G. Philip Rightmire

Department of Anthropology, State University of New York, Binghamton, NY 13901, U.S.A.

H. J. Deacon

Department of Archaeology, University of Stellenbosch, Stellenbosch 7600, South Africa

Comparative studies of Late Pleistocene human remains from Klasies River Mouth, South Africa

The main site at Klasies River Mouth was excavated in 1967–1968, and quantities of shell, animal bones and some human remains were recovered in association with a Middle Stone Age industry. More recent investigation of the caves has clarified aspects of stratigraphy and dating. It is well established that the site was first inhabited during the Last Interglaciation. Two main stages of deposition leading to formation of the (older) LBS and (younger) SAS members can be recognized, and the site was abandoned about 60,000 years ago, perhaps as a consequence of changes in habitat conditions due to climatic forcing. Most of the human bones collected in 1967–1968, and several additional specimens found since 1984, come from the SAS deposits. Two recently excavated fragments of maxillae are from the LBS member.

We report results of comprehensive studies of the Klasies River Mouth teeth, mandibles, upper jaws and other facial pieces, and postcranial material. Measurements and anatomical comparisons confirm that the Klasies Middle Stone Age people differ from Neanderthals and other archaic humans. Mandibles tend to be deeper at the front than posteriorly, and a chin is relatively prominent. Internal symphyseal buttresses are not expressed, and there is no retromolar space. An impression that the morphology is modern extends also to the face and to the parts of the post-cranial skeleton that are preserved. This robust but essentially modern anatomy is coupled with strong sexual dimorphism. A question that remains to be explored is how the Klasies folk compare to contemporary populations present at Qafzeh Cave and Es Skhul. It is apparent that there are some differences between the South African assemblage and those from western Asia. These differences must be checked further, but all three sites may document an early dispersal of modern humanity, perhaps from an African source.

Introduction

The caves at Klasies River Mouth are situated on the southern coast of South Africa, some 40 km to the west of Cape St Francis. Five of the caves and shelter complexes have been assigned numbers, but it is the main site including caves 1, 1A, 1B, 1C and 2 that has been the principal focus of archaeological interest. Excavations carried out over two field seasons in 1967–1968 have been described by Singer & Wymer (1982). During these earlier investigations, much information concerning stratigraphy, paleoenvironment and human occupation at the main site was obtained. It was determined that Middle Stone Age people had used the caves during the earlier part of the Late Pleistocene, for a period of at least 50,000 years. Human remains as well as animal bones, shell, and stone artifacts were collected from the Middle Stone Age levels. Unfortunately, due to the fact that the site was not utilized for intentional burials, human bones are scarce. The remains are also fragmentary. Several lower jaws are reasonably complete, but only small pieces of cranium and a few bits of postcranial material were recovered during the 1967–1968 field seasons. These remains are described as essentially modern in anatomy by Singer & Wymer (1982).

A new research program was initiated at Klasies River Mouth in 1984 by one of us (HJD) working through the University of Stellenbosch. The aims of this series of

investigations are to clarify some aspects of stratigraphy, to obtain materials suitable for dating, and to add to our understanding of the behavior of Middle Stone Age populations. A revised account of the stratigraphy and sedimentology of the main site has been published elsewhere (Deacon & Geleijnse, 1988). It is now well established that the Klasies caves were inhabited nearly 120,000 years ago, during regression from the maximum high sea level stand of the Last Interglacial. Two main stages of subsequent cave infilling and several briefer periods of deposition can be recognized. Multiple short episodes of human occupation are associated with hearths, shell middens and other traces of activity. These layers are separated by naturally accumulated sands incorporating chance inclusion of bones of fish and small mammals derived from bird roosts. Several lines of evidence suggest that the site was abandoned about 60,000 years ago, perhaps as a consequence of climatic and related ecological changes leading to a less productive human habitat.

During the course of the 1984–1989 excavations, several more human fossils have come to light. These include a broken maxilla from the lowermost (LBS) depositional member, a second piece of maxilla containing one tooth from the same level in the main site, the proximal end of an ulna from the overlying (SAS) member and several isolated teeth from the top of the Middle Stone Age sequence. These relics are important because they are some of the oldest from the main site and because they add to the small inventory of bones recovered in good archaeological context that can inform us about the people associated with an early Late Pleistocene, Middle Stone Age way of life. The purpose of this report is to describe this new material and at the same time to provide a systematic reassessment of the more complete remains discovered in 1967–1968. We feel that it will be useful to place on record a comprehensive account covering all of the human bones found as of 1987. Anatomical comparisons should also be carried out, and the Klasies fossils are discussed with reference to Neanderthals from Europe and western Asia, specimens from Qafzeh Cave in Israel, and samples of recent people from South Africa. These studies confirm that the Klasies jaws, teeth and other body parts fall easily within the range of variation exhibited by modern humans.

Stratigraphy and dating of the main site

The main site is a cliff face at right angles to the coast into which a series of side chambers or caves has been cut along a stepped bedrock profile (Figure 1). A ridge parallel to the cliff has helped to anchor the extensive Late Pleistocene accumulation of deposits. The base is a 6 m rockcut bench that is well developed along the coast and is an older Plio-Pleistocene feature (Hendey & Volman, 1986; Deacon & Geleijnse, 1988) known as the minor emergence (Krige, 1927). Caves 1 and 1C are deep chambers in excess of 30 m in length, cut into hard quartzite at the 6 m elevation. Cave 1B by contrast is an overhang, and only the rear of the original chamber, formed at the same elevation, is preserved in this part of the site. As the cone of deposition at the main site built up and the center of accumulation migrated upslope against the overhanging cliff, the lower chambers were blocked off. The upslope part of the depository is a long overhang (cave 1A), and a shelter (cave 2) with a rock floor at 17 m, the elevation of Krige's major emergence. A thickness of over 20 m of deposits accumulated at the main site, and in the process even cave 2 became filled to the roof. This cone of material was truncated by erosion in the Holocene, and perhaps only as little as a third of the original volume has been preserved.

The strata have been divided into a number of members and units (Figure 2). These
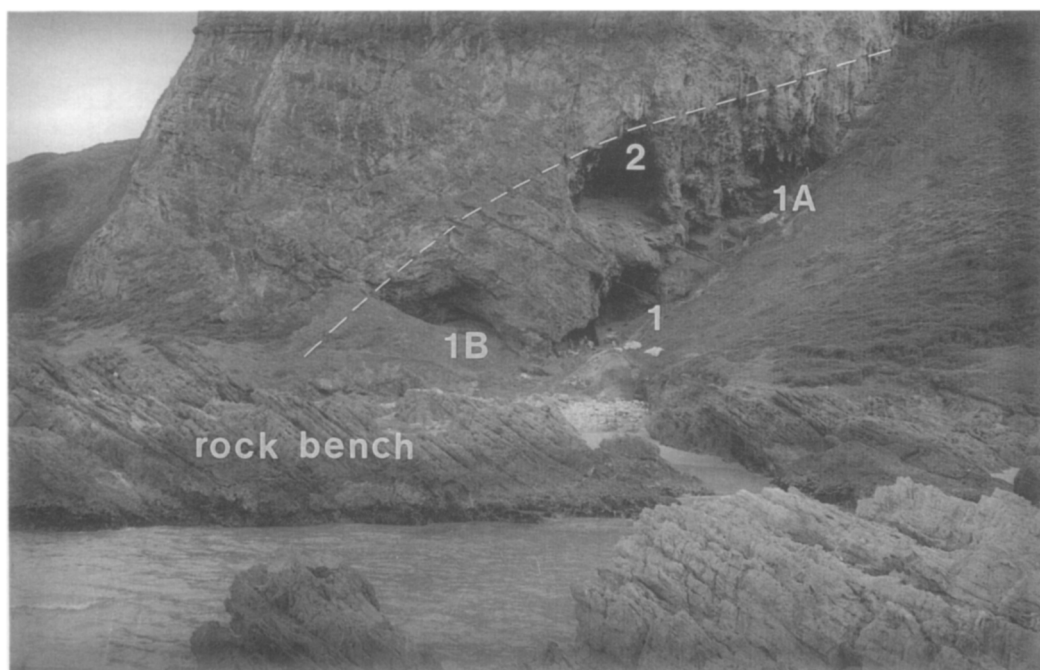
Figure 1. The main site at Klasies River Mouth, made up of several caves and shelters (numbered). Traces of the original cone of deposits occur along the level indicated by the dashed line. Much of this material was removed by erosion in the Holocene, and only a fraction of the original accumulation has been preserved.

complement and extend the division of the sequence into a series of layers by Singer & Wymer (1982). Their layer numbers are given in parentheses where appropriate. The stratigraphically oldest member, LBS (38), overlies a partly calcareous cemented grit on bedrock in most of the area of cave 1 and has an equivalent position in cave 1B. This member represents the first occupation in a near beach situation initiated during the Last Interglacial which ended 118,000 years ago (CLIMAP Project Members, 1984). The deposits consist of sands interbedded with human occupation horizons that include the ash lenses of hearths, Middle Stone Age artifacts, and shell and bone foodwaste. The sand source was a nearby beach (Deacon & Geleijnse, 1988), indicating a sea level near to the present. The last time sea levels were this high was during the Last Interglacial. The dating of the LBS member to oxygen isotope stage 5e is confirmed by two independent oxygen isotope studies of shell samples (Shackleton, 1982; Deacon et al., 1988). These show that the shell from the LBS member grew in an isotopically light interglacial ocean. There is additional confirmation of this age from uranium disequilibrium and aspartic acid dating (Deacon et al., 1988). Human bones recovered from this level were found within an area of about a square meter and were associated with a single shell midden horizon in cave 1A. These finds, consisting of two maxillary fragments, are essentially contemporaneous and are the oldest human remains excavated at Klasies River Mouth.

