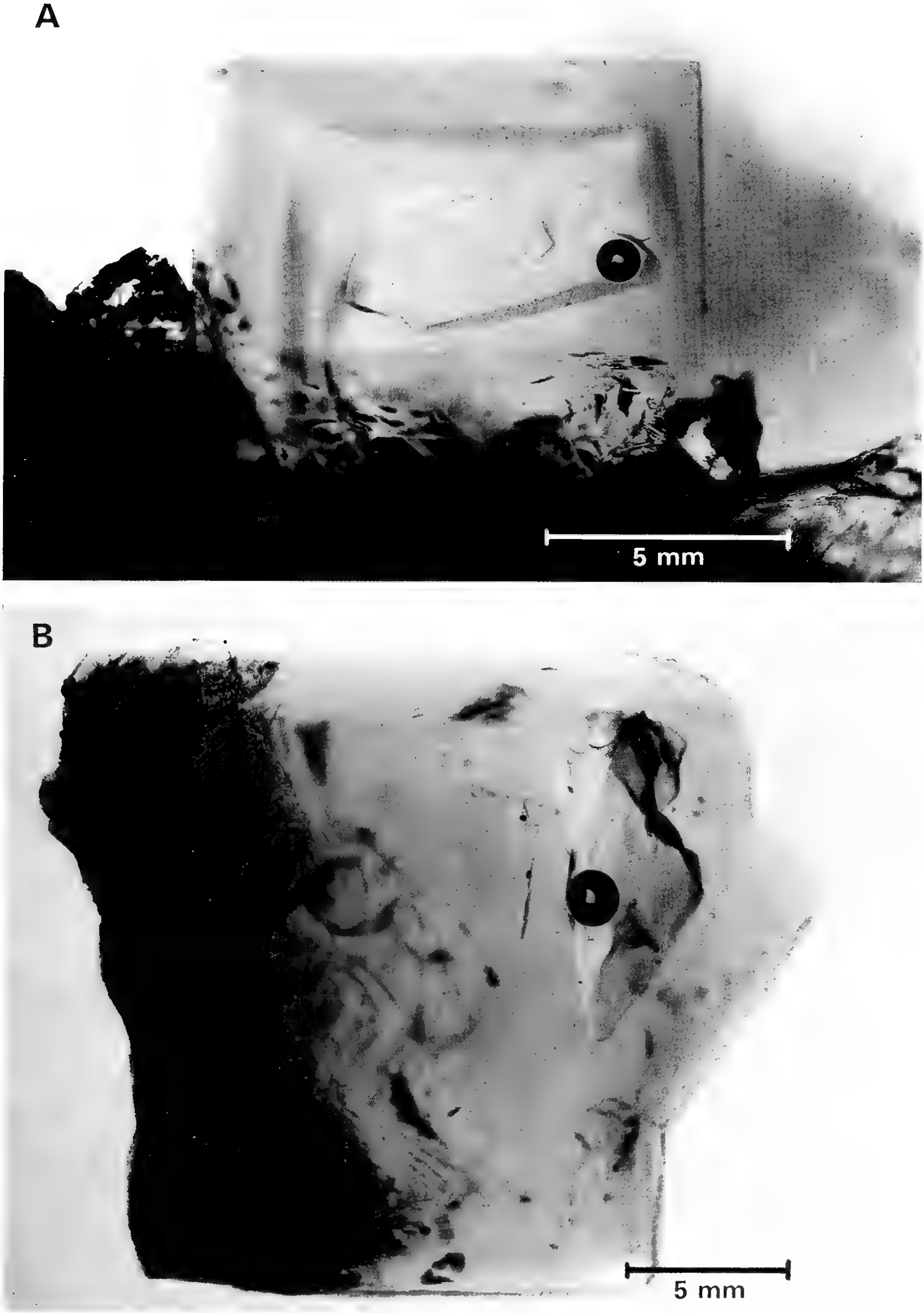


Plate 4

Plate 5

A. BM 1964R,1559. The large inclusion is located in a clear portion of this colour-zoned crystal. The inclusion is elongate in the plane of the paper. The small elongate feature apparently within the inclusion is actually a portion of the inclusion itself extending below the lower wall of the cavity.

B. BM 69124. Purple-zoned crystal (with quartz overgrowth) containing a macroscopic, elongate inclusion parallel to the right-hand cube face of the crystal.