Overlying the LBS is the SAS member, a thick sequence of sands, again with intercalations representing multiple discrete human occupation events. The contact with the underlying strata is sharp and has been described as unconformable (Deacon &
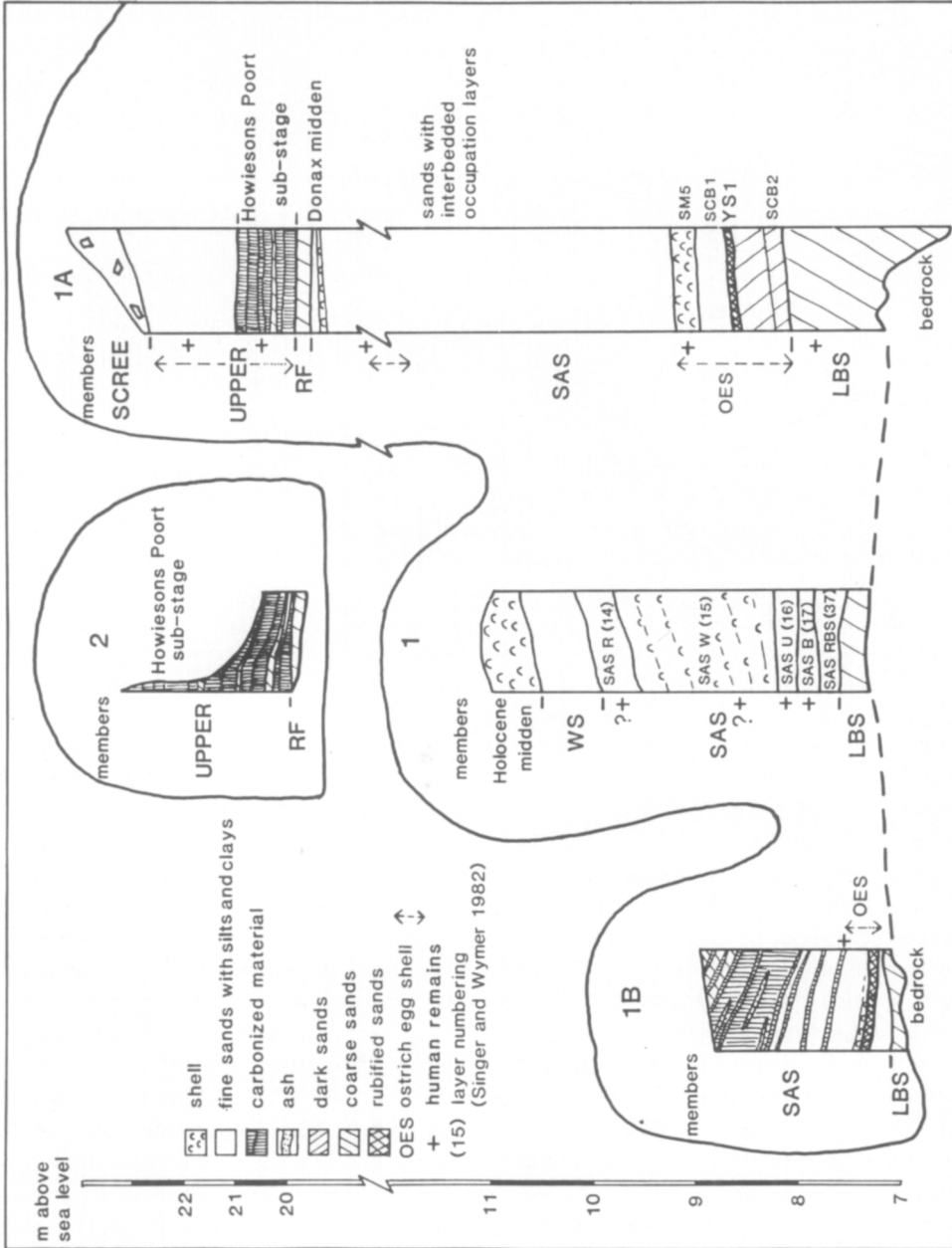
Figure 2. Generalized stratigraphy for caves 1, 1A, 1B and 2 at the main site. See text for details.

Geleijnse, 1988) but locally it is more properly disconformable. In cave 1 the base is marked by a prominent 0·3 m thick carbonaceous layer SAS RBS (37) which can be traced in 1A as a series of units grouped and labeled as SCB1-2. As there is no stratigraphic connection between cave 1B and the rest of main site, indirect means have had to be used to effect a correlation. Of particular interest is the stratigraphic position of the human mandible KRM 41815 in the main site sequence. There are two lines of evidence that apply. Firstly, electron spin resonance measurements on shell from the horizon of the mandible in 1B and the carbonaceous layer (37) in cave 1 group together, indicating a similar age (Goede & Hitchman, 1987). Secondly, the occurrence of ostrich eggshell at the main site is restricted to one horizon in the sequence. The present day surrounds are not a semi-arid karroid habitat suitable for ostriches, but early in the Late Pleistocene there were episodes when ostriches were present in the area. The oldest episode is associated with the mandibular horizon in 1B and deposits directly overlying SCB2 in 1A, and this provides a marker for intrasite correlation. Ostrich eggshell does not occur in the LBS sediments.

It is evident that Singer & Wymer (1982) were in error in assuming that the 1B deposits represent only the oldest pulse of sedimentation. The position of 1B on the outer margin of the cone of deposition means that the sequence in that part of the main site is condensed, and the deposits there are equivalent to four or five times the thickness of material in 1A. Thus, although truncated by later erosion, the 1B deposits still represent a considerable time range. The implication is that the artifact and faunal contents from the 1967–1968 excavations in 1B cannot be used as a valid sample, and to debate the stratigraphic placement or the age of the KRM 41815 mandible on the basis of this assemblage (Binford, 1986; Singer & Wymer, 1986) is inappropriate.

The KRM 41815 mandible is stratigraphically and chronologically younger than the LBS member. The interval of time between the deposition of the LBS and the SAS sediments has still to be established with precision. Oxygen isotope measurements by Talma (Deacon *et al.*, 1988) suggest that deposition of the SAS member took place during stage 5c, and this implies an age in excess of 90,000 years. The relevant aspartic acid age reported for cave 1 (37) is 90,000 years (Bada & Deems, 1975), but there are uncertainties in calibration. For example, if the results are recalibrated using the D/L_{asp} ratio for the oldest sample in the series as dating to 120,000 years, then the age estimate is closer to 100,000 years. While the aspartic acid results probably underestimate rather than overestimate the true age, they are consistent with a high antiquity for the mandible. All evidence to hand makes it improbable that the important 1B find can be significantly younger than 100,000 years, and this vindicates the claims of Singer & Wymer (1982).

Above the base of the SAS member in cave 1 (37) is a series of strata that have been mapped as SAS B (17), SAS U (16), SAS W (15) and SAS R (14). The bulk of the human remains found in the 1967–1968 excavations came from two localized areas in cave 1, Main Cutting A and West Cutting F (Singer & Wymer, 1982: Figure 2.1). Features like hearths show that cave 1 was habitable during the build up of SAS B and SAS U, but SAS W is a steeply dipping talus slope deposit with clear tip lines. The talus formed in the process of blocking off the cave 1 chamber which was then at the foot of the growing pile of sediments accumulating against the cliff face in 1A. The context of all finds in SAS W (15) is geological rather than archaeological. A matrix-supported rubble SAS R (14) occupies a broad channel-like feature against the back slope of SAS W in cave 1. Within this tumble of coarse materials, the clasts range from rounded cobbles and boulders to blocks of speleothems. During the formation of this submember, cave 1 would have served as a

drainage sump for the depository. Within cave 1 there are facies changes, and especially against the walls of the chamber where the post-depositional effects of elutriation of fines by drainage waters are most noticeable, the deposits grade into course clastic rubble making stratigraphic subdivision less certain.

This stratigraphic detail has a bearing on the provenience of human materials particularly in the West Cutting area where 11 specimens are recorded from the SAS R rubble unit, layer 14 (Singer & Wymer, 1982: Table 8.1). An episode of cannibalistic activity can probably explain the localization of human remains recovered from the recent excavations in the LSB member, and a similar argument may be advanced to account for the finds made earlier in the West Cutting if the context of the material is primary rather than secondary. The secondary concentration of human bones in a slope deposit seems improbable, and given the difficulty of distinguishing rubble facies, some if not all of these finds can be in primary context and be associated with the lower (17–16) rather than the upper (15–14) phases of deposition of the SAS member in cave 1. This would imply that the West Cutting remains are closer in age to those in Main Cutting A rather than significantly younger. The vault fragment KRM 41658, from East Cutting T (Singer & Wymer, 1982: Table 8.1), is from a similar stratigraphic position, a few meters up dip from where an ulna associated with ostrich eggshell was found in 1985. The ulna is mineralized, although the containing deposits have been largely decalcified under the present ground water regime. All these fossils from the SAS member in caves 1 and 1A must be penecontemporaneous with the 1B mandible.

A meter thick sand with a few thin occupation horizons, the RF member (22), caps the SAS member and is exposed in caves 1A and 2. The deposits that overlie this have been grouped into the Upper member. Two parietal fragments were recovered from the Upper member in 1967–1968 and the recent excavations have produced in addition several isolated teeth. The dating of the Upper member, including the Howiesons Poort cultural substage of the Middle Stone Age, is beyond the limits of conventional radiocarbon determination. Shackleton (1982) has suggested correlation with isotope stage 3 and a tentative dating of 50,000 years, based on a single oxygen isotope analysis. Additional measurements by Talma (Deacon *et al.*, 1988) are more consistent with the Upper member representing the end of the Last Interglacial *sensu lato*, including the 5a-4 stage transition. This implies an age of more than 60,000 years.

In the top of the Upper member, human use of the site—indicated by the frequency of discrete occupation horizons—diminishes, and the main site was abandoned. The record of Middle Stone Age occupation ends in the first half of the Late Pleistocene and, as at a number of other long sequence sites in southern Africa, the main site was not inhabited again for tens of thousands of years. Colluvial scree deposits, however, continued to accumulate, adding to the height of the cone, and cemented materials show these eventually filled cave 2. This cone was later eroded and truncated by the rising sea of the Holocene. The removal of a large volume of deposits reopened cave 1 for human occupation in the mid-Holocene, some 4000 years ago.

Human remains from Klasies River Mouth

Human fossils recovered from the 1967–1968 excavations have been described by Singer & Wymer (1982). Additional notes and comments on this material have been provided by other authors, principally Bräuer (1984) and Rightmire (1984, 1986). In the present

Table 1   Hominid remains recovered from Middle Stone Age levels at main site, Klasies River Mouth[1]

Description	Location in chamber complex	Stratigraphic level	KRM designation (1967–68 excavations)
1. Right mandibular corpus with P_4 to M_2. Three loose teeth probably belong with this individual.	cave 1	SAS member	13400. Also 14691, 14693 14694?
2. Anterior part of mandibular corpus including symphysis. One loose tooth may belong with this individual.	cave 1	SAS member	14695. Also 14696?
3. Right mandibular corpus with M_1 to M_3.	cave 1	SAS member	16424
4. Left mandibular corpus.	cave 1	SAS member	21776
5. Damaged mandible with left M_1 and M_2, right P_4 and M_1.	cave 1B	base of SAS member	41815
6. Fragment of left maxilla with alveoli and part of palate.	cave 1A	LBS member	—
7. Fragment of left maxilla with M^1.	cave 1A	LBS member	—
8. Frontal fragment, with nasal bones attached.	cave 1	SAS member	16425
9. Left zygomatic bone.	cave 1	SAS member	16651
10. Vault fragment, including parts of right parietal and frontal squama.	cave 1A	SAS member	41658
11. Left clavicle, broken at sternal end.	cave 1	SAS member	26076
12. Proximal end of left radius.	cave 1	SAS member	27889
13. Left first metatarsal.	cave 1	SAS member	—
14. Lumbar vertebra.	cave 1	SAS member	—
15. Proximal portion of right ulna.	cave 1A	SAS member	—

[1] Only the more complete specimens are inventoried here. For a full listing of items from the 1967–68 excavations, see Singer & Wymer (1982).

account, not all of the remains discussed by Singer & Wymer (1982) are touched on, but new observations concerning the jaws and other more complete specimens (Table 1) are offered. There is necessarily some overlap of our treatment with that given in the earlier monograph, but readers wishing to obtain full details of the 1967–1968 discoveries should consult both reports. Human bones found since 1984 (also listed in Table 1) are described here for the first time.

The 1967–1968 mandibles
KRM 13400. KRM 13400 is most of a right mandibular corpus, broken behind M_2 (Figure 3). Crowns of right P_4 to M_2 are still in place. A distal contact facet on M_2 shows that M_3 had erupted fully, but this last molar and nearly all of its alveolus are missing. The sockets for right I_1 to P_3 are eroded, and these teeth are also missing. The front of the jaw is fairly well preserved, although the left incisor alveoli are damaged, and the labial wall of the left canine socket is broken out. This specimen from cave 1 exhibits no blackening or other signs of fire damage.

Like several of the other Klasies jaws, KRM 13400 is rather heavily built. In side view, the upper and lower borders of the corpus are now approximately parallel, but this appearance results from erosion of the sockets which held the anterior dentition. It is clear that the front of the jaw was (appreciably) deeper before this damage occurred. The root of the ramus is lost, and the bone below M_2 is splintered. Enough of this surface remains to show that there is some development of a lateral prominence. This prominence is continued as an irregular superior torus, which reaches forward to the level of P_3. One
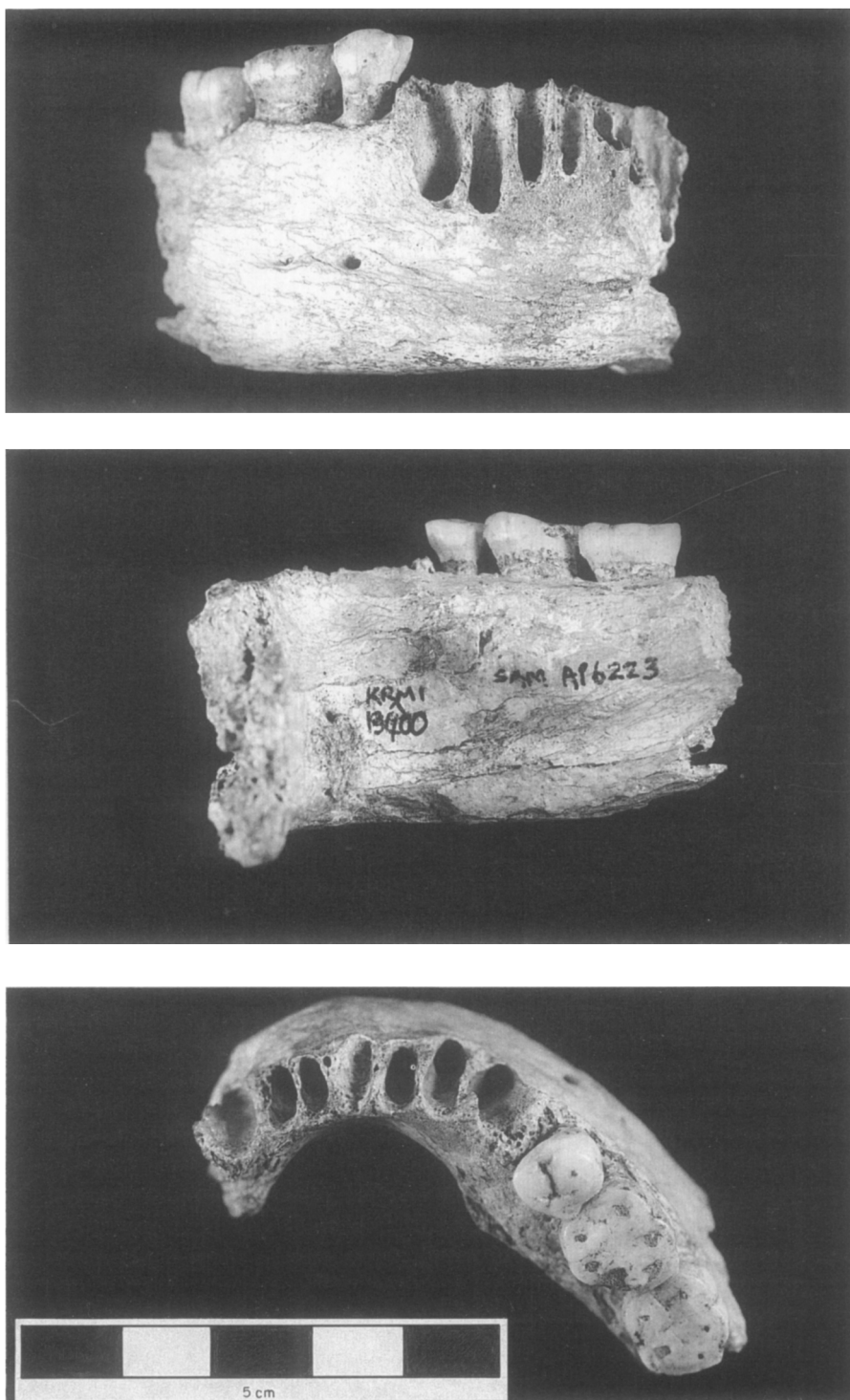
Figure 3. Three views of KRM 13400. Anterolateral, medial and occlusal aspects of this right mandibular corpus are shown. Crowns of P_4, M_1 and M_2 are preserved. KRM 13400 is one of the larger jaws, probably that of a male individual.

mental foramen is located in the torus below M_1, while a second enters the bone at the same depth below P_4. A distinct intertoral sulcus can be followed horizontally, just above the base.

The symphyseal axis is nearly vertical, and at the front of the jaw there is an area of blunt swelling. This eminence broadens below to produce a mental trigone. The trigone itself is not so prominent as in many modern human mandibles, but it does provide evidence of chin formation. On the internal aspect of the symphysis, there is some hollowing just below the alveolar margin, but nothing resembling the shelving planum characteristic of more archaic *Homo* is present. There is no superior transverse torus. A small foramen supraspinosum lies in the midline, and directly below it there is a roughened mound bearing several small projections. The number of separate mental spines cannot be determined.

A notable feature of KRM 13400 is the alveolar prominence, which is strong below M_2 and continues anteriorly as a roughened projection from the body wall. Cracking and displacement of surface bone contributes to additional swelling below the premolar teeth. Some expression of a mandibular torus is evident, however, as suggested by Singer & Wymer (1982). The mylohyoid line is not sharply defined, and the posterior subalveolar fossa forms a low channel which opens onto the flatter sublingual aspect of the corpus. The base is thickened. Digastric impressions are narrow but deep and face posteroinferiorly.

Of the three teeth present in this mandible, the right P_4 is roughly square in occlusal outline. Both the large buccal cusp and the smaller mesiolingual cusp show appreciable wear. Probably a third cusp or cuspulid was expressed on the distal marginal ridge, which is now worn nearly flat. M_1 is larger than M_2. Fissure patterns on both teeth are almost obliterated, but probably M_1 has five principal cusps, all of which show enamel perforation. In addition, the outline of a large *tuberculum intermedium* (C7) can be discerned. M_2 carries five cusps arranged in a Y pattern.

Other loose teeth excavated in proximity to the jaw are presumed to represent the same individual. KRM 14691 is a left first molar, to which a fragment of bone adheres. *Contra* Singer & Wymer (1982), there is no join to KRM 13400. Nevertheless, the tooth is comparable in size, cusp pattern and condition of wear to the molar situated in the mandible. It is reasonable to group not only the M_1 but also the isolated left M_2 (14693) and left M_3 (14694) together.

A premolar numbered KRM 14692 was also found nearby, and Singer and Wymer identify this as the left P_3 "fitting into the appropriate socket" of KRM 13400. The identification of this tooth as P_3 is probably correct, although the chipped and worn state of the crown makes assessment of its morphology difficult. When the specimen is aligned with the alveolar wall of KRM 13400, its crown projects well above the level of the arcade as preserved on the right side. This suggests that the left premolar in fact belongs to a different individual. Despite its archaeological provenience, this tooth should not be grouped with the lower jaw.

KRM 14695. KRM 14695 is the front of a jaw, containing the incisor sockets but no tooth crowns or roots. Both canine alveoli are partially complete, while the rest of the corpus is missing on both sides. Because of damage to the alveolar margin, heights can be estimated only roughly. The jaw is lower than other cave 1 specimens with which it can be compared. There is external swelling at the symphysis, and a central chin eminence is present. Internally, the wall of the corpus drops vertically behind the incisor sockets, and there is

neither a planum nor any sign of a superior transverse torus. Lower in this profile, there is a narrow midline pit, flanked by small tubercles. A larger ridge is present inferiorly, just above the rounded base. Diagastric impressions are not preserved.

Singer & Wymer (1982) report that an isolated lower molar was found "adjacent" to KRM 14695 and may be associated with it. This left lower molar has five cusps. In side view, the two buccal cusps as well as the distal (hypoconulid) are visible in occlusal profile. This trait, and the fact that the mesial and distal roots are widely separated, suggest that the tooth is M_1 rather than M_2. The specimen carries the number 14696.

KRM 16424. KRM 16424 represents an individual which is very small and lightly built, almost surely an (adult) female (Figure 4). Only part of the right corpus and a little of the ramus are present. The external surface of the body has splintered, and cancellous bone is exposed below the P_4 alveolus. The internal contour of the jaw is more complete, although the base is damaged. Sockets for the anterior teeth and for P_3 are missing. All three right molars are in place, but the crown of M_1 is partly blackened and has lost enamel. Discoloration and flaking indicate that the specimen has been burned.