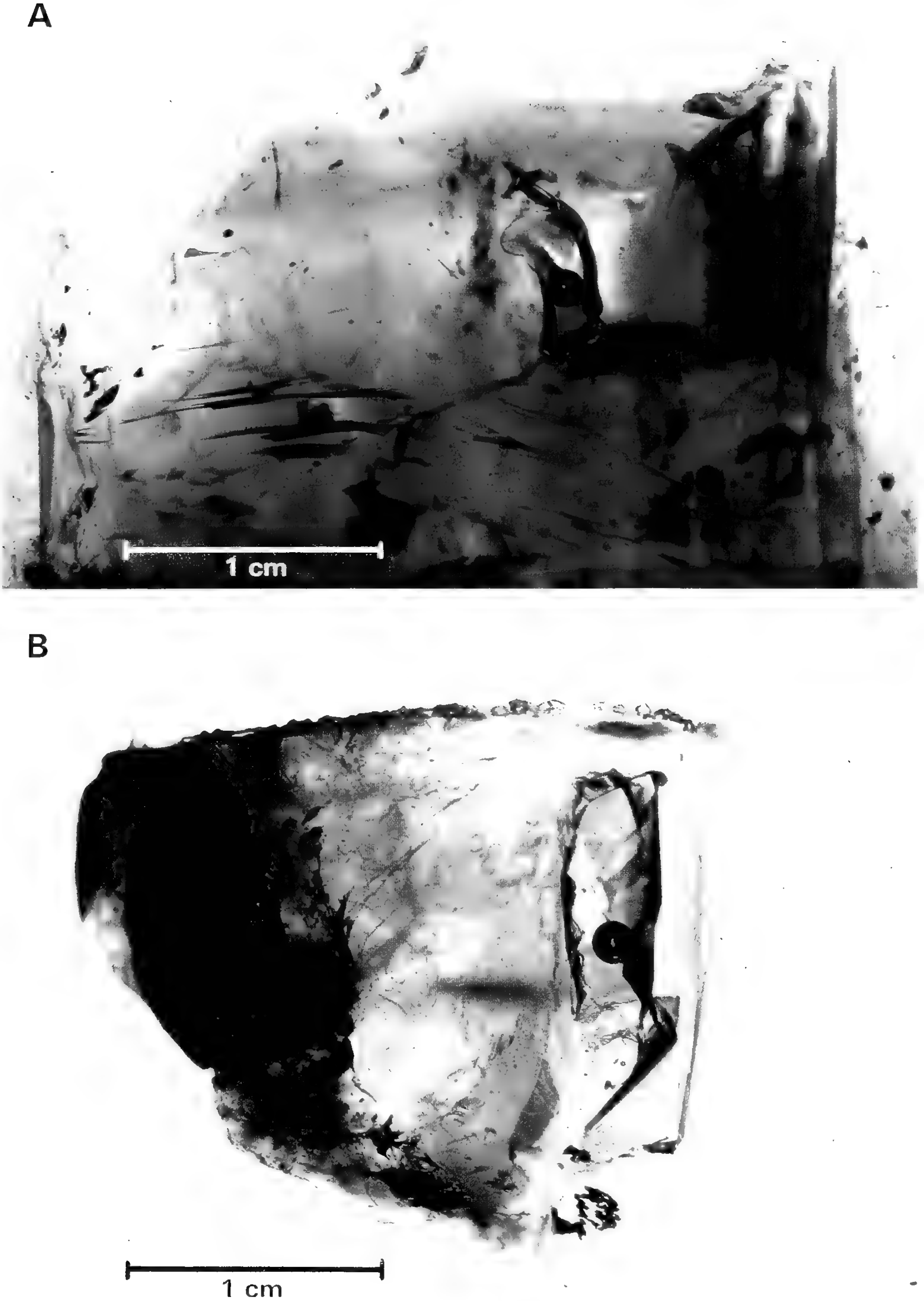


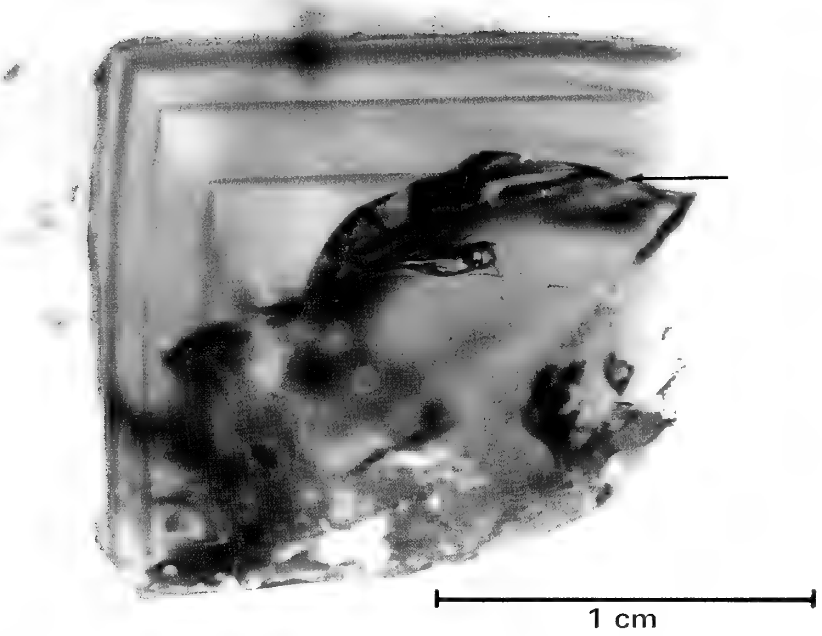
Plate 5

Plate 6

A. BM 46482. The complexly shaped macroscopic inclusion is contained within the clear, innermost zone of the fluorite. A healed fracture, which under the microscope is seen to consist of numerous secondary microscopic aqueous inclusions, is also apparent (arrowed).

B. BM 40238. A group of three irregularly shaped macroscopic inclusions occurs in the centre of the fluorite crystal. The largest inclusion appears to contain two vapour bubbles, but the smaller bubble belongs to the third inclusion.

A



B

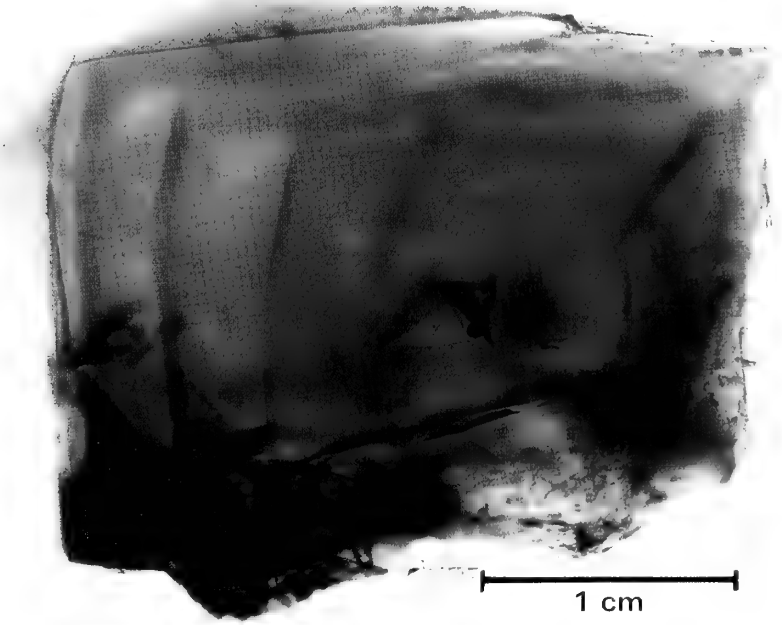


Plate 6

Plate 7

A. BM 56269. Three macroscopic and several smaller inclusions are present. The largest, whose outline is partly obscured by shadows, contains a number of crystalline phases in addition to liquid and vapour. A thin, tubular, 'necked down' portion of this inclusion is shown by the arrow. The other two macroscopic inclusions are aligned roughly parallel to the right hand cube face of the fluorite.

B. BM 56269. Close-up of the crystals contained in the larger inclusion in A (above) viewed in approximately the same orientation. These tiny crystals adhere to the walls of the inclusion and are probably a captured mineral phase or phases. At first they were identified as quartz but in view of the form and habit of many of the crystals, this is probably not the case. Some of them resemble quartz, others an unusual habit of fluorite. However, it has not proved possible to identify them from their morphology alone. The walls of the cavity and its necked down portions (arrowed) are composed of a series of intricate 'steps'. The sides of these steps are parallel to the external cube faces of the host fluorite.