At the position of M_2, the corpus is about 20 mm in height and 13 mm in width. The index of robusticity is therefore relatively high, while absolute dimensions are quite small. Although the body is incomplete, it is apparent that the jaw deepens anteriorly. Little surface detail has survived. Development of the lateral prominence and buccinator gutter is comparable to that seen in gracile modern mandibles. The upper portion of the ramus is missing, but this structure cannot have been high. The alveolar prominence is relatively strong. Anteriorly, the mylohyoid line is expressed as a ridge below M_1.

What remains of the occlusal surface or M_1 shows heavy wear, and dentin is exposed on all the cusps. The five cusps of M_2 are moderately worn and are arranged in a + pattern. The third molar is square in occlusal outline and is smaller than M_2. Five cusps are again arranged in a + configuration. No C6 or C7 is expressed, and there are neither deflecting wrinkles nor crenulate enamel. Small pits on the buccal aspect of M_2 and distal aspect of the M_3 crown may reflect hypoplastic damage.

KRM 21776. KRM 21776 is one of the larger Klasies jaws. A small part of the right corpus, the symphysis, and more of the corpus on the left side are preserved. Sockets for right I_1 and left I_1 to P_4 are slightly damaged, and the alveolus for left M_1 is broken. A little more bone is present posteriorly on the left, but all of the ramus is missing. Surfaces are blackened, especially on the inner aspect of the body and in the alveoli. No teeth have been recovered.

Some of the lateral prominence is intact, and this trends downward from the broken alveolar margin at the level of M_2. The prominence is continued anteriorly as a blunt torus which merges with the base. No intertoral sulcus is formed. A single large mental foramen opens upward below the P_4/M_1 septum. Further forward, the surface of the body is hollowed between the alveolar margin and the base. The base itself is slightly everted, although there are no distinct marginal tubercles. At the symphysis, the chin is expressed as a moderately prominent trigone.

Just below the anterior tooth sockets, the internal aspect of the corpus is faintly concave, but no planum is present. Instead, the surface slopes steeply toward a small pit, located in the midline. Below this pit, a complex of several large genial tubercles is formed. The digastric impressions are roughened. The scars face posteroinferiorly and are separated at
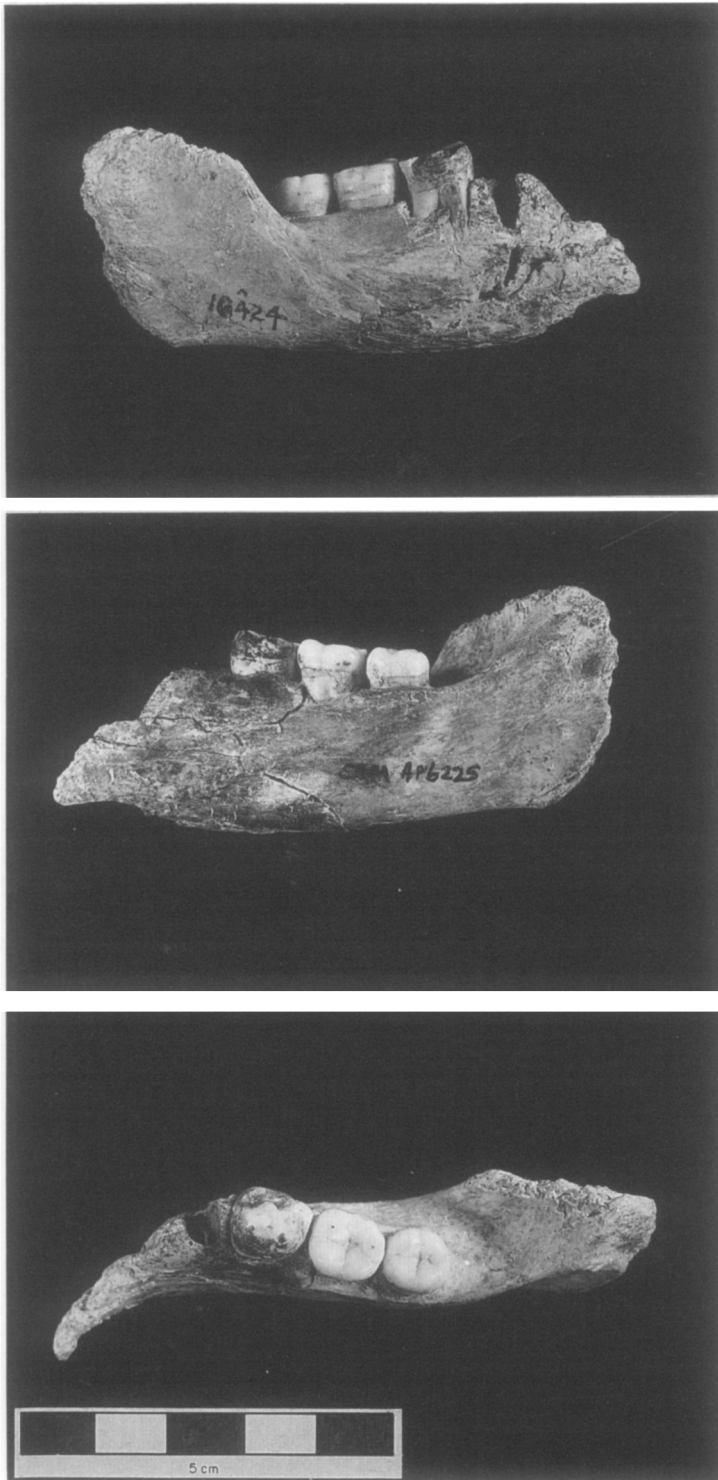
Figure 4. Three views of KRM 16424. Lateral, medial and occlusal aspects of the mandibular corpus are pictured. Crowns of the three right molar teeth are preserved. This small specimen probably represents a female individual.

Figure 5. Occlusal view of KRM 41815. The most complete of the Klasies jaws, this specimen was recovered from the base of the SAS member in cave 1B.

the symphysis by a sharp ridge, oriented sagitally. Otherwise the base is rounded and substantially thickened.

KRM 41815. KRM 41815 was recovered from the base of the SAS member in cave 1B. Although it has sustained some damage, this is the most complete of the Klasies mandibles (Figure 5). All of the right corpus is present, but on this side the angle and posterior part of the ramus are missing. On the left, bone has been lost from the mandibular base below the molars, and the ramus has been only partly reconstructed from fragments. All of the incisor teeth are gone, and the incisor sockets are completely broken away. Empty alveoli for left C to P_4 and right C, P_3 and M_2 shows evidence of extensive resorptive change associated with age and disease. The crowns of left M_1 and M_2 and right P_4 and M_1 are very worn, leaving only roots and some eroded dentin. On the left, M_3 may never have erupted, while on the right only a small pit remains in the area behind the M_2 alveolus.

Because of damage, KRM 41815 is difficult to measure. Corpus height at the position of (right) M_1 is approximately 33 mm, and thickness is 16 mm. Expression of the lateral prominence is comparable to that seen in many modern jaws, and traces of a weak superior torus can be followed anteriorly for some distance. Below C or I_2, this torus merges with the base to produce a tubercle. Tubercles on both sides contribute to formation of a strong trigone at the symphysis. Protrusion of the chin is accentuated by incurvation of the symphyseal face, and the mental eminence is clearly visible when the jaw is viewed from the side.

The alveolar prominence presents a flattened surface, bounded below by a strong mylohyoid line. The subalveolar fossa is only slightly hollowed. The base is rounded posteriorly but becomes thinner toward the front. Although the symphysis is cracked and

some bone is missing from its internal aspect, it is apparent that there is no superior transverse torus. The wall of the corpus slopes downward to an irregular depression. The floor of this hollow is roughened, but no distinct mental spines can be identified. Inferiorly to each side, there are areas of swelling which may represent an incomplete transverse torus. Digastric impressions are clearly marked and meet anteriorly at a small crest set toward the back of the base. Neither here nor in other characters of this jaw described by Singer & Wymer (1982) are there indications of archaic morphology.

The 1967–1968 cranial fragments

Cranial remains recovered from the main site at Klasies are all very incomplete. These include a section of frontal to which the upper ends of both nasal bones are attached, a cheek bone, and numerous vault fragments. The latter are mostly pieces of parietal, some of which are blackened. In a few cases, suture lines are preserved, and details of endocranial morphology can be made out. Maximum thickness readings vary from 7 mm to about 10 mm. All of this material is described by Singer & Wymer (1982), and only the more important specimens are touched on here.

KRM 16425. KRM 16425 is part of a frontal bone (Figure 6). Some of the orbital plate and supraorbital region from the right side, glabella, and the nasofrontal contact are preserved, and the broken nasal bones are still in place. A little of the endocranial aspect is present, and the frontal sinus is exposed. The morphology of KRM 16425 is informative and shows that in this individual a browridge is not developed. Glabella is somewhat inflated, but the superciliary eminence is not strongly projecting in comparison to that of recent African crania. This eminence is distinct from the more lateral aspect of the supraorbital margin. Most of the frontal squama is missing, but it is likely that the forehead would have sloped gently posteriorly. In all respects, there is clear contrast to the anatomy seen in archaic hominids from Africa or Europe. The Klasies bone is very gracile and exhibits none of the brow thickening or supratoral flattening which is present, for example, in the case of Florisbad.

Recently, White (1987) has noted that there are several fine subparallel scratches on the external surface of the KRM specimen, above the superciliary eminence. This damage appears to have been inflicted when the bone was fresh, and the scratches show the microscopic characteristics to be expected in the case of cutmarks left by stone tools. White concludes that this individual was intentionally defleshed, and KRM 16425 provides suggestive evidence for cannibalism at the site.

KRM 16651. KRM 16651 is most of a zygomatic bone from the left side. This specimen is broken along its maxillary border, and some of the temporal process is missing. The bone is large by modern standards but is not noticeably archaic in its anatomy. In comparison to the corresponding part of the Florisbad face, the Klasies fragment seems less robust, and the surface of the cheek is flatter.

KRM 41658. KRM 41658 is the single largest piece of cranial vault collected at the main site. It consists of part of a right parietal attached to a section of frontal squama. A short segment of the sagittal suture can be recognized endocranially. The coronal suture, fully fused, is identifiable as a shallow groove containing small perforations. Thickness at bregma is about 6·5 mm, and maximum thickness measured toward the center of the parietal is 9 mm. Singer & Wymer (1982) suggest that the vault represented by this
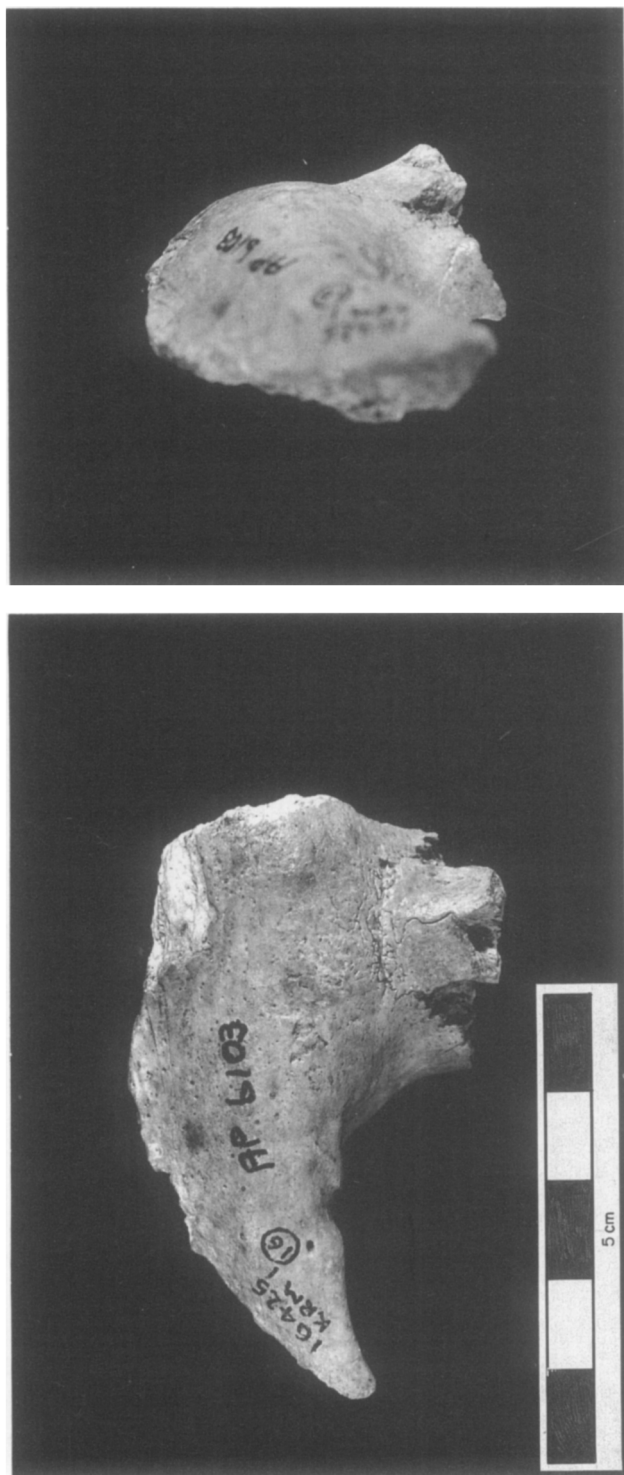
Figure 6. Anterior and lateral views of KRM 16425. Some of the supraorbital region and glabella are preserved, and pieces of both nasal bones are attached to this frontal fragment.

specimen may have been relatively low and narrow, but overall shape of the braincase cannot be determined from isolated pieces of this size. The cranium need not have been especially low, and there is some indication of parietal bossing.

New jaws and teeth from the 1984–1989 excavations

Since 1984, excavations conducted at the main site have produced several hominid fragments. One of the new specimens is a piece of blackened maxilla, recovered from the LBS member low in the cave 1A stratigraphic sequence. A small section of the hard palate is preserved, just to the left side of the midline. Only the posterior walls of the alveoli for left I^1, I^2 and C are still in place. Sockets for P^3 (containing the broken tooth root) and P^4 are more complete, but the cavity for the distobuccal root of left M^1 has been eroded. Parts of the sockets for the lingual and mesiobuccal roots of M^2 are intact, while the rest of the alveolar process is missing. A little of the floor of the nasal cavity is preserved, as is some of the adjacent maxillary sinus. All of the subnasal surface of the jaw is broken away, but the root of the zygomatic process can be traced upward just above M^1.

Because the bone is so incomplete, comparisons with other fossil specimens and recent humans can be carried out only in a limited fashion. Neither the nasal sill nor prosthion is present, so length of the maxillary clivus cannot be measured accurately. However, it is clear that this length is well within the range expected for modern crania. The KRM lower face must be substantially shorter than that of the archaic hominid from Kabwe (Broken Hill). What remains of the alveolar process is relatively heavily constructed. The premolar roots, as judged from the P^3 fragment and the socket for P^4, were not especially large, but the M^1 root system is expanded buccolingually. Here the jaw is widened, and the palate is deep. This specimen is large by modern human standards but is less robust than the jaw of the Kabwe individual. In overall size and proportions, the KRM maxilla seems close to that of Hominid 18 from Laetoli in northern Tanzania.

A second piece of maxilla has been excavated from the same stratigraphic horizon in the LBS member. Only a little of this jaw is preserved, containing part of the socket for left P^4, the crown and root of left M^1 and the mesial wall of the M^2 alveolus. Much of the enamel has cracked away from the worn molar crown, leaving only the dentin stump behind. The arrangement of molar cusps can no longer be determined. Unfortunately, this jaw does not provide much information. The surviving tooth is small, and the bone seems gracile even in comparison to recent human specimens. Along with the cave 1 maxilla, it suggests a substantial level of dimorphism for the Klasies population.

In addition to the jaws, several isolated teeth have been collected. Some are too incomplete to be studied, but one lower premolar has an intact root. Enamel has chipped away from all of the buccal half of the crown, but the small lingual cusp is only slightly worn. Proportions of the part of the crown remaining are consistent with identification of this tooth as a P_3. Mesiodistal length can be estimated as 6·7 mm.

Postcranial remains

Along with mandibles, teeth and bits of braincase, a small number of postcranial specimens have been recovered at the Klasies main site. The 1967–1968 excavations brought to light part of a left clavicle (KRM 26076) and a broken radius (KRM 27889). The clavicle, which has a circumference at midshaft of 31 mm, is slender. The radius, also from the left side, is represented only by its proximal end. The head is badly eroded. Like

Figure 7. Medial aspect of the right ulna recovered from the SAS member in cave 1A. The specimen is broken approximately at midshaft, and only the proximal portion is preserved.

the clavicle, this bone is lightly constructed. Both are described by Singer & Wymer (1982).

Two other specimens collected during the earlier investigations at the site were not catalogued initially as human and have not been described before. One is a first metatarsal from a left foot, found in the SAS member of cave 1. This bone is complete but has sustained some damage. Articular length, treated as a maximum reading, is 56 mm. Both medial and lateral borders of the base are abraded, so measurements of the proximal articular surface cannot be taken accurately. Height of the bone at midshaft is 13·5 mm, and breadth is 12·0 mm. The circumference at midshaft is 43 mm. The plantar aspect and medial side of the head are also broken. In the parts that are preserved, this metatarsal is indistinguishable from that of modern humans.

A lumbar vertebra, picked out of the Klasies fauna by Richard Klein, comes from the uppermost SAS levels of cave 1. Upper and lower borders of the centrum are damaged, and the transverse and superior articular processes are missing. Height of the body taken either ventrally or dorsally is 23 mm. The inferior dorsoventral diameter is 31 mm, and the inferior transverse diameter is 48 mm. Dimensions of the vertebral canal, taken superiorly, are 16·5 mm by 23 mm.

The proximal end of a right ulna was excavated from deposits of the SAS member in 1985. The specimen is broken approximately at midshaft, and all of the distal part is missing (Figure 7). The remaining bone is well preserved, and several measurements can be recorded (see Table 2). In its midshaft and proximal diameters, the KRM ulna is close to the means provided by McHenry *et al.* (1976) for several groups of modern humans. The interosseus crest is blunt rather than projecting, so a measure of midshaft flare is low, as in San populations. Coronoid height is also low, whereas the olecranon process is relatively

Table 2   Ulnar measurements (mm) for the Klasies specimen and for groups of recent *Homo sapiens*[1]

	KRM	San	Australians	Amerindians
4. Midshaft flare	2?	1·7	2·6	3·5
5. Midshaft anteroposterior diameter	12?	11·1	11·6	11·0
6. Trochlear transverse diameter	17	15·9	18·0	17·2
7. Trochlear anteroposterior diameter	18	14·0	17·5	16·3
8. Coronoid height	28	27·5	34·0	32·0
9. Olecranon height	23	18·9	29·9	21·6
10. Trochlear length	22	18·1	21·5	21·1
11. Tuberosity position	—	30·4	31·1	29·9
12. Olecranon length	16	14·2	17·4	17·5
13. Proximal anteroposterior diameter	14	13·4	17·8	16·0
14. Proximal transverse diameter	15	13·1	16·1	13·9

[1] Measurement numbers and definitions correspond to those of McHenry *et al.* (1976). Averages for San, Australians and Amerindians are taken from this source.

large. Other dimensions of the proximal extremity are not exceptional, and neither the tuberosity for *m. brachialis* nor a supinator crest is strongly developed.

Comparisons with other human populations

Measurements for the five KRM mandibles are given in Table 3. Included for comparative purposes are figures for Neanderthals from Europe and western Asia, and data for more modern groups. The remains from Vindija Cave in Yugoslavia are associated with Mousterian tools and resemble other European Neanderthals. In certain features, however, there is said to be an approach to the condition seen in more recent *Homo sapiens* (Wolpoff *et al.*, 1981). The Neanderthal assemblage from Shanidar in Iraq includes three jaws that provide useful information concerning corpus size and form. Qafzeh 9 is the single most complete adult mandible recovered at Qafzeh Cave in Israel. Skeletons excavated from the Mousterian levels at this site show some archaic traits but are generally regarded as more modern anatomically than the Neanderthals (Vandermeersch, 1981).

Unfortunately, there are few jaws from sub-Saharan Africa that can be confirmed as earlier Late Pleistocene in age. Two adult mandibles from Border Cave may represent a Middle Stone Age population, although there is still uncertainty concerning the provenience of these finds within the Border Cave stratigraphic sequence. Both specimens are entirely modern in their morphology, and measurements provided by de Villiers (1973, 1976) need not be listed again here. However, data for recent black South Africans and for a sample of San males are included in the table. Standard dimensions of the corpus are reported. Robusticity is defined as the ratio of breadth to height at the position of M_1, and cross sectional area below M_1 is calculated as though the mandibular body were elliptical in contour.

Lower jaws tend to be variable in size within any human group, and there is substantial overlap in ranges. As a result, dimensions of the mandibular corpus do not effectively distinguish recent populations from earlier representatives of *Homo sapiens*. Neither height nor thickness of the symphysis can be used to separate African blacks from the Vindija Neanderthals, for example, and it is not surprising that the Klasies specimens are within this size range. KRM 21776, one of the larger jaws, has a symphysis which is thinner than any at Shanidar but slightly thicker than average for modern Africans.