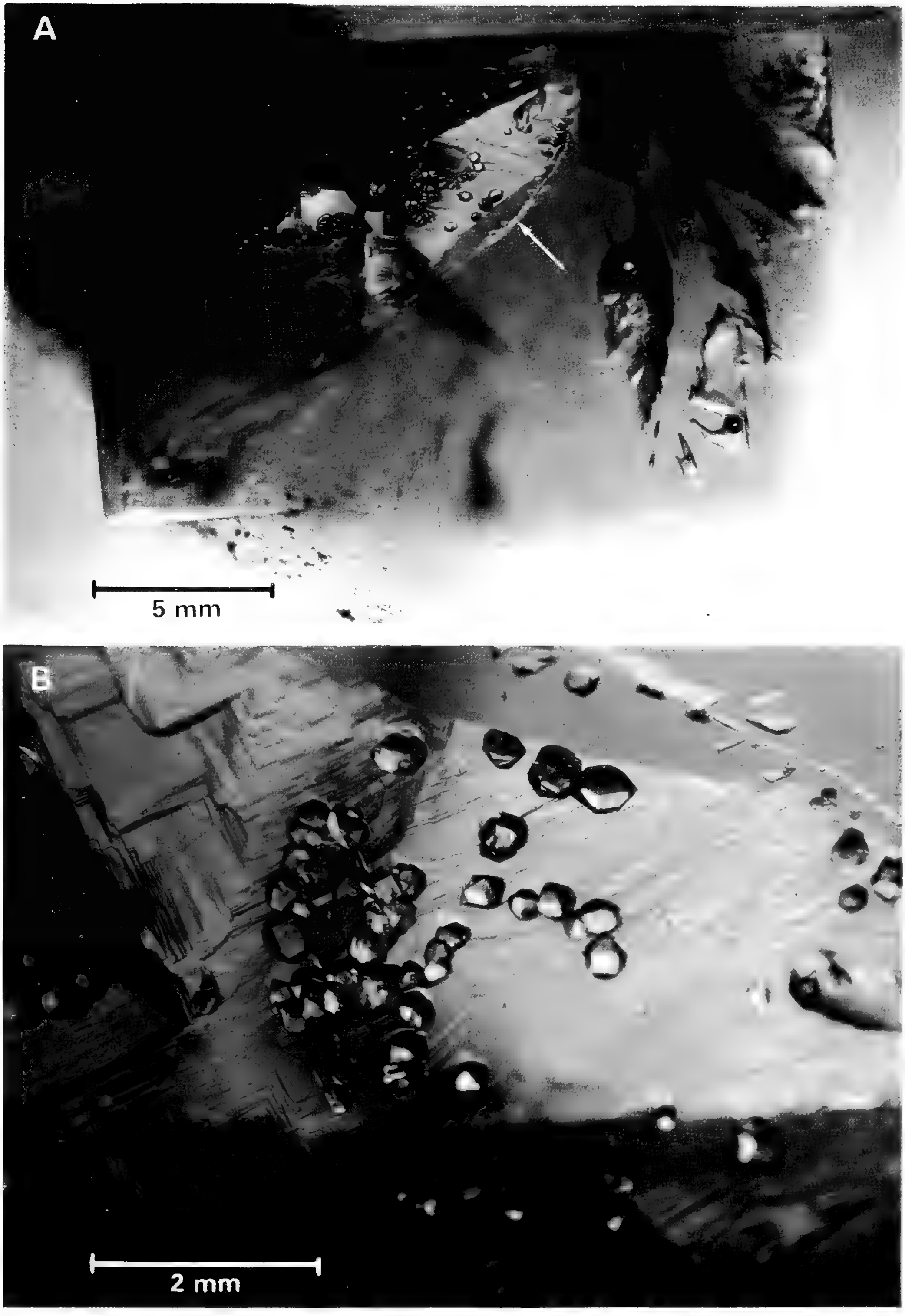


Plate 7

Plate 8

A. BM 56270. Zoned fluorite crystal containing a single macroscopic inclusion. Two smaller inclusions containing smaller vapour bubbles are also visible (arrowed). These probably necked down from the larger cavity. Small triangular depressions (just visible) are present on the inside walls of the cavity. Unidentified, captured crystalline phases (not visible in photograph) similar to those shown in Plate 7 are also present. The large arrow shows the orientation of the photograph in B (below).

B. BM 56270. As A (above), but viewed in a different orientation. A small healed fracture (arrowed) traverses the inclusion and the inner green, colourless and pink inner growth zones, but ends at the base of the outer green colour zone.

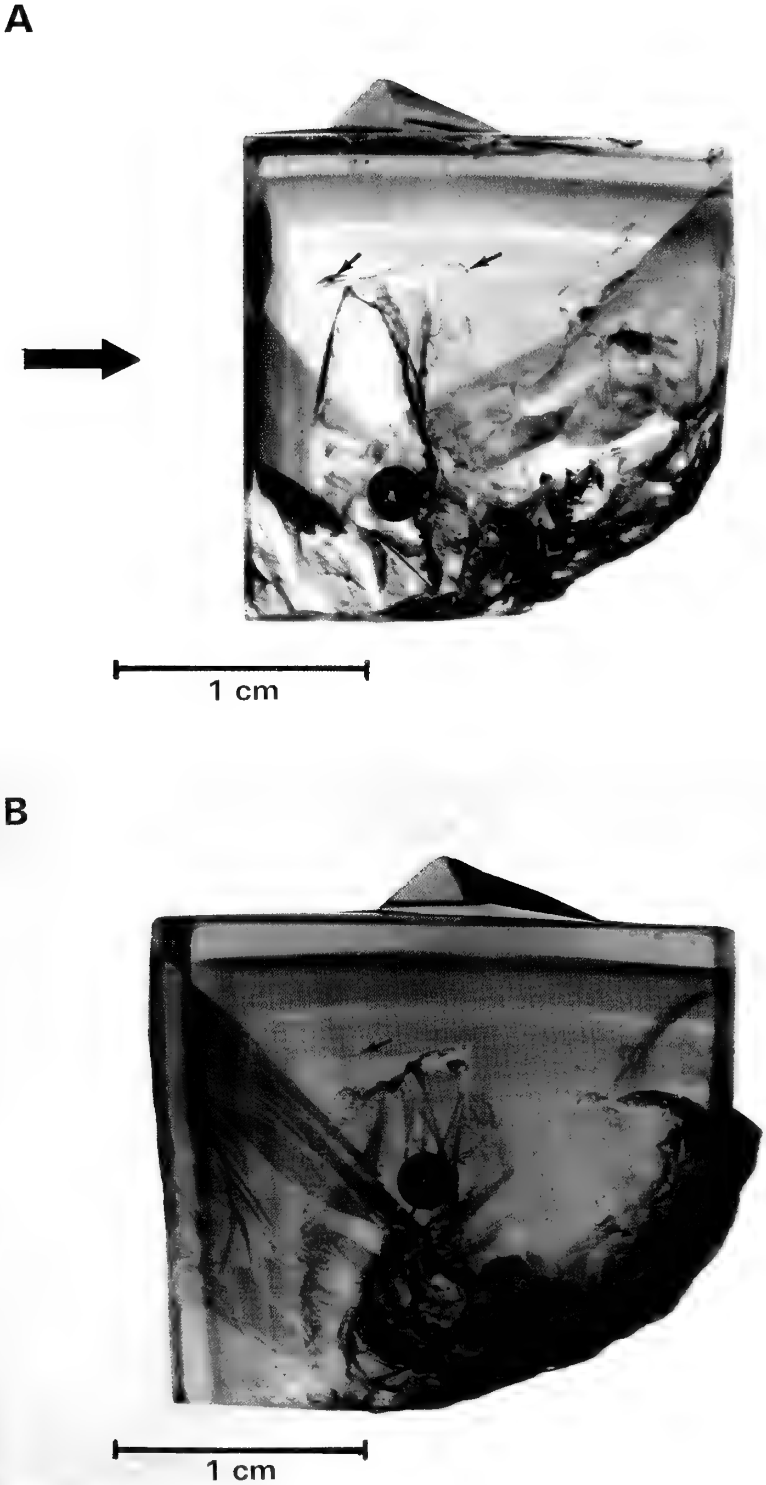


Plate 8

Plate 9

A. BM 56271. A group of several macroscopic and microscopic inclusions apparently located in the outer growth zone of the fluorite crystal. The walls of the largest inclusion (top right) are composed of series of steps with sides parallel to the external cube faces of the host crystal. The inclusions, viewed in a different orientation, (indicated by the arrow) are shown in **B** (below).