Much the same pattern holds for dimensions taken at M_1. Corpus heights at Klasies River Mouth are low in comparison to the Shanidar Neanderthals and Qafzeh 9, similar to the Vindija figures, and still within the range expected for recent humans. KRM 13400 has quite a thick corpus, and robusticity for this individual is high. At the same time, KRM 16424, which in its absolute dimensions in the smallest of the Klasies jaws, also has a relatively high robusticity index. Among living South Africans, it is the San who most closely resemble the Klasies people in this feature.

Size differences within the Klasies assemblage are reflected directly in the cross sectional areas, which range from about 200 mm^2 to well over 400 mm^2. Perhaps more than other measurements of the corpus, these areas underscore the fact that at least one of the jaws is very small, even by modern standards. KRM 16424 also has small teeth, and this individual is likely to be female. Two other Klasies specimens lie well above the averages calculated for South African blacks and San, and it is apparent that these jaws are much more massive. Taken together, the Klasies cross section figures are lower than any recorded at Shanidar or for Qafzeh 9, but areas of about 400 mm^2 would not be out of place among the Vindija Neanderthals.

Comparisons should take into account the development of tori, prominences and other traits as well as corpus measurements. All of the Klasies fossils preserve some anatomical detail, and several are reasonably complete. The four Vindija specimens consist of either the right or left side of the mandible, and the Shanidar 1 jaw is as well preserved as that of any Neanderthal known. Unfortunately, Qafzeh 9 is rather badly damaged and deformed. Comparisons undertaken here are general in scope and are meant to convey an overall impression of how similar (or different) the KRM hominids are to other groups. Since the

Table 3 **Measurements (mm) of mandibles from Klasies River Mouth, central European and western Asian Mousterian localities, and modern African populations**

	Symphysis height[1]	Symphysis thickness	Corpus height[2] at M_1		Corpus thickness[3] at M_1		Robusticity index	Cross sectional area[4]
KRM 13400	(>33)	(15)	(30·5)	31	(18)	(18·5)	59·0	430·9
KRM 14695	(25)	(15)	—	—	—	—	—	—
KRM 16424	—	—	(21)	(22)	—	(12)	54·5	207·2
KRM 21776	(35)	16·5	—	—	(14)	—	—	—
KRM 41815	—	—	(33)	(33)	16	17	48·5	414·5
Vindija Neanderthals[5]	31·1	15·3	(30·3	—	16·0	—	53·7	386·7
Shanidar Neanderthals[6]	37·0	17·6	—	36·1	—	17·6	48·7	499·0
Qafzeh 9[7]	(37)	—	—	35	—	16·6	47·4	456·1
SA black males[8]	34·7	13·5	—	28·8	—	13·6	47·2	307·5
SA black females	33·1	13·5	—	27·7	—	13·1	47·7	284·8
San males	30·5	12·6	—	24·5	—	12·9	53·3	248·1

[1] Symphysis height is taken along the axis of symphyseal inclination, and thickness is measured approximately at a right angle to this axis. Where there is damage to a specimen, ( ) indicates uncertainty.

[2] Corpus height is measured in two ways. Minimum dimensions taken externally are given in the left column. Vertical heights measured internally are given on the right.

[3] Corpus thickness treated as a minimum is reported in the left column. Breadth taken with the caliper arm held parallel to the occlusal surface of the tooth row is given on the right.

[4] Area (mm^2) is computed as height x thickness x 1/4 π.

[5] Averages for three Vindija Neanderthals are taken from Wolpoff *et al.* (1981).

[6] Averages for three Shanidar individuals are calculated from data in Trinkaus (1983).

[7] Corpus dimensions are reported by Vandermeersch (1981).

[8] Averages for 50 South African black males, 50 black females, and 14 San males are given by de Villiers (1976).

ramus is missing or broken for all of the Klasies jaws, features of the lateral corpus and the symphyseal region are emphasized throughout.

The heavy Shanidar 1 jaw exhibits a moderately strong lateral prominence that is continued anteriorly as a superior torus. Marginal tori are weaker, while the anterior marginal tubercles are large. The degree of relief present on the lateral corpus is comparable to that seen in European Neanderthals. Trinkaus (1983) describes the symphyseal face as "slightly retreating, clearly lacking a prominent mental protuberance". However, a mental trigone is present, and this provides some evidence of chin formation. On the internal aspect of the symphysis, there is a short alveolar plane ending at a "moderately developed" superior transverse torus. The inferior torus is projecting. Another important feature of Shanidar 1 is the large retromolar space, separating the distal aspect of M_3 from the anterior margin of the ascending ramus. Such a gap is common in the jaws of Neanderthals from Europe, and it is usually taken to be a correlate of pronounced midfacial prognathism.

The Vindija specimens are similar. The corpus of Vi 206 is only slightly higher at the symphysis than posteriorly at the position of the molars, and there is little tendency for the jaw to deepen toward the front. Both this individual and Vi 231 exhibit some incurving of the symphyseal profile below the incisor sockets, and a low mental eminence is present. In a third jaw, the symphysis is vertical and flattened. Wolpoff et al. (1981) argue that the Vindija people show more signs of chin formation than are characteristic of other Neanderthals, but it is apparent that the thickened symphysis is not fully modern in morphology. Internally, both superior and inferior transverse tori are well developed. As in most Neanderthal mandibles, there is a retromolar space, suggesting relatively anterior placement of the entire tooth row.

The Klasies hominids depart from the morphology seen at Shanidar and Vindija in several respects. KRM 13400 is one of the larger jaws, in which erosion of the incisor alveoli has reduced the anterior height of the corpus, causing the upper and lower borders of the body to appear parallel. Singer & Wymer (1982) emphasize this trait, but it is at least partly a consequence of damage. In its original state, the jaw would have been higher at the front. The symphyseal profile is vertical rather than receding, and there is a low mental eminence. A chin is clearly present in two more of the Klasies specimens, including the jaw from cave 1B, and in KRM 21776 the symphyseal face is hollowed above the everted base. Here the trigone stands out in moderate relief, and even this more robust Klasies individual can be distinguished from archaic humans.

Where the internal aspect of the corpus is preserved, it can be ascertained that symphyseal buttresses are never strongly developed. Neither KRM 13400 nor KRM 21776 shows any shelving alveolar planum, and instead the profile drops steeply toward the thickened base. No superior or inferior tori are formed. KRM 14695 is similar, and only in the case of KRM 41815 is there a suggestion that an inferior torus is expressed. Tori occur much more frequently in archaic jaws, including those of the "advanced" Neanderthals of Vindija Cave. Even in the Qafzeh specimens, which appear modern in other respects, there is (variable) internal buttressing. Qafzeh 9, for example, has a strong superior torus, although there is no inferior transverse swelling.

One further point of difference from the Neanderthals is the placement of the tooth row in relation to the ascending ramus. Only a little of the ramus is preserved for KRM 16424, but more of this structure can be reconstructed for KRM 41815. In the latter individual, the jaw is most complete on the right side, where M_2 and M_3 have been lost. However, it is

Table 4   Length and breadth dimensions (mm) of teeth from Klasies River Mouth, central European and western Asian Mousterian localities, and modern African populations

	P_4		M_1		M_2		M_3	
	MD	BL	MD	BL	MD	BL	MD	BL
KRM 13400[1] (right)	7·8	9·1	12·8	11·2	12·0	10·6	—	—
(left)[2]	—	—	12·9	11·0	12·5	10·4	11·9	9·8
KRM 14696[3]	—	—	12·1	11·2	—	—	—	—
KRM 16424	—	—	—	—	9·3	8·7	8·5	8·0
Vindija Neanderthals[4]	—	—	11·3	11·1	11·6	11·8	11·9	11·8
Shanidar Neanderthals[5]	7·1	8·8	10·9	10·7	11·6	11·2	11·8	11·2
Qafzeh[6]	7·8	9·2	12·1	12·1	11·4	11·7	12·6	11·5
SA black males[7]	7·4	9·6	11·4	10·9	11·1	10·7	11·2	10·6
SA black females	7·3	9·4	11·1	10·6	10·7	10·5	10·9	10·3

[1] Measurements of the KRM teeth are not corrected for interproximal wear. Most MD lengths are underestimates, to which as much as 0·5 mm should be added.

[2] The left molars were found near the KRM 13400 jaw and probably represent the same individual. These teeth are given separate numbers (KRM 14691, 14693 and 14694).

[3] KRM 14696 was picked up close to the mandible numbered KRM 14695.

[4] Averages for three Vindija Neanderthals are taken from Wolpoff *et al.* (1981).

[5] Averages for four Shanidar individuals are calculated from measurements given by Trinkaus (1983).

[6] Averages for the Qafzeh people are reported by Vandermeersch (1981).

[7] Data for South African blacks are taken from Jacobson (1982).

clear that if M_3 were in position, the crown of this tooth would lie partly posterior to the leading edge of the ramus. A large retromolar fossa of the sort common in Neanderthals is not developed, and it is likely that the teeth and jaws are less projecting in the Klasies population.

Dimensions of selected teeth from the main site are reported in Table 4. Only premolars and molars are associated with the mandibles, and the number of specimens that can be measured is quite small. All of the teeth recovered with the jaw from cave 1B are too heavily worn to be utilized. The Klasies material can be compared to the Neanderthals from Vindija Cave and Shanidar, and to the Qafzeh assemblage described by Vandermeersch (1981). Also included in the table are dental data for modern black South Africans.

Of the two Klasies individuals for which more than a single tooth is preserved, one has molars that equal or exceed those of the Neanderthals in length. Both M_1 and M_2 of KRM 13400 are longer than averages determined for the Vindija and Shanidar people, while M_3 is about the same in its mesiodistal dimension in all three populations. Molar breadths for KRM 13400 are close to the Neanderthal means, or a little less in the case of M_3. These measurements suggest that the Klasies molars are elongated relative to those of the Neanderthals. Especially in the case of the Vindija people, the cheek teeth have a square appearance. In comparison to the Qafzeh averages, the first and second molars of KRM 13400 are again slightly lengthened, whereas M_3 is short and reduced in breadth. Overall differences are slight, however, and neither the Klasies individual nor the more archaic hominids depart very much from the tooth sizes expected in modern Africans. Measurements of KRM 13400 fall within the ranges for length and breadth reported for South African blacks by Jacobson (1982).

A second Klasies jaw carries molars that are small by any standard. The M_2 and M_3 of KRM 16424 are shorter and much narrower than the teeth of Neanderthals or the Qafzeh people. In both mesiodistal and buccolingual diameters, these molars approach the low

ends of the ranges given for South African blacks by Jacobson (1982). This information reinforces the impression already gained from mandibular morphology that KRM 16424 is female.

One additional specimen that should be treated comparatively is the proximal ulna found at the main site in 1985. As noted previously, this bone is similar in its dimensions to those of recent humans. In a few respects, including its reduced lateral flare at midshaft and relatively low coronoid height, the ulna resembles that of a San individual, but it cannot be linked to this population on so little evidence. Another feature of interest is the orientation of the semilunar notch. The direction in which this surface opens is dependent on the heights of both the olecranon and the coronoid processes. An index obtained by dividing measurement 9 of Table 2 by measurement 8 tends to be relatively low in modern humans, reflecting a tendency for the notch to face proximoanteriorly. Index values calculated from data given by McHenry *et al.* (1976) range from 67·5 for Amerindians to 86·4 for Australians. Averages for intermediate groups are close to 70. The figure for the Klasies ulna is 82·1, which is toward the high side for recent people.

Neanderthal values are generally greater. An example is provided by four individuals from Shanidar which have indices of 85·5 to 88·7, suggesting that the olecranon is relatively prominent (Trinkaus, 1983). Here the trochlear notch opens more directly forward. This difference in articular orientation is not likely to affect the range of movement allowed at the joint itself. Trinkaus & Churchill (1988) argue from radial as well as ulnar morphology that Neanderthals were able to rotate the forearm powerfully with the elbow partly flexed, but the significance of this ability is unclear. In any case, the Klasies ulna, which lacks strong crests associated with muscle attachment, is more lightly constructed than is characteristic of Neanderthals.

Discussion

The caves at Klasies River Mouth preserve a highly significant record of human occupation in the Middle Stone Age. Skeletal parts recovered in secure context within the LBS and SAS deposits of the main site are not plentiful, but this collection now includes a number of important items. The Klasies assemblage is far more substantial than those from other Middle Stone Age localities such as Die Kelders and Equus Cave, where only teeth and a broken mandible have been recovered (Grine & Klein, 1985). A more complete cranium, two lower jaws, and other fragments are reported to have come from ancient levels at Border Cave (Beaumont, 1980). However, some of this material was discovered by guano diggers, and its original provenience within the sequence of cave deposits may be questioned. It is clear that human bones from the Klasies main site constitute the principal evidence relating to early Late Pleistocene populations in southern Africa (Deacon & Schuurman, in press).

Measurements coupled with anatomical comparisons confirm that the Klasies specimens differ from the bones of archaic people in a number of respects. Although the mandibles are not much smaller than those of Neanderthals from Shanidar or European localities, the corpus tends to be deeper at the front than posteriorly, and a chin eminence is relatively prominent. None of the jaws exhibits a superior transverse torus, and only one shows traces of an inferior torus. These internal symphyseal buttresses are common in Neanderthals, and a strong superior torus is present also in the jaw of Qafzeh 9. In KRM

41815, which is complete enough to allow reconstruction of the posterior tooth row in relation to the ramus, there is no retromolar space. The cheek teeth themselves are elongated in comparison to those of the Neanderthals, but their dimensions fall within the range of variation expected for recent black South Africans.

This impression that the morphology is modern extends also to the face, represented by pieces of the frontal and the cheekbone, and to the vault. Postcranial elements from the 1967–1968 excavations are indistinguishable from the bones of living people, and the new ulna from the SAS member has none of the distinctive features of Neanderthals. Whether the Klasies folk should be recognized as somewhat robust but otherwise similar to San is uncertain, however, given such limited skeletal material. There are a few points of resemblance, but the question of a special relationship to San can be explored only as more information becomes available. Perhaps it is unlikely that such a relationship can be documented very fully, considering that the Klasies caves were inhabited prior to 60,000 years ago. After this early Late Pleistocene phase of occupation, not only Klasies River Mouth but also some other sites in southern Africa seem to have been abandoned, probably as a consequence of habitat change due to climatic forcing. If population numbers dropped significantly for long periods, then it will be difficult to detect morphological links between Middle Stone Age people and the Late Stone Age groups who succeed them. The latter show up in the archaeological record only after an interval of some 50,000 years.

Individuals from Middle Stone Age levels in the main site differ appreciably in size. Several of the mandibles are large, while another is quite small and lightly built. One of the maxillae from the LBS member is also robust, with a deep palate and alveoli that are widened to accommodate thick molar roots. A second maxillary fragment from the same stratigraphic horizon must come from a much more gracile face. Of course these damaged specimens cannot be sexed accurately, but it is fair to assume that the larger individuals are males. One such jaw is KRM 13400, which has a corpus cross sectional area of about 430 mm^2. This mandible stands in contrast to KRM 16424, for which the calculated corpus area is just over 200 mm^2. If the smaller specimen is female, then a comparison of the two should shed some light on sexual dimorphism in the Klasies population.

Corpus dimensions provide one basis for study, and the ratio of male measurement to female measurement ($\times 100$) gives a simple index of sex difference. Corpus heights taken at the position of M_1 for KRM 13400 and KRM 16424 establish an index of 140·9. A corresponding figure cannot be obtained for Neanderthals from Shanidar, as all of the mandibles from this site are judged to be male (Trinkaus, 1983). One of the larger jaws (Vi 231) from Vindija Cave paired with a probable female (Vi 226) gives a ratio of 122·6 which is higher than the value of 115·5 calculated for a sample of European Neanderthals by Frayer & Wolpoff (1985). Dimorphism for the South African blacks of Table 3 is only 103·9. When corpus thickness is measured, KRM 13400 and KRM 16424 yield a ratio of 154·1, which is far larger than the figure of 103·8 obtained for recent Africans.

Tooth dimensions show much the same pattern. Dimorphism in breadth of the mandibular second molar is 120·6 at Klasies River Mouth. Frayer & Wolpoff (1985) report a value of 104·8 for European Neanderthals and a range of 101·0 to 109·4 for diverse samples of hunter-gathering, agricultural and urban human populations. The ratio calculated for South African blacks (Table 4) is 101·9. Breadth of M_2 thus displays a considerable range of dimorphism in human groups, and this variation is said to be highly correlated with dimorphism in body size (Frayer & Wolpoff, 1985 and references therein).

By this measure, the level of sex difference apparent at Klasies River Mouth is exceptionally great.

It should be noted that the ratios obtained for the Klasies specimens will be misleading, if one jaw or the other is far from the norm for the appropriate sex within the ancient population. The choice of KRM 13400 as a male is not unreasonable, as other mandibles in the collection are equally large. KRM 16424 may be an especially small female, although this individual shows no signs, apart from a few tiny pits in the molar enamel, of growth related pathology. To the extent that KRM 16424 is more gracile than an average female, the Klasies indices will be too high. Nevertheless, contrasts in corpus dimensions and tooth size are striking, relative to the dimorphism observed in Neanderthals and particularly in comparison to the situation observed in modern Africans. There are indications that a substantial amount of dimorphism is reflected also in other Klasies body parts, such as the face and vault. Both large and small individuals occur together in the oldest levels at the site, as well as in deposits of somewhat younger age.

Sexual dimorphism in human populations is frequently linked to nutrition, but the most common pattern is one in which differences between males and females decrease in response to nutritional inadequacies. Males are more susceptible to growth impairment under dietary stress and will approach females in body size (Stini, 1985). Since the Klasies people seem to display great size dimorphism, perhaps over a long period of time, there is here no obvious sign of generalized undernutrition. Explanations involving food supply may still be offered, however, and it is possible that females may have depended heavily on certain foods or have been denied access to others. Such circumstances can lead to an increase in size difference between the sexes, as documented for example by the prehistoric populations of St. Catherines Island, Georgia (Larsen, 1982).

Whether a nutritional hypothesis can account for the dimorphism observed at Klasies River Mouth, and how a scenario of this sort could be confirmed in an ancient Stone Age context, are questions not easily answered. Evidence concerning subsistence is available, and it is known that the main site inhabitants ate shellfish, meat obtained from various sea and land animals, and plant materials like geophytes (Klein, 1976, 1983; Deacon, 1989). There is a possibility that human flesh was consumed as well (White, 1987). But the extent of variability in the diet, and the ways in which different foods were distributed to individuals, remain obscure.

Apart from the issues of dimorphism and diet, it should be emphasized that the Klasies bones generally conform to the anatomy expected for modern humans. This is significant, in that the material is associated unequivocally with Middle Stone Age artifacts in a sedimentary sequence extending into Last Interglacial times. Fossils from the LBS member must be close to 120,000 years in age, while mandibles, teeth and other remains from the SAS levels are likely to be in the order of 100,000 years old, as determined from several lines of evidence. These dates should now be regarded as well established and subject to only minor revision as new information is obtained.

During this earlier part of the Late Pleistocene, only Neanderthals were present in Europe. The record is still incomplete for much of Asia including the Far East, but these regions seem also to have been inhabited by archaic populations. Whether such groups contributed to the emergence of more modern people or were instead replaced between 50,000 and 30,000 years ago by anatomically advanced humans originating elsewhere is currently debated (Smith & Spencer, 1984; Mellars & Stringer, 1989). Where populations from this crucial time period have been sampled at all adequately, there is increasingly firm

evidence suggesting replacement rather than local evolutionary continuity (Stringer & Andrews, 1988).

Much recent attention has focused on Africa, partly as a result of genetic studies that point to this continent as the source for nuclear DNA haplotypes (Wainscoat *et al.*, 1986), mitochondrial DNA genotypes (Cann *et al.*, 1987) and non-DNA polymorphisms (Cavalli-Sforza *et al.*, 1988) distributed among living humans. These findings support the view that anatomically modern people were present in sub-Saharan Africa at a relatively early date. In fact this idea was advanced more than a decade ago, by investigators commenting on Border Cave as well as Klasies River Mouth (Beaumont *et al.*, 1978; Rightmire, 1979). Bräuer argued a more explicit case for an African origin of southwest Asian and European populations in 1984. Some of these links remain tenuous, and it is particularly difficult to identify clear ties between broken crania from sites such as Florisbad or the Omo and (any) recent groups (Rightmire, 1986). Nevertheless, the Klasies assemblage continues to underscore the importance of southern Africa to the emergence of *Homo sapiens sapiens*.