B. BM 56271. Viewed in this orientation the complex stepped nature of the walls of the largest cavity are clearly visible. The overall shape of this inclusion approximates to a negative cubic crystal. All but one of the inclusions (arrowed) are located in the outer portion of the fluorite crystal.

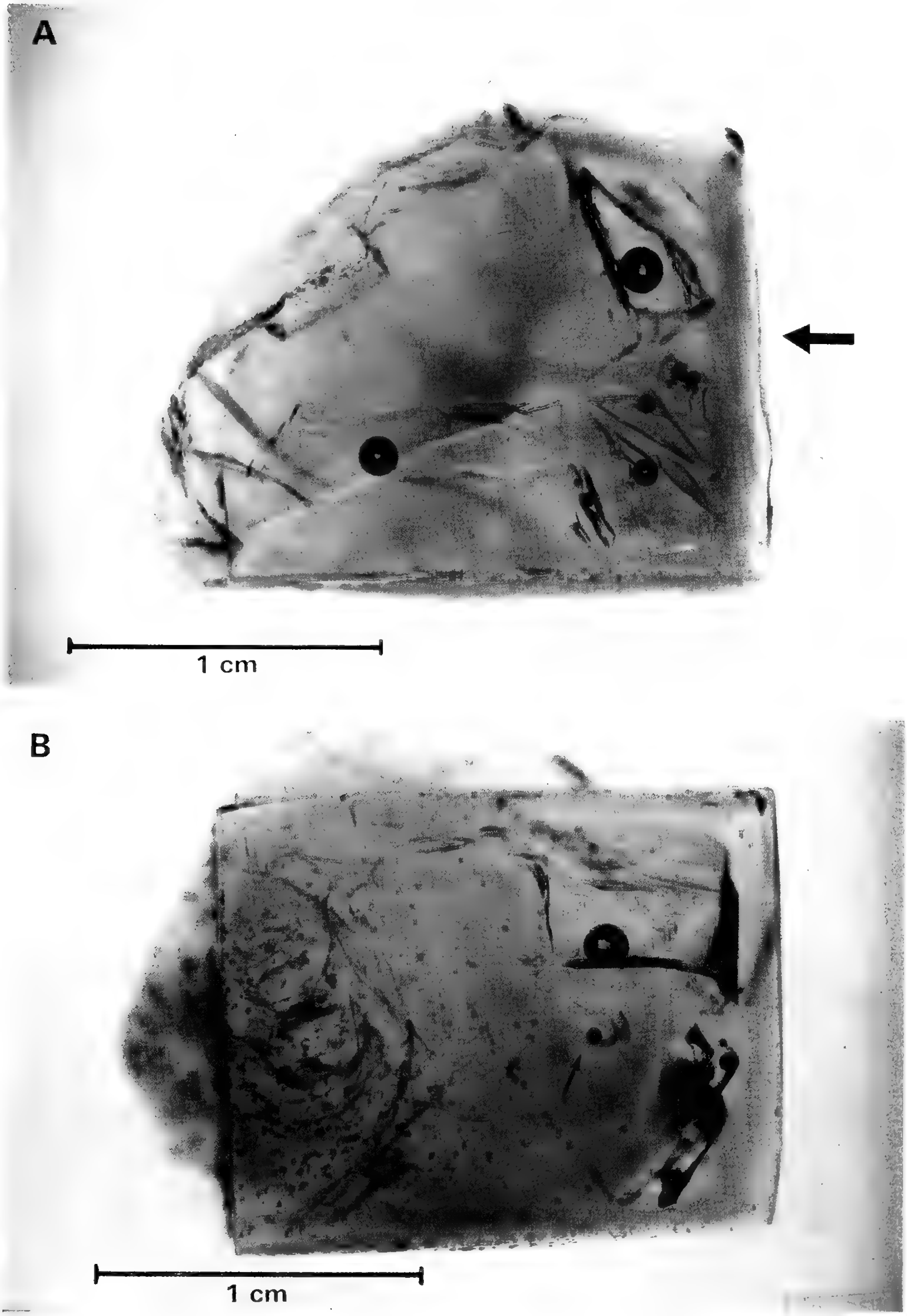


Plate 9

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