Information provided by Klasies River Mouth must be considered in the light of new dates reported for sites in southwestern Asia. Both stone artifacts and animal teeth recovered at Qafzeh in Israel have been used to obtain estimates ranging from 92,000 years to 115,000 years for the age of levels in this cave containing human skeletons (Schwarcz *et al.*, 1988; Valladas *et al.*, 1988). The collection from Qafzeh includes 16 individuals, described by Vandermeersch (1981). Qafzeh 9 is reasonably complete, and measurements of the cranium group it with other robust but anatomically modern specimens. The form of the brow and sinus cavity are in keeping with this assessment, as are characters of the face, temporal bone and occiput. The mandible carries a bony chin, even if an internal buttress is also well developed. Pelvic and limb bones show departures from Neanderthal morphology (Trinkaus, 1984). Qafzeh 6 is similar to Qafzeh 9 in overall shape of the braincase, although the supraorbital torus is more prominent and the face is broader. These differences suggest that Qafzeh 6 is male. At the same time, the facial skeleton is relatively short, and there is less protrusion of the maxillary alveolar process and the anterior dentition. Although the back of the cranium is very incomplete, it is apparent that there is no occipital bun.

The cave at Skhul has also been redated, following the application of electron spin resonance methods to bovid teeth excavated from the deposits yielding human remains. These remains, formerly thought to be at most 40,000 years old, now appear to approach 101,000 years in age (Stringer *et al.*, 1989). The Skhul assemblage consists of parts of at least ten skeletons widely recognized as anatomically akin to modern people. Some male (?) crania have large faces and rather well developed supraorbital tori, but measurements show that there is less midfacial prognathism than is characteristic of Neanderthals (Howells, 1975). The mandibles display chin eminences. Postcranial bones are generally similar to those of European Upper Paleolithic humans (Trinkaus, 1984).

While the skulls from Skhul and Qafzeh are certainly robust and may share a few features wtih Neanderthals, they speak to the presence in southwestern Asia of anatomically modern populations. In possessing relatively strong brows, a protruding glabellar region, and internal buttressing of the symphysis in the lower jaw, some of these individuals also differ from the hominids resident at Klasies River Mouth. The extent of such differences must be checked further before it can be claimed that the Asian and South African assemblages provide firm evidence for regional differentiation. A key question is whether the Skhul and Qafzeh people resemble Upper Paleolithic Europeans, while the

Klasies remains show more similarities to Africans. If patterns of interpopulation variation were already established by the onset of Last Interglacial times, then modern humans must have dispersed still earlier, perhaps from an African source.

Acknowledgements

References

Bada, J. & Deems, L. (1975). Accuracy of dates beyond the C-14 dating limit using the aspartic acid racemization reaction. *Nature* **255**, 218–219.

Beaumont, P. B. (1980). On the age of Border Cave hominids 1-5. *Palaeontol. Afr.* **23**, 21–33.

Beaumont, P. B., de Villiers, H. & Vogel, J. C. (1978). Modern man in sub-Saharan Africa prior to 49 000 years B.P.: a review and evaluation with particular reference to Border Cave. *S. Afr. J. Sci.* **74**, 409–419.

Binford, L. R. (1986). Reply to Singer and Wymer: on Binford on Klasies River Mouth: response of the excavators. *Curr. Anthrop.* **27**, 57–62.

Bräuer, G. (1984). A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, pp. 327–410. New York: Liss.

Cann, R., Stoneking, M. & Wilson, A. C. (1987). Mitochondrial DNA and human evolution. *Nature* **325**, 31–36.

Cavalli-Sforza, L. L., Piazza, A., Menozzi, P. & Mountain, J. (1988). Reconstruction of human evolution: bringing together genetic, archaeological and linguistic data. *Proc. Nat. Acad. Sci.* **85**, 6002–6006.

CLIMAP Project Members (1984). The Last Interglacial ocean. *Quat. Res.* **21**, 123–224.

Deacon, H. J. (1989). Late Pleistocene paleoecology and archaeology in the southern Cape, South Africa. In (P. Mellars & C. Stringer, Eds) *The Human Revolution. Behavioural and Biological Perspectives on the Origins of Modern Humans*, pp. 547–564. Edinburgh: Edinburgh University Press.

Deacon, H. J. & Geleijnse, V. B. (1988). The stratigraphy and sedimentology of the main site sequence, Klasies River, South Africa. *S. Afr. Archaeol. Bull.* **43**, 5–14.

Deacon, H. J. & Schuurman, R. (in press). The origins of modern people: the evidence from Klasies River. In (G. Bräuer & F. H. Smith, Eds) *Continuity or Replacement: Controversies in Homo sapiens Evolution*. Rotterdam: Balkema.

Deacon, H. J., Talma, A. S. & Vogel, J. C. (1988). Biological and cultural development of Pleistocene people in an Old World southern continent. In (J. R. Prescott, Ed.) *Early Man in the Southern Hemisphere*, pp. 523–531. Adelaide: Department of Physics and Mathematical Physics, University of Adelaide.

de Villiers, H. (1973). Human skeletal remains from Border Cave, Ingwavuma District, Kwa Zulu, South Africa. *Ann. Trans. Mus.* **28**, 229–256.

de Villiers, H. (1976). A second adult human mandible from Border Cave, Ingwavuma District, Kwa Zulu, South Africa. *S. Afr. J. Sci.* **72**, 212–215.

Frayer, D. W. & Wolpoff, M. H. (1985). Sexual dimorphism. *Ann. Rev. Anthrop.* **14**, 429–473.

Goede, A. & Hitchman, M. A. (1987). Electron spin resonance analysis of marine gastropods from coastal archaeological sites in southern Africa. *Archaeometry* **29**, 163–174.

Grine, F. E. & Klein, R. G. (1985). Pleistocene and Holocene human remains from Equus Cave, South Africa. *Anthrop.* **8**, 55–98.

Hendey, Q. B. & Volman, T. P. (1986). Last Interglacial sea levels and coastal caves in the Cape Province, South Africa. *Quat. Res.* **25**, 189–198.

Howells, W. W. (1975). Neanderthal man: facts and figures. In (R. Tuttle, Ed.) *Paleoanthropology, Morphology and Paleoecology*, pp. 389–407. The Hague: Mouton.

Jacobson, A. (1982). *The Dentition of the South African Negro*. Anniston: Higginbotham.

Klein, R. G. (1976). The mammalian fauna of the Klasies River Mouth sites, South Africa. *S. Afr. Archaeol. Bull.* **31**, 75–98.

Klein, R. G. (1983). The Stone Age prehistory of southern Africa. *Ann. Rev. Anthrop.* **12**, 25–48.

Krige, A. V. (1927). An examination of the Tertiary and Quaternary changes of sea level in South Africa. *Ann. Univ. Stellenbosch* **A-5**, 1–81.

Larsen, C. S. (1982). The anthropology of St. Catherines Island 3. Prehistoric human biological adaptation. *Anthrop. Pap. Am. Mus. Nat. Hist.* **57**, 157–270.

Mellars, P. & Stringer, C., Eds (1989). *The Human Revolution. Behavioural and Biological Perspectives on the Origins of Modern Humans.* Edinburgh: Edinburgh University Press.

McHenry, H. M., Corruccini, R. S. & Howell, F. C. (1976). Analysis of an early hominid ulna from the Omo basin, Ethiopia. *Am. J. phys. Anthrop.* **44**, 295–304.

Rightmire, G. P. (1979). Implications of Border Cave skeletal remains for later Pleistocene human evolution. *Curr. Anthrop.* **20**, 23–35.

Rightmire, G. P. (1984). *Homo sapiens* in sub-Saharan Africa. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence,* pp. 295–325. New York: Liss.

Rightmire, G. P. (1986). Africa and the origins of modern humans. In (R. Singer & J. K. Lundy, Eds) *Variation, Culture and Evolution in Arican Populations,* pp. 209–220. Johannesburg: Witwatersrand University Press.

Schwarcz, H. P., Grün, R., Vandermeersch, B., Bar-Yosef, O., Valladas, H. & Tchernov, E. (1988). ESR dates for the hominid burial site of Qafzeh in Israel. *J. hum. Evol.* **17**, 733–737.

Shackleton, N. J. (1982). Stratigraphy and chronology of the Klasies River Mouth deposits: oxygen isotope evidence. In (R. Singer & J. Wymer) *The Middle Stone Age at Klasies River Mouth in South Africa,* pp. 194–199. Chicago: University of Chicago Press.

Singer, R. & Wymer, J. (1982). *The Middle Stone Age at Klasies River Mouth in South Africa.* Chicago: University of Chicago Press.

Singer, R. & Wymer, J. (1986). On Binford on Klasies River Mouth: response of the excavators. *Curr. Anthrop.* **27**, 56–57.

Smith, F. H. & Spencer, F., Eds (1984). *The Origins of Modern Humans: A World Survey of the Fossil Evidence.* New York: Liss.

Stini, W. A. (1985). Growth rates and sexual dimorphism in evolutionary perspective. In (R. I. Gilbert, Jr. & J. H. Mielke, Eds) *The Analysis of Prehistoric Diets,* pp. 191–226. Orlando: Academic Press.

Stringer, C. B. & Andrews, P. (1988). Genetic and fossil evidence for the origin of modern humans. *Science* **239**, 1263–1268.

Stringer, C. B., Grün, R., Schwarcz, H. P. & Goldberg, P. (1989). ESR dates for the hominid burial site of Es Skhul in Israel. *Nature* **338**, 756–758.

Trinkaus, E. (1983). *The Shanidar Neandertals.* New York: Academic Press.

Trinkaus, E. (1984). Western Asia. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence,* pp. 251–293. New York: Liss.

Trinkaus, E. & Churchill, S. E. (1988). Neandertal radial tuberosity orientation. *Am. J. phys. Anthrop.* **75**, 15–21.

Valladas, H., Reyss, J. L., Joron, J. L., Valladas, G., Bar-Yosef, O. & Vandermeersch, B. (1988). Thermoluminescence dating of Mousterian "Proto-Cro-Magnon" remains from Israel and the origin of modern man. *Nature* **331**, 614–616.

Vandermeersch, B. (1981). *Les Hommes Fossiles de Qafzeh (Israel).* Paris: CNRS.

Wainscoat, J. S., Hill, A. V. S., Boyce, A. L., Flint, J., Hernandez, M., Thein, S. L. *et al.* (1986). Evolutionary relationships of human populations from an analysis of nuclear DNA polymorphisms. *Nature* **319**, 491–493.

White, T. D. (1987). Cannibals at Klasies? *Sagittarius* **2**, 7–9.

Wolpoff, M. H., Smith, F. H., Malez, M., Radovčić, J. & Rukavina, D. (1981). Upper Pleistocene human remains from Vindija Cave, Croatia, Yugoslavia. *Am. J. phys. Anthrop.* **54**, 499–545.